Université Libre de Bruxelles
Faculté des sciences
Service d'Eco-Ethologie Evolutive

Institut Royal des Sciences Naturelles de Belgique
Section d'Evaluation Biologique

Structure des assemblages de fourmis le long d'un gradient d'aridité situé dans le Chaco sec paraguayen.

Thèse
présentée pour obtenir le grade de
Docteur en Sciences Biologiques
par
Thibaut Delsinne

2007

Devant le jury composé de:

Guy JOSENS: Université Libre de Bruxelles	Président
Olivier HARDY: Université Libre de Bruxelles	Secrétaire
Jérôme ORIVEL: Université Paul Sabatier (Toulouse, France)	Rapporteur
Olivier MISSA: Université de York (United Kingdom)	Rapporteur
Yves ROISIN: Université Libre de Bruxelles	Promoteur
Maurice LEPONCE: Institut Royal des Sciences Naturelles de Belgique	Co-promoteur

A mes parents, pour toujours veiller sur moi.

Remerciements

En cours préparatoire, le professeur nous avait demandé de citer la profession que nous souhaiterions exercer plus tard. J'avais écrit dans mon cahier "entomologiste" à côté d'une belle image de cétoine dorée. J'ai maintenant 29 ans et ma fascination pour la Vie, la Nature, les Insectes est toujours aussi forte. En réalisant ce travail de thèse, j'ai pu vivre et aller jusqu'au bout de ma passion.

C'est la raison pour laquelle je remercie chaleureusement le Dr. Maurice Leponce et le Professeur Yves Roisin pour m'avoir accueilli et encadré au sein de leurs unités de recherche afin que je puisse concrétiser mes rêves. Maurice, j'ai appris énormément à tes côtés. La qualité de ton écoute, ton esprit critique, ta patience, ta disponibilité, tes conseils toujours pertinents, ton soutien amical ont contribué à l'aboutissement de cette thèse. Tu m'as également donné une grande liberté dans l'organisation de mes recherches. Merci pour ta confiance. Yves, ton intelligence et ta perspicacité m'ont toujours impressionné. Je te remercie pour ton exigence et ta sincérité. Quand tu dis "cet article est bon", ça fait extrêmement plaisir car il est alors certain que "cet article est bon"! Yves et Maurice, permettez-moi de continuer à vous utiliser comme modèles.

Je remercie le Professeur Guy Josens pour me faire l'honneur de présider le jury de cette thèse. Je remercie également le Dr. Olivier Hardy, le Dr. Jérôme Orivel et le Dr. Olivier Missa d'avoir accepté d'examiner et d'évaluer ce travail. Je remercie également le Profeseur Guy Josens et le Dr. Jean-Christophe de Biseau d'Hauteville pour les conseils et les suggestions donnés lors des comités d'accompagnement.

Un travail de doctorat ne peut pas se faire seul. Une thèse est une expérience scientifique mais aussi humaine. J'ai eu la chance, alors que j'étais loin des miens, de travailler au sein d'une équipe chaleureuse, conviviale, amicale et accueillante. Pour ces années fort sympathiques, je remercie le chef de la section d'Evaluation Biologique, le Dr. Pierre Devillers, ainsi que tous les membres de la section et les étudiants au passage plus ou moins long: René-Marie Lafontaine, Roseline et Dilou Beudels, Didier Vangeluwe, Isabelle Bachy, Chris Kerwyn, Yves Laurent, Laurence Theunis, Géraldine Kapfer, Géraldine de Montpellier, David Monticelli, Yves Braet, Thibaud Rigot, David Cammaerts. Un merci spécial à Yves Laurent pour développer la documentation photographique de mes charmantes bestioles.

J'exprime ma profonde gratitude envers Julien Cillis (I.R.Sc.N.B., microscopie à balayage) pour l'énorme travail de qualité qu'il a réalisé en photographiant en microscopie électronique les fourmis collectées. Merci aussi à Jérôme Constant (I.R.Sc.N.B., entomologie) pour les dépannages en tubes, colle, etc.! Je remercie Patricia Féron (ULB - Service d'Eco-Ethologie Evolutive) pour son dévouement et sa grande gentillesse.

Quatre missions d'échantillonnages ont permis d'obtenir une quantité de matériel biologique suffisamment importante pour répondre aux objectifs de la thèse. Ceci n'aurait pu être possible sans l'appui du Dr. John Kochalka du "Museo Nacional de Historia Natural del Paraguay". Merci aussi à "la Secretaría del Ambiente" (SEAM) pour m'avoir accordé l'autorisation de collecter et d'exporter des fourmis du Chaco paraguayen.
Le travail de terrain a été effectué efficacement et dans la bonne humeur en compagnie de Bolivar Garcete-Barrett, Victor Filippi, Jorge Jara, César Bénilez et Carlos Aguilar Julio ("Museo Nacional de Historia Natural del Paraguay"). Merci également à Véronique Olivier

pour m'avoir accompagné et aidé en 2004. Je vous remercie tous d'avoir partagé avec moi les joies du terrain: les centaines de Winkler, les roues crevées, les ensablements, les problèmes mécaniques (le Chaco ne ménage pas les voitures), les routes indiquées sur la carte qui n'existent plus, le manque d'eau pour les ablutions (voire pour la boisson), le soleil écrasant, les levers matinaux, les tiques, les puces, les moustiques et ce qui rend peut-être le plus fou, les milliers d'Hyménoptères et/ou de Diptères attirés par notre sueur et allant la chercher aussi bien sur le front et dans le cou que dans les narines et dans les oreilles!

Atteindre les différentes localités n'a donc pas toujours été évident et y travailler non plus. Merci à toutes les personnes qui nous ont accueillis, nous ont permis d'établir notre camp sur leur terrain et nous ont laissé installer des Winkler chez eux: les gardes du Parc National Teniente Enciso, les habitants de l'Estancia María Vicenta, les militaires du Fortín Mayor Infante Rivarola, la "Fundación para el desarrollo sustentable del Chaco" (DeSdel Chaco), les employés du "Programa de Desarrollo Duradero del Chaco" (ProdeChaco), l'école d'agriculture de Mariscal Estigarribia, l'"Estación experimental del Chaco central" à côté de Cruce de Los Pioneros. Vous avez tous accepté d'emblée de nous aider. Merci pour votre générosité.
Je remercie également Enrique Bragayrac, "gerente del Parque Nacional Medanos del Chaco" pour nous avoir permis d'atteindre et d'établir des camps dans des localités difficiles (Siracua, Fortín Mister Long). Si la mission 2003 a été un succès, c'est principalement grâce à toi. Je remercie Albrecht Glatzle de l'"Iniciativa para la Investigación y Transferencia de Tecnologia Agraria Sostenible" (INTTAS) pour la documentation et les données climatiques qu'il m'a fournies.

Je remercie du fond du coeur Careca. En 2002, j'effectuais mes premiers pas dans le Chaco sec paraguayen. Ne parlant ni ne comprenant l'espagnol, j'avoue que je n'étais pas toujours très fier! Merci pour m'avoir aidé spontanément à revenir du Chaco sec paraguayen et pour m'avoir hébergé à Mariscal Estigarribia en attendant le bus TransChaco qui devait me ramener à Asunción. Lors de toutes les missions suivantes, nous nous sommes revus et à chaque reprise tu renouvelais ton aide (c'est bien tombé que tu sois mécanicien!). Bref, merci!

Romina et Bolivar, merci pour m'avoir reçu chez vous. Mes séjours à Asunción resteront d'excellents souvenirs grâce à vous. Merci de m'avoir traité en ami dès le premier jour.

J'adresse mes vifs remerciements au Dr. Fatima Mereles ("Facultad de Ciencias Químicas, universidad Nacional de Asunción") et au Dr. Frieda Billiet (Jardin Botanique de Meise) pour avoir participé à l'identification des espèces d'arbres et d'arbustes chaquéens. Je remercie aussi le Dr. Alex Wild et le Dr. William MacKay pour leur contribution à l'identification des fourmis collectées.

J'adresse un grand merci au Dr. Jacques Herbauts pour m'avoir accueilli au sein de son laboratoire du Jardin Massart (ULB) où j'ai pu analyser les propriétés physico-chimiques de mes échantillons de sol. Mon séjour chez toi reste un excellent souvenir, en grande partie grâce à ta gentillesse inépuisable. Je remercie Wolff Gruber pour m'avoir aussi conseillé pendant les analyses.

L'anglais de mes articles a souvent été amélioré grâce à la relecture de mes amies Lorraine Berry et Nihara Gunawardene. Le Chapitre 2 a aussi bénéficié des commentaires de Jennifer Boyle. Merci à toutes.

Je remercie tous ceux qui m'ont fait confiance et ont cru à l'intérêt de la problématique de cette thèse. En m'octroyant leur soutien financier, ils m'ont permis de me consacrer sereinement et à plein temps à la réalisation et à l'achèvement de ces travaux. Pour cela, je remercie:

- le Fonds pour la formation à la Recherche dans l'Industrie et dans l'Agriculture (FRIA) pour avoir financé mes recherches pendant quatre années;
- le Fonds National de la Recherche Scientifique (FNRS) pour m'avoir accordé trois bourses de voyage;
- le Fonds Léopold III pour l'Exploration et la Conservation de la Nature, pour m'avoir permis d'effectuer ma première mission;
- la Fondation Léon et Henri FREDERICQ (Classe des Sciences de l'Académie Royale de Belgique) pour avoir facilité ma participation au "Ant Course 2004";
- la Fondation David et Alice van BUUREN, pour m'avoir soutenu lors de la réalisation de ma cinquième année doctorale.

J'ai déjà pu apprécier à maintes reprises la valeur de l'amitié. J'ai la chance que mes amis soient très nombreux. Je ne les cite donc pas tous mais tous doivent savoir à quel point ils ont été, sont et seront toujours importants pour moi.

De même, ma famille m'est vitale. Merci à mes parents, mon frère, mes soeurs, mes oncles et tantes, mes cousins et cousines et tous mes autres proches d'avoir toujours été une source intarissable d'affection et de soutien.

Por fin, quiero agradecer a mi corazón, mi preciosa por su amor y por ser perfecta para mi. Tu presencia y tus palabras de ánimo me han permitido terminar este trabajo con energía, ganas y placer. Mi Tania, te adoro aún más que las hormigas!

Résumé de la thèse

Contexte: L'importance écologique des fourmis dans les écosystèmes terrestres justifie qu'elles soient considérées comme groupe cible pour des actions de conservation. De plus, de par leur abondance, leur facilité de récolte et leur réponse à des perturbations, elles présentent un potentiel intéressant comme groupe indicateur précoce de l'état de santé des écosystèmes. Par contre, pour le choix d'aires à protéger, leur utilité comme intégrateur des conditions de milieu par rapport à des indicateurs classiques tels que les assemblages de plantes n'est pas clairement établie. En d'autres termes, répondent-elles plus finement que les plantes à différentes conditions de milieu et dans ce cas doit-on s'attendre à trouver au sein de formations végétales comparables plusieurs types d'assemblages de foumis? Si tel est le cas, la méthode utilisant les assemblages de végétaux pour sélectionner les sites à protéger peut ne pas permettre une conservation efficace de la diversité des fourmis. Ce type de problématique s'aborde bien le long de gradients environnementaux. Pour faciliter l'interprétation des résultats en terme de réponse aux facteurs abiotiques il est préférable de limiter le nombre de facteurs qui varient en même temps. Dans ce sens, le Chaco sec paraguayen représente un système très favorable: faible déclivité, faibles variations de températures moyennes mais gamme très étendue de conditions de pluviométrie (350mm à 1000mm de précipitations moyennes annuelles) et des sols variables (texture limoneuse à sableuse). L'aridité est l'un des principaux facteurs pouvant limiter la diversité des fourmis soit directement en exerçant un stress physiologique sur les espèces, soit indirectement en limitant la productivité primaire de l'habitat. Les conditions édaphiques peuvent également avoir une influence en affectant par exemple la survie des colonies qui nidifient dans le sol.

Objectifs: Les principaux buts de la thèse sont (1) de déterminer l'influence de l'aridité et des conditions édaphiques sur la distribution et la structure des assemblages de fourmis terricoles du sol en forêts tropicales sèches, (2) mettre en évidence les mécanismes qui facilitent la coexistence des espèces de fourmis à l'échelle locale, (3) déterminer si à l'échelle régionale les fourmis et les plantes répondent de façon similaire aux conditions du milieu.

Méthode: Onze localités ont été échantillonnées le long d'un transect régional long de 400km. Au niveau de chaque localité, trois transects élémentaires longs de 200m et séparés les uns des autres par 200m ont été effectués. La myrmécofaune a été échantillonnée à l'aide de 20 pièges à fosse et de 20 Winkler par transect élémentaire. La végétation de chaque site a été caractérisée sur base de l'abondance de 45 espèces d'arbres ou d'arbustes caractéristiques de la flore chaquéenne. Les propriétés physico-chimiques du sol ont également été mesurées. A fine échelle, l'organisation spatio-temporelle d'un assemblage a été étudié dans une localité de référence.

Résultats: Au total, plus de 50.000 spécimens correspondant à 206 espèces de fourmis ont été collectés avec en moyenne (± SD) 62 ± 10 espèces par localité. Pour un même effort d'échantillonnage, le nombre d'espèces de fourmis récoltées à l'aide des pièges à fosse augmente avec l'aridité et une tendance inverse est observée pour les Winkler. Puisque les Winkler peuvent entraîner une sévère sous-estimation de la diversité des fourmis d'un habitat, seules les données des pièges à fosse sont utilisées pour la suite des analyses. La diversité locale α des assemblages de fourmis n'apparaît corrélée ni à l'aridité, ni aux conditions édaphiques. En revanche, ces facteurs, et spécialement la texture du sol, influencent la composition des assemblages. Trois complexes myrmécofauniques sont mis en évidence: le premier dans la localité la plus sèche (350mm) et la plus sableuse (>90% de sable dans la fraction minérale du sol), le second dans la localité la plus humide (1000mm, sol argilo-limoneux) et le dernier dans des localités présentant de larges conditions de pluviométrie (350-850mm) et de sol (limoneux à sablo-limoneux). Les plantes répondent encore plus finement à ces facteurs abiotiques. A l'échelle locale, l'établissement d'une ségrégation spatio-temporelle fine des espèces de fourmis lors de l'exploitation des ressources alimentaires facilite la coexistence interspécifique. Cette ségrégation est engendrée par l'existence de deux compromis: l'un entre les capacités des espèces à dominer et à découvrir les ressources et l'autre entre la capacité de dominance et la tolérance aux températures élevées.

Conclusions: Nos résultats contredisent l'hypothèse selon laquelle les fourmis répondent plus finement que les plantes aux conditions du milieu. A l'échelle du gradient étudié, une augmentation de l'aridité n'affecte pas la diversité des fourmis. La productivité de l'habitat ne semble pas déterminer la richesse des assemblages et la tolérance à l'aridité semble répandue au sein des Formicidae. La texture du sol apparaît être le facteur le plus déterminant des distributions spatiales observées. Dans le Chaco sec paraguayen, une sélection des sites à protéger sur base des assemblages végétaux est susceptible de maximiser la conservation de la diversité biologique des fourmis. Notre étude de la distribution de la myrmécofaune, basée sur la plus large gamme de pluviométrie envisagée à ce jour, pourra constituer le point de départ d'un suivi des assemblages de fourmis dominantes du Chaco sec paraguayen dans le but d'investiguer l'impact des changements climatiques globaux sur ces organismes.

Table des matières

Introduction générale

> "Although our tools are more advanced, in many ways the science of biodiversity is not much farther along than medicine was in the Middle Ages. We are still at the stage, as it were, of cutting open bodies to find out what organs are inside. The low investment in and slow pace of biodiversity research might be tolerable were it not for the overwhelmingly rapid destruction of the natural world. Without hyperbole we can truthfully say that we are almost out of time to save much of the diversity of life on Earth."
> (Hubbell, 2001).

1. Cadre conceptuel et sémantique de la thèse.

1.1. Diversité biologique.

De nombreuses définitions de la "diversité biologique", également appelée "biodiversité", ont été proposées. DeLong (1996) par exemple en discute 85! La plus communément citée est celle donnée à l'article 2 de la Convention sur la Diversité Biologique (C.B.D.) ratifiée par plus de 150 nations lors de la Conférence de Rio de Janeiro, en 1992. Selon ce texte, la diversité biologique est la "variabilité des organismes vivants de toute origine y compris, entre autres, les écosystèmes terrestres, marins et autres écosystèmes aquatiques et les complexes écologiques dont ils font partie; cela comprend la diversité au sein des espèces et entre espèces ainsi que celle des écosystèmes" (http://www.cbd.int/doc/legal/cbd-un-fr.pdf). Ainsi la diversité biologique est hiérarchisée et concerne à la fois des éléments génétiques (gènes, chromosomes, etc.), organismiques (populations, espèces, genres, etc.) et écologiques (habitats, biomes, etc.) (Gaston et Spicer, 2004). Dans le cadre de cette thèse, nous nous concentrerons sur l'aspect organismique de la diversité et nous utiliserons donc la définition plus restreinte employée par Magurran (2004) selon laquelle la diversité biologique est "the variety and abundance of species in a defined unit of study."

1.2. Assemblage d'espèces, facteurs déterminants et domaines d'échelles.

Un assemblage d'espèces est un ensemble d'espèces liées phylogénétiquement, présentes au sein d'une même unité spatio-temporelle mais n'exploitant pas nécessairement les mêmes ressources du milieu (Fauth *et al.*, 1996). La composition et l'abondance relative des différentes espèces d'un assemblage sont influencées par des facteurs abiotiques (dont font partie les facteurs climatiques, édaphiques ou topographiques), biotiques (comme la compétition, la prédation, la présence de parasites ou de mutualistes), historiques et stochastiques. Ces facteurs opèrent à de multiples échelles spatiales et temporelles, souvent de façon simultanée et interactive. Les structures générées peuvent donc être observées sur un continuum d'échelles spatiales s'étendant du point d'échantillonnage à l'échelle planétaire, en passant par l'échelle locale, régionale et continentale (Wiens, 1989; Levin, 1992; Beever *et al.*, 2006). A chaque niveau spatial et temporel correspond une organisation de la diversité biologique. Whittaker (1960, 1972) a différencié, entre autres, les diversités α et γ correspondant aux structures biologiques observées réciproquement à l'échelle locale et régionale. Il a également défini la diversité β comme étant la variation dans la composition spécifique entre localités d'une même région. Chaque niveau d'organisation de la diversité biologique constitue une entité qui justifie une description et une étude particulières. Les domaines d'échelles sont néanmoins interdépendants (Levin, 1992). Par conséquent, des structures et des processus ne peuvent être compris que si des allers et retours sont effectués entre les différentes échelles (Blondel, 1995). Par exemple, les changements climatiques globaux modifient la distribution des organismes à l'échelle locale et des interactions interspécifiques locales peuvent générer des ségrégations ou des associations d'espèces observables à l'échelle régionale. Décrire la structure des assemblages d'espèces à de multiples échelles spatio-temporelles et déterminer les facteurs qui les génèrent, les maintiennent ou les modifient sont des objectifs devenus indispensables du fait de la crise écologique contemporaine (Gaston, 2000).

2. Crise de la diversité biologique.

2.1. Une crise globale.

La diversité biologique est gravement menacée. Les taux d'extinctions des espèces animales et végétales n'ont jamais été aussi élevés au cours de l'histoire de l'humanité que lors de ces 50 dernières années (Millennium Ecosystem Assessment [MEA], 2005). Ils sont estimés être actuellement 100 à 1000 fois supérieurs à ce qu'ils étaient avant l'apparition de l'homme (Pimm *et al.*, 1995). Les causes de ce déclin sont la disparition, la fragmentation et la dégradation des habitats, les changements climatiques globaux, l'introduction d'espèces envahissantes, la surexploitation des habitats et la pollution (MEA, 2005). Ces multiples facteurs agissent souvent en synergie et leurs effets s'accélèrent (Woodruff, 2001; Travis, 2003; Wilson, 2003; Thomas *et al.*, 2004; Didham *et al.*, 2005). Les taux actuels d'extinctions pourraient être multipliés par 10 dans 50 ans (MEA, 2005). La crise de la diversité biologique est générale: elle affecte tous les écosystèmes et tous les groupes taxonomiques (Wilson, 1993; McKinney, 1999; Pimm, 2002).

2.2. Les forêts tropicales sèches en crise.

En comparaison des efforts de recherche et de sensibilisation menés en faveur des forêts tropicales humides, les forêts sèches des zones tropicales et subtropicales ont reçu peu d'attention (Redford *et al.*, 1990; Olson et Dinerstein, 2002; Sánchez-Azofeifa *et al.*, 2005a; Prance, 2006). Entre 1945 et 2004, environ 86% des articles scientifiques traitant des forêts tropicales concernaient les forêts humides et seulement 14% les forêts sèches (Sánchez-Azofeifa *et al.*, 2005b; sur base des articles listés dans le "Science Citation Index"). Pourtant, ces habitats sont considérés comme les plus menacés des formations forestières tropicales (Janzen, 1988; Mooney *et al.*, 1995; Miles *et al.*, 2006) et nécessitent des actions de conservation immédiates (Olson et Dinerstein, 2002; Sánchez-Azofeifa *et al.*, 2005a).

2.3. Les insectes en crise.

Plus de 925.000 espèces d'insectes ont été décrites, ce qui correspond à environ 76% des espèces animales connues (Grimaldi et Engel, 2005). Entre 4 et 10 millions d'espèces seraient encore à découvrir (Novotny *et al.*, 2002; Ødegaard *et al.*, 2005; Ødegaard, 2006). Si ces estimations s'avèrent exactes, à peine 10 à 20% de l'entomofaune mondiale est connue! Contrastant avec cette diversité gigantesque, moins de 1% des espèces décrites sont reconnues être menacées de disparition (IUCN, 2006) et seulement 70 extinctions ont été documentées au cours des 600 dernières années (Dunn, 2005). Ces chiffres faussement optimistes reflètent à la fois le manque d'études concernant la diversité des insectes et la difficulté de les réaliser (Kellert, 1993; McKinney, 1999; Dunn, 2005; Samways, 2007). Les suivis portant sur des taxons et des régions bien documentés (généralement les Lépidoptères en milieux tempérés européens ou américains), révèlent que les déclins des populations d'insectes sont de magnitude égale ou supérieure à ceux observés chez des groupes plus couramment étudiés tels que les mammifères, les oiseaux ou les plantes vasculaires (McKinney, 1999; Thomas *et al.*, 2004). Beaucoup d'insectes ont un temps de génération bref, répondent finement aux conditions du milieu (Oliver *et al.*, 1998; French, 1999) et ont une répartition géographique restreinte (Yeates *et al.*, 2002). Ces caractéristiques rendent les insectes particulièrement vulnérables aux changements environnementaux (Thomas *et al.*, 2004; Dunn, 2005). Dunn (2005) écrit même: "the biodiversity crisis is undeniably an insect biodiversity crisis".

3. Les fourmis.

3.1. Avantages des fourmis pour les études en biologie de la conservation.

Les fourmis sont, parmi les insectes, l’un des taxons les plus abordables pour des études en biologie de la conservation car:

- Elles sont diversifiées mais non excessivement. Jusqu'à présent 20 sous-familles, 288 genres et un peu plus de 12.000 espèces sont identifiés (Bolton, 2003; Saux *et al.*, 2004; Agosti et Johnson, 2005). Hölldobler et Wilson (1990) estiment qu'il existerait environ 350 genres et 20.000 espèces.

- Elles sont abondantes dans quasiment tous les écosystèmes terrestres. En Amazonie par exemple leur biomasse est quatre fois supérieure à celle de tous les vertébrés (Fittkau et Klinge, 1973).
- Elles jouent un rôle clé dans le fonctionnement des écosystèmes (Hölldobler et Wilson, 1990; Folgarait, 1998; Passera et Aron, 2005). Elles interviennent à divers niveaux trophiques et sont en particulier des prédateurs d'arthropodes (Jeanne, 1979; Novotny *et al.*, 1999) et des nécrophages majeurs (Bestelmeyer et Wiens, 2003). Elles jouent un rôle important dans l'enrichissement et l'aération des sols (MacMahon *et al.*, 2000; Boulton *et al.*, 2003; Wagner et Jones, 2006) ainsi que dans la dispersion des graines (Andersen *et al.*, 2000; Retana *et al.*, 2004). Elles entretiennent des symbioses facultatives ou obligatoires avec plus de 465 espèces de plantes réparties dans 52 familles (Jolivet, 1996), ainsi qu'avec des milliers d'espèces d'arthropodes (Hölldobler et Wilson, 1990), de champignons et de micro-organismes (Currie *et al.*, 1999, 2003; Schultz et McGlynn, 2000; Mueller *et al.*, 2001).
- Elles répondent rapidement aux perturbations du milieu et aux changements environnementaux (Andersen, 1995, 1997a; Kaspari et Majer, 2000).
- La majorité des espèces ayant des colonies sessiles, elles sont échantillonnables toute l’année (Alonso, 2000). Cette caractéristique rend les fourmis également pertinentes pour des études de suivi des assemblages ("monitoring") (Kaspari et Majer, 2000).
- Elles sont facilement collectées selon un protocole standardisé adopté par différentes équipes de recherche au niveau mondial: le protocole "Ants of the Leaf Litter" (Agosti et Alonso, 2000). Ce protocole a été mis au point dans les forêts tropicales humides et il reste cependant nécessaire d'en vérifier l'applicabilité dans une variété plus large d'habitats dont les forêts tropicales sèches.

Ces propriétés font que les fourmis sont de plus en plus intégrées à des programmes de suivi et d’évaluation de sites (Andersen *et al.*, 2002, 2004; Underwood et Fisher, 2006). Par exemple, elles servent d'indicateur pour la réhabilitation des sites miniers en Australie (Majer, 1983; Bisevac et Majer, 1999; Majer et Nichols, 1998; Hoffmann *et al.*, 2000). Pour optimiser le potentiel informatif des fourmis en biologie de la conservation, il est essentiel de connaître les facteurs qui déterminent la distribution des espèces et la structure des assemblages sur de multiples échelles spatio-temporelles.

3.2. Facteurs influençant la distribution des espèces de fourmis.

3.2.1. Echelles planétaire et continentale.

Les phénomènes évolutifs de diversification et de mise en place des myrmécofaunes jouent un rôle prépondérant dans les distributions et diversités observées à ces vastes échelles spatiales. La dérive des continents sous l'effet de la tectonique des plaques a provoqué des isolements géographiques propices à la différenciation des taxons. Par exemple, Lattke (2003) liste 62 genres néotropicaux dont l'origine et la diversification se sont probablement effectuées au cours de l'isolement de l'Amérique du Sud, après la fragmentation du Gondwana et avant la connexion avec l'Amérique du Nord. Les taxons les plus remarquables sont les fourmis champignonnistes (*Atta, Acromyrmex, Mycetophylax*...), les fourmis légionnaires (*Eciton, Labidus, Neivamyrmex*...) et les *Cephalotes*. Au sein d'un continent les phénomènes historiques, liés par exemple à l'orogénèse ou aux variations climatiques du pléistocène, ont eu aussi un impact profond sur les distributions actuelles (Andersen, 1997a; Lattke, 2003). Ainsi le soulèvement des Andes a empêché la colonisation du Chili par des taxons autrement largement répandus et diversifiés en Amérique du Sud tels que les *Crematogaster*, Attini, Cephalotini, Dacetini, et Ecitoninae (Lattke, 2003).

A ces niveaux d'analyse spatiale, on observe une diminution de la richesse spécifique avec la latitude (Kusnezov, 1957; Jeanne, 1979; Ward, 2000). Ce patron est observé chez de nombreux organismes et plus de 30 hypothèses ont été proposées pour l'expliquer (Willig *et al.*, 2003). Celle ayant reçu le plus de support est l'hypothèse de limitation d'énergie. Aux faibles latitudes, les températures et les précipitations sont plus élevées ce qui favorise la production primaire nette des plantes. La biomasse produite (l'énergie) est ensuite redistribuée aux autres membres de l'habitat via les chaînes trophiques. Plus la productivité de l'habitat est élevée, plus la diversité biologique peut être importante (Hawkins *et al.*, 2003; Evans *et al.*, 2005; Clarke et Gaston, 2006). Les patrons de diversité observés chez les fourmis correspondent aux prédictions de cette hypothèse puisque la richesse spécifique de la myrmécofaune augmente le long d'un gradient de production primaire nette, allant des déserts nord-américains aux forêts tropicales d'Equateur (Kaspari *et al.*, 2000). Cependant, l'influence importante des processus historiques et évolutifs à ces larges échelles spatiales et la contribution de différents "pools" d'espèces le long du gradient latitudinal compliquent l'interprétation des patrons de diversité observés (Gotelli et Ellison, 2002; Clarke et Crame, 2003; Currie et Francis, 2004; Qian et Ricklefs, 2004; Ricklefs, 2004; Rahbek *et al.*, 2007).

3.2.2. Echelle régionale.

Il n'existe pas de consensus pour définir l'étendue d'une région (ni celle d'une localité). La délimitation doit être réalisée de façon pragmatique en fonction du taxon et des objectifs de recherche considérés (Blondel, 1995; Magurran, 2004). La notion peut-être la plus importante est, qu'à cette échelle, le "pool" d'espèces est virtuellement identique sur l'ensemble de la superficie étudiée. A ce niveau de résolution spatiale, l'hétérogénéité du milieu influence de façon importante la distribution des espèces et leurs abondances relatives en fonction de leur physiologie, de leur capacité de dispersion ou de leur tolérance aux perturbations. Ainsi, le type d'habitat (Vasconcelos, 1999), son degré de fragmentation (Suarez *et al.*, 1998; Gibb et Hochuli, 2002; Brühl *et al.*, 2003; Vasconcelos *et al.*, 2006), le régime des incendies (York, 2000; Farji-Brener *et al.*, 2002; Hoffmann, 2003; Andersen *et al.*, 2006; Arnan *et al.*, 2006), ou la pression d'herbivorie exercée sur la végétation (Bestelmeyer et Wiens, 1996, 2001) conditionnent la distribution des fourmis au sein d'une région.

De nombreuses études ont cherché à déterminer la structure des assemblages de fourmis en fonction de l'altitude (Kusnezov, 1957; Olson, 1994; Fisher 1996, 1998, 1999, 2002, 2004; Samson *et al.*, 1997; Ward, 2000; Sanders, 2002; Sanders *et al.*, 2003a; Botes *et al.*, 2006). Deux patrons principaux ont été obtenus: soit la richesse spécifique diminue avec l'altitude, soit une plus grande richesse est trouvée aux altitudes moyennes [ce second cas étant plus souvent observé dans les régions tropicales que tempérées (Ward, 2000)]. Dans les régions arides, la relation peut toutefois être positive (Sanders *et al.*, 2003a). De nombreux facteurs co-varient avec l'altitude, en particulier la température et la pluviométrie, ce qui rend difficile la détermination des processus responsables des patrons observés. Plusieurs hypothèses explicatives, certainement non exclusives (faisant intervenir le climat, l'histoire, la géographie, les interactions biotiques, etc.), ont été proposées. L'une des plus probantes est à nouveau l'hypothèse de limitation d'énergie. L'altitude où la production primaire nette est la plus élevée est celle où la richesse spécifique est la plus importante. D'autre part, le fait que la surface disponible des habitats diminue avec l'altitude peut contribuer à la mise en place de certains des patrons observés (Rahbek, 1995; Sanders, 2002; Dunn *et al.*, 2007).

Les facteurs édaphiques peuvent influencer la structure des assemblages de fourmis et les distributions régionales, soit directement en affectant l'établissement et la survie des colonies qui nidifient dans le sol, soit indirectement par leur impact sur les caractéristiques de la végétation (productivité, diversité, etc.) (Johnson, 1992, 2000; Bestelmeyer et Wiens, 2001; Vasconcelos *et al.*, 2003). Cependant le sol a rarement été pris en considération dans les études concernant la diversité des fourmis et comme le fait remarquer Kaspari (2000) "whereas a gardener or botanist can speak volumes on how pH, drainage, and other soil properties influence the plant community, ant ecologists can say little about how soil properties influence ant communities".

L'aridité est l'un des principaux facteurs susceptibles de limiter la distribution des organismes, soit en contrôlant la production primaire nette (hypothèse de limitation d'énergie), soit en exerçant un stress physiologique sur les espèces (Mittelbach *et al.*, 2001; Hawkings *et al.*, 2003; Engelbrecht *et al.*, 2007). Cependant peu d'études ont tenté de déterminer son influence sur la structure des assemblages de fourmis à l'échelle régionale (Tableau 0-1). En outre, elles n'ont été réalisées qu'au sein d'écosystèmes désertiques. Les résultats obtenus ne sont pas concluants. Deux études ont montré une diminution de la richesse spécifique avec l'aridité (Davidson, 1977; Marsh, 1986). Trois autres n'ont mis en évidence aucune relation (Morton et Davidson, 1988; Medel, 1995; Pfeiffer *et al.*, 2003). Pour ces dernières, les effets négatifs liés à une diminution des précipitations ont pu être masqués par une hétérogénéité des conditions édaphiques au sein de la région étudiée (Morton et Davidson, 1988; Medel, 1995) ou par l'existence d'un gradient de température opposé à celui d'aridité (Pfeiffer *et al.*, 2003). D'autre part, ces études se sont focalisées sur les espèces granivores. La variabilité spatio-temporelle de la ressource, les pressions de compétition exercées par d'autres granivores (rongeurs, oiseaux) et le degré de spécialisation des espèces vis-à-vis de ce régime alimentaire ont pu influencer les patrons de distribution obtenus (Morton et Davidson, 1988; Medel, 1995). Des études complémentaires sont donc indispensables si l'on souhaite déterminer l'impact de l'aridité sur la structure des assemblages de fourmis.

Les gradients environnementaux peuvent engendrer des différences structurelles entre assemblages de localités aux conditions contrastées. Cependant, les limites à la capacité de dispersion, inhérentes à chaque espèce, font que des localités aux conditions abiotiques similaires mais éloignées peuvent supporter des assemblages différents. C'est ce que Nekola et White (1999) ont nommé "the decay of assemblage similarity". La distance géographique est donc un facteur à ne pas négliger lors d'études concernant la diversité biologique.

3.2.2. Echelle locale.

C'est à l'échelle locale que les interactions entre organismes ont lieu. A ce niveau de résolution spatiale, la compétition interspécifique est réputée être le mécanisme principal structurant les assemblages de fourmis (Hölldobler et Lumsden, 1980; Levings et Franks, 1982; Vepsalainen et Pisarski, 1982; Savolainen et Vepsäläinen, 1988, 1989; Hölldobler et Wilson, 1990; Andersen et Patel, 1994; Perfecto, 1994; Basu, 1997; Davidson, 1998; Sanders *et al.*, 2003b), bien qu'il soit reconnu que la prédation (Gotelli 1993, 1996) et le parasitisme (Adler *et al.*, 2007; Lebrun et Feener, 2007) puissent également avoir une influence.

L'intensité de la compétition interspécifique est toutefois conditionnée par l'amplitude des perturbations et des facteurs de stress qui s'exercent sur l'assemblage (Andersen, 1995, 1997a). On appelle perturbation tout processus qui *détruit* de la biomasse (un incendie par exemple); un facteur est dit stressant lorsqu'il *limite* la productivité de l'habitat (ou simplement des fourmis). C'est le cas des températures élevées (Andersen, 1995, 1997a). L'aridité est suspectée être également un facteur de stress pour les fourmis mais, comme nous l'avons vu, ceci reste à déterminer avec précision. L'intensité de la compétition est généralement maximale dans les habitats peu perturbés et où les conditions abiotiques sont peu stressantes (Andersen, 1995, 1997a, 1997b).

Une relation unimodale est classiquement observée entre la richesse spécifique d'un assemblage et l'abondance des espèces compétitivement dominantes qui le composent (Andersen, 1992; Morrison, 1996; Parr *et al.*, 2005). La partie ascendante de la relation est supposée correspondre à une amélioration des conditions abiotiques, c'est-à-dire à une diminution du stress ou des perturbations. Toutes les espèces, qu'elles aient des habilités compétitives (espèces "dominantes") ou non ("subordonnées"), bénéficient initialement de l'amélioration des conditions et la richesse spécifique de l'assemblage augmente. Cependant, l'abondance croissante des dominantes et donc l'intensité croissante de la compétition entraîne ensuite une réduction du nombre d'espèces.

La compétition interspécifique peut avoir pour conséquence la formation de combinaisons d'espèces ("règles d'assemblages"). Cela signifie que certaines espèces sont plus souvent associées (d'autres plus souvent ségrégées) que ce qui serait observé si la composition des assemblages était générée de façon aléatoire (Diamond, 1975; Gotelli et Graves, 1996). Ce mécanisme peut, par exemple, être à l'origine des compositions qui furent observées au sein des assemblages de fourmis sur trois îles de Polynésie (Morrison, 1996). Entre 30 et 36 espèces de fourmis furent collectées sur chaque île. Trois de ces espèces exhibaient une forte dominance à la fois numérique et comportementale (forte agressivité) et présentaient des aires de distribution ségrégées spatialement. Chaque espèce dominante était, en outre, associée à un ensemble d'espèces subordonnées différent. Morrison (1996) fait cependant remarquer que les patrons observés peuvent résulter soit des interactions compétitives entre espèces, soit des affinités de chaque espèce pour un type d'habitat particulier.

L'intensité et la fréquence des interactions compétitives peuvent être atténuées grâce à une ségrégation des espèces selon leur taille (Hutchinson, 1959; Grant, 1972) car la gamme des ressources alimentaires et des microhabitats qu'une espèce exploite est en effet fonction de sa morphologie (Davidson, 1978; Eastlake Chew et Chew, 1980; Gotelli et Ellison, 2002; Sarty *et al.*, 2006; Kaspari et Weiser, 2007). D'autre part, des ségrégations spatiales, trophiques ou temporelles peuvent s'établir afin de faciliter la coexistence des espèces au sein d'un même habitat (Schoener, 1974; Fellers, 1987; Albrecht et Gotelli, 2001; Thomas et Holway, 2005).

On distingue classiquement la compétition par interférence et celle par exploitation. Il s'agit respectivement, d'une part de la capacité à empêcher activement les espèces compétitrices d'accéder aux ressources (par exemple, par la mise en place de territoires ou par des agressions directes), et d'autre part de la capacité à trouver et utiliser une ressource et ce faisant d'en priver les compétiteurs. Fellers (1987) a mis en évidence une corrélation négative (un "trade-off") entre le temps nécessaire à la découverte d'une source de nourriture et la dominance exercée sur cette ressource. Les espèces subordonnées ("opportunists") sont capables de localiser rapidement les ressources mais en sont exclues lorsque les espèces agressives ("extirpators") arrivent à leur tour. Une troisième catégorie ("insinuators") est constituée d'espèces qui parviennent à s'immiscer près de la source de nourriture et à en dérober discrètement aux deux autres catégories (Wilson, 1971; Fellers, 1987). La hiérarchie peut toutefois être modifiée dans les habitats où les conditions de température sont souvent stressantes. En effet, dans ces milieux, la corrélation négative "découverte-dominance" est associée à une seconde corrélation opposant la dominance des espèces à leur capacité à tolérer les températures élevées (Bestelmeyer, 2000; Cerdá *et al.*, 1998a, 1998b; Retana et Cerdá, 2000; mais voir Santini *et al.*, 2007). L'intrication de ces deux compromis permet une ségrégation temporelle fine des espèces. Ceci est suspecté être la raison pour laquelle les milieux arides et semi-arides supportent souvent un plus grand nombre d'espèces de fourmis que ce qui pourrait être attendu sous des conditions abiotiques stressantes (Cerdá *et al.*, 1998a). Cependant, les connaissances concernant l'impact de ces deux compromis sur l'organisation des assemblages et la coexistence des espèces de fourmis sont encore fragmentaires. Leurs conséquences sur l'exploitation spatiale des ressources n'ont, par exemple, jamais été investiguées. D'autre part, la compétitivité des espèces de fourmis dépend du type de ressource alimentaire à défendre (Gibb, 2005) et il serait intéressant d'étudier si cela modifie les structures spatio-temporelles d'exploitation des ressources alimentaires engendrées par les deux compromis.

3.3. Fidélité spatiale entre les assemblages de fourmis et de plantes.

Pour répondre à l'ampleur de la crise biologique actuelle, des actions de conservation rapides et efficaces sont indispensables. Puisque le temps, les moyens financiers et humains sont limités et que le manque de connaissances taxonomiques (en particulier en ce qui concerne les insectes et autres invertébrés) est limitant, il est judicieux de tenter d'identifier certaines espèces ou groupes d'espèces dont les patrons de diversité seraient représentatifs de ceux d'une majorité de taxons (espèces bioindicatrices; "bioindicators", "surrogates", "predictor sets") et/ou dont la protection permettrait de maximiser celle de la diversité biologique (espèces parapluies; "umbrella species") (Kremen *et al.*, 1993; New, 1995; Oliver et Beattie, 1996; Lawton *et al.*, 1998; McGeoch, 1998; Oliver *et al.*, 1998; Alonso, 2000; Basset *et al.*, 2004; Kati *et al.*, 2004; Moreno *et al.*, 2007).

Les formations végétales sont classiquement utilisées afin de sélectionner les aires prioritaires à protéger. Elles sont en effet supposées être des indicateurs fiables de la diversité biologique globale d'un habitat car elles sont censées intégrer de nombreux facteurs environnementaux (sol, pluviométrie, altitude, température, etc.) et car la majorité des organismes terrestres dépendent directement ou indirectement des plantes pour se nourrir ou s'abriter (Scott *et al.*, 1993; Panzer et Schwartz, 1998; Alonso, 2000). Elles sont également faciles à échantillonner et sont commodes à utiliser pour définir une liste d'unités de conservation dans des textes légaux.

Cette méthode n'est valide que si les autres organismes à protéger présentent vis-à-vis des végétaux une haute fidélité spatiale [celle-ci étant définie comme "the degree to which assemblages from different phylogenic groups co-occur in space and time" (Oliver *et al.*, 1998)]. Ainsi un réseau d'aires protégées basé sur la maximisation de la complémentarité entre assemblages de plantes devrait être complémentaire pour les autres taxons (Su *et al.*, 2004). Les études ayant cherché à vérifier la congruence des patrons de complémentarité de végétaux et d'insectes ont produit des résultats parfois contradictoires. Par exemple, en utilisant les fourmis comme modèle, certaines études ont mis en évidence une fidélité spatiale (Negi et Gadgil, 2002; Pfeiffer *et al.*, 2003), d'autres non (Oliver *et al.*, 1998[1]; Englisch *et al.*, 2005). Il est probable que la variabilité des résultats s'explique par la diversité des échelles spatiales considérées par chaque étude. Les assemblages analysés sont en effet distants les uns des autres de quelques dizaines de mètres (Englisch *et al.*, 2005) à plusieurs centaines de

---

[1] Dans cette étude, les données concernant les fourmis sont groupées à celles de trois familles de Coléoptères.

kilomètres (Pfeiffer *et al.*, 2003). Englisch *et al.* (2005) émettent l'hypothèse qu'une fidélité spatiale entre plantes et fourmis n'est observable qu'à large échelle spatiale ("coarse-scale"). Si tel est le cas, l'utilisation des végétaux comme taxon "parapluie" permettant la protection des fourmis à l'échelle régionale pourrait être envisagée.

4. Objectifs de la thèse.

En réponse:

- à l'intérêt des fourmis comme groupe d'invertébrés informatif en biologie de la conservation;
- au manque de connaissances relatives à l'effet de l'aridité et du sol sur la distribution des assemblages de fourmis;
- à l'intérêt d'étudier, à des fins prédictives, l'impact d'une aridité croissante dans un contexte de changements climatiques;

nous avons choisi d'étudier un système écologique unique représenté par les forêts du Chaco sec paraguayen. Unique car il s'agit d'un large continuum forestier peu dégradé et très peu peuplé, soumis à de très faibles variations d'altitude et de température moyenne mais présentant de larges variations de pluviométrie et de conditions édaphiques.

Plus spécifiquement, les objectifs visés par ce travail de thèse étaient de:

1. Vérifier l'applicabilité du protocole d'échantillonnage des assemblages de fourmis "Ants of the Leaf Litter" (Agosti et Alonso, 2000) dans les forêts tropicales sèches. L'existence d'une méthode fiable, performante et standardisée d'échantillonnage est effectivement un prérequis indispensable à des études concernant la diversité biologique.
2. Etudier l'influence exercée par l'aridité et les conditions édaphiques sur la structure des assemblages de fourmis du Chaco sec paraguayen.
3. Mettre en évidence les mécanismes qui permettent la coexistence des espèces de fourmis en examinant (1) les ségrégations trophiques, temporelles et spatiales présentées lors de l'exploitation des ressources alimentaires par un assemblage de référence; (2) les patrons de co-occurrence spatiale des espèces au sein de la région et des localités étudiées.
4. Déterminer si, à l'échelle régionale, les patrons de distribution des assemblages de fourmis et de végétaux (arbres et arbustes) sont congruents.

5. Développer les connaissances taxonomiques des Formicidae du Chaco sec paraguayen.

La Figure 0-1 présente la méthodologie qui fut employée afin de remplir ces objectifs.

5. Site d'étude: le Chaco sec paraguayen.

5.1. Le Gran Chaco: origine, relief, climat.

Le Gran Chaco constitue le second plus vaste biome forestier d'Amérique du Sud après la forêt du Bassin Amazonien. Il s'étend entre 16° et 34° de latitude Sud et 58° et 67° de longitude Ouest. Il se situe donc entre la Cordillère des Andes et le plateau brésilien (Figure 0-2). Sa superficie est d'environ 996.000km² répartis entre trois pays: l'Argentine (633.000km²; soit 63,5%), le Paraguay (240.000km²; 24%) et la Bolivie (124.000km²; 12,5%) (Prado, 1993; Noss *et al.*, 2002). Une zone supplémentaire brésilienne de faible superficie (9000km²) est couverte par une végétation présentant des affinités avec celle du Gran Chaco mais son statut chaquéen est contesté par Prado (1993).

Ce biome s'est développé sur une vaste plaine d'origine Quaternaire formée par des apports éoliens et fluviaux de sédiments issus de l'érosion de la Cordillère des Andes. La plaine s'élève progressivement d'est en ouest mais sa déclivité est faible. Par exemple, le Chaco paraguayen a une pente de 0,23% (Gorham, 1973).

Situé au coeur de l'Amérique du Sud, loin des influences océaniques, le Gran Chaco possède un climat continental subtropical (Fariña Sánchez, 1973). D'est en ouest, la pluviométrie annuelle moyenne passe de 1400 à 350mm (Figure 1-1 du Chapitre 1). Plus de 80% des pluies se produisent pendant l'été austral, de décembre à avril (Figure 0-3) (Gorham, 1973; Ramella et Spichiger, 1989). On différencie le Chaco humide (1000 à 1400mm de précipitation moyenne annuelle) et le Chaco sec (350-1000mm) (Figure 0-2).

Les températures annuelles moyennes suivent un gradient décroissant nord-sud, variant de +26°C à +17°C. Au cours de l'année, de fortes variations de température peuvent avoir lieu (de -10°C à >40°C) (Prado, 1993). Les températures les plus chaudes coïncident avec la période des pluies (Figure 0-4).

Les données climatiques utilisées dans le cadre de cette thèse proviennent de 29 stations météorologiques réparties de façon homogène sur l'ensemble du Chaco paraguayen (Gorham, 1973). Chacune des 11 localités échantillonnées était située à moins de 60km de la station météorologique la plus proche. Les moyennes sont calculées à partir de données récoltées sur une période de 30 ans (1951 à 1980) (Ramella et Spichiger, 1989). D'autre part, les gardes du Parc National Teniente Enciso (la localité de référence) ont fourni des relevés quotidiens de températures et de précipitations couvrant la période 1996-2004 (Figures 0-3 et 0-4).

5.2. Faune et flore.

La diversité biologique du Gran Chaco est importante mais le taux d'endémisme est faible (Noss *et al.*, 2002). On y a recensé 150 espèces de mammifères (dont 12 endémiques), 409 oiseaux nicheurs (7 endémiques), 177 reptiles (17 endémiques) et 60 amphibiens (8 endémiques).

La végétation du Gran Chaco serait constituée d'environ 2000 espèces (>90 d'endémiques). Les assemblages végétaux sont influencés principalement par la pluviométrie. Deux grandes unités de végétation sont définies: l'unité xérophytique et la mésoxérophytique qui correspondent respectivement à la végétation du Chaco sec et du Chaco humide. Ces deux unités regroupent plusieurs formations végétales dont la structure et la distribution dépendent des conditions édaphiques (Devillers et Devillers-Terschuren, 1996 [Habitats "Physis" de l'unité 4B.6]; Mereles, 2005). Au sein du Chaco paraguayen, par exemple, une vingtaine de formations différentes sont reconnues (Figure 0-5). La végétation du Chaco sec est dense et basse (3-10m), avec toutefois quelques arbres émergents pouvant atteindre 15-20m.

5.3. Occupation humaine, menaces et réserves naturelles.

Le début de la colonisation du Gran Chaco par l'Homme débute probablement il y a 12.000 ans (Kruck *et al.*, 1998) mais a toujours été limitée. L'avantage de cette faible pression anthropique est que plus de 70% du biome est encore considéré comme intact (Noss *et al.*, 2002). Ceci est particulièrement marqué dans les parties paraguayennes et boliviennes.

Le Chaco paraguayen représente 60% du territoire national mais seulement 2,5% de la population s'y est établie. Sur les 130.000 habitants qui le peuplent, 80.000 sont regroupés dans les agglomérations (Krug *et al.*, 1998). La densité de la population est de ce fait inférieure à 1hab/km² sur la majorité du territoire.

Les principales menaces pesant sur le Gran Chaco sont l'exploitation forestière et l'élevage extensif qui entraînent des problèmes de désertification, d'érosion et de salinisation des sols (Abril et Bucher, 1999; Bucher et Huszar, 1999; Bonino et Araujo, 2005; Abril *et al.*, 2005; Boletta *et al.*, 2006). Dans le Chaco paraguayen la déforestation a toutefois diminué de 5 à 14% entre 2000 et 2005 (Mereles, 2005). Le Paraguay a créé 6 grands parcs nationaux qui conservent environ 7% du Chaco sur ce territoire (17.403km²). En outre, le Paraguay et la Bolivie tentent de mettre en place un corridor biologique protégé dans le but de relier leurs différentes réserves naturelles. Si ce projet aboutit, une unité continue de 29.922, 21km² (3% du Gran Chaco) serait ainsi protégée (Bragayrac[2], comm. pers., 2003). Pour comparaison, la Belgique a une superficie de 30.528km²!

En 2005, dans le cadre de son programme "L'Homme et la biosphère" (MAB), l'UNESCO a ajouté une surface du Chaco paraguayen de 75.000km² à son réseau mondial des réserves de biosphère[3].

5.4. Fourmis du Gran Chaco.

A partir d'une recherche bibliographique exhaustive, de visites de collections muséologiques et d'un échantillonnage partiel, Alex Wild a listé 124 espèces de fourmis dont la présence est attestée dans le Chaco paraguayen (Alex Wild, comm. pers., 2007). Cette diversité correspond à 43 genres et 9 sous-familles (Tableau 0-2). La liste est loin d'être complète car, avant la présente étude, aucun échantillonnage visant spécifiquement les fourmis n'avait été réalisé dans le Chaco paraguayen. Les seules études en rapport avec les Formicidae ont concerné *Acromyrmex landolti* car cette fourmi champignonniste est l'une des principales pestes en milieu agricole tropical (Schultze-Kraft, 1998; Michels *et al.*, 2001).

Les études s'interrogeant sur l'écologie des assemblages de fourmis ont été réalisées exclusivement dans le Chaco argentin. Elles ont traité de l'influence de l'herbivorie sur la structure des assemblages (Bestelmeyer et Wiens, 1996) et de celle de la température sur l'activité des espèces, l'exploitation des ressources alimentaires et les interactions de

---

[2] Enrique Bragayrac est l'un des co-responsables paraguayens du projet. Il était également à la tête des Parcs Nationaux "Médanos del Chaco" et "Teniente Enciso" pendant la période correspondant à la réalisation de ma thèse.

[3] Des informations concernant le programme MAB de l'UNESCO sont disponibles sur le site internet:
http://www.unesco.org/mab/mabProg_fr.shtml
D'autre part, des informations concernant la réserve de biosphère du Chaco paraguayen sont accessibles au site:
http://www.unesco.org/mabdb/br/brdir/directory/biores.asp?mode=all&code=PAR+02

compétition (Bestelmeyer, 1997, 2000). Elles ont été accomplies à l'intérieur d'un carré de 10km de côté où au moins 104 espèces de fourmis ont été collectées à l'aide de pièges à fosse et d'appâts de thon. Une classification en groupes fonctionnels a été proposée mais il est difficile de l'utiliser en dehors de la zone étudiée car 50% des fourmis n'ont pu être identifiées jusqu'à l'espèce.
Enfin, l'applicabilité du protocole "Ants of the Leaf Litter" a été confirmée dans les forêts du Chaco humide (Leponce *et al.*, 2004), ce qui a permis l'étude de la structure spatiale des fourmis au sein d'ilôts forestiers du Chaco humide argentin (Theunis *et al.*, 2005).

Ces données limitées montrent à quel point les connaissances concernant la taxonomie, la diversité et l'écologie des fourmis du Gran Chaco sont rudimentaires.

6. Organisation de la thèse.

Les résultats obtenus au cours du travail de thèse sont présentés dans cinq chapitres destinés à répondre à chacun des cinq objectifs présentés précédemment. Ils sont rédigés en anglais et ont la forme d'articles. Ils s'intitulent:

1. **"Rainfall influence the ant sampling in dry forests".**
   Ce premier chapitre traite de la méthodologie utilisée dans le cadre de la thèse. Il s'interroge sur l'applicabilité du protocole "Ants of the Leaf Litter" (Agosti et Alonso, 2000) dans les forêts tropicales sèches. L'influence de l'aridité sur la capacité des pièges à fosse et des Winkler à collecter des fourmis est particulièrement étudiée. Les résultats obtenus seront exploités dans les chapitres 3 à 5.

2. **"Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage".**
   A l'échelle locale, la compétition interspécifique est suspectée être le principal facteur déterminant la structure des assemblages de fourmis. Pour faciliter la coexistence des espèces, des mécanismes de ségrégations trophiques, temporelles et spatiales peuvent se mettre en place, en particulier lors de l'exploitation des ressources alimentaires. Comment les espèces dominantes, aux écologies souvent voisines, se partagent-elles les ressources?

3. **"Spatial co-occurrence in ground-foraging ant assemblages along an aridity gradient in the Paraguayan dry Chaco".**

Une seconde conséquence attendue de la compétition interspécifique est la création d'associations ou d'exclusions d'espèces. Le but de ce chapitre est la recherche de tels patrons de distribution à la fois à l'échelle locale et régionale.

4. **"Influence of aridity and soil on the distribution and diversity of ant assemblages and dominant plant species in the Paraguayan dry Chaco".**

Les deux précédents chapitres ont tenté de mettre en évidence la compétition interspécifique et ses conséquences sur les assemblages de fourmis. Celui-ci a pour but de distinguer les influences respectives de l'aridité, des conditions édaphiques et de la distance géographique. Les patrons de complémentarité des assemblages de fourmis sont comparés à ceux des végétaux afin de vérifier l'hypothèse de l'existence d'une fidélité spatiale entre ces deux types d'organismes.

5. **"Taxonomic structure of ant assemblages along aridity gradients".**

Ce chapitre complète le précédent en s'interrogeant sur l'influence de l'aridité (et des conditions édaphiques) sur la distribution des genres et sous-familles de fourmis. Les résultats obtenus dans le Chaco sec paraguayen sont complétés par une réanalyse de données issues de la littérature, provenant de quatre études ayant échantillonné des assemblages de fourmis le long de gradients d'aridité.

Les résultats présentés dans ces cinq chapitres sont ensuite réunis dans une discussion générale sur les influences principales structurant les assemblages de fourmis du Chaco sec paraguayen.

Références bibliographiques.

Abril, A., Barttfeld, P., Bucher, E.H., 2005. The effect of fire and overgrazing disturbes on soil carbon balance in the Dry Chaco forest. Forest Ecology and Management 206: 399-405.

Abril, A., Bucher, E.H., 1999. The effects of overgrazing on soil microbial community and fertility in the Chaco dry savannas of Argentina. Applied Soil Ecology 12: 159-167.

Adler, F.R., LeBrun, E.G., Feener, D.H.Jr., 2007. Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. The American Naturalist 169: 323-333.

Agosti, D., Alonso, L.E., 2000. The ALL protocol: a standard protocol for the collection of ground-dwelling ants. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 204-206. Smithsonian Institution Press, Washington, D.C.

Agosti, D., Johnson, N.F., Editors 2005. Antbase. www.antbase.org. Version (05/2005).

Albrecht, M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126, 134-141.

Alonso, L.E., 2000. Ants as indicators of diversity. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 80-88. Smithsonian Institution Press, Washington, D.C.

Andersen, A.N., 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. American Naturalist 140: 401-420.

Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography 22: 15-29.

Andersen, A.N., 1997a. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24: 433-460.

Andersen, A.N., 1997b. Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology [online] 1: 8. http:// www.consecol.org/vol1/iss1/art8/

Andersen, A.N., Azcarate, F.M., Cowie, I.D., 2000. Seed selection by an exceptionally rich community of harvester ants in the Australian seasonal tropics. Journal of Animal Ecology 69: 975-984.

Andersen, A.N., Fisher, A., Hoffmann, B.D., Read, J.L., Richards, R., 2004. Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecology 29: 87-92.

Andersen, A.N., Hertog, T., Woinarski, J.C.Z., 2006. Long-term fire exclusion and ant community structure in an Australian tropical savanna: congruence with vegetation succession. Journal of Biogeography 33: 823-832.

Andersen, A.N., Hoffmann, B.D., Müller, W.J., Griffiths, A.D., 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. Journal of Applied Ecology 39: 8-17.

Andersen, A.N., Patel, A.D., 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. Oecologia 98: 15-24.

Arnan, X., Rodrigo, A., Retana, J., 2006. Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. Journal of Biogeography 33: 1246-1258.

Basset, Y., Mavoungou, J.F., Mikissa J.B., Missa, O., Miller, S.E., Kitching, R.L., Alonso, A., 2004. Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. Biodiversity and Conservation 13: 709-732.

Basu, P., 1997. Competition hierarchy in the ground foraging ant community in a wet evergreen forest (Western Ghats, India): role of interference behaviour. Current Science 73:173–179.

Beever, E.A., Swihart, R.K., Bestelmeyer, B.T., 2006. Linking the concept of scale to studies of biological diversity: evolving approaches and tools. Diversity and Distributions 12: 229-235.

Bestelmeyer, B., 1997. Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. Journal of Arid Environments 35: 297-310.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. Journal of Animal Ecology 69: 998-1009.

Bestelmeyer, B.T., Wiens, J.A., 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecological Applications 6: 1225-1240.

Bestelmeyer, B.T., Wiens, J.A., 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. Ecological Applications 11: 1123-1140.

Bestelmeyer, B.T., Wiens, J.A., 2003. Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands. Journal of Arid Environments 53: 373-386.

Bisevac, L., Majer, J.D., 1999. Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia. Restoration Ecology 7: 117-126.

Blondel, J., 1995. Biogéographie. Approche écologique et évolutive. Masson, Paris, 297 pp.

Boletta, P.E., Ravelo, A.C., Planchuelo, A.M., Grilli, M., 2006. Assessing deforestation in the Argentine Chaco. Forest Ecology and Management 228: 108-114.

Bolton, B. 2003. Synopsis and Classification of Formicidae. Memoirs of the American Entomological Institute, Vol. 71. Gainesville, FL. 370 pp.

Bonino, E.E., Araujo, P., 2005. Structural differences between a primary and a secondary forest in the Argentine Dry Chaco and management implications. Forest Ecology and Management 206: 407-412.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P., Chown, S.L., 2006. Ants, altitude and change in the northern Cape Floristic Region. Journal of Biogeography 33: 71-90.

Boulton, A.M., Jaffee, B.A., Scow, K.M., 2003. Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota. Applied Soil Ecology 23: 257-265.

Brühl, C.A., Eltz, T., Linsenmair, E.K., 2003. Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity and Conservation 12: 1371-1389.

Bucher, E.H., Huszar, P.C., 1999. Sustainable management of the Gran Chaco of South America: ecological promise and economic constraints. Journal of Environmental Management 57: 99-108.

Cerdá, X., Retana, J., Cros, S., 1998a. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12: 45-55.

Cerdá, X., Retana, J., Manzaneda, A., 1998b. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117: 404-412.

Clarke, A., Crame, A.J., 2003. The importance of historical processes in global patterns of diversity. In: Blackburn, T.M., Gaston, K.J., Macroecology: concepts and consequences, pp. 130-151. Blackwell Publishing, Oxford.

Clarke, A., Gaston, K.J., 2006. Climate, energy and diversity. Proceedings of the Royal Society of London B. 273: 2257-2266.

Currie, C.R., Scott, J.A., Summerbell, R.C., Malloch, D., 1999. Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. Nature 398: 701-704.

Currie, C.R., Wong, B., Stuart, A.E., Schultz, T.R., Rehner, S.A., Mueller, U.G., Sung, G-H., Spatafora, J.W., Straus, N.A., 2003. Ancient tripartite coevolution in the attine ant-microbe symbiosis. Science 299: 386-388.

Currie, D.J., Francis, A.P., 2004. Regional versus climatic effect on taxon richness in Angiosperms: reply to Qian and Ricklefs. American Naturalist 163: 780-785.

Davidson, D.W., 1977. Species diversity and community organization in desert seed-eating ants. Ecology 58: 711-724.

Davidson, D.W., 1978. Size variability in the worker caste of a social insect (*Veromessor pergandei* Mayr) as a function of the competitive environment. American Naturalist 112: 523-532.

Davidson, D.W., 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecological Entomology 23: 484-490.

DeLong Jr., D.C., 1996. Defining biodiversity. Wildlife Society Bulletin 24: 738–749.

Devillers, P., Devillers-Terschuren, J., 1996. A classification of South American habitats. IRSNB, Brussels, and Institute of Terrestrial Ecology, Huntingdon.

Diamond, J.M., 1975. Assembly of species communities. pp. 342-444 in: Ecology and evolution of communities. M.L. Cody and J.M. Diamond (eds). Harvard University Press, Cambridge.

Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M., Gemmell, N.J., 2005. Are invasive species the drivers of ecological change? Trends in Ecology and Evolution 20: 470-474.

Dunn, R.R., 2005. Modern insect extinctions, the neglected majority. Conservation Biology 19: 1030-1036.

Dunn, R.R., McCain, C.M., Sanders, N.J., 2007. When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. Global Ecology and Biogeography 16: 305-312.

Eastlake Chew, A., Chew, R.M., 1980. Body size as a determinant of small-scale distributions of ants in evergreen woodland southeastern Arizona. Insectes Sociaux 27: 189-202.

Engelbrecht, B.M.; Comita, L.S.; Condit, R.; Kursar, T.A.; Tyree, M.T.; Turner, B.L.; Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80-82.

Englisch, T., Steiner, F.M., Schlick-Steiner, B.C., 2005. Fine-scale grassland assemblage analysis in Central Europe: ants tell another story than plants (Hymenoptera: Formicidae; Spermatophyta). Myrmecologische Nachrichten 7: 61-67.

Evans, K.L., Warren, P.H., Gaston, K.J., 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80: 1-25.

Fariña Sánchez, T., 1973. The climate of Paraguay.. In: Gorham, J.R. (ed.). Paraguay: ecological essays, pp. 33-38. Academy of the Arts and Sciences of the Americas, Miami, FL.

Farji-Brener, A.G., Corley, J.C., Bettinelli, J., 2002. The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. Diversity and Distributions 8: 235-243.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J. Jr., van Buskirk, J., McCollum, S.A., 1996. Simplifying the jargon of community ecology: a conceptual approach. American Naturalist 147: 282-286.

Fellers, J.H. 1987. Interference and exploitation in a guild of woodland ants. Ecology 68, 1466-1478.

Fisher, B.L., 1996. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. Fieldiana Zoology 85: 93-108.

Fisher, B.L., 1998. Ant diversity patterns along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the Western Masoala Peninsula, Madagascar. Fieldiana Zoology 90: 39-67.

Fisher, B.L., 1999. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andohahela, Madagascar. Fieldiana Zoology 94: 129-147.

Fisher, B.L., 2002. Ant diversity patterns along an elevational gradient in the Réserve Spéciale de Manongarivo, Madagascar. Boissiera 59: 311-328.

Fisher, B.L., 2004. Diversity patterns of ants (Hymenoptera: Formicidae) along an elevational gradient on Monts Doudou in Soutwestern Gabon. California Academy of Sciences Memoir 28: 269-286.

Fittkau, E.J., Klinge, H., 1973. On the biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica 5: 2-14.

Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7: 1221-1244.

French, K., 1999. Spatial variability in species composition in birds and insects. Journal of Insect Conservation 3: 183-189.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405: 220-227.

Gaston, K.J., Spicer, J.I., 2004. Biodiversity: an introduction, second edition. Blackwell Publishing, Oxford, 208pp.

Gibb, H., 2005. The effect of a dominant ant, *Iridomyrmex purpureus*, on resource use by ant assemblages depends on microhabitat and resource type. Austral Ecology 30: 856-867.

Gibb, H., Hochuli, D.F., 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106: 91-100.

Gorham, J.R., 1973. The Paraguayan Chaco and its rainfall. In: Gorham, J.R. (ed.). Paraguay: ecological essays, pp. 39-60. Academy of the Arts and Sciences of the Americas, Miami, FL.

Gotelli, N.J., 1993. Ant lion zones: causes of high-density predator aggregations. Ecology 74, 226-237.

Gotelli, N.J., 1996. Ant community structure: effects of predatory ant lions. Ecology 77, 630-638.

Gotelli, N.J., Ellison, A.M., 2002. Assembly rules for New England ant assemblages. Oikos 99: 591-599.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Institution, Washington, 368 pp.

Grant, P.R., 1972. Convergent and divergent character displacement. Biological Journal of the Linnean Society 4: 39-68.

Grimaldi, D., Engel, M.S., 2005. Evolution of the insects. Cambridge University Press, Cambridge. 755pp.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 24: 3105-3117.

Hoffmann, B.D., 2003. Responses of ant communities to experimental fire regimes on rangelands in the Victoria River District of the Northern Territory. Austral Ecology 28: 182-195.

Hoffmann, B.D., Griffiths, A.D., Andersen, A.N., 2000. Responses of ant communities to dry sulfur deposition from mining emissions in semi-arid tropical Australia, with implications for the use of functional groups. Austral Ecology 25: 653-663.

Hölldobler, B., Lumsden, C.J., 1980. Territorial strategies in ants. Science 210: 732-739.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Cambridge: Bellknap Press.732 pp.

Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey. 375pp.

Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93: 145-159.

IUCN (Species Survival Commission of the World Conservation Union) 2006**:** 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>.

Janzen, D., 1988. Tropical dry forests. The most endangered major tropical ecosystem. In: Wilson, E.O. ed., Biodiversity, pp. 130-137. National Academy of Sciences/Smithsonian Institution, Washington, D.C.

Jeanne, R.L., 1979. A latitudinal gradient in rates of ant predation. Ecology 60: 1211-1224.

Johnson, R.A., 1992. Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. Oecologia 89:118-124.

Johnson, R.A., 2000. Habitat segregation based on soil texture and body size in the seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus.* Ecological Entomology 25: 403–412.

Jolivet, P., 1996. Ants and plants: an example of coevolution. Blackhuys, Leiden, Netherlands. 303 pp.

Kaspari, M., 2000. A primer on ant ecology. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 9-24. Smithsonian Institution Press, Washington, D.C.

Kaspari, M., Majer, J.D., 2000. Using ants to monitor environmental change. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 89-98. Smithsonian Institution Press, Washington, D.C.

Kaspari, M., O'Donnell, S., Kercher, J.R., 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. American Naturalist 155: 280-293.

Kaspari, M., Weiser, M., 2007. The size-grain hypothesis: do macroarthropods see a fractal world? Ecological Entomology 32: 279-282.

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Testing the value of six taxonomic groups as biodiversity indicators at a local scale. Conservation Biology 18: 667-675.

Keel, S., Gentry, A.H., Spinzi, L., 1993. Using vegetation analysis to facilitate the selection of conservation sites in eastern Paraguay. Conservation Biology 7: 66-75.

Kellert, S.R., 1993. Values and perceptions of invertebrates. Conservation Biology 7: 845-855.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7: 796-808.

Kruck, W., Barboza, F., Carlini, A., Hoffmann, R., Medina Netto, A., Mereles, F., 1998. Chaco: protección y uso sostenible. Proyecto Sistema Ambiental del Chaco 1992-97. Dirección de Ordenamiento Ambiental, Ministerio de Agricultura y Ganadería, Paraguay (DOA-MAG) e Instituto Federal de Geociencias y Recursos Naturales, Alemania.

Kusnezov, N., 1957. Numbers of species of ants in faunae of different latitudes. Evolution 11: 298-289.

Lattke, J.E., 2003. Biogeografía de las hormigas neotropicales. In: Fernández, F. (ed.). Introducción a las hormigas de la región Neotropical, pp. 65-85. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391: 72-76.

Lebrun, E.G., Feener, D.H.Jr., 2007. When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. Journal of Animal Ecology 76: 58-64.

Leponce, M., Theunis, L., Delabie, J.H.C., Roisin, Y., 2004. Scale dependence of diversity measures in a leaf-litter ant assemblage. Ecography 27: 253-267.

Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. Ecology 73: 1943-1967.

Levings, S.C., Franks, N.R., 1982. Patterns of nest dispersion in a tropical ground ant community. Ecology 63: 338-344.

MacMahon, J.A., Mull, J.F., Crist, T.O., 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Annual Review of Ecology and Systematics 31: 265-291.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell Publishing, Oxford, 256 pp.

Majer, J.D., 1983. Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. Environmental Management 7: 375-383.

Majer, J.D., Nichols, O.G., 1998. Long-term recolonization patterns of ants in Western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. Journal of Applied Ecology 35: 161-182.

Marsh, A.C.,1986. Ant species richness along a climatic gradient in the Namib Desert. Journal of Arid Environments 11: 235–241.

McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73: 181-201.

McKinney, M.L., 1999. High rates of extinction and threat in poorly studied taxa. Conservation Biology 13: 1273-1281.

Medel, R.G., 1995. Convergence and historical effects in harvester ant assemblages of Australia, North America, and South America. Biological Journal of the Linnean Society 55: 29-44.

Mereles, M.F., 2005. Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay. Rojasiana 6: 5-48.

Michels, K., Cromme, N., Glatzle, A., Schultze-Kraft, R., 2001. Biological control of leaf-cutting ants using forage grasses: nest characteristics and fungus growth. Journal of Agronomy and Crop Science 187: 259-267.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. Journal of Biogeography 33: 491-505.

Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: biodiversity synthesis. World Resource Institute, Washington, D.C., 86 pp.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82: 2381-2396.

Mooney, H.A., Bullock, S.H., Medina, E., 1995. Introduction. In: Bullock, S.H, Mooney, H.A, Medina, E., 1995. Seasonally dry tropical forests, pp. 1-8. Cambridge University Press, Cambridge.

Moreno, C.E., Sánchez-Rojas, G., Pineda, E., Escobar, F., 2007. Shortcuts for biodiversity evaluation: a review of terminology and recommendations for the use of target groups, bioindicators and surrogates. International Journal of Environment and Health 1: 71-86.

Morrison, L.W., 1996. Community organization in a recently assembled fauna: the case of Polynesian ants. Oecologia 107: 243-256.

Morton, S.R., Davidson, D.W., 1988. Comparative structure of harvester ant communities in arid Australia and North America. Ecological Monographs 58: 19-38.

Mueller, U.G., Schultz, T.R., Currie, C.R., Adams, R.M.M., Malloch, D., 2001. The origin of the attine ant-fungus mutualism. The Quaterly Review of Biology 76: 169-197.

Negi, H.R., Gadgil, M., 2002. Cross-taxon surrogacy of biodiversity in the Indian Garhwal Himalaya. Biological Conservation 105: 143-155.

Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26: 867-878.

New, T.R., 1995. An introduction to invertebrate conservation biology. Oxford University Press, Oxford. 194pp.

Noss, A., Mares, M.A., Diaz, M.M., 2002. The Chaco. In: Mittermeier, R.A., Mittermeier, C.G., Robles-Gil, P., Pilgrim, J.D., Fonseca, G., Brooks, T.M., Konstant, W.R. (eds): Wilderness. Earth's last wild places, pp. 165-172. Cemex, Mexico City.

Novotny, V., Basset, Y., Auga, J., Boen, W., Dal, C., Drozd, P., Kasbal, M., Isua, B., Kutil, R., Manumbor, M., Molem, K., 1999. Predation risk for herbiorous insects on tropical vegetation: a search for enemy-free space and time. Australian Journal of Ecology 24: 477-483.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. et Drozd, P., 2002. Low host specificity of herbivorous insects in a tropical forest. Nature 416: 841-844.

Ødegaard, F., 2006. Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. Biodiversity and Conservation 15: 83-105.

Ødegaard, F., Diserud, O.H., Østbye, K., 2005. The importance of plant relatedness for host utilization among phytophagous insects. Ecology Letters 8: 612-617.

Oliver, I., Beattie, A.J., 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecological Applications 6: 594-607.

Oliver, I., Beattie, A.J., York, A., 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. Conservation Biology 12: 822-835.

Olson, D.M., 1994. The distribution of leaf littr invertebrates along a Neotropical altitudinal gradient. Journal of Tropical Ecology 10: 129-150.

Olson, D.M., Dinerstein, E., 2002. The global 200: priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89: 199-224.

Panzer, R., Schwartz, M.W., 1998. Effectiveness of a vegetation-based approach to insect conservation. Conservation Biology 12: 693-702.

Parr, C.L., Sinclair, B.J., Andersen, A.N., Gaston, K.J., Chown, S.L., 2005. Constraint and competition in assemblages: a cross-continental and modeling approach for ants. The American Naturalist 165: 481-494.

Passera, L., Aron, S., 2005. Les fourmis. Comportement, organisation sociale et évolution. CNRC-CRC, Ottawa. 480 pp.

Perfecto, I., 1994. Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. Oecologia 98: 184-192.

Pfeiffer, M., Chimedregzen, L., Ulykpan, K., 2003. Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. Journal of Biogeography 30: 1921-1935.

Pimm, S.L., 2002. The dodo went extinct (and other ecological myths). Annals of the Missouri Botanical Garden 89: 190-198.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M. 1995. The future of biodiversity. Science 269: 347–350.

Prado, D.E., 1993. What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco. V. Candollea 48: 145-172.

Prance, G.T., 2006. Tropical savannas and seasonally dry forests: an introduction. Journal of Biogeography 33: 385-386.

Qian, H., Ricklefs, R.E., 2004. Taxon richness and climate in Angiosperms: is there a globally consistent relationship that precludes region effects? American Naturalist 163: 773-779.

Rahbek, C., 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18: 200-205.

Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B., Graves, G.R., 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society of London B. 274: 165-174.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639-680.

Redford, K.H., Taber, A., Simonetti, J.A., 1990. There is more to biodiversity than the tropical rain forests. Conservation Biology 4: 328-330.

Retana, J., Cerdá, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123: 436-444.

Retana, J., Picó, X., Rodrigo, A., 2004. Dual role of harvesting ants as seed predators and dispersers of a non-myrmechorous Mediterranean perennial herb. Oikos 105: 377-385.

Ricklefs, R.E., 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters 7: 1-15.

Samson, D.A., Rickart, E.A., Gonzales, P.C., 1997. Ant diversity and abundance along an elevational gradient in the Philippines. Biotropica 29: 349-363.

Samways, M.J., 2007. Insect conservation: a synthetic management approach. Annual Review of Entomology 52: 465-487.

Sánchez-Azofeifa, A.G., Kalacska, M., Quesada, M., Calvo-Alvarado, J.C., Nassar, J.M., Rodríguez, J.P., 2005a. Need for integrated research for a sustainable future in tropical dry forests. Conservation Biology 19: 285-286.

Sánchez-Azofeifa, A.G., Quesada, M., Rodríguez, J.P., Nassar, J.M., Stoner, K.E., Castillo, A., Garvin, T., Zent, E.L., Calvo-Alvarado, J.C., Kalacska, M., Fajardo, L., Gamon, J.A., Cuevas-Reyes, P., 2005b. Research priorities for neotropical dry forests. Biotropica 27: 477-485.

Sanders, N.J., 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography 25: 25-32.

Sanders, N.J., Moss, J., Wagner, D., 2003a. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12: 93-102.

Sanders, N.J., Gotelli, N.J., Heller, N.E., Gordon, D.M. 2003b. Community diassembly by an invasive species. PNAS 100: 2474-2477.

Santini, G., Tucci, L., Ottonetti, L., Frizzi, F., 2007. Competition trade-offs in the organisation of a Mediterranean ant assemblage. Ecological Entomology 32: 319-326.

Sarty, M., Abbott, K.L., Lester, P.J., 2006. Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149: 465-473.

Saux, C., Fisher, B.L., Spicer, G.S., 2004. Dracula ant phylogeny as inferred by nuclear 28S rDNA sequences and implications for ant systematics (Hymenoptera: Formicidae: Amblyoponinae). Molecular Phylogenetics and Evolution 33: 457-468.

Savolainen, R., Vepsäläinen, K., 1988. A competitive hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51: 135-155.

Savolainen, R., Vepsäläinen, K., 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. Oikos 56: 3-16.

Schoener T.W., 1974. Resource partitioning in ecological communities. Science 185, 27-39.

Schultz, T.R., McGlynn, T.P., 2000. The interactions of ants with other organisms. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 35-44. Smithsonian Institution Press, Washington, D.C.

Schultze-Kraft, R., 1998. Biologicol control of the leaf-cutting ant *Acromyrmex landolti* using forage grass species. Diplomarbeit, Universität Hohenheim und Institut für Pflanzenproduktion und Agrarökologie in den Tropen und Subtropen. 93 pp.

Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Croves, G., Anderson, H., Caicco, S., D'erchia, F., Edwards Jr., T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123. 41 pp.

Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conservation Biology 18: 167-173.

Suarez, A.V., Bolger, D.T., Case, T.J., 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79: 2041-2056.

Theunis, L., Gilbert, M., Roisin, Y., Leponce, M., 2005. Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. Insectes Sociaux 52: 366-377.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, E., 2004. Extinction risk from climate change. Nature 427: 145-148.

Thomas, M.L., Holway, D.A., 2005. Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. Journal of Animal Ecology 74: 532-542.

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London B., 270: 467-473.

Underwood, E.C., Fisher, B.L., 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132: 166-182.

Vasconcelos, H.L., 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiversity and Conservation 8: 409-420.

Vasconcelos, H.L., Macedo, A.C.C., Vilhena, J.M.S., 2003. Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. Studies on Neotropical Fauna and Environment 38: 115-124.

Vasconcelos, H.L., Vilhena, J.M.S., Magnusson, W.E., Albernaz, A.L.K.M., 2006. Long-term effects of forest fragmentation on Amazonian ant communities. Journal of Biogeography 33: 1348-1356.

Vepsäläinen, K., Pisarski, B., 1982. Assembly of island ant communities. Annales Zoologici Fennici 19: 327-335.

Wagner, D., Jones, J.B., 2006. The impact of harvester ants on decomposition, N mineralization, litter quality, and the availability of N to plants in the Mojave Desert. Soil Biology and Biochemistry 38: 2591-2601.

Ward, P.S., 2000. Broad-scale patterns of diversity in leaf litter ant communities. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 99-121. Smithsonian Institution Press, Washington, D.C.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution and Systematics 34: 273-309.

Wilson, E.O., 1971. The Insect Societies. The Belknap Press of Harvard University Press. 548 pp.

Wilson, E.O., 1993. La diversité de la vie. Editions Odile Jacob, Paris, 496 pp.

Wilson, E.O., 2003. L'avenir de la vie. Editions du Seuil, Paris, 285 pp.

Woodruff, D.S., 2001. Declines of biomes and biotas and the future of evolution. PNAS 98: 5471-5476.

Yeates, D.K., Bouchard, P., Monteith, G.B., 2002. Patterns and levels of endemism in the Australian wet tropics rainforest: evidence from flightless insects. Invertebrate Systematics 16: 605-619.

York, A., 2000. Long-term effects of frequent low-intensity burning on ant communities in coastal blackbutt forests of southeastern Australia. Austral Ecology 25: 83-98.

Tableau 0-1: Résultats des études traitant de l'influence de l'aridité sur la structure des assemblages de fourmis à l'échelle régionale.

Région et nombre de localités (n)	Etendue du gradient (1)	Myrmécofaune étudiée	Méthode d'échantillonnage	Richesse spécifique totale observée	Corrélation (2) entre pluviométrie et diversité α		Similarité faunique (3)	Référence
					Richesse spécifique	Indice de Shannon		
Sud-Ouest des Etats-Unis n= 10	76-276	Granivores	Appâts (graines)	16	**r =0.83; P=0.003**	**r =0.73; P=0.017**	$0 \leq \text{So} \leq 0.86$ $\text{So}_{moy} \pm \text{SD} = 0.38 \pm 0.24$	Davidson, 1977; Morton et Davidson, 1988
Désert de Namib n=11	16-95	Formicidae	Pitfall avec appâts (fromage + sirop)	27	**r=0.97; P<0.001**	-	-	Marsh, 1986
Australie n=19	119-568	Granivores	Appâts (graines)	91	r=0.30; P=0.212	r =0.197; P=0.419	$0 \leq \text{So} \leq 0.59$ $\text{So}_{moy} \pm \text{SD} = 0.15 \pm 0.11$	Morton et Davidson, 1988
Argentine/Chili n=16	43-332	Granivores	Appâts (graines)	21	r =0.105; P=0.698 (4)	-	-	Medel, 1995
Mongolie n=10	84-197	Surtout granivores	Appâts (graines/sucre) + chasse à vue	26	r = -0.007; P=0.983	r =0.15; P>0.05	$0 \leq \text{MH} \leq 0.98$ $\text{MH}_{moy} \pm \text{SD} = 0.22 \pm 0.33$ $0 \leq \text{So} \leq 0.71$ $\text{So}_{moy} \pm \text{SD} = 0.27 \pm 0.18$	Pfeiffer *et al.*, 2003

(1) Pluviométrie annuelle moyenne (mm/an).

(2) "Pearson product moment correlations"; les corrélations significatives sont indiquées **en gras**.

(3) Les indices de similarité utilisés sont: So = indice de Sørensen et MH= indice de Morisita-Horn. Leurs valeurs sont comprises entre 0 [quand les assemblages comparés n'ont aucune espèce commune] et 1 [assemblages similaires]. Les valeurs minimales, maximales et moyennes (± SD) sont données.

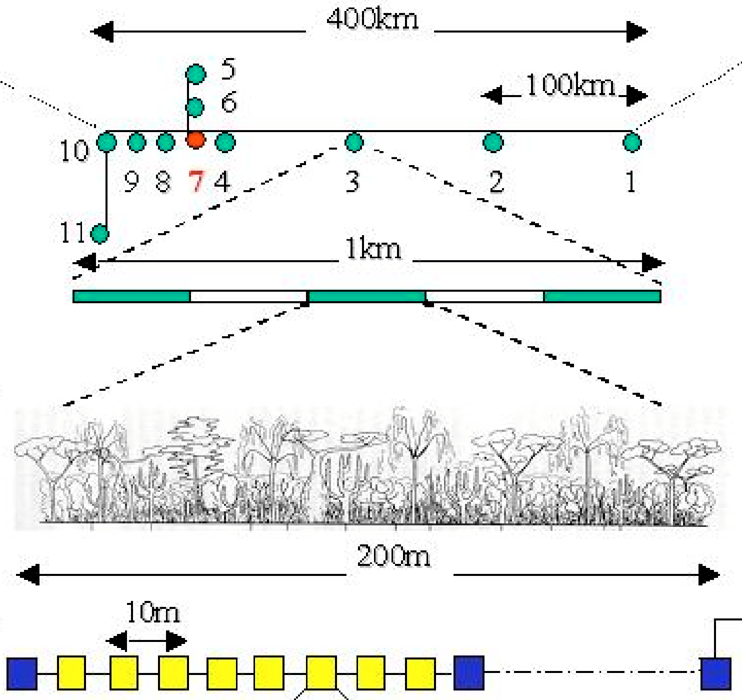
(4) L'absence de corrélation entre la diversité α et la pluviométrie reste valide lorsque les localités argentines et chiliennes sont analysées séparément. On obtient alors respectivement: r = -0.259, P=0.442, n=11 et r =0.567, P=0.319, n=5.

Tableau 0-2: Liste des sous-familles et genres de fourmis présents dans le Chaco paraguayen (Alex Wild, comm. pers., 2007).

Sous-famille	Genre	Nombre d'espèces[(1)]
Amblyoponinae	*Amblyopone*	1
Cerapachyinae	*Acanthosticus*	1
Dolichoderinae	*Anillidris*	1
-	*Dolichoderus*	1
-	*Dorymyrmex*	5 (+1)
-	*Forelius*	2 (+3)
-	*Gracilidris*	1
-	*Linepithema*	3
Ecitoninae	*Labidus*	2
-	*Neivamyrmex*	4 (+1)
Ectatomminae	*Ectatomma*	4
-	*Gnamptogenys*	2
-	*Typhlomyrmex*	1
Formicinae	*Brachymyrmex*	4 (+1)
-	*Camponotus*	12 (+5)
-	*Paratrechina*	1 (+1)
Myrmicinae	*Acromyrmex*	9 (+3)
-	*Apterostigma*	1
-	*Atta*	2
-	*Cephalotes*	12
-	*Crematogaster*	5 (+1)
-	*Cyphomyrmex*	1 (+1)
-	*Megalomyrmex*	1
-	*Mycetophylax*	1
-	*Mycetosoritis*	1
-	*Myrmicocrypta*	1
-	*Nesomyrmex*	1 (+2)
-	*Pheidole*	11 (+6)
-	*Pogonomyrmex*	4
-	*Pyramica*	3
-	*Rogeria*	1 (+1)
-	*Solenopsis*	6 (+5)
-	*Strumigenys*	1
-	*Trachymyrmex*	1 (+3)
-	*Tranopelta*	1
-	*Wasmannia*	1
Ponerinae	*Anochetus*	1
-	*Dinoponera*	1
-	*Hypoponera*	1 (+2)
-	*Leptogenys*	1
-	*Odontomachus*	1 (+1)
-	*Pachycondyla*	2
Pseudomyrmecinae	*Pseudomyrmex*	8
TOTAL: 9 sous-familles	**43 genres**	**124 (+37) = 161 espèces**

(1) Les nombres entre parenthèses sont des morpho-espèces. Cette liste prend en compte une partie des fourmis collectées dans le cadre de cette thèse (trois localités).

Gradient d'aridité:



Plantes: protocole adapté d'après Keel *et al.*, 1993

Fourmis: protocole A.L.L. (Agosti et Alonso, 2000)

Sol:
- Texture (%sable, %limon, % argile)
- pH
- [Chlorides]

Ecologie:
Partage des ressources alimentaires (localité de référence; localité 7)

Pièges à fosse

Winkler

Figure 0-1: Méthodologie employée afin de répondre aux objectifs de la thèse.

Le long d'un gradient d'aridité (1000mm à 350mm de précipitation moyenne annuelle) traversant le Chaco sec paraguayen, la myrmécofaune et la végétation de 11 localités furent échantillonnées entre 2001 et 2004. L'échantillonnage se fit toujours en septembre ou novembre afin d'éviter les températures extrêmes connues pour modifier l'activité des fourmis dans le Gran Chaco (Bestelmeyer, 2000). La localité 7 (Parc National Teniente Enciso) fut notre localité de référence et fut échantillonnée en 2001, 2002 et 2004 afin de vérifier la stabilité temporelle de la structure des assemblages de fourmis.

La distance de base séparant les localités était de 100km. Celle-ci fut affinée autour de la localité de référence. Des localités perpendiculaires au gradient d'aridité furent également échantillonnées. Les localités étaient ainsi séparées les unes de autres par 20 à 400km. Le but de cet agencement était de comparer des assemblages de plantes et de fourmis présents dans des conditions abiotiques similaires (de sol et/ou d'aridité) mais à des distances géographiques différentes afin de (1) distinguer les influences respectives de l'aridité, des conditions édaphiques et de la distance géographique sur les patrons de diversité obtenus **(objectif 2)**, (2) tester si les assemblages de fourmis répondent plus finement que les plantes aux conditions du milieu (**objectif 4**).

Au niveau de chaque localité, trois transects de 200m furent collectés le long d'une ligne d'un kilomètre. Le protocole "Ants of the Leaf Litter" (A.L.L.) fut appliqué pour collecter les fourmis. Au niveau de 20 points espacés de 10m, les fourmis sont collectées par piège à fosse ("24h-pitfall trap") et par Winkler. Le Winkler est un dispositif permettant d'extraire la faune des litières. Pour cela, la litière de feuilles mortes présente à l'intérieur d'un quadrat de 1m² est ramassée, tamisée et placée dans un sac mini-Winkler pendant 24h (Fisher, 1998). L'extraction des insectes se fait ensuite de façon passive: ils se déplacent, notamment afin de tenter de fuir la dessication progressive de la litière, et tombent dans un sachet rempli d'alcool disposé au bas du sac mini-Winkler. La comparaison des myrmécofaunes collectées par ces deux méthodes répond aux **objectifs 1 et 5**.

Le long de chaque transect de 200m, la présence et l'abondance de 45 espèces végétales sont relevées dans une bande de 2m de largeur (la surface étudiée par localité est donc de 0,12ha). Les 45 espèces d'arbres ou d'arbustes sélectionnées sont caractéristiques du Chaco sec paraguayen (Mereles, 2005), communes et identifiables sur le terrain. Ce protocole est basé sur celui de Keel *et al.* (1993) mis au point dans les forêts humides du Paraguay. Dans ces forêts, plus diversifiées que celles du Chaco sec, une surface de 0,1ha suffisait à caractériser l'assemblage végétal.

Un échantillon de sol a été ramassé au début, au milieu et à la fin de chaque transect de 200m (carrés bleus). Des analyses ont été réalisées au sein du laboratoire du Dr. Herbauts (ULB, Jardin Massart) afin de déterminer la texture, le pH et la concentration en chlorides des échantillons (se référer au chapitre 4 pour les protocoles d'analyses).

Enfin, une expérience à base d'appâts a été réalisée au niveau de la localité de référence afin d'étudier les ségrégations trophiques, temporelles et spatiales présentées par les fourmis de cet assemblage lors de l'exploitation des ressources alimentaires (**objectif 3**).

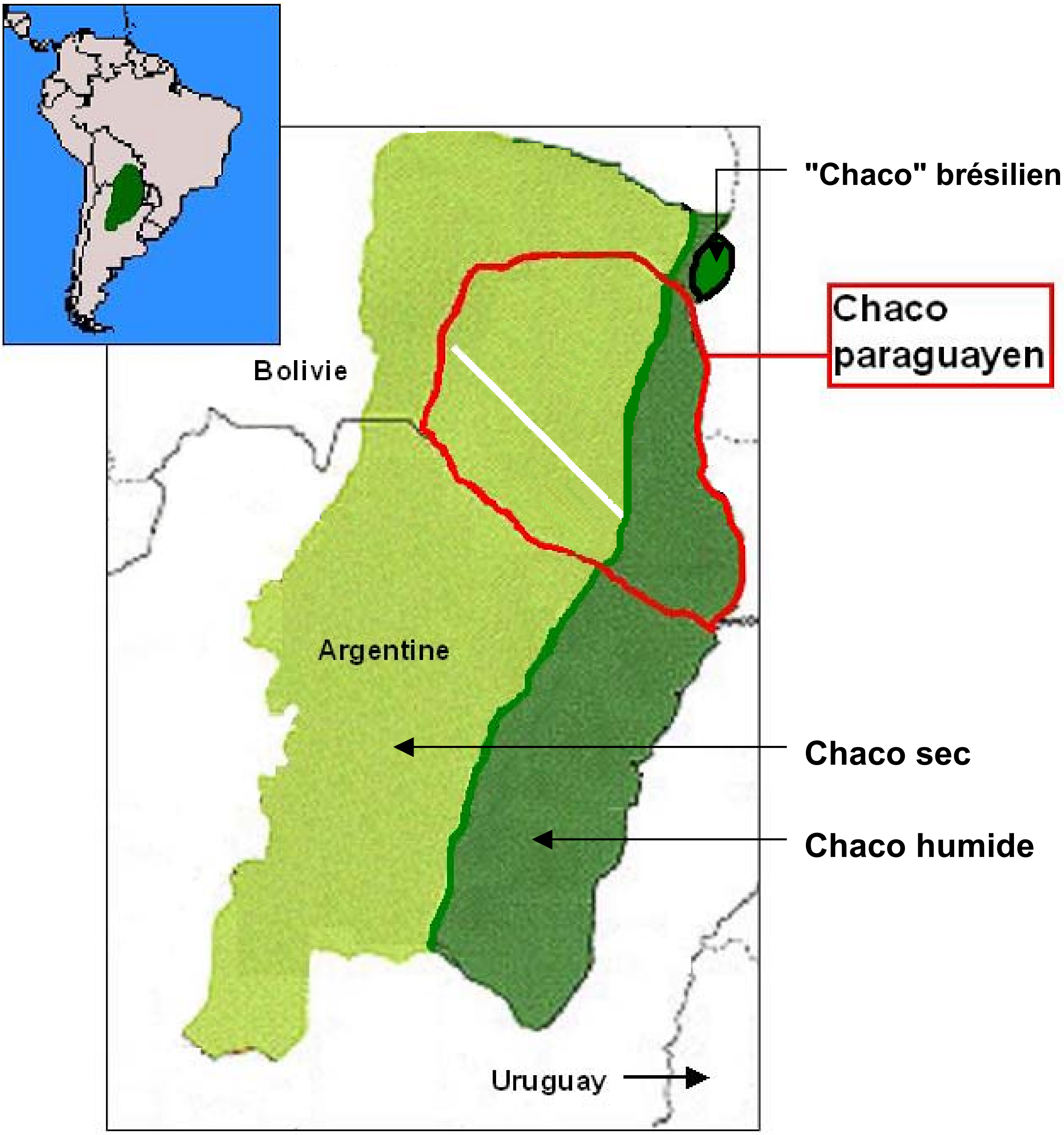


Figure 0-2: Le Gran Chaco, la plus vaste forêt sèche d'Amérique du Sud. On différencie le Chaco humide (1000 à 1400mm de précipitation moyenne annuelle) et le Chaco sec (350-1000mm). Il n'existe pas de consensus concernant l'existence d'une végétation chaquéenne sur le territoire brésilien (Prado, 1993). Le transect étudié fait 400km.

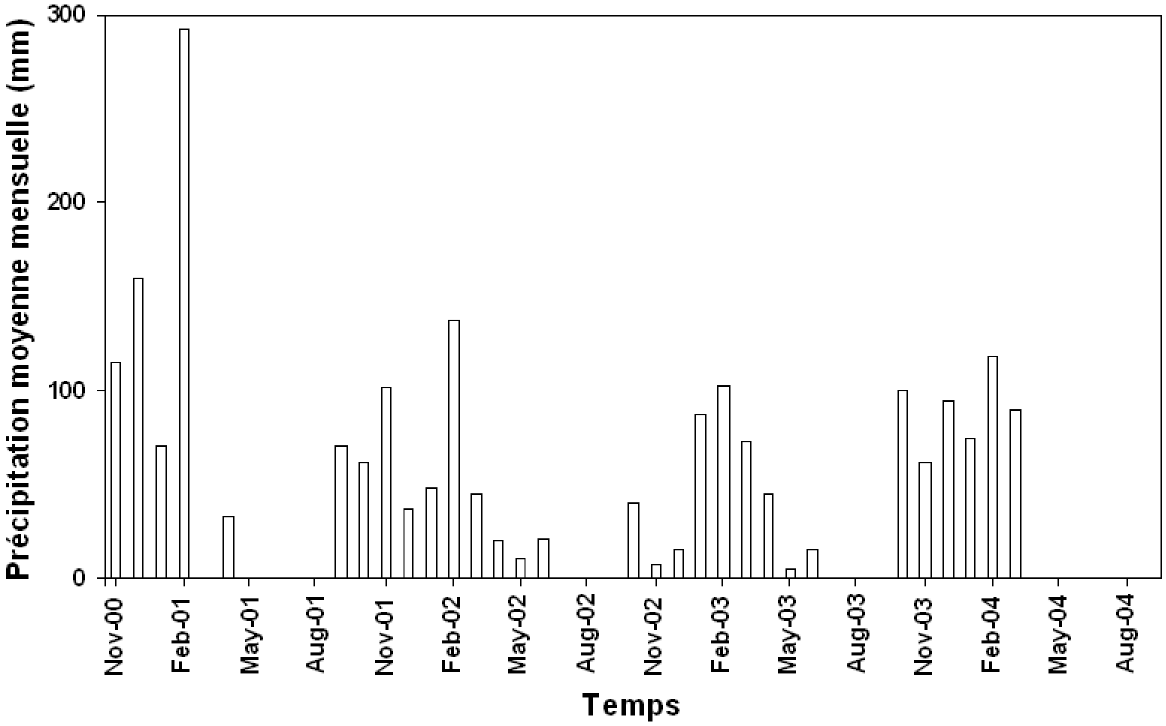


Figure 0-3: Précipitations mensuelles moyennes de novembre 2000 à septembre 2004 au Parc National Teniente Enciso, la localité de référence.

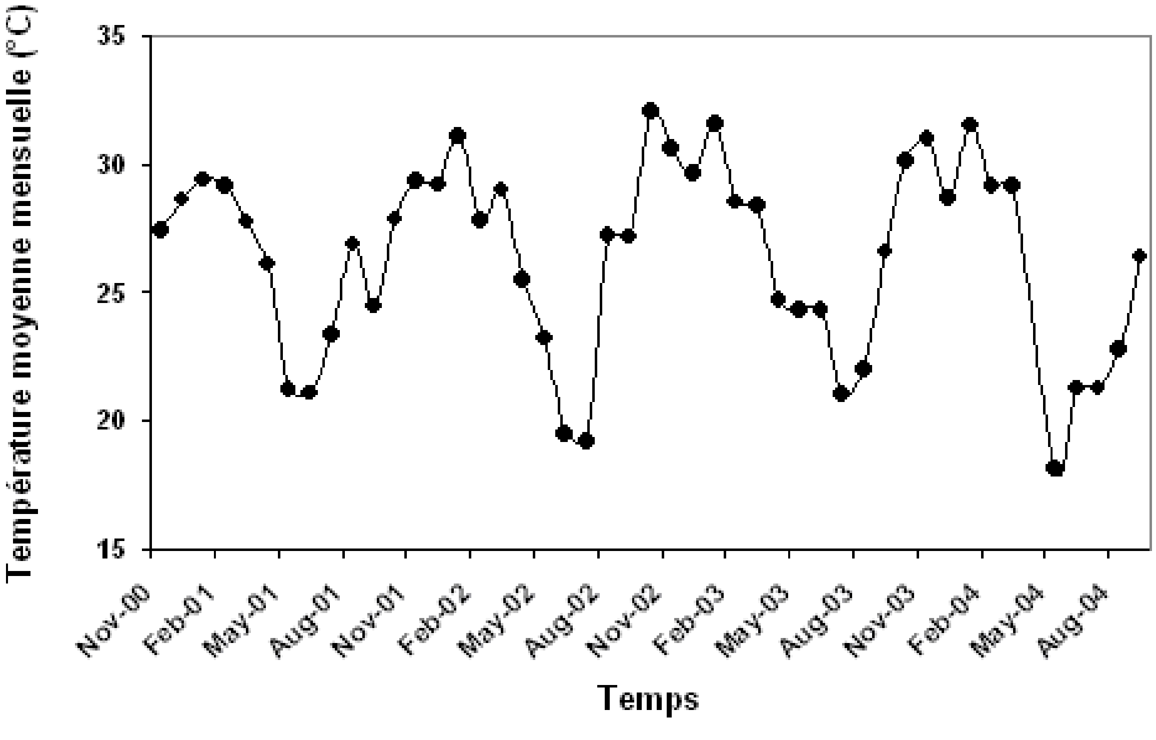
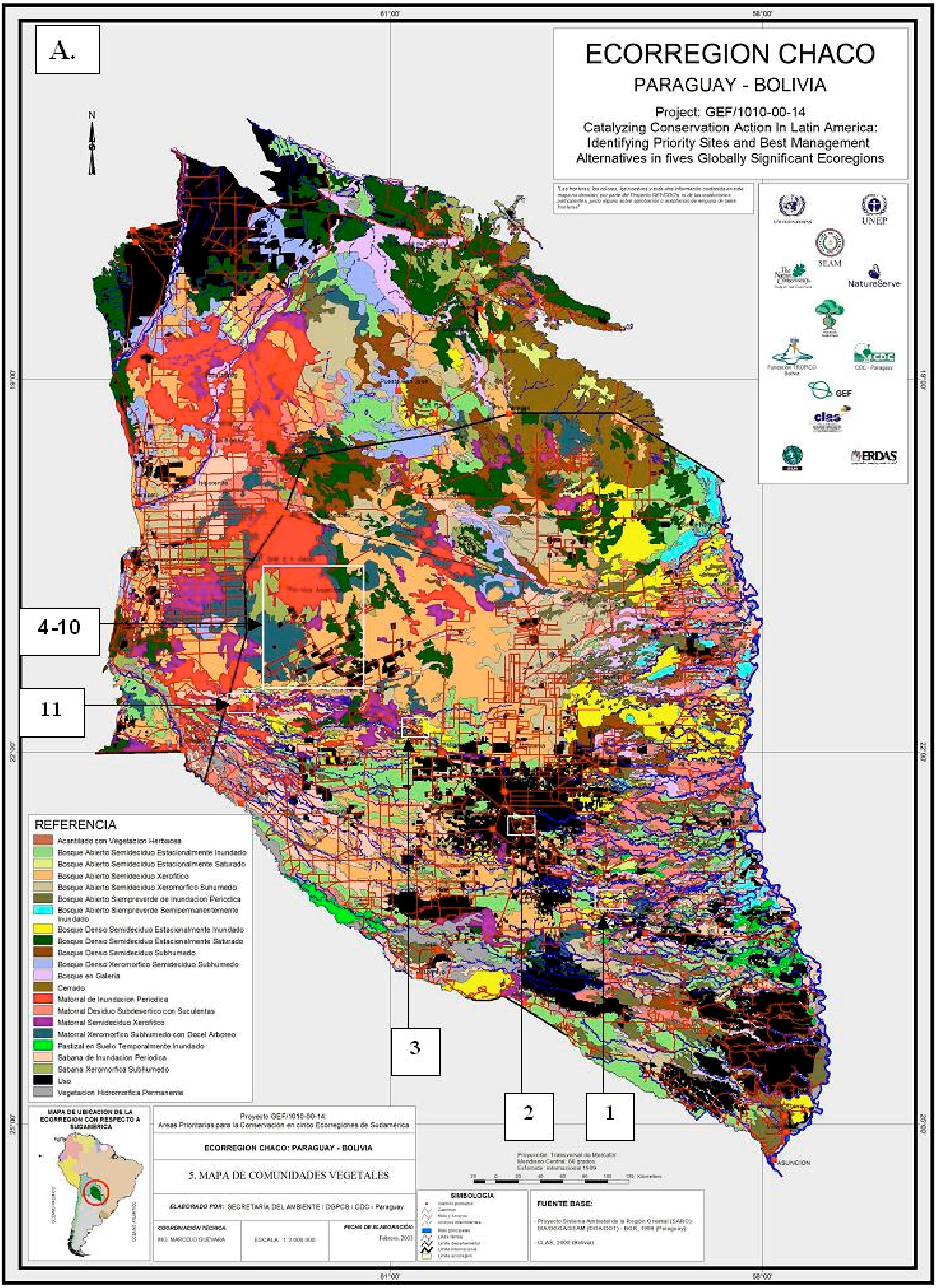


Figure 0-4: Températures mensuelles moyennes de novembre 2000 à septembre 2004 au Parc National Teniente Enciso, la localité de référence.


A.
ECORREGION CHACO
PARAGUAY - BOLIVIA
Project: GEF/1010-00-14
Catalyzing Conservation Action In Latin America:
Identifying Priority Sites and Best Management
Alternatives in fives Globally Significant Ecoregions
UNEP
SEAM
NatureServe
CDC - Paraguay
GEF
clas
ERDAS
N
61°00'
58°00'
19°00'
22°00'
25°00'
4-10
11
3
2
1
ASUNCION
REFERENCIA
Acantilado con Vegetacion Herbacea
Bosque Abierto Semideciduo Estacionalmente Inundado
Bosque Abierto Semideciduo Estacionalmente Saturado
Bosque Abierto Semideciduo Xerofitico
Bosque Abierto Semideciduo Xeromorfico Subhumedo
Bosque Abierto Siempreverde de Inundacion Periodica
Bosque Abierto Siempreverde Semipermanentemente Inundado
Bosque Denso Semideciduo Estacionalmente Inundado
Bosque Denso Semideciduo Estacionalmente Saturado
Bosque Denso Semideciduo Subhumedo
Bosque Denso Xeromorfico Semideciduo Subhumedo
Bosque en Galeria
Cerrado
Matorral de Inundacion Periodica
Matorral Desiduo Subdesertico con Suculentas
Matorral Semideciduo Xerofitico
Matorral Xeromorfico Subhumedo con Docel Arboreo
Pastizal en Suelo Temporalmente Inundado
Sabana de Inundacion Periodica
Sabana Xeromorfica Subhumedo
Uso
Vegetacion Hidromorfica Permanente
MAPA DE UBICACION DE LA ECORREGION CON RESPECTO A SUDAMERICA
Proyecto GEF/1010-00-14:
Areas Prioritarias para la Conservación en cinco Ecoregiones de Sudamérica
ECORREGION CHACO: PARAGUAY - BOLIVIA
5. MAPA DE COMUNIDADES VEGETALES
ELABORADO POR: SECRETARÍA DEL AMBIENTE / DGPCB / CDC - Paraguay
COORDINACIÓN TÉCNICA:
ING. MARCELO GUEVARA
ESCALA: 1:3.000.000
FECHA DE ELABORACIÓN:
Febrero, 2003
SIMBOLOGIA
FUENTE BASE:
- CLAS, 2000 (Bolivia)
Kilometers

B.

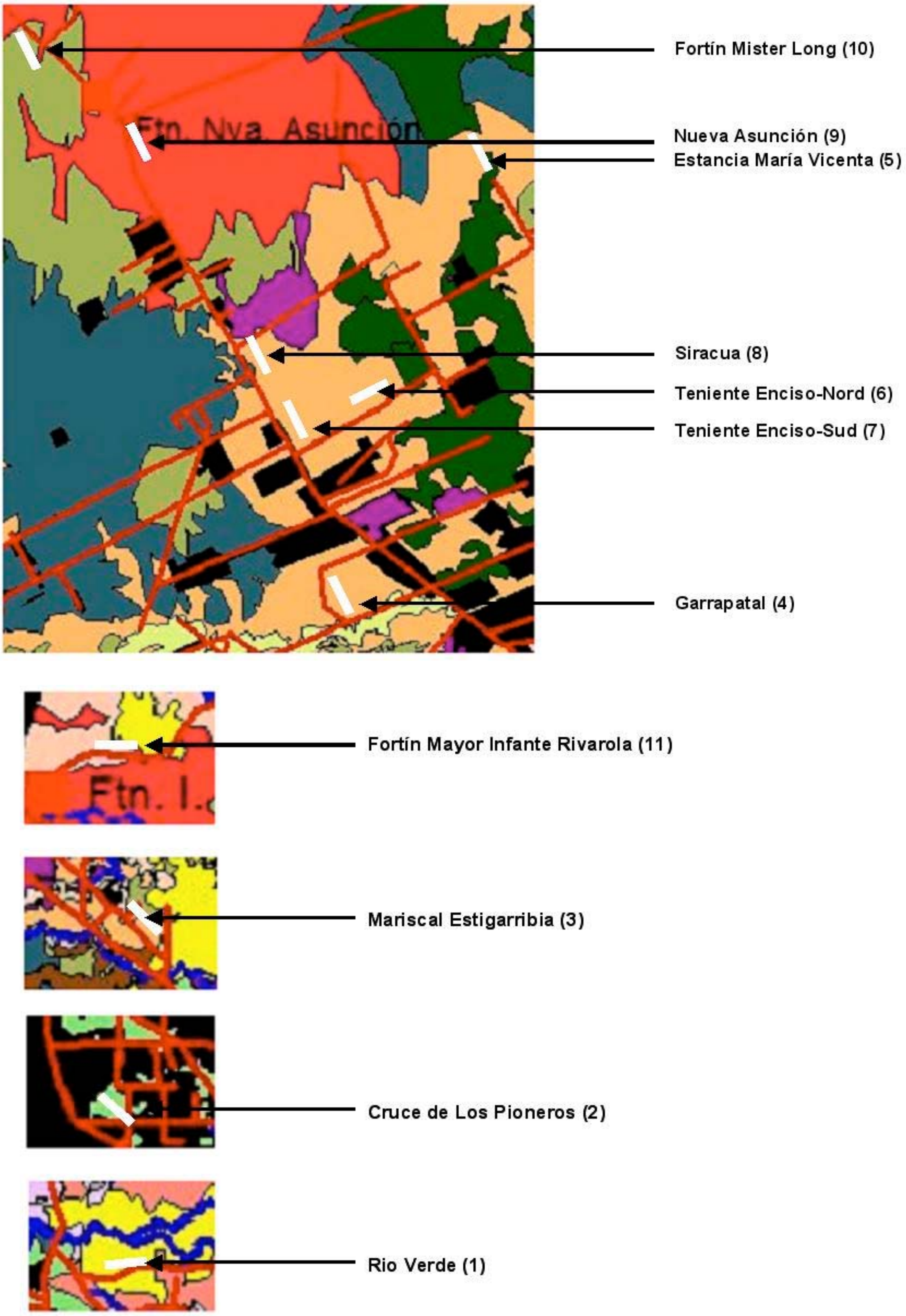


Figure 0-5: (A) Végétation du Chaco paraguayen et bolivien. (B) Détails de la végétation au niveau des 11 localités étudiées. Les traits blancs symbolisent les transects de 1km le long desquels les assemblages de plantes et de fourmis furent échantillonnés.

LRH: Delsinne, Leponce, Theunis, Braet, and Roisin

RRH: Rainfall Influences Ant Sampling

Rainfall Influences Ant Sampling in Dry Forests

Thibaut Delsinne[1,2,3], Maurice Leponce[1], Laurence Theunis[1, 2], Yves Braet[1], and Yves Roisin[2]

[1]: Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, BELGIUM.

[2]: Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral and Evolutionary Ecology - CP 160/12, 1050 Brussels, BELGIUM.

Received: ; revision accepted:

---

[3] Corresponding author; e-mail: Thibaut.Delsinne@sciencesnaturelles.be

ABSTRACT

The standardized "Ants of the Leaf Litter" protocol aims at facilitating the use of ground-foraging and litter-dwelling ants in biodiversity assessment and monitoring programs. It was initially developed to characterize assemblages from tropical rain forests and is based on two main techniques: Winkler extractions and pitfall traps. Here we tested to what extent this protocol was adapted to tropical dry forests and affected by the rainfall regime. Our 10 study sites were located along an aridity gradient (average annual rainfall: 350-1300mm) in the Gran Chaco. The number of species collected per sampling effort increased with aridity for pitfalls but followed an opposite trend for Winkler samples. This trend could be explained by the low daytime foraging activity in the leaf litter during drought periods. In arid and semi-arid regions the good performance of pitfalls was probably related to their 24h operation and to the attractiveness of the water they contained. Our results stress that the Winkler method used in the Ants of the Leaf Litter protocol may not be cost-effective during periods of drought and may lead to severe underestimations of litter ant diversity in tropical dry forests.

RESUMEN

El objetivo del protocolo estándar para la colección de hormigas que habitan en el suelo y la hojarasca ("Ants of the Leaf Litter") es facilitar el uso de las hormigas en la estimación de la biodiversidad y en los programas de monitoreo. Este protocolo fue desarrollado inicialmente para caracterizar los ensamblajes de las hormigas de los bosques tropicales y se basa principalmente en dos técnicas: el extractor Winkler y las trampas de caída. En este estudio nosotros evaluamos hasta qué punto este protocolo se ajustó a los bosques secos tropicales y fue afectado por el régimen de lluvia. Nuestros 10 sitios de muestreo fueron localizados a lo largo de un gradiente de aridez (la media anual de lluvia: 350-1300mm) en el Gran Chaco. El número de especies colectadas por esfuerzo de muestreo incrementó con la aridez para las trampas de caída pero siguió una tendencia opuesta para las muestras de Winkler. Esta tendencia puede ser explicada por la baja actividad de forrajeo en la hojarasca en el día y durante los periodos secos. El buen desempeño de las trampas de caída en las regiones áridas y semiáridas podría estar relacionado a su funcionamiento de día y noche y al atractivo del agua que ellas contenían. Nuestros resultados enfatizan que el método de Winkler usado en el protocolo "Ants of the Leaf Litter" puede ser ineficiente durante los periodos secos y puede llevar a una severa baja estimación de la diversidad de las hormigas de la hojarasca en los bosques secos tropicales.

Key words: A.L.L. protocol; conservation; Formicidae; Gran Chaco; rapid biodiversity assessment; sampling method evaluation.

AMONG INSECTS, ANTS APPEAR TO BE ONE OF THE MOST INFORMATIVE AND TRACTABLE GROUP FOR biodiversity evaluation and monitoring because of their ecological and numerical dominance (Folgarait 1998, Underwood and Fisher 2006), their perennial nests (Alonso & Agosti 2000), their quick response to environmental changes (Kaspari & Majer 2000) and their relative ease of identification (Brown 2000). The standardized "Ants of the Leaf Litter" protocol (hereafter called A.L.L. protocol) for collecting ground-dwelling ants (Agosti & Alonso 2000) was established to allow a qualitative comparison of ant community structure at different localities, the basic information needed to design conservation policies (Fisher 1999, 2005). This protocol relies on 200m transects, along which 1m² litter samples are taken for Winkler extraction and pitfall traps are placed at 10m intervals. These two methods are the most efficient for sampling litter-dwelling and ground-foraging ants in rainforest ecosystems (Delabie *et al*. 2000). Further techniques such as dead wood inspection or baiting may be added to collect more species, depending on the survey objectives (Agosti & Alonso 2000). The A.L.L. protocol has mainly been developed for tropical rain forests (Agosti *et al*. 2000) and it is still necessary to verify its applicability in a larger set of climates. To this purpose, Winkler and pitfall samples were recently compared in forests of Tennessee (Martelli *et al*. 2004), Florida (King & Porter 2005), and France (Groc 2006). In all these studies, the authors collected more species with Winkler than with pitfall traps, and advised to combine both methods to sample the ant assemblage.

Here, the A.L.L. protocol based on Winkler extractions and pitfall traps was carried out in dry forests along a gradient of aridity to test the effect of rainfall on (1) the efficiency of both methods in terms of species richness and species occurrences collected; (2) their faunal complementarity; and (3) the fraction of the whole assemblage captured per A.L.L. transect. The Gran Chaco plains, divided into the wet Chaco (1000-1400 mm of average annual rainfall) and the dry Chaco (350-1000 mm), appear as ideal for such a study because of their flat topography and wide rainfall range spread along a regular gradient (Fig. 1-1).

In arid and semi-arid ecosystems, rainfall occurs as sporadic pulse events separated by drought periods of variable duration (Reynolds *et al*. 2004, Schwinning *et al*. 2004). As rainfall is known to influence the activity of ant assemblages on a seasonal scale (Whitford 1978, Reddy & Venkataiah 1990, Lindsey & Skinner 2001), we hypothesized that rainfall pulses could have an immediate effect on ant foraging and, consequently, on the efficiency of the sampling protocol. In this paper, we tested this hypothesis by comparing samples taken during drought or after rainfall, and by simulating rainfall in experimental quadrats.

METHODS

STUDY SITES.—The study was conducted between 1998 and 2004 in the dry and wet Paraguayan Chaco and in the wet Argentinean Chaco. Ten localities, distant from each other by 20-800km and distributed along the aridity gradient (Fig. 1-1), were sampled at the end of the dry season, in September and October, when temperature and rainfall increased. This sampling period was selected in order to avoid the extremely high or low temperatures, which may occur during the dry or wet season respectively (Ramella & Spichiger 1989), because extreme temperatures limit the foraging of some Chacoan ant species (Bestelmeyer 2000, Delsinne *et al*. 2007). The habitats are a continuum of xeromorphic forests in the dry Chaco and mesoxeromorphic forests in the wet Chaco (Mereles 2005).

SAMPLING PROTOCOL.—Ants were sampled according to the standardized A.L.L. protocol (Agosti & Alonso 2000). Overall, 26 A.L.L. transects were carried out: six in localities 1 and 7, which were our reference localities for the wet and dry Chaco respectively, three in localities 2, 5, and 10 and one in the other localities (Fig. 1-1).

The A.L.L. protocol consists of a line-transect of 20 sampling points spaced at 10m intervals. One Winkler and one pitfall sample are taken at each point. For Winkler extractions, the leaf litter present inside a 1m²-quadrat is collected and sifted and its fauna is extracted with a mini-Winkler apparatus (Fisher 1998). The Winkler extraction is based on the passive desiccation of the leaf litter, forcing the ants to find a more favorable environment and their nest mates (Krell *et al*. 2005). Standard extraction time is 48 hours. However, a preliminary test, consisting in the extraction of 100 Winkler samples for both 24 and 48 hours, was conducted in the wettest locality (1 on Fig. 1-1) to determine if the extraction time could be reduced to 24 hours. Pitfall traps consisted in 70mm-diameter drinking cups, containing water and a drop of detergent, operating for 24 hours.

INFLUENCE OF A NATURAL RAINFALL PULSE.—In reference locality 7, three transects were sampled in September 2001 and three in September 2004. The data from this locality was used to study the influence of a recent rainfall event on the efficiency of the collection method. In September 2001, the mean ambient temperature at this locality was 28°C and six rainfall pulses (totalling 147mm of precipitation) had occurred in the 40 days preceding sampling, one of them (a 15mm pulse) occurring the day before. In September 2004, the mean ambient temperature was 26.5°C and no rainfall had occurred in the preceding 4 months. In all other localities, no rainfall event occurred the day before sampling.

INFLUENCE OF SIMULATED RAINFALL PULSES.—In September 2004, 23 pairs of $1m^2$ quadrats were randomly selected in the dry Chaco (10, 8 and 5 samples in localities 7, 6 and 10 respectively [Fig. 1-1]). In each pair, one quadrat was sprinkled with 2 litres of water while the other, 1m away, was used as a control. The leaf litter was collected and sifted 90 minutes after the beginning of the experiment and its fauna was extracted with a mini-Winkler apparatus for 24 hours.

ANALYSES.—All workers were identified to species or morphospecies. Reproductives were excluded from the analyses because only workers certify the presence of an established colony (Longino *et al*. 2002). Species occurrences (*i.e.* presence/absence) in samples were used as surrogate of abundance (*i.e.* number of workers) because ants are spatially aggregated due to their sociality (Longino 2000) and because colony sizes may strongly vary among species (Hölldobler & Wilson 1990, pp. 160-164). As a consequence, a single trap may collect numerous individuals of a rare species (Longino 2000).

For each reference locality, a matched rank-occurrence plot (Longino & Colwell 1997) was computed to study the complementarity between pitfall and Winkler samples. The graph consisted of a standard rank-occurrence plot for pitfall traps ("the reference method" *sensu* Longino & Colwell [1997]) and the corresponding occurrences of the species collected with Winkler extractors. This graphical method is efficient to reveal the degree of correspondence between two sampling methods and to detect species that are rare in samples from one method but common in samples from the other (Longino & Colwell 1997).

In addition, complementarity between pitfall and Winkler samplings was expressed by the complement of the NNESS index (Trueblood *et al*. 1994):

$$\begin{aligned}\text{Complementarity}_{PW/k} &= 1 - \text{NNESS}_{PW/k}\\ &= 1 - \{\text{ESS}_{PW/k} / [(\text{ESS}_{PP/k} + \text{ESS}_{WW/k})/2]\}\end{aligned}$$

Where $\mathrm{ESS}_{PW\,/\,k}$ is the expected number of species shared for random draws (without replacement) of *k* occurrences from pitfall samples (*P*) and *k* occurrences from Winkler samples (*W*). When *k* is small, the index is highly sensitive to the occurrences of the most frequent ant species. When *k* increases, the influence of rarer species is emphasized. Complementarity was calculated for *k*=1, *k*=64 and *k*=128. Complementarity ranges from 0, if pitfall and Winkler samples are not complementary (*i.e.* they collect the same species) to 1, if species collected by the 2 methods are totally different. The software program BiodivR 1.0 (Hardy 2005) was used to compute the indices.

To investigate the sampling completeness of the A.L.L. transects in both the wet and dry Chaco, the number of species collected with 1 to 6 A.L.L. transects was compared with the total number of species recorded in the reference localities by a larger set of methods and at other sampling dates. These records corresponded to the minimum total number of species present at the reference sites and represented a thorough inventory based on a high number of samples (1943 samples in the reference locality of the wet Chaco and 3458 samples in the reference locality of the dry Chaco) from diverse methods (pitfall traps, Winkler samples, dead wood and soil inspections, hand collection, carbohydrate and protein baits).

RESULTS

CALIBRATION OF THE WINKLER EXTRACTION TIME.— A preliminary test showed that 93 percent (7048) of the individuals, 98 percent (532) of the species occurrences and 100 percent (67) of the species collected after 48 hours were collected in the first 24 hours. After these results, a 24h extraction time was adopted throughout the sampling program.

COMPARATIVE METHOD EFFICIENCY.—At the end of the dry season, the efficiency of both Winkler and pitfall samplings was related to the aridity (Fig. 1-2). A positive linear correlation existed between the number of species collected per Winkler transect and the annual mean precipitation (Pearson product moment correlation analysis, *N*=26 transects, *r* = 0.70, *P*<0.0001). The opposite trend was observed for pitfall transects (*r* = -0.76, *P*<0.00001) while no correlation was obtained when both collection methods were combined (*r* = -0.24, *P*=0.24). A similar result was obtained for species occurrences against rainfall (with Winkler transects: *r* = 0.73, *P*<0.0001; with pitfall transects: *r* = -0.74, *P*<0.00001 and with both methods combined: *r* = -0.31, *P*=0.12).

INFLUENCE OF A RAINFALL PULSE ON METHOD EFFICIENCY.—In the dry Chaco (locality 7 on Fig. 1-1), when no rainfall occurred the preceding 4 months, a single A.L.L. Winkler transect collected only 5 ± 7 (± mean SD) species and 9 ± 13 species occurrences. This was significantly less than previous collections after rainfall in 2001, where 30 ± 4 species and 87 ± 18 species occurrences were recorded (t-test, df=4, t-test values = 5.41 and 5.99, *P*<0.006 and 0.004 for species and species occurrences respectively).

In contrast, the rainfall pulse did not significantly influence the efficiency of a single A.L.L. pitfall transect in terms of species richness (wet year/dry year: 45 ± 5 / 45 ± 7) and species occurrences (224 ± 44 / 179 ± 14) (t-test, df=4, t-test values = -0.07 and 1.69, *P*=0.95 and 0.17 for species and species occurrences respectively).

More species were collected with 60 pitfalls than with 60 Winkler but, for a similar common number of occurrences, Winkler extractions were as efficient as pitfall traps in terms of species collected (Fig. 1-3).

INFLUENCE OF A SIMULATED RAINFALL PULSE ON WINKLER EFFICIENCY.—For an identical number of samples, wet 1m²-quadrats collected 9-fold more species and 21-fold more occurrences than control quadrats (Table 1-1). Both the mean number of workers and occurrences per sample in the watered quadrats were higher than in the control quadrats (Table 1-1, Mann-Whitney rank sum test, $P<0.001$).

PITFALL AND WINKLER COMPLEMENTARITY.—These analyses were restricted to the data sets of the reference localities 1 and 7. For the latter, only data from the rainy year were analysed. In the wet Chaco, six A.L.L. transects yielded 90 ant species (Fig. 1-4A). Winkler samples alone recorded 76 species and pitfall traps alone 48 species. In the dry Chaco, after rainfall, three A.L.L. transects yielded 91 ant species (Fig. 1-4B). Pitfall traps were more efficient (64 species) than Winkler extractions (51 species).

Pitfall and Winkler complementarity was higher in the dry Chaco than in the wet Chaco (26 percent and 35 percent of shared species respectively) (Figs. 1-4A and 1-4B; Table 1-2). In the wet Chaco, frequent ants were globally the same by either method, and rare species collected in pitfall traps were also found in Winkler samples (Fig. 1-4A). However, frequent ant species were different according to the sampling method in the dry Chaco (Fig. 1-4B).

SAMPLING COMPLETENESS.—In order to collect around 50 percent of the total ant fauna known from the reference locality so far, the minimum sampling effort is one A.L.L. transect combining both Winkler and pitfall traps in the dry Chaco during a rainy year. Two such transects would be necessary in the dry Chaco during a period of drought and up to five such transects in the wet Chaco (Table 1-2).

DISCUSSION

EFFECTIVENESS OF THE COLLECTION METHODS.—Winkler and pitfall sampling efficiency, in terms of both species and species occurrences per A.L.L. transect, was dependent of the rainfall regime with opposite trends for the two methods.

Ant species density is generally positively correlated with the leaf litter thickness (Kaspari 1996, Theunis *et al.* 2005). Although this factor could have influenced the Winkler sampling in this study, the drought occurring in the driest localities during and before the sampling campaigns seems to be the main cause of the Winkler inefficiency. This hypothesis is supported by the increased efficiency of the Winkler extraction in the dry Chaco reference locality after a natural or artificial rainfall. The absence of leaf litter nesting specialists may be an additional explanation. Indeed, in the dry Chaco reference locality, no ant colonies were encountered in the leaf litter even after careful searches (Delsinne, pers. obs.), probably because the microclimatic conditions inside the leaf litter were too stressful. All discovered nests were subterranean.

The overall better performance of pitfalls in dry environments may be explained by the fact that these traps also run during the night when temperature is less stressful. In addition, the water contained in the pitfall may actually attract workers. This would explain the strong negative correlation between pitfall efficiency and rainfall. In the Mexican Sonoran Desert (mean annual rainfall = 346mm; [Bestelmeyer & Schooley 1999]), in the Argentinean dry Chaco (rainfall = 500mm; [Bestelmeyer & Wiens 1996]) and in the Australian Gibson Desert (rainfall = 220mm; [Gunawardene & Majer 2005]) ant assemblages were also collected by pitfall traps but their efficiency was not as noteworthy as in our study, possibly because the preservative used in these studies (*i.e.* propylene glycol, a 70 percent mixture of ethylene glycol/ethanol and ethylene glycol respectively) neither attracts nor repels ants (Bestelmeyer *et al*. 2000). To our knowledge, whether ants possess the capacity to detect water sources from a distance (*e.g.* by detecting water vapor in a dry environment) is still unknown.

Pitfall traps generally perform better in habitats with a low leaf litter cover (Melbourne 1999) and in open rather than closed habitats (Parr & Chown 2001, Fisher & Robertson 2002). Dry Chacoan forests are seasonally deciduous (Ramella & Spichiger 1989). At the end of the dry season (*i.e.* during the sampling period), the majority of trees and shrubs are without leaves.

Consequently, at that time the leaf litter depth and the canopy openness were maximal. These environmental conditions may have influenced the pitfall sampling and may have contributed to the observed higher pitfall efficiency in the dry Chaco compared to the wet Chaco.

METHOD COMPLEMENTARITY.—Pitfall and Winkler complementarity was higher in the dry Chaco than in the wet Chaco. Diurnal and nocturnal differences in ant activity and ant assemblage composition may be more pronounced in the dry Chaco than in the wet Chaco due to stressful environmental conditions. It would be interesting to collect the leaf litter at night in the dry Chaco. We predict that the complementarity between methods would decrease. In a similar way, pitfalls could be operated at different times of the day to document the daily pattern of ant activity.

INVENTORY COMPLETENESS.—There are 150 ant species currently known from the dry subtropical forests of the wet Chaco reference locality 1. A single A.L.L. Winkler/pitfall transect collected 29 percent of them. This is slightly lower than the 36 percent obtained in the Atlantic region with the same methods (Delabie, pers. comm., result obtained in 1ha of cocoa plantation where 134 species were collected by a combination of 17 methods). By contrast, depending of the local rainfall history, a single A.L.L. Winkler/pitfall transect collected between 39 percent and 52 percent of the currently documented ant fauna of the dry Chaco reference locality 7. This good performance could illustrate the high complementarity between the fauna captured by pitfalls (active ground-foraging, thermophilic or nocturnal species and also possibly ants attracted by water) and by Winkler after rainfall, when cryptic subterranean nesting species forage in the leaf litter. Nevertheless, this apparently good sampling performance could also be the result of an underestimated local species richness and a longer-term collection effort at the reference locality would be required to discard this eventuality.

CONCLUSION.—Every sampling technique suffers from biases (Bestelmeyer *et al*. 2000, Longino 2000) and none allows the collection of the whole ant fauna locally present (Longino *et al*., 2002). Here, a single pitfall/Winkler A.L.L. transect collected at least one-third of the local assemblage. The A.L.L. protocol, which was initially developed for tropical rain forests, seemed also efficient for sampling ant assemblages in dry forests. Nevertheless, we have underlined the strong influence of rainfall on the efficiency of Winkler sampling in dry forests, and its consequences on the complementarity of methods and on the completeness of standardized A.L.L. transects. During drought periods, Winkler extractions are not cost-effective and pitfalls traps should be used in the context of rapid assessments of the ant fauna.

ACKNOWLEDGMENTS

We thank John Kochalka, Bolívar Garcete-Barrett, Victor Filippi, Jorge Jara, César Bénilez, Carlos Aguílar Julio from the "Museo Nacional de Historia Natural del Paraguay", the guards from Teniente Enciso National Park and Véronique Olivier for their help during fieldwork or administrative procedures. Alex Wild from University of Arizona and Jacques H.C. Delabie from the “laboratório de Mirmecologia” of the USC-CEPLAC at Itabuna (Brazil) supervised a part of the ant identifications. This study was made possible by financial support from the “Fonds pour la Formation à la Recherche dans l’Industrie et l’Agriculture” and the "Fonds de la Recherche Scientifique - FNRS" (Belgium). Nihara Gunawardene greatly improved the English version. Tania Milena Arias Penna translated the abstract into Spanish.

LITERATURE CITED

AGOSTI, D., AND L. E. ALONSO. 2000. The A.L.L. protocol. A standard protocol for the collection of ground-dwelling ants. In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 204-206. Smithsonian Institution Press, Washington DC.

AGOSTI, D., J. MAJER, L. E. ALONSO, AND T. R. SCHULTZ. (eds). 2000. Sampling ground-dwelling ants: case studies from the world's rain forests. Curtin University of Technology, Perth, Western Australia.

ALONSO, L. E., AND D. AGOSTI. 2000. Biodiversity studies, monitoring, and ants: an overview. In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 1-8. Smithsonian Institution Press, Washington DC.

BESTELMEYER, B. T. 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Anim. Ecol. 69: 998-1009.

BESTELMEYER, B. T., AND R. L. SCHOOLEY. 1999. The ants of the southern Sonoran desert: community structure and the role of trees. Biodivers. Conserv. 8: 643-657.

BESTELMEYER, B. T., AND J. A. WIENS. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecol. Appl. 6: 1225-1240.

BESTELMEYER, B. T., D. AGOSTI, L. E. ALONSO, R. F. BRANDÃO, W. L. BROWN JR., J. H. C. DELABIE, AND R. SILVESTRE. 2000. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 122-144. Smithsonian Institution Press, Washington DC.

BROWN, W. L. JR. 2000. Diversity of ants. In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 45-79. Smithsonian Institution Press, Washington DC.

COLWELL, R. K. 2004. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL: <purl.oclc.org/estimates>.

DELABIE, J. H. C., B. L. FISHER, J. D. MAJER, AND I. W. WRIGHT. 2000. Sampling effort and choice of methods. In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 145-154. Smithsonian Institution Press, Washington DC.

DELSINNE T., Y. ROISIN, AND M. LEPONCE. 2007. Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage. J. Arid Environ. 71: 29-44.

FISHER, B. L. 1998. Ant diversity patterns along an elevational gradient in the Réserve Spéciale Naturelle Intégrale d'Andringitra, Madagascar. Fieldiana Zool. (n.s.) 85: 93-108.

FISHER, B. L. 1999. Improving inventory efficiency: a case study of leaf litter ant diversity in Madagascar. Ecol. Appl. 9: 714-731.

FISHER, B. L. 2005. A model for a global inventory of ants: a case study in Madagascar. Proc. Calif. Acad. Sci. 56: 86-97.

FISHER, B. L., AND H. G. ROBERTSON. 2002. Comparison and origin of forest and grassland ant assemblages in the high plateau of Madagascar (Hymenoptera: Formicidae). Biotropica 34: 155-167.

FOLGARAIT, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers. Conserv. 7: 1221-1244.

GROC, S. 2006. Diversité de la myrmécofaune des Causses aveyronnais. Comparaison de différentes méthodes d'échantillonnage. DESUPS Diplôme d'Études Supérieures de l'Université Paul Sabatier.

GUNAWARDENE, N. R., AND J. D. MAJER. 2005. The effect of fire on ant assemblages in the Gibson Desert Nature Reserve, Western Australia. J. Arid Environ. 63: 725-739.

HARDY, O. 2005. BiodivR 1.0. A program to compute statistically unbiases indices of species diversity within samples and species similarity between samples using rarefaction principles. Université Libre de Bruxelles.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The Ants. Cambridge: Bellknap Press.

KASPARI, M. 1996. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76: 443-454.

KASPARI, M., AND J. D. MAJER. 2000. Using ants to monitor environmental change. In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 89-98. Smithsonian Institution Press, Washington DC.

KING, J. R., AND S. D. PORTER. 2005. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. Environ. Entomol. 34: 1566-1578.

KRELL, F.-T., A. Y. C. CHUNG, E. DEBOISE, P. EGGLETON, A. GIUSTI, K. INWARD, AND S. KRELL-WESTERWALBESLOH. 2005. Quantitative extraction of macro-invertebrates from temperate and tropical leaf litter and soil: efficiency and time-dependent taxonomic biases of the Winkler extraction. Pedobiologia 49: 175-186.

LINDSEY, P. A., AND J. D. SKINNER. 2001. Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. J. Arid Environ. 48: 551-568.

LONGINO, J. T. 2000. What to do with the data? In D., Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity, pp. 186-203. Smithsonian Institution Press, Washington DC.

LONGINO, J. T., AND R. K. COLWELL. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecol. Appl. 7: 1263-1277.

LONGINO, J. T., J. CODDINGTON, AND R. K. COLWELL. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology 83: 689-702.

MARTELLI, M. G., M. M. WARD, AND A. M. FRASER. 2004. Ant diversity sampling on the southern Cumberland Plateau:a comparison of litter sifting and pitfall trapping. Southeast. Nat. 3: 113-126.

MELBOURNE, B. A. 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. Aust. J. Ecol. 24: 228-239.

MERELES, M. F. 2005. Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay. Rojasiana 6: 5-48.

PARR C. L., AND S. L. CHOWN. 2001. Inventory and bioindicator sampling: testing pitfall and Winkler methods with ants in a South African savanna. J. Insect. Conserv. 5: 27-36.

RAMELLA, L., AND R. SPICHIGER. 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639-680.

REDDY, M. V., AND B. VENKATAIAH. 1990. Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid savanna. Int. J. Biometeorol. 34: 49-59.

REYNOLDS, J. F., P. R. KEMP, K. OGLE, AND R. J. FERNÁNDEZ. 2004. Modifying the "pulse-reserve" paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141: 194-210.

SCHWINNING, S., O. E. SALA, M. E. LOIK, AND J. R. EHLERINGER. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141: 191-193.

THEUNIS, L., M. GILBERT, Y. ROISIN, AND M. LEPONCE. 2005. Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. Insect. Soc. 52: 366-377.

TRUEBLOOD, D. D., E. D. GALLAGHER, AND D. M. GOULD. 1994. Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnol. Oceanogr. 39: 1440-1454.

UNDERWOOD, E. C., AND B. L. FISHER. 2006. The role of ants in conservation monitoring: if, when, and how. Biol. Conserv. 132: 166-182.

WHITFORD, W. G. 1978. Structure and seasonal activity of Chihuahua Desert ant communities. Insect. Soc. 25: 79-88.

TABLE 1-1. *Results of the artificial rainfall pulse experiment.*

	Watered quadrats (*N*=23)	Control quadrats (*N*=23)	Mann-Whitney rank sum test
Mean number of workers/sample (±SD)	29.6 ± 41.8	0.2 ± 0.5	$P<0.001$
Total number of workers	681	5	
Mean number of occurrences/sample (±SD)	3.6 ± 2.0	0.2 ± 0.5	$P<0.001$
Total number of species occurrences	83	4	
Total number of species	37	4	

TABLE 1-2. *Pitfall and Winkler complementarity and A.L.L. transect completeness for reference localities of the wet and dry Chaco.*

	Wet Chaco Locality 1	**Dry Chaco** Locality 7, drought	**Dry Chaco** Locality 7, after rainfall
Winkler/Pitfall complementarity[a]:			
1-NNESS (*k*=1)	0.37	-	0.76
1-NNESS (*k*=64)	0.32	-	0.59
1-NNESS (*k*=128)	0.33	-	0.56
Total species richness[b]:	≥150	≥126	≥126
Mean percent of species collected with:			
1 A.L.L. transect	29	39	52
2 A.L.L. transects	38	52	64
3 A.L.L. transects	43	59	72
4 A.L.L. transects	48	-	-
5 A.L.L. transects	51	-	-
6 A.L.L. transects	54	-	-

[a] For the wet Chaco, 6 transects were used to compute the complementarity indices. For the dry Chaco after a rainfall, 3 transects were used. No indices were calculated for the dry Chaco during a drought because Winkler collected very few ants.

[b] Total species richness values represent the total number of species collected at the reference localities so far. Hence, they correspond to a minimal value of the ant fauna present in the reference localities.

FIGURE 1-1. Study sites distributed along the aridity gradient of the Gran Chaco plains. Dotted lines are isolines of mean annual rainfall. Localities are: 1: Pilcomayo N.P., 2: Chaco N.P., 3: Río Verde, 4: Cruce de Los Pioneros, 5: Garrapatal, 6: Estancia María Vicenta, 7: Teniente Enciso N.P., 8: Siracua, 9: Nueva Asunción, 10: Fortín Mayor Infante Rivarola.

FIGURE 1-2. Number of species collected per A.L.L. transect by (A) pitfall traps, (B) by Winkler extractions and (C) by both methods combined along the aridity gradient. Lines are the linear fitting of the plots. Empty symbols correspond to the 3 transects collected after a rainfall event at the dry Chaco reference locality.

FIGURE 1-3. Occurrence-based rarefaction curves (Coleman method of EstimateS 7.5, [Colwell 2004]) of 3 pooled A.L.L. transects for Winkler and pitfall catches after a rainfall event (2001) and during a dry year (2004) at the dry Chaco reference locality (locality 7 on Fig. 1-1).

FIGURE 1-4. Matched rank/occurrence plots of ants collected with pitfall and Winkler samples (A) at the wet Chaco reference locality (90 species collected) and (B) at the dry Chaco reference locality after a rainfall (91 species collected).

FIGURE 1-1.

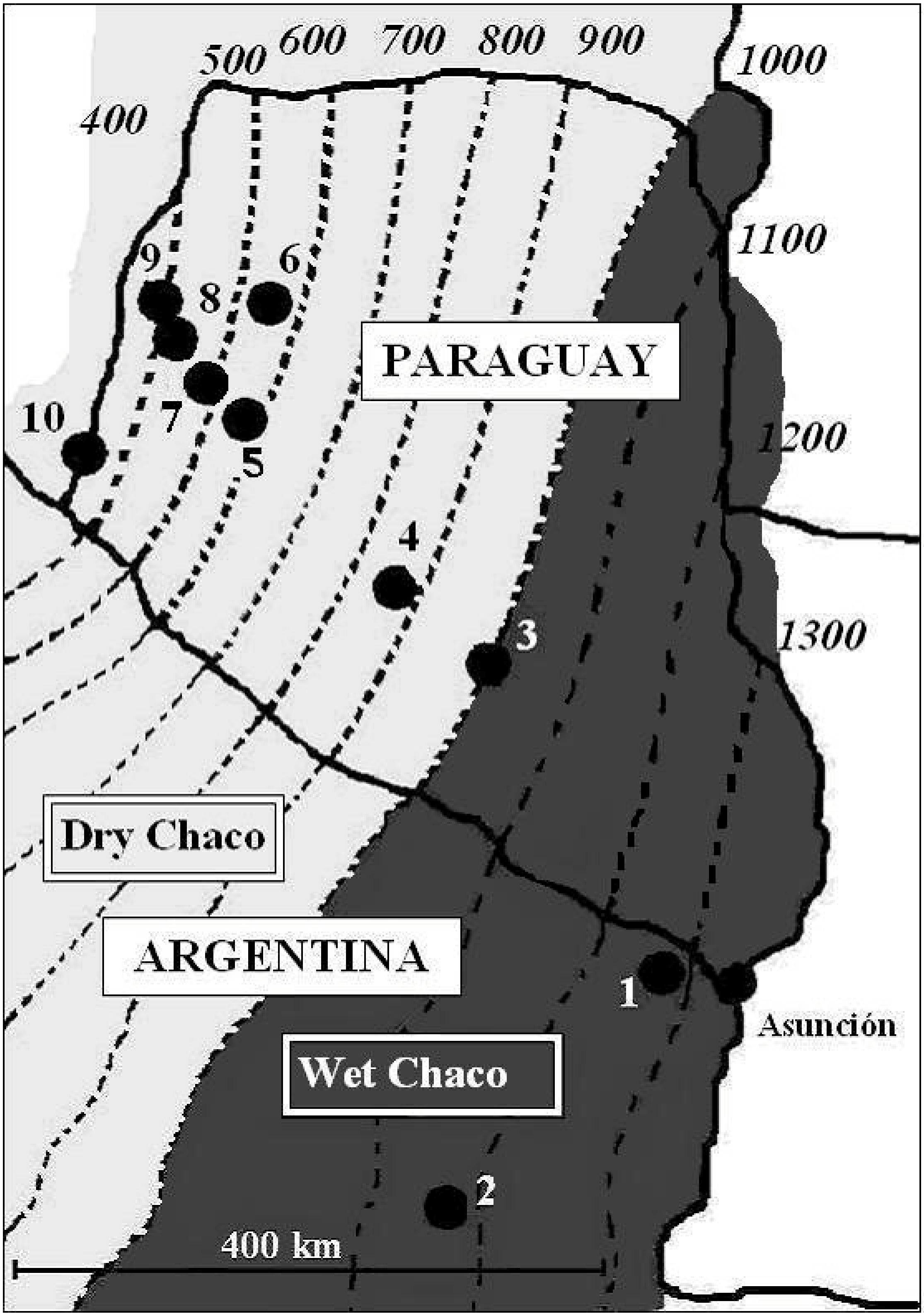

400
500
600
700
800
900
1000
1100
1200
1300
PARAGUAY
ARGENTINA
Dry Chaco
Wet Chaco
Asunción
1
2
3
4
5
6
7
8
9
10
400 km

FIGURE 1-2.

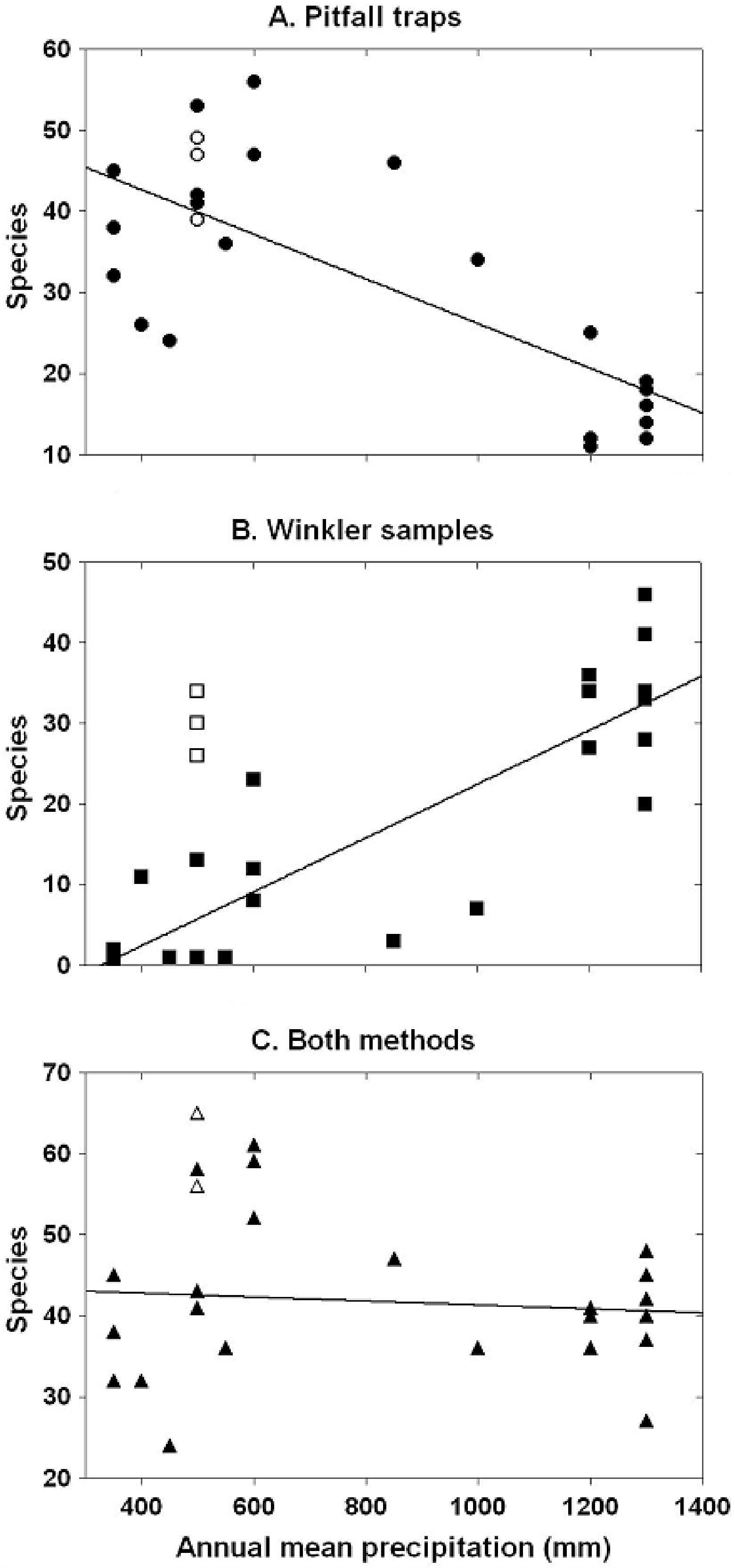

A. Pitfall traps
60
50
40
30
20
10
Species
B. Winkler samples
50
40
30
20
10
0
Species
C. Both methods
70
60
50
40
30
20
Species
400
600
800
1000
1200
1400
Annual mean precipitation (mm)

FIGURE 1-3.

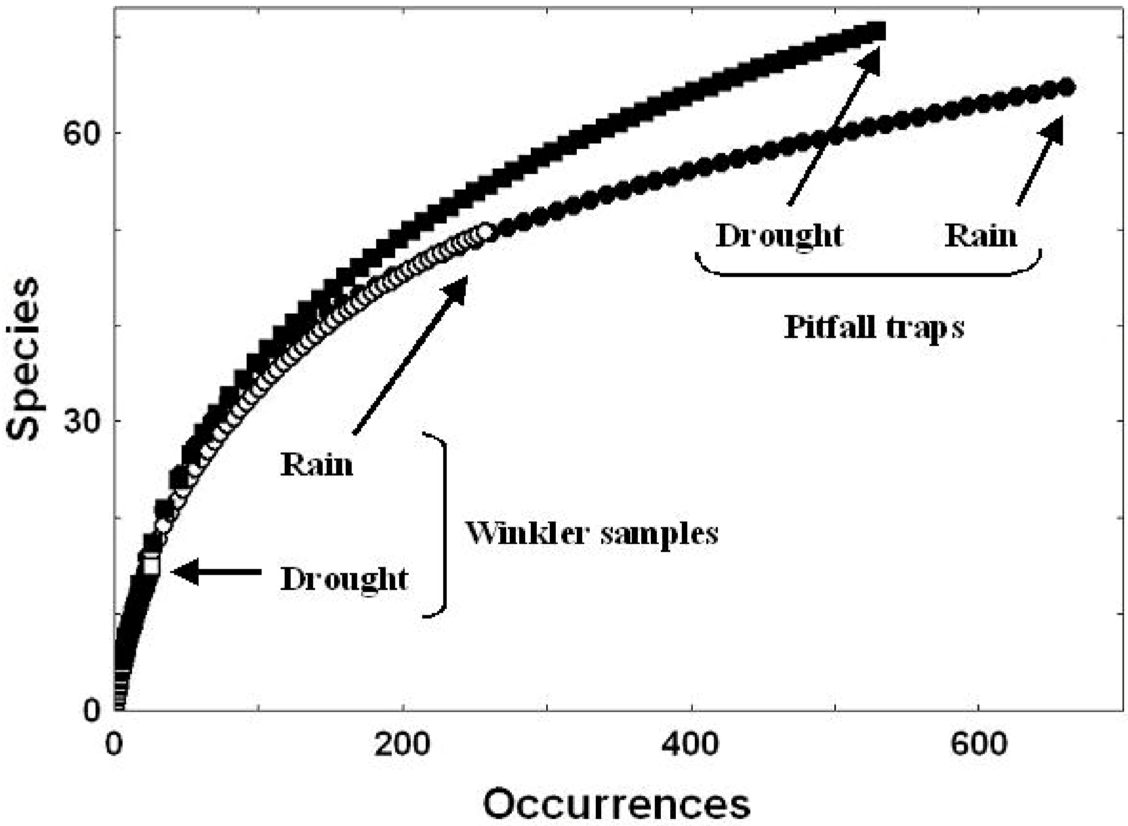
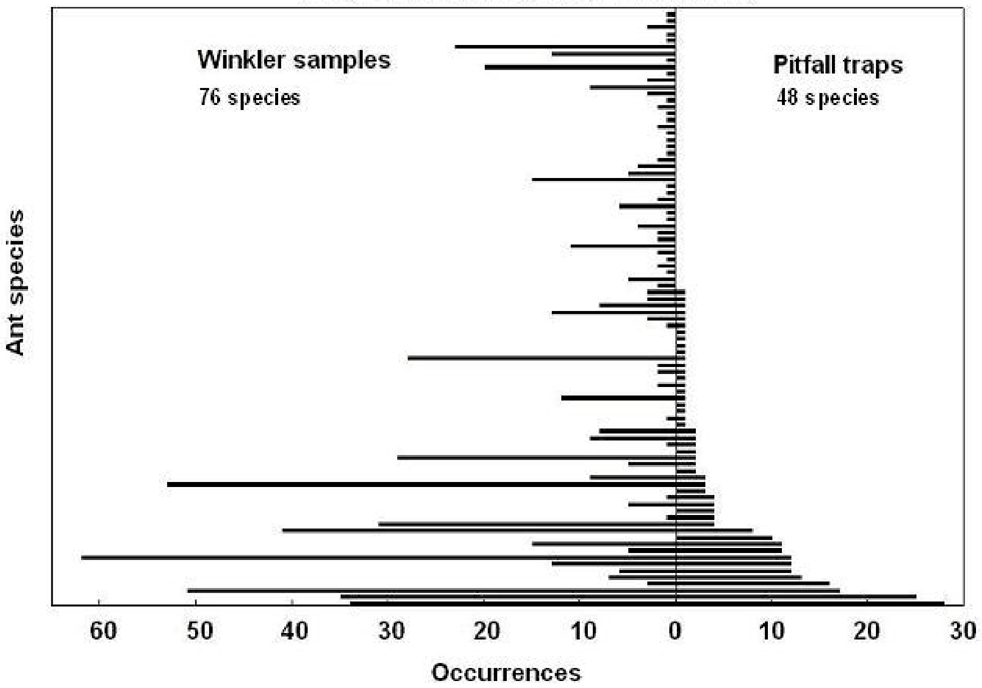
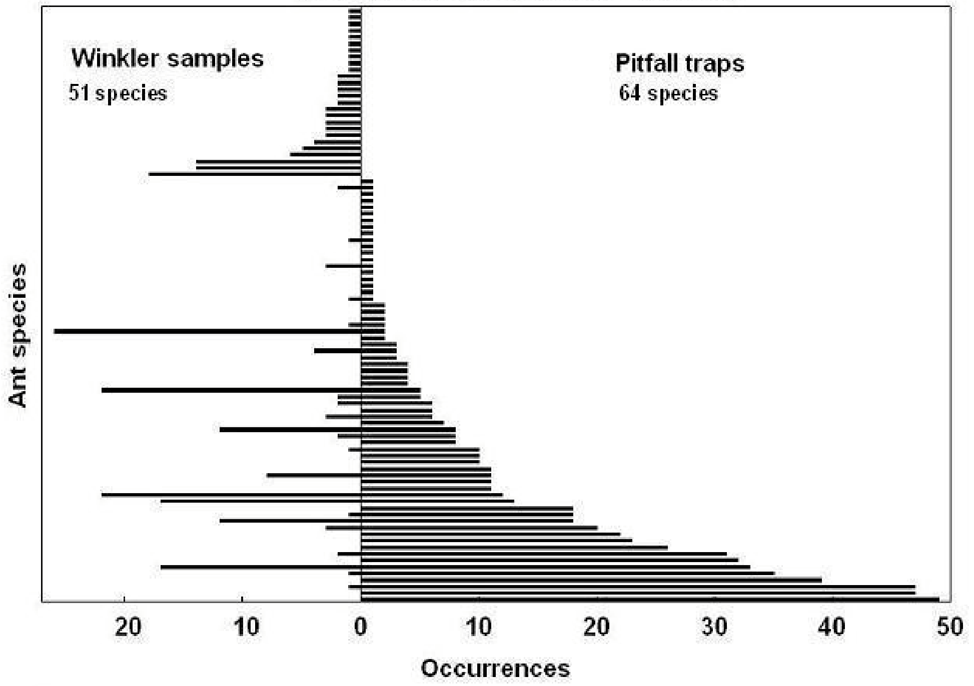

Species
0
30
60
Occurrences
0
200
400
600
Drought
Rain
Pitfall traps
Rain
Winkler samples
Drought

FIGURE 1-4.

A. Wet Chaco (Locality 1, n=6 transects)
(Mean annual precipitation : 1300 mm)



B. Dry Chaco (Locality 7, after rainfall, n=3 transects)
(Mean annual precipitation: 500 mm)



Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage.

DELSINNE Thibaut[1,2]*, **ROISIN Yves**[2], **LEPONCE Maurice**[1]

[1]: Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, BELGIUM.
Thibaut.Delsinne@naturalsciences.be;
Maurice.Leponce@naturalsciences.be

[2]: Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral and Evolutionary Ecology - CP 160/12, 1050 Brussels, BELGIUM.
yroisin@ulb.ac.be

*: Corresponding author.
Tel: +32 (0) 2 627 43 64
Fax: +32 (0) 2 649 48 25

Journal of Arid Environments 71 (2007) 29–44

Journal of Arid Environments

www.elsevier.com/locate/jaridenv

Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage

T. Delsinne[a,b,*], Y. Roisin[b], M. Leponce[a]

[a]Conservation Biology Section, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, 1000 Brussels, Belgium
[b]Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral & Evolutionary Ecology—CP 160/12, 1050 Brussels, Belgium

Received 12 September 2005; received in revised form 22 January 2007; accepted 24 February 2007
Available online 24 April 2007

Abstract

In arid habitats ant temporal foraging results from a set of trade-offs between species food discovery and food domination ability and between species thermal tolerance and behavioral dominance. We investigated how this set of trade-offs structures the spatial co-occurrence of ants during foraging, hence focusing on interspecific competition. The consequences of food type on the spatio-temporal foraging structure were also studied because food preferences were expected to optimize the restricted foraging time and space of thermophilic species. The food partitioning between 24 species attracted to protein or carbohydrate baits was studied in a dry forest of the Paraguayan Chaco. Baits were spaced at one meter intervals and inspected every 15 min over 90-min sessions conducted during mornings and afternoons. Null model analyses revealed a temporal food partitioning during afternoon sessions and a spatial partitioning, influenced by both thermal conditions and interspecific competition. Bait type did not influence the spatio-temporal foraging. Unexpectedly, evidence of interspecific competition was scarce and avoidance rather than overt conflicts appeared to be the rule of thumb. Overall, the spatio-temporal food exploitation at a small scale was affected by temperature and stochastic processes. This demonstrates that chance structures ant foraging even in constraining arid environments.

Keywords: Food partitioning; Formicidae; Interspecific competition; Null model analysis; Species coexistence; Temperature

---

*Corresponding author. Conservation Biology Section, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, 1000 Brussels, Belgium. Tel.: +32 2 627 43 64; fax: +32 2 649 48 25.

E-mail addresses: Thibaut.Delsinne@naturalsciences.be (T. Delsinne), yroisin@ulb.ac.be (Y. Roisin), Maurice.Leponce@naturalsciences.be (M. Leponce).

0140-1963/$ - see front matter
doi:10.1016/j.jaridenv.2007.02.007

1. Introduction

Space, food type and time are the three most important niche axes which may be partitioned among species in order to facilitate their coexistence (Schoener, 1974). In ground-foraging ant assemblages species coexistence is eased by temporal segregations occurring at seasonal (Fellers, 1989; Greenslade, 1971; Herbers, 1989; Levings, 1983; Lynch, 1981; Rissing, 1988) and nycthemeral scales (Bernstein, 1974; de Biseau et al., 1997; Vepsäläinen and Savolainen, 1990). At even shorter temporal scales (60–90 min), food exploitation is also temporally segregated among species depending on their resource discovery and food dominance abilities (Fellers, 1987; Wilson, 1971). Competitive hierarchy theory predicts the existence of three categories of species classified according to their food exploitation behavior: "opportunists", "insinuators" and "extirpators". Opportunists are subordinate species, capable of finding food quickly but which are displaced when extirpators, aggressive ant species, arrive later. Insinuators are discreet ant species able to steal food pieces from opportunists and extirpators (Davidson, 1998; Wilson, 1971). This classical trade-off between resource discovery and resource dominance abilities has been demonstrated in various temperate and tropical ant assemblages (Andersen, 1992, 1995, 1997; Perfecto, 1994; Savolainen and Vepsäläinen, 1989).

Nevertheless at the same short time scale ant competitive hierarchy is modified in habitats where thermal conditions may be stressful, as in arid or semi-arid habitats (Bestelmeyer, 2000; Cerdá et al., 1998a; 1998b; Retana and Cerdá, 2000). In particular, Bestelmeyer (2000) attracting ants with tuna baits in the Argentinean dry Chaco has demonstrated that the trade-off between food resource discovery and food resource domination is associated with a second one opposing thermal tolerance to behavioral dominance. Extirpators were most active at moderately high temperatures whereas opportunists were active at extreme ones. This set of trade-offs structures the ant temporal foraging (Bestelmeyer, 2000) and allows arid environments to support a higher diversity of ant species than expected under these stressful conditions (Cerdá et al., 1998a). Our aim here was to refine the Bestelmeyer study on temporal foraging, bringing to the fore the simultaneous presence of species, by a spatio-temporal foraging analysis taking into account also the species co-occurrence at baits, hence focusing on interspecific competition. This spatio-temporal analysis was performed at a small scale and with a randomization algorithm (null model) allowing the distinction between deterministic and purely stochastic patterns (Gotelli and Graves, 1996; Ribas and Schoereder, 2002). In addition we considered the influence of the type of the food resource by using not only proteins but also carbohydrates as baits.

Ant preferences for a certain food are suspected to occur when the nutrients contained in the food are usually less available or more limited in the environment (Kay, 2004). We hypothesized that in arid or semi-arid habitats species with narrow thermal requirements exhibit a food preference in order to optimize their restricted foraging time. Ant competitiveness is affected by food type, quantity and/or patchiness (Chew and de Vita, 1980; de Biseau et al., 1997; Detrain et al., 2000; Gibb, 2005; McGlynn and Kirksey, 2000; Vepsäläinen and Savolainen, 1990). However, it is still unclear how this may affect spatially and temporally the ant foraging at the assemblage level.

To attain our objectives we: (1) first verified the influence of the set of trade-offs on the temporal foraging activity of the assemblage considered before (2) to study the dynamic of the ant spatial foraging overlap and (3) the consequences of food type on spatio-temporal foraging patterns.

2. Materials and methods

2.1. Study site

The study site was located inside Teniente Enciso National Park in northeastern Paraguay (Lat: S 21°12′; Long: W 61°39′). The habitat is a xeromorphic forest called "Quebrachal" (Ramella and Spichiger, 1989). The upper vegetation stratum is composed of emerging trees (*Aspidosperma quebracho-blanco* Schlechtendal 1861 and *Chorisia insignis* Kunth 1822) and treelike cacti (*Stetsonia coryne* (Salm-Dyck) Britton and Rose 1920, *Cereus stenogonus* Schumann 1899). The lower vegetation stratum is composed of shrubs (*Ruprechtia triflora* Grisebach 1879, *Capparis* spp. and *Ziziphus mistol* Grisebach 1874). The ground vegetation includes bromeliads (*Bromelia* spp., *Dyckia* spp.) and cacti (*Opuntia* spp., *Cereus* spp., *Cleistocactus baumannii* (Lemaire) Lemaire 1861) (Ramella and Spichiger, 1989). Precipitations range between 500 and 800 mm per year (Ramella and Spichiger, 1989), mean temperature is 26 °C.

2.2. Experimental protocol

Experiments were conducted in September 2002 in nine contiguous 4 × 4 m plots, covering a total area of 144 m^2. The studied area was elected in order to maximize the homogeneity in terms of exposure to the sun, soil texture and leaf-litter cover. Each plot consisted of a grid with 25 points at 1 m intervals (Fig. 1). The plot constituted the experimental unit. Bait sessions were carried out with protein (3 g of natural canned tuna fish) or carbohydrate baits

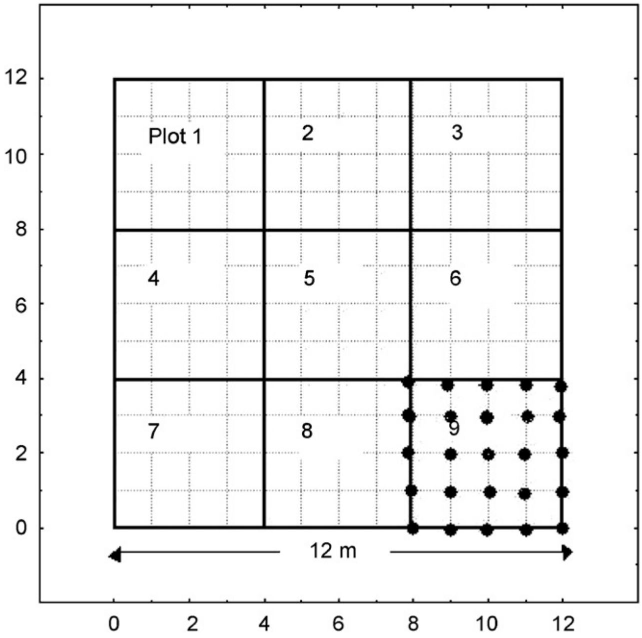


Fig. 1. Experimental protocol. Nine contiguous 4 × 4 m plots covering a total area of 144 m^2 were studied. Each plot was constituted of a grid of 25 baiting points at 1 m interval (illustrated in Plot 9).

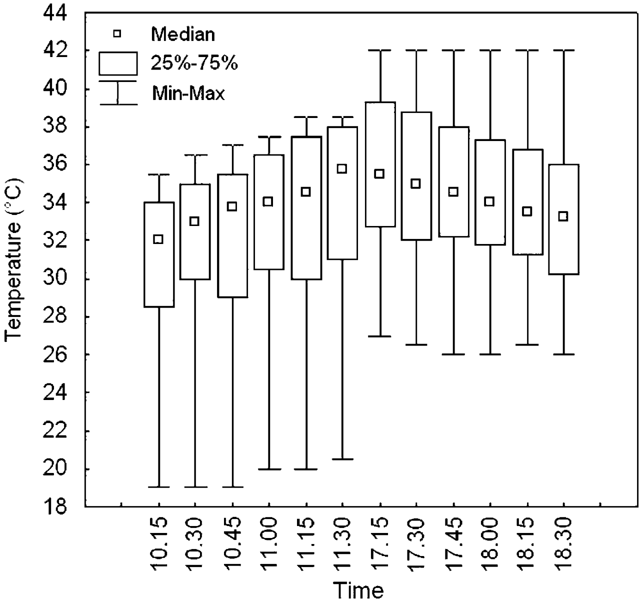


Fig. 2. Atmospheric temperature (°C) over time during the experiment.

(two drops of liquid honey). Baits were installed on a 2 cm-side square of aluminum foil that prevented ants from foraging below the bait. Ant species attracted to each bait were identified and their abundances noted every 15 min over a 90 min period (= 6 successive records). Voucher specimens were collected for later identification in the laboratory. All collected ants were identified to species or morphospecies.

We conducted 18 baiting sessions including four "food resource–time of day" combinations consisting of 3 "honey/morning" (75 baits), 5 "honey/afternoon" (125 baits), 7 "tuna/morning" (175 baits) and 3 "tuna/afternoon" sessions (75 baits). Morning sessions were from 10.00–11.30 h and afternoon sessions from 17.00–18.30 h. In total, our study was based on 450 baits and 2700 (450 baits × 6 records) data collection points.

Each plot was studied two or three times but with a different combination separated by more than 48 h. At the end of each experiment, baits were cleared to avoid a food saturation of the habitat.

To evaluate temperature influence upon observed foraging patterns, ambient air temperature was measured every 15 min during the experiments, from which mean temperature was calculated for each baiting session (Fig. 2). It is likely that ants are more sensitive to ground temperature rather than to that of the ambient air. However, we assumed that these variables were correlated.

2.3. Analyses of ant foraging

- *Food preferences.* For the nine most frequent ant species, we tested food preferences by Chi-square analyses of contingency tables of species occurrences accompanied by Yates corrections for continuity.

- *Influence of temperature*. The Pearson product moment correlation was calculated (1) between temperature and the occurrence of each frequent ant species and (2) between temperature and the abundance of every frequent ant species. If occurrences or abundances increased with temperature, this indicates that thermal conditions may influence the ability of ants to discover or to dominate baits, respectively.
- *Behavioral dominance*. We noted any aggressive behavioral interactions (biting or stinging) that occurred between ant species at baits. The number of times that a given species initiated an attack indicated its aggressiveness, which is a critical trait of behaviorally dominant ant species (i.e. extirpator ants) (Fellers, 1987; Wilson, 1971).
- *Food exploitation and recruitment strategy*. To classify the frequent ant species and to investigate their recruitment strategy we represented the cumulative abundance of ants at baits as a function of time from the beginning to the end of the baiting session. By definition, opportunistic ant species are abundant at baits at the beginning of the baiting session and then, decrease in abundance at the benefit of extirpator species. The abundance of insinuator species is independent of time.

2.4. Null model analysis

To determine the stochastic and deterministic parts of observed patterns of species occurrences and abundances at baits, we compared the observed matrices (see below) to those expected under the null hypothesis of random occurrence/abundance of species and generated by null model randomizations (Gotelli and Graves, 1996).

2.4.1. Matrices of data

Temporal analysis. Rows of the data matrix represented species foraging at least once at baits. Columns corresponded to the time from the start of the experiment. Entries in the matrix consisted of the number of bait occurrences for each species. The data obtained for the four "food resource–time of day" combinations were analyzed separately.

Spatial analysis. Rows of the data matrix represented species while columns represented baits. Entries in the matrix consisted of the species abundance at each bait. The data obtained for the four "food resource–time of day" combinations and for the six sampling points in time following the start of the experiment were analyzed separately. Only species that occurred at least at one bait during the given observation time were included in this analysis. Points common to two contiguous plots were excluded from the analysis.

2.4.2. Quantification of spatial and temporal foraging overlaps between species

To quantify spatial and temporal foraging overlaps, we calculated the Pianka index of niche overlap between each pair of species (Pianka, 1973):

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i}p_{1i}}{\sqrt{\sum_{i=1}^{n}(p_{2i}^2)(p_{1i}^2)}}.$$

In this formula, O_{12} is the overlap between species 1 and 2, p_{1i} and p_{2i} represent the utilization of time i (for temporal analyses) or bait i (for spatial analyses) by species 1 and 2, respectively. Pianka index is symmetric, so $O_{12} = O_{21}$, and ranges from 0, for pairs of species that share no spatial or temporal resource state, to 1, for pairs that present an identical resource utilization. To describe the observed spatial and temporal foraging overlaps of the entire ant assemblage, we calculated the observed mean and variance of foraging overlap indices for each data matrix.

We compared the values with those derived from 1000 iterations. All null model simulations were performed with Ecosim software (Gotelli and Entsminger, 1999). We used the randomization algorithm 3 (RA3) of Winemiller and Pianka (1990) which corresponds to a simple reshuffling of each row of the matrix and which is often recommended to create null matrices (Gotelli and Graves, 1996). All resources (time or bait) were considered equiprobable. We did not use any adjustments for multiple tests because we were interested in the overall pattern of which data sets showed significance and which did not.

2.4.3. Interpretation of results

If ant species forage at the same time or at the same location more often than expected by chance it can be interpreted as an effect of abiotic factor (Albrecht and Gotelli, 2001; Gotelli and Graves, 1996). Here, temperature was the more plausible abiotic factor constraining ant foraging (Bestelmeyer, 2000). By contrast, interspecific competition tends to segregate ant species more often than expected (Albrecht and Gotelli, 2001; Gotelli and Graves, 1996; Sale, 1974).

The study of foraging overlap variances informs about the ant assemblage structure. An internal guild structure in the assemblage, in which some species pairs are very similar in resource use while others are very dissimilar, leads to an observed variance index superior to those generated by null models (Albrecht and Gotelli, 2001; Winemiller and Pianka, 1990). No guild structure can be demonstrated when the indice is inferior.

3. Results

3.1. Ecology of ants attracted to baits

Overall baits attracted 24 species (Table 1). Most baits were exploited by a single ant species during the time of the experiment. Only 28% of baits attracted more than one species (up to 4) (Fig. 3). The "food resource–time of day" combination did not influence the mean number of species per bait (one-way ANOVA, $df = 3$, $P = 0.55$).

Only nine direct interspecific aggressions were observed at baits. *Pseudomyrmex denticollis* attacked *Wasmannia auropunctata* ($n = 2$) and *Pheidole radoszkowskii* ($n = 1$). *Camponotus crispulus* attacked *Ps. denticollis* ($n = 4$), *Solenopsis* sp. A attacked *W. auropunctata* ($n = 1$) and this latter species attacked *Solenopsis* sp. B ($n = 1$). A conflict generally resulted in the retreat of the species attacked. A single aggressive intraspecific interaction was observed between *Ps. denticollis* workers.

The numerical dominance of six ant species was influenced by temperature. Their abundances were either negatively ($n = 4$ species) or positively ($n = 2$) correlated with temperature (Pearson product moment correlation analysis, $P \leqslant 0.05$, Table 1). Identical results were obtained by considering their occurrences (number of baits visited by contrast to number of individuals observed in the area) according to the temperature indicating that temperature also influenced bait discovery for these six ant species.

Table 1
Ant species collected during the study with baits ($n = 450$)

Species attracted to baits ($n = 24$)	Percentage of occurrences at baits (%)	Food preferences	Correlation between ant abundance and temperature ($P \leqslant 0.05$)
Pseudomyrmex denticollis	46.9	Proteins**	Positive
Camponotus crispulus	10.0	Proteins**	No
Pheidole radoszkowskii	7.1	No	Negative
Wasmannia auropunctata	5.8	No	No
Pheidole sp. A	5.6	No	Negative
Brachymyrmex aphidicola	4.7	No	Negative
Brachymyrmex leuderwaldti	4.4	No	Negative
Crematogaster quadriformis	4.2	No	No
Forelius brasiliensis	4.2	Proteins***	Positive
Camponotus termitarius	3.6		
Pheidole jelskii	2.9		
Pheidole vafra	2.4		
Camponotus crassus	2.0		
Solenopsis sp. A	2.0		
Solenopsis sp. B	2.0		
Forelius nigriventris	1.6		
Ectatomma edentatum	0.7		
Pheidole sp. B	0.7		
Pheidole sp. C	0.7		
Solenopsis sp. C	0.7		
Pseudomyrmex acanthobius	0.4		
Ectatomma brunneum	0.2		
Ectatomma permagnum	0.2		
Odontomachus chelifer	0.2		

The percentage of the total number of bait used by each species is given. Food and temperature preferences of the nine most frequent ant species attracted to baits are indicated. Food preferences were tested by Chi-square analyses of contingency tables of species occurrences with Yates corrections for continuity. Correlation between the abundance of each species and temperature were calculated by Pearson product moment correlation analyses (**$P \leqslant 0.01$; ***$P \leqslant 0.001$).

Among the nine most frequent ant species attracted to baits, 3 exhibited a food preference, always for tuna baits (*Ps. denticollis*, $\chi^2 = 6.603$, $df = 1$, $P \leqslant 0.01$; *Ca. crispulus*, $\chi^2 = 9.133$, $df = 1$, $P \leqslant 0.01$; *Forelius brasiliensis*, $\chi^2 = 14.118$, $df = 1$, $P \leqslant 0.001$, Table 1). *Ca. crispulus* and *Ps. denticollis,* two relatively large ant species (over 1 cm) foraged mainly solitarily or in small groups and never recruited massively (maximal abundance at bait of 15 and 10 workers, respectively). *Ps. denticollis* was by far the most frequent species attracted to baits (Table 1). The other seven frequent ants whose workers are small (around 1 or 2 mm), often recruited massively (over 100 workers at some baits) over the 90 min period.

For each ‘‘food resource–time of day’’ combination, we plotted the cumulative abundance of ants at baits over time. With the exception of *Crematogaster quadriformis*, all species exhibited a similar curve for each combination. We thus represented the pooled data (Fig. 4). Among the nine most frequent species, abundance at baits of *Brachymyrmex aphidicola*, *B. leuderwaldti*, *Ph. radoszkowskii*, *Pheidole* sp. A and *W. auropunctata* globally

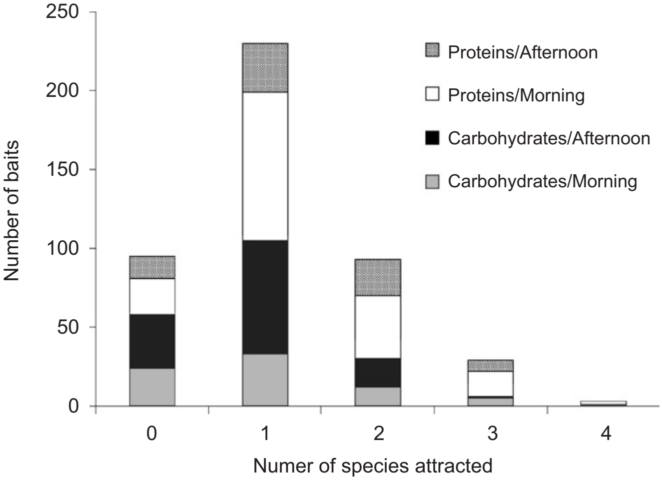


Fig. 3. Number of ant species attracted to baits ($n = 450$).

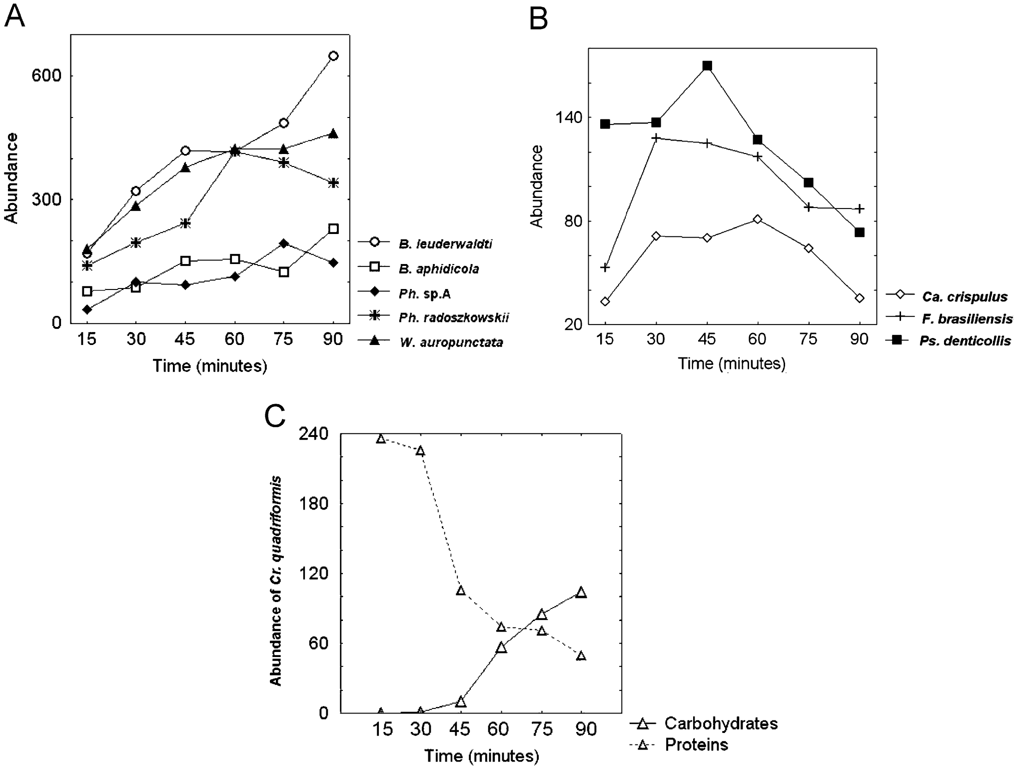


Fig. 4. Cumulative abundance at baits of the nine frequent ant species as a function of time. Five species are considered as extirpators because their cumulative abundance increased along with time (A). *Pseudomyrmex denticollis* is classified as opportunist because globally abundant at baits at the beginning of the baiting session and then scarcer (B). Two species exhibited an intermediate pattern (B). *Crematogaster quadriformis* behavior (C) is function of food type (see text).

increased over time, as expected for extirpators (Fig. 4A). The opposite was globally observed for *Ps. denticollis*, as expected for opportunists. *F. brasiliensis* and *Ca. crispulus* exhibited an intermediate pattern (Fig. 4B). *Cr. quadriformis* displayed an extirpator behavior for carbohydrates and an opportunist behavior for proteins (Fig. 4C).

3.2. Temporal foraging overlap

Temperature constrained the temporal foraging of ants (at both protein or carbohydrate baits) only during afternoons (observed mean indices greater than expected, Table 2).

An internal guild structure of the ant assemblage was revealed (observed variance greater than expected, Table 2) except during afternoons with proteins.

3.3. Spatial foraging overlap

In most cases ants were not constrained spatially to exploit particular baits (Table 3, 15 out of 24 observed mean indices not different from those generated by null models). However, at the end of morning sessions temperature influenced the spatial foraging structure (mean indices were greater than expected). By contrast, at the end of afternoon sessions, interspecific competition appeared as a structuring factor (mean indices were lower than expected).

Only at the end of morning experiments a guild structure was revealed (observed variance indices greater than expected, Table 3).

Food type did not influence the spatial foraging structure of the ant assemblage (similar results obtained with tuna or honey baits for mean or variance indices, Table 3).

All results of temporal and spatial null model analyses remained valid when the most frequent ant species was discarded from analyses. Therefore, they were valid for the whole assemblage and not distorted by the overdominance of *Pseudomyrmex denticollis.*

3.4. Spatial distribution of ants

Fig. 5 represents, for every frequent species and all unfrequent species cumulated, baits where the species were observed. Because bait type did not influence the spatio-temporal

Table 2
Determination of stochastic or deterministic influences on the observed pattern of temporal food resource exploitation and study of the ant assemblage structure

Food resource–time of day combination	Observed vs expected mean indices	Observed vs expected variance indices
Proteins–morning	$0.69 = 0.69$ n.s.	$0.09 > 0.07$***
Carbohydrates–morning	$0.76 = 0.76$ n.s.	$0.07 > 0.04$**
Proteins–afternoon	$0.8 > 0.76$***	$0.02 < 0.03$ n.s.
Carbohydrates–afternoon	$0.60 > 0.57$*	$0.1 > 0.07$***

Observed means or variances of temporal foraging overlap indices are compared with those expected under random for each "food resource–time of day" experiments. Expected values were calculated as the average temporal overlap in 1000 randomized assemblages generated by the randomization algorithm 3 of Ecosim (*$P \leqslant 0.05$; **$P \leqslant 0.01$; ***$P \leqslant 0.001$).

Table 3
Determination of stochastic or deterministic influences on the observed pattern of spatial food resource exploitation and study of the ant assemblage structure

	Morning		Afternoon	
Time (min)	Proteins	Carbohydrates	Proteins	Carbohydrates
Means of spatial overlap indices (observed vs expected values)				
15	0<0.01 n.s.	0<0.03**	0.04>0.03 n.s.	0<0.02 n.s.
30	0.04>0.02**	0.01<0.03 n.s.	0.01<0.03 n.s.	0<0.02 n.s.
45	0.03>0.01 n.s.	0.01<0.02 n.s.	0.04>0.03 n.s.	0.02 = 0.02 n.s.
60	0.02>0.01 n.s.	0.01<0.03 n.s.	0.0<0.04*	0.01<0.02 n.s.
75	0.02>0.01 n.s.	0.02 = 0.02 n.s.	0.0<0.04**	0<0.02***
90	0.08>0.01***	0.08>0.02**	0<0.03***	0<0.02***
Variances of spatial overlap indices (observed vs expected values)				
15	0<0.01 n.s.	0<0.01**	0.02>0.01 n.s.	0<0.01 n.s.
30	0.02>0.01 n.s.	0<0.01 n.s.	0<0.01 n.s.	0<0.01 n.s.
45	0.01 = 0.01 n.s.	0<0.01 n.s.	0.02>0.01 n.s.	0.01 = 0.01 n.s.
60	0.02>0.01 n.s.	0<0.01 n.s.	0<0.01 n.s.	0<0.01 n.s.
75	0.01 = 0.01 n.s.	0.02>0.01 n.s.	0<0.01*	0<0.01***
90	0.05>0.01**	0.07>0.01**	0<0.01***	0<0.01**

Observed means or variances of spatial foraging overlap indices are compared with those expected under random for each "food resource–time of day" experiments. Expected values were calculated as the average spatial overlap in 1000 randomized assemblages.

foraging overlap patterns, data for both resources were combined. Bait occurrences gave an indication over the extent of the foraging area for every species inside the studied 144 m^2. *Pseudomyrmex denticollis* exploited almost every available bait. Contrastingly, the other eight frequent species exploited a restricted number of baits, which were often clustered. This was particularly obvious for *Ph. radoszkowskii*, *Ph.* sp. A, *Ca. crispulus* and *W. auropunctata*. The foraging areas of these species virtually did not overlap. *Brachymyrmex leuderwaldti* and *B. aphidicola* were able to exploit baits present inside the foraging area of these species because, rather than foraging over a group of baits, they often exploited a single one which was exclusively dominated due to a high recruitment (Fig. 4). The largest species (*Ps. denticollis* and *Ca. crispulus*) were also those who exploited the largest number of baits (Table 1 and Fig. 5).

4. Discussion

4.1. Influence of the set of trade-offs on temporal ant foraging

The trade-off between food resource discovery and food resource domination (Fellers, 1987; Wilson, 1971) existed globally. We recognized five extirpators, one opportunist and two intermediate species. Furthermore, infrequent ant species possibly corresponded to insinuators since this behavior is often exhibited by cryptic ant species (Wilson, 1971). Temperature influenced both bait discovery and dominance abilities of frequent ant species as described by Bestelmeyer (2000) in the Argentinean Chaco (400 km away from our study site). *Forelius brasiliensis* was the most thermophilic species and exhibited a foraging

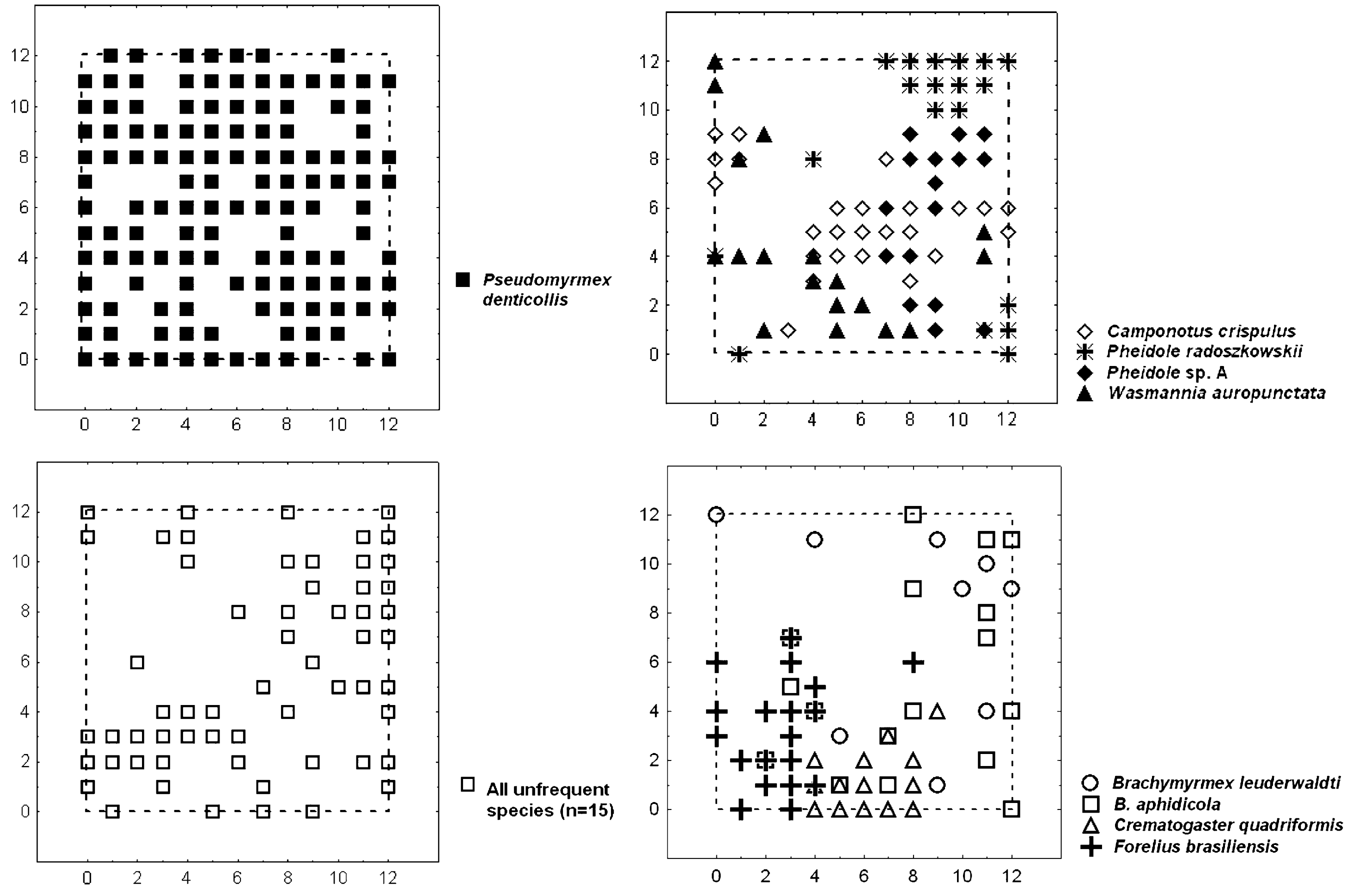


Fig. 5. Bait occupancy by species. For every frequent ants and all unfrequent species cumulated, baits where species was noted at least once during all baiting sessions are indicated.

behavior (fast worker displacement with raised abdomen) typical of thermophilic ants such as *Cataglyphis rosenhaueri* (Cerdá, 2001; Cerdá and Retana, 2000). Extirpators were competitive non-thermophilic ant species (*Brachymyrmex* spp., *Pheidole* spp., *Wasmannia auropunctata*), and opportunists were subordinate thermophilic ones (*Forelius* spp.). It appears that the coexistence of numerically dominant ant species was allowed by the coexistence of these two guilds. An internal guild structure in the assemblage was confirmed. It was sometimes difficult to establish the guild to which a particular species belongs, as for *Pseudomyrmex denticollis* (aggressive and thermophilic species whose cumulated abundance pattern was typical of opportunists), or for *Cr. quadriformis* (which appeared to change its food exploitation strategy according to food nature).

However, temperature and chance rather than interspecific competition structured the temporal foraging at the assemblage level. Indeed, during afternoons temperature strongly structured the temporal foraging but during mornings temporal foraging did not differ from random.

Interspecific conflicts observed at baits were rare and moreover, were rarely initiated by extirpators, which are supposed to be the most aggressive species (Wilson, 1971). Avoidance could be a typical interference behavior among ants. Fellers (1987) specified that interference between species in his study occurred on around 55% of the occasions when two or more species used the same bait and that avoidance behavior accounted for half of these observed interactions. Yanoviak and Kaspari (2000) also found a low frequency of aggresive bait defense at ground in a seasonally wet tropical forest of Panama. However, Bestelmeyer (2000) indicated that non-aggressive encounters between taxa were relatively infrequent at his baits and did not integrate them in his analyses.

Nevertheless, the apparent absence of interspecific competition in our temporal study may be an artifact. The high density of baits at small spatial-scale may allow subordinate species to move to a second bait when extirpators arrived at the first exploited. Hence, although a species turnover at one particular bait existed, at the scale of a whole baiting session, the coexistence time of the guild was increased. We never observed this directly but noted that 21% of the baits were never exploited by any ant species and that half of them (51%) attracted only a single species. This is rather unusual with bait experiments. Only invasive tramp-species are known to monopolize baits exclusively (Davidson, 1998). Here ants were confronted with unusually high quantities of food which could modify their foraging behaviors.

4.2. *Influence of the set of trade-offs on spatial ant foraging*

Our results show that ants in a semi-arid habitat adjust their foraging behavior to environmental conditions very finely in space. Variance indices of spatial foraging overlap indicated that several guilds foraged at the end of morning experiments (thermophilic and non-thermophilic ants probably) and only one guild foraged at the end of afternoon experiments, (non-thermophilic dominant and aggressive species which had excluded submissive thermophilic ants). In the morning, ants were able to forage randomly on the entire soil surface but when temperature became stressful (at the end of morning experiments), ants foraging was aggregated possibly around microsites where temperature was lower. Under high temperatures, only thermophilic ants were able to explore the environment randomly before being excluded by non-thermophilic ants as the temperature cooled down (at the end of the afternoon experiments). To sum up, the set of trade-offs structured the spatial ant foraging when thermal conditions were stressful. When temperature was not too high (during mornings), bait spatial exploitation appeared stochastic.

Among species recognized as extirpators, two strategies of space occupation were observed (Fig. 5). Baits exploited by *Ph. radoszkowskii*, *Ph.* sp. A and *W. auropunctata* were clustered. It is plausible that these species defended a foraging area and only exploited baits located inside their territory (= "territorial species" following the three-leveled competition hierarchy of Savolainen and Vepsäläinen, 1988). Conversely, *B. aphidicola* and *B. leuderwaldti* seemed to defend a punctual food resource rather than a foraging area (= "encounterers species" of Savolainen and Vepsäläinen, 1988). They controlled the bait thanks to a massive recruitment, which allowed them to dominate it even inside the foraging area of other extirpators.

In numerous organisms as diverse as birds (Hyman, 2005), lizards (Trigosso-Venario et al., 2002) or termites (Kaib et al., 2002), it was observed that neighboring individuals avoid each other in order to reduce energetically expensive fighting. It was called the "dear-enemy phenomenon" (Fisher, 1954). In ants this effect also exists. Gordon (1989) has shown that *Pogonomyrmex barbatus* workers confronted with conspecifics from neighboring colonies detered foraging more frequently than with ants from geographically distant colonies. This behavior was also observed during interspecific encounters in two desert *Pheidole* species (Langen et al., 2000).

Here, a "dear-enemy" effect between interspecific neighboring colonies could explain: (1) a very low number of conflicts at baits; (2) no-overlap of foraging areas (Fig. 5) and small mean spatial foraging overlaps (Table 3); (3) a weak interspecific competition effect on the spatio-temporal foraging (Tables 2 and 3); (4) a very small number of baits exploited by more than a single species (Fig. 3).

Because abiotic conditions in arid and semi-arid habitats strongly constrain the ant foraging, the cost of fighting in these environments may be particularly strong and may allow the establishment of "a dear-enemy phenomenon" more easily than in temperate or tropical habitats. More studies are necessary to examine the importance of avoidance between neighboring interspecific colonies, its occurrence according to habitat type and season and its impact on space use and species coexistence.

Although a "dear-enemy phenomenon" may explain our observations, nonexclusive alternative hypotheses may also be proposed. *First*, our baiting protocol may have saturated the habitat with high quality food, decreasing the spatial foraging of ants. Indeed, optimal foraging theory (MacArthur and Pianka, 1966) predicts that the number of microhabitats visited by species during foraging decreases when the set of food resource increases. *Second,* it is possible that some areas were unfavorable due to high predation risks. High densities of antlion larvae, known to influence the spatial distribution of ants (Gotelli, 1993, 1996), were noted in some small patches of the studied area. *Third,* as we discussed above temperature appeared to influence strongly the foraging strategies exhibited by ants and it is not excluded that the majority of species in semi-arid habitat forage only near their nest entrance to decrease their exposure to stressful temperature.

4.3. Food type influence on spatio-temporal foraging

Food preferences were highlighted for three frequent ant species, always for proteins. As we predicted, two of them are thermophilic species: *Pseudomyrmex denticollis* and *Forelius* *brasiliensis*. Temperature restricted the foraging time and space of these species, which in turn exhibited a strong food selectivity to optimize their foraging. Kay (2004) found that species with relatively easy access to carbohydrates preferred proteins. In this direction, *Forelius* spp. are mainly plant nectar consumers. However, protein food preference of *Forelius brasiliensis* could be an artifact due to temperature constraints. Indeed, *F. brasiliensis* is a hot temperature specialist and only the experiment with the hottest temperature conditions (around 42 °C) was really attractive for this species and was carried out with protein baits. During this extremely hot episode, *F. brasiliensis* was the only ant species present at baits (sometimes along with *Ps. denticollis*). *Forelius* species forage usually in open areas under direct sunlight and rarely in forest where non-thermophilic and aggressive species are favored (Bestelmeyer, 1997, 2000). However, when ambient air temperature was high, and hence when competitors were less favored, the subordinate *Forelius* spp. were able to expand their foraging area into the leaf-litter. More replicates at very high temperature are necessary to confirm food preferences of *F. brasiliensis*.

Cr. quadriformis appeared to adapt its foraging behavior according to the bait nature, confirming that bait exploitation by ants could be different according to the food resource (de Biseau et al., 1997; Sanders and Gordon, 2000). However, even if we observed specific food preferences and foraging behavior changes according to food nature, it appears that this did not affect the global foraging at the assemblage scale.

Although it was possible that food preference may be confounded by texture preference (Kaspari and Yanoviak, 2001), we believe that bait exploitation was weakly biased by texture. Canned tuna contains water and salts, proteins and fats in solution, which were probably attractive to both liquid and solid feeders and we assumed honey to be thick enough to be exploited by both ant groups. In the future, it would be more precise to use nutrient solutions of sucrose or casein as Kay (2004) at the cost of realism (Kaspari and Yanoviak, 2001).

4.4. General conclusions

In hot and dry habitats the set of trade-offs between species food discovery and food domination ability and between species thermal tolerance and competitive dominance strongly influence the temporal foraging of ants (Bestelmeyer, 2000). The set of trade-offs has also consequences on the spatial co-occurrence of species during foraging. Nonetheless, temperature and chance rather than interspecific competition deeply structure the spatio-temporal foraging at the assemblage level. As for food preferences, no effect was detected at the assemblage scale. An interspecific "dear-enemy phenomenon" may explain the scarcity of evidences of interspecific competition. Albrecht and Gotelli (2001) already demonstrated the part of chance in the structure of the ant spatio-temporal foraging at both seasonal and nycthemeral scales in grassland ant assemblages from North America. Our results suggest that this finding can be extended to smaller spatio-temporal scales and to more constraining habitats as arid environments.

Acknowledgments

This study was made possible by financial support of the "Fonds pour la formation à la Recherche dans l'Industrie et l'Agriculture" and the King Leopold III Fund for Nature Exploration and Conservation. We thank the guards from Teniente Enciso National Park, John Kochalka, Bolivar Garcete-Barrett and Victor Filippi from the "Museo Nacional de Historia Natural del Paraguay" for their help during fieldwork or administrative procedures. Alex Wild from University of California at Davis and William MacKay from the Laboratory for Environmental Biology (University of Texas, El Paso) confirmed the ant identifications. The manuscript benefited from comments by two anonymous referees, Géraldine Kapfer, Laurence Theunis and René-Marie Lafontaine (RBINS). Lorraine Berry and Jennifer Boyle greatly improved the English version.

References

Albrecht, M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126, 134–141.

Andersen, A.N., 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. American Naturalist 140, 401–420.

Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography 22, 15–29.

Andersen, A.N., 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24, 433–460.

Bernstein, R.A., 1974. Seasonal food abundance and foraging activity in some desert ants. American Naturalist 108, 490–498.

Bestelmeyer, B.T., 1997. Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. Journal of Arid Environments 35, 297–310.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. Journal of Animal Ecology 69, 998–1009.

Cerdá, X., 2001. Behavioural and physiological traits to thermal stress tolerance in two Spanish desert ants. Etología 9, 15–27.

Cerdá, X., Retana, J., 2000. Alternative strategies by thermophilic ants to cope with extreme heat: individual versus colony level traits. Oikos 89, 155–163.

Cerdá, X., Retana, J., Cros, S., 1998a. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12, 45–55.

Cerdá, X., Retana, J., Manzaneda, A., 1998b. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117, 404–412.

Chew, R.M., de Vita, J., 1980. Foraging characteristics of a desert ant assemblage: functional morphology and species separation. Journal of Arid Environments 3, 75–83.

Davidson, D.W., 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecological Entomology 23, 484–490.

de Biseau, J.-C., Quinet, Y., Deffernez, L., Pasteels, J.-M., 1997. Explosive food recruitment as a competitive strategy in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). Insectes Sociaux 44, 59–73.

Detrain, C., Tasse, O., Versaen, M., Pasteels, J.M., 2000. A field assessment of optimal foraging in ants: trail patterns and seed retrieval by the European harvester ant *Messor barbatus*. Insectes Sociaux 47, 56–62.

Fellers, J.H., 1987. Interference and exploitation in a guild of woodland ants. Ecology 68, 1466–1478.

Fellers, J.H., 1989. Daily and seasonal activity in woodland ants. Oecologia 78, 69–76.

Fisher, J.B., 1954. Evolution and bird sociality. In: Huxley, J., Hardy, A.C., Ford, E.B. (Eds.), Evolution As A Process. Allen & Unwin, London, pp. 71–83.

Gibb, H., 2005. The effect of a dominant ant, *Iridomyrmex purpureus*, on resource use by ant assemblages depends on microhabitat and resource type. Australian Ecology 30, 856–867.

Gotelli, N.J., 1993. Ant lion zones: causes of high-density predator aggregations. Ecology 74, 226–237.

Gotelli, N.J., 1996. Ant community structure: effects of predatory ant lions. Ecology 77, 630–638.

Gotelli, N.J., Entsminger, G.L., 1999. Ecosim: null model software for ecology, version 3.0. Aquired Intelligence Inc. and Kesey-Bear 〈http://homepages.together.net/~gentsmin/ecosim.html〉.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Institution, Washington, pp. 368.

Gordon, D.M., 1989. Ants distinguish neighbors from strangers. Oecologia 81, 198–200.

Greenslade, P.J.M., 1971. Interspecific competition and frequency changes among ants in Solomon islands coconut plantations. Journal of Applied Ecology 8, 323–352.

Herbers, J.M., 1989. Community structure in north temperate ants: temporal and spatial variation. Oecologia 81, 201–211.

Hyman, J., 2005. Seasonal variation in response to neighbors and strangers by a territorial songbird. Ethology 111, 951–961.

Kaspari, M., Yanoviak, S.P., 2001. Bait use in tropical litter and canopy ants—evidence of differences in nutrient limitation. Biotropica 33, 207–211.

Kaib, M., Franke, S., Francke, W., Brandl, R., 2002. Cuticular hydrocarbons in a termite: phenotypes and a neighbour-stranger effect. Physiological Entomology 27, 189–198.

Kay, A., 2004. The relative availabilities of complementary resources affect the feeding preferences of ant colonies. Behavioral Ecology 15, 63–70.

Langen, T.A., Tripet, F., Nonacs, P., 2000. The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants. Behavioral Ecology and Sociobiology 48, 285–292.

Levings, S.C., 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. Ecological Monographs 53, 435–455.

Lynch, J.F., 1981. Seasonal, successional, and vertical segregation in a Maryland ant community. Oikos 37, 183–198.

MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. American Naturalist 100, 603–609.

McGlynn, T.P., Kirksey, S.E., 2000. The effects of food presentation and microhabitat upon resource monopoly in a ground-foraging ant (Hymenoptera: Formicidae) community. Revista de Biologia Tropical 48, 629–642.

Perfecto, I., 1994. Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. Oecologia 98, 184–192.

Pianka, E.R., 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4, 53–74.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44, 639–680.

Retana, J., Cerdá, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123, 436–444.

Ribas, C., Schoereder, J.H., 2002. Are all ant mosaics caused by competition? Oecologia 131, 606–611.

Rissing, S.W., 1988. Dietary similarity and foraging range of two seed-harvester ants during resource fluctuations. Oecologia 75, 362–366.

Sale, P.F., 1974. Overlap in resource use, and interspecific competition. Oecologia 17, 245–256.

Sanders, N.J., Gordon, D.M., 2000. The effects of interspecific interactions on resource use and behavior in a desert ant. Oecologia 125, 436–443.

Savolainen, R., Vepsäläinen, K., 1988. A competitive hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51, 135–155.

Savolainen, R., Vepsäläinen, K., 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. Oikos 56, 3–16.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27–39.

Trigosso-Venario, R., Labra, A., Niemeyer, H.M., 2002. Interactions between males of the lizard *Liolaemus tenuis*: roles of familiarity and memory. Ethology 108, 1057–1064.

Vepsäläinen, K., Savolainen, R., 1990. The effect of interference by Formicine ants on the foraging of Myrmica. Journal of Animal Ecology 59, 643–654.

Wilson, E.O., 1971. The Insect Societies. The Belknap Press of Harvard University Press, pp. 548.

Winemiller, K.O., Pianka, E.R., 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecological Monographs 60, 27–55.

Yanoviak, S.P., Kaspari, M., 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos 89, 259–266.

Spatial co-occurrence in ground-foraging ant assemblages along an aridity gradient in the Paraguayan dry Chaco.

DELSINNE Thibaut (1, 2), **LEPONCE Maurice (1)**, **ROISIN Yves (2)**

[1]: Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, BELGIUM.

[2]: Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral and Evolutionary Ecology - CP 160/12, 1050 Brussels, BELGIUM.

Abstract

One of the expected structuring effects of interspecific competition is to segregate species spatially. In ground-foraging ant assemblages, competition is expected to be higher in habitats with low stress. As a consequence, ant species should exhibit a higher level of segregation in these habitats. Here, we used a null model approach to study the spatial co-occurrence of ants along an aridity gradient in order to verify this expectation. Analyses were carried out at regional and local scales on ant fauna, on consubfamilial and on congeneric species. At a regional scale, aridity itself rather than competition seems to influence the ant distribution. At a local scale, evidence of non-random patterns was almost absent and species segregation was not correlated with aridity for all taxonomic levels studied. The random spatial co-occurrence pattern of ants during foraging may allow arid and semi-arid habitats to support a higher number of species than expected under these stressful conditions.

Keywords

Assemblage structure, Formicidae, interspecific competition, null model, related species, species coexistence, species segregation, stress.

Evidence of interspecific competition in ground-foraging ant assemblages includes the observation of dominance hierarchies (Vepsäläinen and Pisarski, 1982; Savolainen and Vepsäläinen, 1988; Basu, 1997), species displacements at food resources (Fellers, 1987) and interspecific aggression (Möglich and Alpert, 1979; Adams and Traniello, 1981; Gordon, 1988). One of the expected structuring effects of competition is to prevent the occurrence of some species combinations in assemblages as a consequence of the exclusion of subordinate species by superior competitors (Diamond, 1975). Examples indicating spatial segregation between ants are nest overdispersion (Levings and Traniello, 1981; Levings and Franks, 1982), territoriality (Savolainen and Vepsäläinen, 1988), fidelity for particular foraging areas (Hölldobler, 1976; Hölldobler and Lumsden, 1980), extension of foraging area by subordinate species after the experimental exclusion of a dominant (Haering and Fox, 1987; Perfecto, 1994) and the observation of a smaller spatial co-occurrence of species than expected under random conditions (Gotelli and Arnett, 2000; Gotelli and McCabe, 2002; Sanders et al., 2003). Nevertheless, the structuring effect of competition on the spatial co-occurrence of ant species may be a function of the habitat studied and of the spatial scale considered (Gotelli and Ellison, 2002). Investigating the co-occurrence of species in bogs and forests in New England, Gotelli and Ellison (2002) found a possible effect of competition in forests, but not in bogs, at a regional scale and no evidence in both habitats at a local scale.

In ant assemblages, interspecific competition is expected predominantly at sites with low stress and/or low disturbance (Heatwhole, 1989; Andersen, 1995, 1997; Parr et al., 2005). As a consequence, the spatial segregation of species may also be expected to be higher at sites with low environmental stress. In this study, the spatial co-occurrence of ant species was investigated with a null model approach, at both regional and local scales along an aridity gradient (average annual rainfall: 350-1000mm). We hypothesized that interspecific competition increases with rainfall (i.e. with a decrease of the aridity stress) and we thus expected (1) an exclusion of species between localities and (2) a decrease of local species co-occurrence with rainfall. The Paraguayan dry Chaco plains are ideal for this study because of their flat topography and wide rainfall range (Fariña Sánchez, 1973; Ramella and Spichiger, 1989).

Along with a spatial segregation, competition may also cause a temporal and/or trophic divergence between species (Schoener, 1974). Nevertheless, these divergences generally do not exclude the existence of a spatial segregation (Schoener, 1974; Deffernez et al., 1990). Here, ant assemblages were collected with pitfall traps because they allow focus on the space exploitation by ants during foraging due to their 24 sampling ability.

Competition is also expected to be stronger between related rather than phylogenetically distant species because relatives should display more morphological and ecological similarities (Dietrich and Wehmer, 2003). For instance in Australia, the dominant *Iridomyrmex purpureus* affects the exploitation of baits by other *Iridomyrmex* species in particular (Gibb and Hochuli, 2004; Gibb, 2005). In these conditions, relatives should exhibit high levels of mutual exclusion. In addition, a dilution effect may lessen the competitive effects when analyses concern a whole fauna (Gilpin and Diamond, 1982). In this paper, we complemented the investigation of the all assemblages by the study of consubfamilial and congeneric species to test if interspecific competition influences their spatial co-occurrence.

METHODS

Study sites and sampling protocol

The study was conducted between 2001 and 2004 in the Paraguayan dry Chaco. Ten localities spaced between 20 and 400km were spread along an aridity gradient (Figure 3-1). These sites were sampled at the end of the dry season, in September-November, when temperature and rainfall increased. This sampling period was selected in order to avoid the extremely high or low temperatures, which may occur during the dry or wet season respectively (Ramella and Spichiger, 1989), because extreme temperatures appear to limit the foraging of some Chacoan ant species (Bestelmeyer, 2000, Delsinne et al., 2007). The habitats are a continuum of xeromorphic forests (Ramella and Spichiger, 1989; Mereles 2005). Mean annual temperature of localities is comprised between 24 and 26°C (Fariña Sánchez, 1973).

Ants were sampled along a transect of 20 pitfall traps spaced at 10m intervals. Three transects, spread along a 1km-long line and separated from each other by 200m, were carried out per locality. Pitfall traps are the most effective method of documenting ground-foraging ant diversity in the dry Chaco (Delsinne et al., submitted) and consisted of 70mm-diameter drinking cups, containing water and a drop of detergent, operating for 24 hours.

Co-occurrence analyses

Co-occurrence analyses were carried out at regional and local scales. At the regional scale, data were organized in a presence (1)/absence (0) matrix where rows represented species and columns corresponded to the 10 localities. At the local scale, rows still represented species but columns corresponded to the 60 pitfall traps.

The C-score of Stone and Roberts (1990) was used to quantify the average amount of co-occurrence in the matrices. This index is recommended for such study because has good statistical properties, when used with an appropriate null model (Gotelli, 2000). The C-score is the average number of checkerboard units calculated for all possible species pairs. A checkerboard unit is a submatrix of the form:

	Locality (or pitfall) x	Locality (or pitfall) y
Ant species i	1	0
Ant species j	0	1

For any pair of species, the number of checkerboard units equals (Ri - S) (Rj - S) where S is the number of localities (or pitfalls) containing both species and Ri and Rj are the number of localities (or pitfalls) where species i and j were collected (i.e. the row total for species i and j). Thus, the C-Score measures the inclination for species to not co-occur. If the space exploitation of species in the assemblage is structured by interspecific competition, the observed C-score should be higher than expected by chance (as a consequence of spatial segregation or exclusion). Inversely, the observation of an unusually small C-score indicates that species are more aggregated than expected.

To determine the stochastic and deterministic parts of observed species co-occurrence in each matrix, the observed C-score value was compared to those expected under the hypothesis of random co-occurrence of species and generated by null models (Gotelli and Graves, 1996). All null model simulations were performed with EcoSim Version 7 software (Gotelli and Entsminger, 2006). We used a "row sum fixed - column sum fixed" null model [=SIM 9 *sensu* Gotelli (2000)] with a sequential swap algorithm (Gotelli and Entsminger, 2001) to generate 5000 randomly constructed assemblages from each observed matrix. This method is recommended for such study, when the C-score index is used (Gotelli, 2000; Gotelli and Entsminger, 2001). In this model, ant species occur with the same frequency in both the randomly and observed assemblages. It is particularly pertinent for ant assemblages which are characterized by a number of rare species, as it is the case for instance in the Argentinean Chaco (Leponce et al., 2004). In addition, the sampling effort (60 pitfall traps) is considered as sufficient to have a representative inventory of the local assemblage (Delsinne et al., submitted). Every localities have also the same number of species in both simulated and observed assemblages. Thus, if a locality corresponded to a better habitat for ants than the others, this aspect was maintained in the simulated assemblages. Along with interspecific competition, distance between localities and local abiotic conditions may also influence the species distribution and it is also probable that each species responds to these factors idiosyncratically. Because data are lacking to determine precisely which locality is more suitable for ants than others, the SIM9 simulation is the most conservative approach, even if it may not be the most biologically realistic.

At a local scale, we used both the SIM9 simulation (i.e. if some pitfall traps were placed in more favourable microhabitats and collected more species, it was also conserved in the null assemblages) and a "row sum fixed - column sum equiprobable" null model [= SIM2 *sensu* Gotelli (2000)]. In the latter, each species is randomly and equiprobably re-shuffled within each pitfall traps. It is realistic because at each locality, we tried to place traps in as homogenous forest as possible.

The statistical significance was calculated as the frequency of simulated C-score values equal to or more extreme than the observed C-score (one-tailed test). We did not use Bonferroni correction on significance levels, because this approach has been criticized for mathematical and logical reasons (Moran, 2003; Nakagawa, 2004) and because we were interested in the overall pattern of which data sets showed significance and which did not.

The effect of interspecific competition on the spatial co-occurrence of consubfamilial and congeneric ant species was explored by constructing submatrices from every original matrix. In these submatrices, columns of the original matrix were conserved but only consubfamilial or congeneric species were included. Analyses were only performed for the most frequent subfamilies and the most diverse genera to avoid the construction of matrices with just 1 or 2 species (e.g.Pseudomyrmecinae) and to avoid the analyses on just infrequent species (e.g. Ecitoninae).

Differences among subfamilies or genera in their spatial co-occurrence patterns

To determine if some subfamilies or genera are more structured by competition than others (i.e. have relatively larger C-scores) at both regional and local scales, we constructed presence/absence submatrices where columns corresponded to the 10 localities (regional scale) or to the 60 pitfall traps (local scale) and where rows represented only the species belonging to the subfamilies (or genera) studied. An additional column was created to indicate the subfamily (or genera) of the species. Then, 5000 simulated matrices were created. Simulations did not alter the structure of the matrix but just reshuffled subfamily or genera labels among the different species. For each subfamily or genera separately, a mean C-score and variance were calculated for both observed and simulated data and were compared to determine whether the mean and variance C-score among guilds is larger or smaller than expected by chance. An unusually large variance would mean that some subfamilies (or genera) have species with low levels of spatial co-occurrence (= high C-score) and others with high levels. Inversely, an unusually small variance would mean that the spatial co-occurrence among subfamilies (or genera) is more similar than expected by chance.

Aridity influence

To compare results between localities with different aridity conditions, a standardized effect size (hereafter SES) was calculated for each matrix and submatrix. An effect size is calculated by standardizing the difference between observed and simulated C-score values as:

$$SES = (Iobs - Isim)/ SDsim$$

where Iobs is the C-score observed, Isim is the mean of the 5000 simulated C-score values and SDsim, their standard deviation.

A single sample *t* test is used to verify the null hypothesis that SES did not differ from zero. Assuming a normal distribution of deviations, ±95% of the SES values should be less than 2 and greater than -2. When SES is greater than +2, species significantly co-occur less than expected by chance ($P<0.05$) (i.e. possible effect of interspecific competition). At the opposite, when SES is less than -2, species are significantly more aggregated than expected ($P<0.05$).

The Pearson product moment correlation was calculated between mean annual rainfall and SES values. If SES values increase with rainfall, this indicates that competition most likely determines the spatial co-occurrence of species at sites with low stress (i.e. less arid).

RESULTS

Spatial co-occurrence at the regional scale

Figure 3-2 represents the presence/absence of species belonging to the most frequent and diverse genera along the aridity gradient. Overall, ant species co-occurred in the Paraguayan Chaco much less than expected by chance (Table 3-1). At the subfamily level, a segregation pattern was also observed, except for Dolichoderinae. At the the genera level, only *Camponotus* species co-occurred less than expected (Table 3-1). Moreover, the spatial co-occurrence among subfamilies was more similar than expected by chance (Variance observed/expected ± SD: 0.028/0.332 ± 0.298 ; P(obs<exp)=0.028) but did not differ from random among genera (0.376/0.413 ± 1.120, P(obs<exp) = 0.299).

Spatial co-occurrence at the local scale

Overall, evidence of non-random co-occurrence was scarce. Only 11 (16%) and 14 (20%) co-occurrences were non-random with the SIM9 and SIM2 algorithms respectively (Table 3-2). Less aggregations were found with SIM9 than with SIM2: 2 (18% of the significant results) and 9 (64%) respectively. No evidence was brought out concerning differences among subfamilies or genera in terms of their spatial co-occurrence (P<0.05).

Influence of aridity

The spatial co-occurrence observed at the assemblage level and for every subfamily and genus studied, was never significantly correlated with aridity (Table 3-2). As an example, Figure 3-3 illustrates the relationship between aridity and local standardized C-scores obtained for the all ant fauna with the SIM9 algorithm. Nevertheless, the 4 significant aggregations obtained with SIM2 for all species (Table 3-2) were found in localities situated at the extremity of the aridity gradient (mean annual rainfall: 350-600mm) and the only one segregation obtained with SIM9 for all species (Table 3-2; Figure 3-3) was found in locality 10, the driest locality (350 mm).

DISCUSSION

At the regional scale, ant species co-occurred less than expected under chance conditions. A similar result was found in other regions and habitats (Gotelli and Arnett, 2000; Gotelli and Ellison, 2002). This pattern may be caused by a spatial exclusion of competitive species as predicted by Diamond's Assemblage Rule (Diamond, 1975). However, species segregation may also be due to other factors such as history or different habitat requirements (Sfenthourakis et al., 2005). Here, species may segregate due to different aridity tolerances rather than competition. Indeed, dessication resistance increases with worker body size (Hood and Tschinkel, 1990) and in this aspect, the 185 species studied constituted a very heterogeneous group from the tiny *Solenopsis* species (worker size: ~1mm long) to the huge *Dinoponera mutica* (~3cm). When analyses were carried out on groups represented by variable species (i.e. on the all ant fauna and on subfamilies) a spatial segregation was observed, but when analyses concerned congeneric species, the regional distribution did not differ from random although competition effects were expected more evident at this taxonomic level. The exception is the *Camponotus* genus, which is a heterogeneous taxa in terms of species body size (Fernández, 2003). Moreover, the spatial co-occurrence among subfamilies is more similar than expected by chance, probably because an identical factor (aridity) structures their regional distribution.

At a local scale, our findings did not support that interspecific competition produces a strong structuring effect on the spatial co-occurrence of ants. When pitfall traps were considered as equiprobable (SIM2), little evidence of species aggregations were obtained, especially in the driest localities. This suggests that some microhabitats were more favourable for ants than others. When pitfall characteristics were maintained in the null model (SIM9), results rarely differed from a co-occurrence expected by chance. In addition, although SIM2 and SIM9 are not prone to Type I error, the null hypothesis may have been rejected ~10% of the time even if the matrix is random (at $P<0.05$) (Gotelli, 2000). Taken this possible error in consideration, existence of a non-random co-occurrence of species is still weaker. This result is congruent with the observation of a random pattern in local ant assemblages of bogs and forests in New England (Gotelli and Ellison, 2002). In addition, contrary to our prediction, aridity did not affect the intensity of competition for space since no correlation existed between aridity and the co-occurrence indices (standardized C-scores). Even in supposedly more competitive consubfamilial and congeneric species, competition did not appear to have a strong influence on the spatial co-occurrence, agreeing with results found with other taxa by Sfenthourakis et al. (2005). It is possible that taxonomic relationships are not a good approximation for ecological similarities and interspecific competition may be expected to be higher between species belonging to a same guild or functional group. Nevertheless, congeneric or consubfamilial ant species are often categorized in a same functional group (Andersen, 1995, 1997) and ground-foraging ants mainly belong to the same guild of generalists and scavengers of dead insects (Carroll and Janzen, 1973).

Our results were surprising since during a study of bait exploitation by ants in locality 6 (Figure 3-1), 4 of the 9 frequently attracted species exploited a small, often clustered number of baits, leading to non-overlapped areas of food exploitation (Delsinne et al., 2007) and suggesting a spatial segregation of species.

Several reasons may explain why interspecific competition evidences are weak and spatial co-occurrence mainly random. Firstly ant species may differ sufficiently in their foraging strategies, body size and/or resource exploitation, such that they compete weakly even if they forage at a same time (Andersen et al., 2000; Sarty et al., 2006). Also competition may change with the growth of the ant colony, with the intensity of its food needs and with the season (Herbers, 1985). Ant assemblages were sampled just after the end of the dry season, which is suspected to be a stressful period for a majority of ant colonies. It is possible that competition is more important later in the year. Interspecific competition may be counterbalanced by other factors such as the presence of parasites (Adler et al., 2007; Lebrun and Feener, 2007). Also, intraspecific competition may be higher than interspecific competition, allowing the coexistence of inferior competitors (Johnson, 2001; Parr et al., 2005). Moreover in ant assemblages, an individual species probably compete with a "constellation of species" (=diffuse competition). The total direct and indirect competitive effects sometimes facilitate species coexistence (Davidson, 1980, 1985).

Ant species may be mainly segregated along a nycthemeral axis, allowing competitors to exploit a same place but at different times of the day (Schoener, 1974; Albrecht and Gotelli, 2001). In arid and semi-arid habitats, the temporal segregation may be made easier by the existence of important temperature variations in a single day. Each species forages during a laps of time allowed by its thermal tolerance (Cerdá et al., 1997, 1998; Bestelmeyer, 2000; Thomas and Holway, 2005).

Competition may be conditional. Indeed, territoriality is correlated with the presence of stable and rich food supply which may be easily defended (Carroll and Janzen, 1973, Hölldobler and Lumsden, 1980). Since ground-foraging ants mainly scavenge on dead insects (Carroll and Janzen, 1973), a highly unpredictably distributed resource, the maintenance of spatial segregation with competitors should not be adaptative (Hölldobler and Lumsden, 1980). In this case, ant workers forage randomly till they find a food source which they will defend if necessary. This explanation is in accord with the fact that at baits, the spatial overlap between species is firstly random and then structured by interspecific competition (Delsinne et al., 2007). It is also congruent with the fact that, in Australia, effects of the exclusion of the dominant *Iridomyrmex sanguineus* were only detectable at baits and not on pitfall catches (Andersen and Patel, 1994) and that the composition of food resource alters the competitive behaviour of ground-foraging ants (Sanders and Gordon, 2003; Gibb, 2005). In arid and semi-arid habitats, thermal conditions probably exacerbate the existence of these "spatiotemporal territories" (*sensu* Hölldobler and Lumsden, 1980), since they influence the spatial exploitation of food resources (Delsinne et al., 2007).

Conclusion

The key issue of this study is not to determine if interspecific competition exists in ant assemblages of the Paraguayan dry Chaco but to what extent it structures the spatial co-occurrence of species. At a regional scale, aridity rather than competition is probably the structuring factor. At a local scale, spatial co-occurrence is mainly random, plausibly helped by a temporal segregation under the influence of temperature. Interspecific competition appears limited at the defense of food resources and foraging areas may hence overlap. An assemblage with more overlap may support more species than with less overlap (Pianka, 1974). The random foraging of ants in arid and semi-arid environments probably contributes to the fact that these habitats support a higher diversity than expected under these stressful conditions. Comparative studies should be undertaken (for instance along altitudinal or thermal gradients) in order to determine if the random co-occurrence of foraging ants is restricted to arid and semi-arid habitats or if it is characteristic of all ground-foraging ant assemblages.

ACKNOWLEDGEMENTS

We thank John Kochalka, Bolivar Garcete-Barrett, Victor Filippi, Jorge Jara, César Bénilez, Carlos Aguilar Julio from the "Museo Nacional de Historia Natural del Paraguay", the guards from Teniente Enciso National Park and Véronique Olivier for their help during fieldwork or administrative procedures. This study was made possible by financial support from the “Fonds pour la Formation à la Recherche dans l’Industrie et l’Agriculture” and the "Fonds de la Recherche Scientifique - FNRS" (Belgium). Nihara Gunawardene greatly improved the English version.

REFERENCES

Adams E.S., Traniello, J.F.A., 1981. Chemical interference competition by *Monomorium minimum* (Hymenoptera: Formicidae). Oecologia 51: 265-270.

Adler, F.R., LeBrun, E.G., Feener, D.H.Jr., 2007. Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. The American Naturalist 169: 323-333.

Albrecht, M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126: 134-141.

Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. J. Biogeogr. 22: 15-29.

Andersen, A.N., 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. J. Biogeogr. 24: 433-460.

Andersen, A.N., Azcárate, F.M., Cowie, I.D., 2000. Seed selection by an exceptionally rich community of haverster ants in the Australian seasonal tropics. Journal of Animal Ecology 69: 975-984.

Andersen, A.N., Patel, A.D., 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. Oecologia 98: 15-24.

Basu, P., 1997. Competition hierarchy in the ground foraging ant community in a wet evergreen forest (Western Ghats, India): role of interference behaviour. Current Science 73:173–179.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Anim. Ecol. 69: 998-1009.

Carroll, C.R., Janzen, D.H., 1973. Ecology of foraging by ants. Annual Review of Ecology and Systematics 4: 231-257.

Cerdá, X., Retana, J., Cros, S., 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. Journal of Animal Ecology 66: 363-374.

Cerdá, X., Retana, J., Manzaneda, A., 1998. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117: 404-412.

Davidson, D.W., 1980. Some consequences of diffuse competition in desert seed-eating ants. The American Naturalist 116:92-105.

Davidson, D.W., 1985. An experimental study of diffuse competition in harvester ants. The American Naturalist 125:500-506.

Deffernez, L., Champagne, P., Verhaeghe, J.-C., Josens, G., Loreau, M., 1990. Analysis of the spatio-temporal niche of foraging grassland ants in the field. Insectes Sociaux 37: 1-13.

Delsinne, T., Roisin, Y., Leponce, M., 2007. Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage. J. Arid Environ. 71: 29-44.

Delsinne T., Leponce M., Theunis L., Braet Y and Roisin Y. Rainfall influence the ant sampling in dry forests. Biotropica, under revision.

Diamond, J.M., 1975. Assembly of species communities. pp. 342-444 in: Ecology and evolution of communities. M.L. Cody and J.M. Diamond (eds). Harvard University Press, Cambridge.

Dietrich, B., Wehmer, R., 2003. Sympatry and allopatry in two desert ant sister species: how do *Cataglyphis bicolor* and *C. savignyi* coexist? Oecologia 136: 63-72.

Fariña Sánchez, T., 1973. The climate of Paraguay. pp. 33–38. In: Gorham, J.R. (ed.). Paraguay: ecological essays. Academy of the Arts and Sciences of the Americas, Miami, FL.

Fellers, J.H., 1987. Interference and exploitation in a guild of woodland ants. Ecology 68: 1466-1478.

Fernández, F., 2003. Subfamilia Formicinae. pp. 299-306. In: Fernández, F. (ed.). Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia. XXVI + 398p.

Gibb, H., 2005. The effect of a dominant ant, *Iridomyrmex purpureus*, on resource use by ant assemblages depends on microhabitat and resource type. Aust. Ecol. 30: 856-867.

Gibb, H., Hochuli, D.F., 2004. Removal experiment reveals limited effects of a behaviorally dominant species on ant assemblages. Ecology 85: 648–657.

Gilpin, M.E., Diamond, J.M., 1982. Factors contributing to non-randomness in species co-occurrences on islands. Oecologia 52: 75-84.

Gordon, D.M., 1988. Nest-plugging: interference competition in desert ants (*Novomessor cockerelli* and *Pogonomyrmex barbatus*). Oecologia 75: 114-118.

Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. Ecology 81: 2606-2621.

Gotelli, N.J., Arnett, A.E., 2000. Biogeographic effects of red fire ant invasion. Ecology letters 3: 257-261.

Gotelli, N.J., Ellison, A.M., 2002. Assembly rules for New England ant assemblages. Oikos 99: 591-599.

Gotelli, N.J., Entsminger, G.L., 2001. Swap and fill algorithms in null model analysis: rethinking the knight's tour. Oecologia 129: 281-291.

Gotelli, N.J., Entsminger, G.L., 2006. EcoSim: null models software for ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT05465. http://garyentsminger.com/ecosim.htm.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Institution, Washington, 368 pp.

Gotelli, N.J., McCabe, D.J., 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. Ecology 83: 2091-2096.

Haering, R., Fox, B.J., 1987. Short-term coexistence and long-term competitive displacement of two dominant species of *Iridomyrmex*: the successional response of ants to regenerating habitats. The Journal of Animal Ecology 56: 495-507.

Heatwhole, H., 1989. Changes in ant assemblages across an arctic treeline. Revue d'entomologie du Québec 34: 10-22.

Herbers, J.M., 1985. Seasonal structuring of a north temperate ant community. Insectes Sociaux 32: 224-240.

Hölldobler, B., 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav. Ecol. Sociobiol. 1: 3-44.

Hölldobler, B., Lumsden, C.J., 1980. Territorial strategies in ants. Science 210: 732-739.

Hood G.W., Tschinkel, W.R., 1990. Dessication resistance in arboreal and terrestrial ants. Physiological Entomology 15: 23-35.

Johnson, R.A., 2001. Biogeography and community structure of North American seed-harvester ants. Annu. Rev. Entomol. 46: 1-29.

Lebrun, E.G., Feener, D.H.Jr., 2007. When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. Journal of Animal Ecology 76: 58-64.

Leponce, M., Theunis, L., Delabie, J.H.C., Roisin, Y., 2004. Scale dependence of diversity measures in a leaf-litter ant assemblage. Ecography 27: 253-267.

Levings, S.C., Franks, N.R., 1982. Patterns of nest dispersion in a tropical ground ant community. Ecology 63: 338-344.

Levings, S.C., Traniello, J.F.A., 1981. Territoriality, nest dispersion, and community structure in ants. Psyche 88: 265-319.

Mereles, M.F., 2005. Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay. Rojasiana 6: 5-48.

Möglich, M.H.J., Alpert, G.D., 1979. Stone dropping by *Conomyrma bicolor* (Hymenoptera: Formicidae): a new technique of interference competition. Behav. Ecol. Sociobiol. 6: 105-113.

Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403-405.

Nakagawa, S., 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behavioral Ecology 15: 1044-1045.

Parr, C.L., Sinclair, B.J., Andersen, A.N., Gaston, K.J., Chown, S.L., 2005. Constraint and competition in assemblages: a cross-continental and modeling approach for ants. The American Naturalist 165: 481- 494.

Perfecto, I., 1994. Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. Oecologia 98: 184-192.

Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci. USA 71: 2141-2145.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639-680.

Sanders, N.J., Gordon, D.M., 2003. Resource-dependent interactions and the organization of desert ant communities. Ecology 84: 1024-1031.

Sanders, N.J., Gotelli, N.J., Heller, N.E., Gordon, D.M. 2003. Community diassembly by an invasive species. PNAS 100: 2474-2477.

Sarty, M., Abbott, K.L., Lester, P.J., 2006. Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149: 465-473.

Savolainen, R., Vepsäläinen, K., 1988. A competitive hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51: 135-155.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Sfenthourakis, S., Tzanatos, E., Giokas, S., 2005. Species co-occurrence: the case of congeneric species and a causal approach to patterns of species association. Global Ecology and Biogeography 15: 39-49.

Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. Oecologia 85: 74-79.

Thomas, M.L., Holway, D.A., 2005. Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. Journal of Animal Ecology 74: 532-542.

Vepsäläinen, K., Pisarski, B., 1982. Assembly of island ant communities. Ann. Zool. Fennici 19: 327-335.

TABLE AND FIGURE LEGENDS

Table 3-1. Regional co-occurrences. The C-score index was calculated for the ant fauna and the main ant subfamilies and genera (C-scores observed). The mean C-score expected was calculated from 5000 randomly generated matrices created with the SIM9 algorithm (C-scores expected ± SD). The P-values indicate the probability that the observed index is larger than expected by chance. Statistically significant results are written in bold. The number of species for each taxonomic level is also given (No. of species).

Table 3-2. Local co-occurrence and the influence of aridity. Average standardized effect sizes (SES) of the local C-scores were calculated for the ant fauna, the main subfamilies and genera with both the SIM9 and SIM2 algorithms (n=10 localities). The number of significant segregations and associations at $P<0.05$ is given. Numbers in brackets indicate the locality (see Figure 3-1) for which a significant result was obtained. For each taxonomic level, the correlation between the 10 local SES and aridity was calculated by Pearson product moment correlation analyses.

Figure 3-1. Study sites distributed along the aridity gradient of the Paraguayan Chaco plains. Isolines of mean annual rainfall are indicated. Localities are: (1) Río Verde; (2) Cruce de Los Pioneros; (3) Mariscal Estigarribia; (4) Garrapatal; (5) Teniente Enciso National Park-Northern side; (6) T.Enciso N.P.-Southern side; (7) Siracua; (8) Nueva Asunción; (9) Fortín Mayor Infante Rivarola; (10) Fortín Mister Long.

Figure 3-2. Species distribution along the aridity gradient. Each dot represents the species occurrence in one of the 10 localities. Each row represents a different species. Species are sorted from the most to the less widely distributed. All species belonging to Ponerinae and Ectatomminae are presented. Only the most diverse genera are presented for Formicidae (*Brachymyrmex, Camponotus*), Myrmicinae (*Solenopsis, Pheidole*) and Dolichoderinae (*Dorymyrmex, Forelius*).

Figure 3-3. Influence of aridity on local co-occurrence. For each locality, an average standardized effect size of the local C-score (=standardized C-score) was calculated with the SIM9 algorithm for all the ant fauna (n=10 localities). The dotted line indicates the approximate level of statistical significance ($P<0.05$). A single C-score value is above the dotted line, indicating that in only one locality the spatial co-occurrence was lower than expected by chance. The solid line is the linear fitting of the plot. The relationship is not significant (Pearson product moment correlation analyses: $r = -0.63$; $P=0.052$).

TABLES

Table 3-1

Taxa	No. of species	C-scores observed	C-scores expected ± SD	P(obs>exp)
All species	185	2.23	2.17 ± 0.01	**<0.00001**
Subfamilies				
Dolichoderinae	22	1.91	1.86 ± 0.05	0.179
Ectatomminae	7	1.86	1.47 ± 0.17	**0.034**
Formicinae	31	2.00	1.78 ± 0.04	**0.0004**
Myrmicinae	106	2.29	2.26 ± 0.01	**0.013**
Ponerinae	9	2.00	1.56 ± 0.14	**0.012**
Genera				
Brachymyrmex	8	1.86	1.79 ± 0.15	0.277
Camponotus	20	2.16	1.85 ± 0.09	**0.005**
Dorymyrmex	11	1.13	1.16 ± 0.10	0.614
Forelius	9	2.50	2.37 ± 0.13	0.169
Pheidole	28	2.43	2.42 ± 0.05	0.336
Solenopsis	28	2.88	2.90 ± 0.04	0.690

Table 3-2

				Correlation with aridity	
Taxa	Average SES ± SD (n=10)	No. of segregations (P<0.05) [localities]	No. of associations (P<0.05) [localities]	Partial correlation coefficients	P values
Algorithm:Fixed-Fixed (SIM9)					
All species	0.85 ± 0.78	1 [10]	0	-0.63	0.052
Subfamilies					
Dolichoderinae	0.10 ± 1.07	1 [1]	0	0.57	0.085
Formicinae	0.34 ± 1.03	0	0	0.50	0.142
Myrmicinae	1.33 ± 0.98	3 [3, 5, 8]	1 [2]	0.23	0.515
Genera					
Camponotus	0.35 ± 1.29	1 [2]	1 [6]	0.41	0.242
Pheidole	0.61 ± 1.03	1 [4]	0	0.19	0.599
Solenopsis	1.01 ± 1.01	2 [5, 9]	0	-0.19	0.592
Algorithm:Fixed-Equiprobable (SIM2)					
All species	-1.92 ± 2.28	0	4 [4, 7, 8, 10]	0.40	0.248
Subfamilies					
Dolichoderinae	-1.35 ± 1.35	0	1 [8]	0.20	0.574
Formicinae	-0.70 ± 0.98	0	1 [4, 6]	0.23	0.517
Myrmicinae	-0.02 ± 1.26	1 [5]	1 [8]	0.52	0.122
Genera					
Camponotus	-0.91 ± 0.90	0	2 [4, 10]	0.17	0.627
Pheidole	1.02 ± 1.21	3 [1, 5, 7]	0	0.23	0.516
Solenopsis	0.48 ± 0.82	1 [3]	0	-0.08	0.834

FIGURES

Figure 3-1

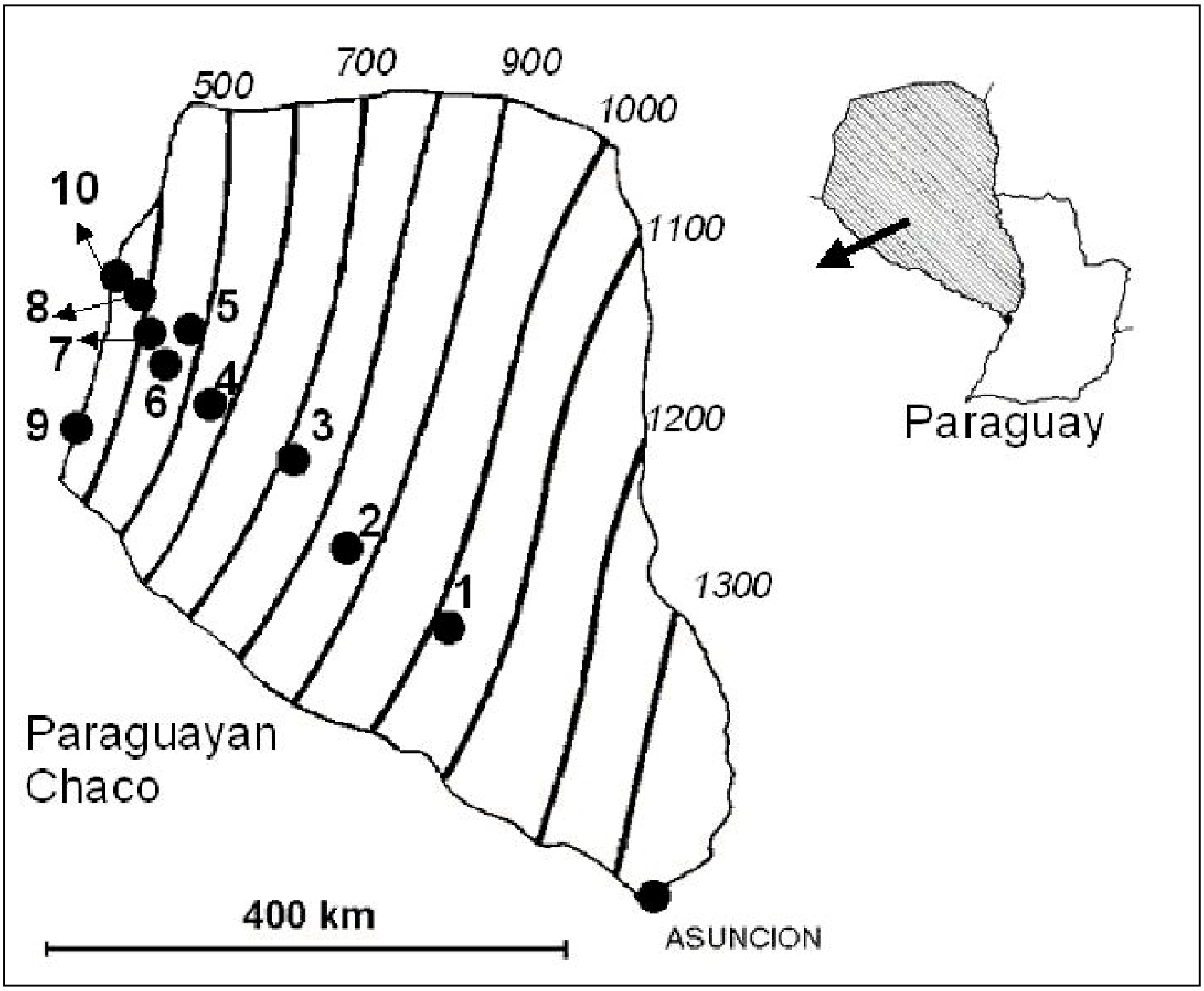


Figure 3-2

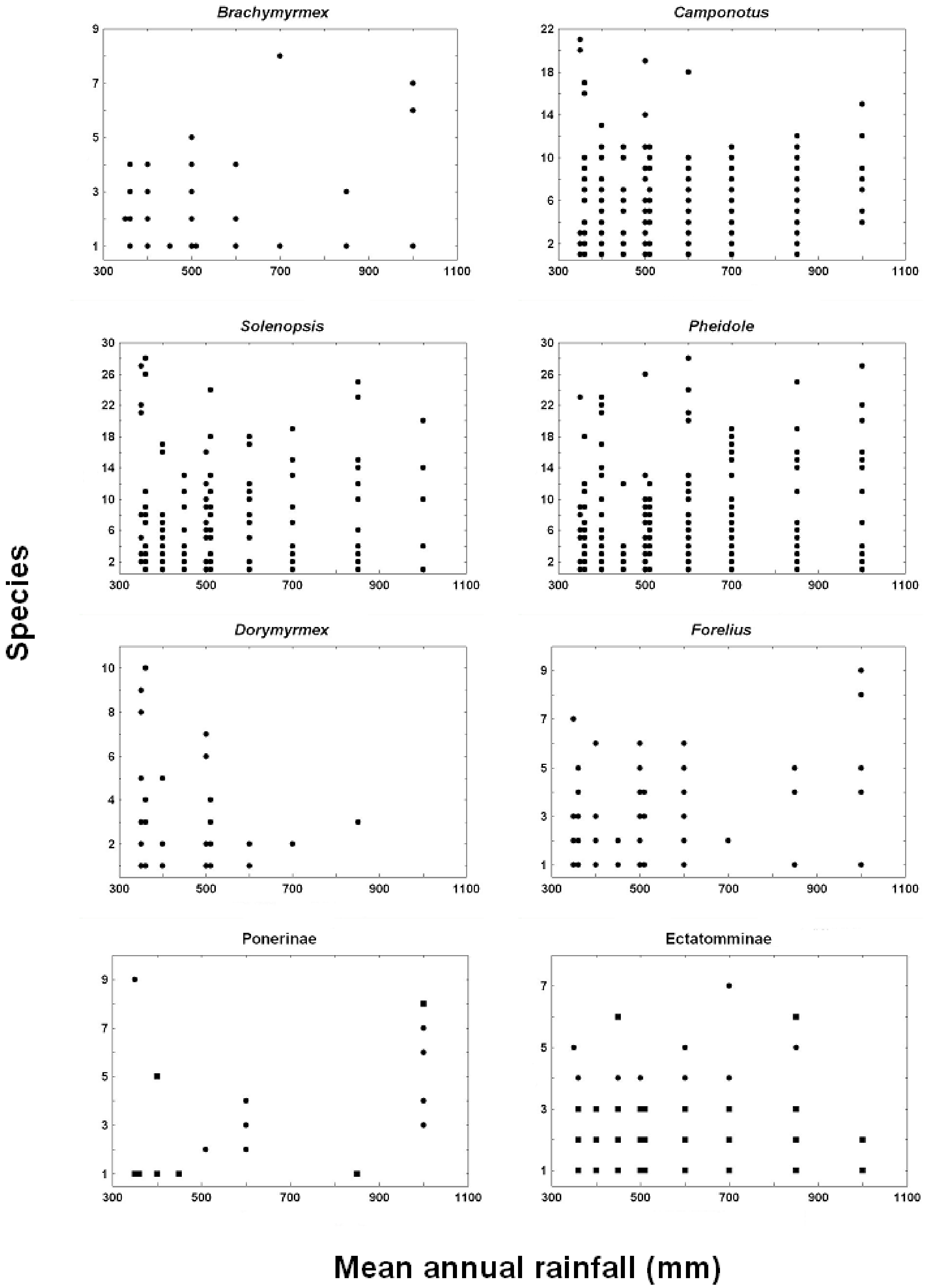
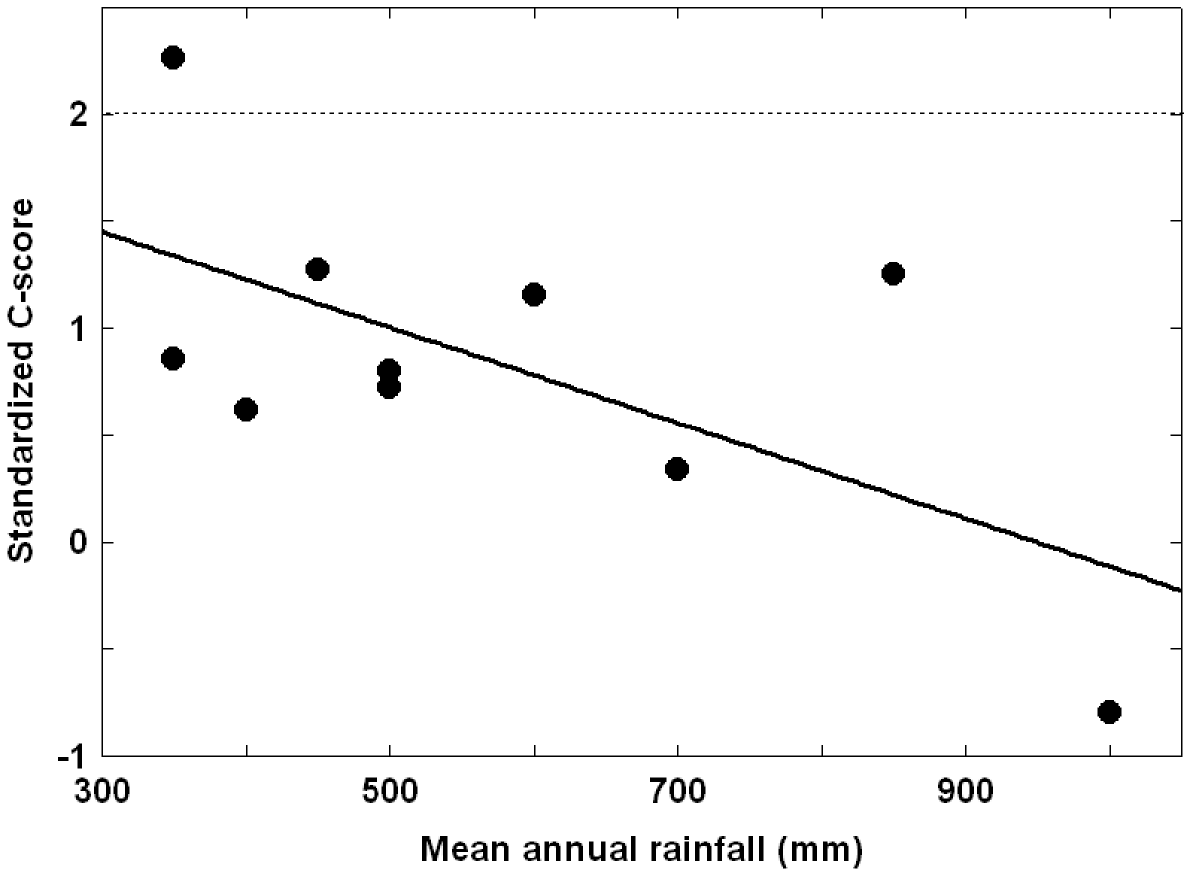

Brachymyrmex
Camponotus
Solenopsis
Pheidole
Dorymyrmex
Forelius
Ponerinae
Ectatomminae
Species
Mean annual rainfall (mm)
300
500
700
900
1100

Figure 3-3


Standardized C-score
2
1
0
-1
300
500
700
900
Mean annual rainfall (mm)

Influence of aridity and soil on the distribution and diversity of ant assemblages and dominant plant species in the Paraguayan dry Chaco.

DELSINNE Thibaut[1, 2], LEPONCE Maurice[1], HERBAUTS Jacques[3], ROISIN Yves[2]

[1]: Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, BELGIUM.

[2]: Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral and Evolutionary Ecology - CP 160/12, 1050 Brussels, BELGIUM.

[3]: Université Libre de Bruxelles, Jardin Jean Massart, Chaussée de Wavre 1850, CP320, 1160 Brussels, BELGIUM.

Abstract

Aim. Ants like plants are sessile organisms and are tractable for conservation purposes. We were interested in studying the influence of aridity and soil on the α and β-diversities of ant assemblages and in comparing the response of dominant plants to these factors.

Location. Ants and plants were sampled along a 400km-long transect covering a mean annual rainfall range of 350-1000mm. Temperature and topography variations were low along this transect located in the Paraguayan dry Chaco.

Methods. Along elementary 200m-long transects, ants were collected by pitfall traps and the abundance of 45 characteristic tree and shrub species was recorded. In complement physicochemical properties of the soil were measured.

Results. Overall, 197 ant species were collected with a median of 39 species per elementary transect. The mean Morisita-Horn index was 0.43 and 0.58 for ants and plants respectively. Ant α-diversity was neither related to aridity nor to edaphic properties. By contrast, the ant composition was more related to soil than to rainfall conditions. Three faunal complexes were observed: one in the most arid and sandy locality, another one in the most humid locality at the border of the wet Chaco, and a third one found in localities with a large range of precipitations and soils. Plants responded even more finely to these factors.

Main conclusions. Our results suggest that, in the Paraguayan dry Chaco, dominant plants appear as a good umbrella group for site selection aimed at species conservation. For ants and even more for plants, soil conditions appear as a more determining factor for species distribution than aridity. Furthermore aridity did not decrease ground-foraging ant diversity.

Keywords

α-diversity, β-diversity, cross-taxon congruency, faunal complementarity, rainfall, soil texture, species richness, surrogate taxa, tropical dry forest.

Under the present context of rapid biodiversity losses and climate changes (Pimm et al., 1995; Thomas et al., 2004), it is urgent to obtain baseline informations about the diversity patterns of organisms and to understand how these patterns are affected by the environment (Gaston, 2000). This necessary knowledge is particularly lacking for invertebrates (New, 1995) despite their central role in ecosystems (Wilson, 1987; Grimaldi and Engel, 2005) and sensitivity to extinction (New, 1995; Chapman and Bourke, 2001; Dunn, 2005). Among insects, ants appear as one of the most informative and tractable group for biodiversity evaluation and monitoring because they are ubiquitous, abundant and ecologically important (Folgarait, 1998; Underwood and Fisher, 2006).

Plants are often advocated as surrogates for reserve selection aimed at species conservation because most terrestrial organisms directly or indirectly depend on plants for food or shelter (Scott et al., 1993; Panzer and Schwartz, 1998). This method is valid only if other taxa respond to environmental changes in ways similar to plant assemblages (Oliver et al., 1998; Su et al., 2004). However invertebrates are generally suspected to respond more finely than plants (Andersen et al., 2004).

Climate is known to be a major factor influencing both the local diversity (= α-diversity) and the variation in species distribution among localities within a region (= β-diversity). Aridity may limit the distribution of species either directly through the physiological tolerance of each species, or indirectly through the control of habitat productivity (Kaspari et al., 2000; Mittelbach et al., 2001; Hawkings et al., 2003; Engelbrecht et al., 2007). Basic knowledge about the influence of aridity on the α and β-diversities of ground-foraging ants is still fragmentary. Studies conducted so far are few, generally concerned subsets of the ant assemblage and sometimes produced opposite results. For instance, species richness of North American seed-eating ants (Davidson, 1977) and of ants from the Namib desert (Marsh 1986) were positively correlated with rainfall while no such relationship was found in Australia (Morton and Davidson, 1988) or in Mongolia (Pfeiffer et al., 2003). An absence of relationship was supposed to be the result of either a thermal gradient running contrarily to the rainfall gradient and counterbalancing the negative effects of aridity (Pfeiffer et al., 2003) or of a high edaphic variability within the study area, leading to the conclusion that rainfall was a poor predictor of the amount of productivity along the study gradient (Morton and Davidson, 1988). These surveys were restricted to deserts and almost nothing is known about the ant response in a wider range of aridity variations.

The aims of the present study are (1) to measure the influence of aridity and soil on the α and β-diversities of ground-foraging ant assemblages along an extended aridity gradient (350-

1000mm mean annual rainfall) in dry Chacoan forests of Paraguay and (2) to test whether ant and plant assemblages presented congruent spatial patterns. In order to discard the influence of temperature, the study was carried out between the 24 and 26°C isolines of mean annual temperature. Because both environmental gradients and dispersal limitation of species can cause a decay of assemblage similarity between increasingly distant localities (Nekola and White, 1999), we tried to control the possible confounding effects of geographic distance by comparing assemblages in localities separated by similar distances and corresponding to contrasted or close rainfall and soil conditions.

METHODS

Study sites and sampling protocol.

The study was conducted between 2001 and 2004 in the Paraguayan dry Chaco plains, which appear as ideal for such study because of their wide rainfall range and flat topography allowing to discard altitudinal influences (Fariña Sánchez, 1973; Ramella and Spichiger, 1989). In an attempt to distinguish the effects of aridity from the effects of geographic distance, localities were sampled at 100km intervals, either along the aridity gradient or perpendicularly, and this spacing was reduced to a 20km interval around locality 7, our reference locality. Overall, 11 localities were sampled (Figure 4-1). Samplings were carried out at the beginning of the wet season, in September-November (Table 4-1), when temperature and rainfall increased. This period was selected in order to avoid the extreme temperatures which may limit the foraging of some Chacoan ant species (Bestelmeyer, 2000; Delsinne et al., 2007), and because at that time the leaf litter depth was maximal. Our reference locality was sampled in 2001, 2002 and 2004 to evaluate inter-annual variations in the local ant composition. The habitats along the gradient were a continuum of xeromorphic forests (Ramella and Spichiger, 1989; Mereles, 2005) except in locality 10 where the vegetation consisted in xeromorphic shrubs ("matorral"). Several soil properties were measured in 8 localities spread along the gradient: pH, concentration of chlorides and soil texture (i.e. relative proportions of sand, silt and clay in the mineral soil fraction); see Appendix 4-1 for detailed protocols.

Ants were sampled along linear transects of 20 pitfall traps spaced at 10m intervals. Three transects, spread along a 1km-long line and separated from each other by 200m, were carried out per locality (except in localities 5 and 7-2002 with 1 and 2 transects, respectively). During the season considered, pitfall traps are the most effective method to document ant diversity in the dry Chaco (Delsinne et al., submitted) and consisted in 70mm-diameter drinking cups, containing water and a drop of detergent, operating for 24 hours. All workers were identified to species or morphospecies. Reproductives were excluded from the analyses because only workers certify the presence of an established colony (Longino et al., 2002). Species occurrences in samples were used as surrogate of abundance because ants are spatially aggregated due to their sociality (Longino, 2000) and because colony sizes may strongly vary among species (Hölldobler and Wilson, 1990).

In parallel to the ant sampling, the abundance of 45 characteristic trees and shrubs (Ramella and Spichiger, 1989; Mereles, 2005) (species list in Appendix 4-2) was determined within a 1 meter strip on either side of the three 200-m long transects at all localities (except in localities 4 and 9 with no vegetation transect and locality 6 with 2 transects).

Influence of aridity (mean annual rainfall) on ant α-diversity.

The Spearman rank order correlation was calculated between ant α-diversity and aridity and between ant α-diversity and edaphic variables. Analyses were restricted to 3 measures of α-diversity, calculated with EstimateS 7.5. (Colwell, 2004):

(1) Chao2 estimation of total local species richness. This nonparametric estimator provides minimum estimates of species richness based on the number of rare species:

$$S_{Chao2} = S_{obs} + Q_1^2/2Q_2$$

where S_{obs} is the local species richness observed, Q_1 the number of species that occur in one sample only (unique species) and Q_2 the number of species that occur in two samples (duplicates) (Colwell and Coddington, 1994). This estimator performs generally well even for "hyperdiverse" organisms, such as insects (Colwell and Coddington, 1994; Leponce et al., submitted);

(2) Rarefied species richness (Coleman method). This approach is necessary when the assemblages compared are sampled with different intensity or success (Gotelli and Colwell, 2001) as it is the case in this study (see Delsinne et al., submitted);

(3) Gini coefficient (i.e. the complement of Simpson index). It is considered as one of the most meaningful and robust diversity measures (Magurran, 2004) and informs on the variance of the species distribution. It is expressed as:

$$\text{Gini coefficient} = 1 - D = 1 - \Sigma p_s^2$$

where D is the Simpson index and p_s the relative frequency of species s (with s =1, 2,..., n) in the locality under study. This index expresses the probability that two ants drawn at random from the study locality belong to different species (Magurran, 2004). It is almost insensitive to species richness but is heavily influenced by the weight of the most abundant species and rises (from 0 to 1) as the assemblage becomes more even.

Ordination of ant and plant assemblages.

To ordinate species assemblages, we used detrended correspondance analysis (DCA), with the Community Analysis Package, version 2.13 (Henderson and Seaby, 2002) Ordinations were also performed after having downweighted the influence of rare species. In this case, the abundance of species rarer than the frequency of the commonest species divided by 5 were downweighted in proportion to their frequency.

Complementarity (= dissimilarity) of ant and plant assemblages.

Complementarity describes the difference between two localities in terms of the species they support (Vane-Wright et al., 1991). The mean of the cell values of a complementarity matrix is a measure of overall β-diversity (Legendre et al., 2005; Tuomisto and Ruokolainen, 2006). The complementarity of ant and plant assemblages between all different locality pairs was expressed by the complement of the NNESS index (Trueblood et al., 1994) which is given by:

$$1\text{- NNESS}_{ij/k} = 1 - \{\text{ESS}_{ij/k} / [(\text{ESS}_{ii/k} + \text{ESS}_{jj/k})/2]\}$$

where $\text{ESS}_{i\ j\ /\ k}$ is the expected number of species shared for random draws (without replacement) of k occurrences from localities i and j. When k is small, the index is highly sensitive to the occurrences of the most frequent species. When k increases, the influence of rarer species is emphasized. If result patterns change when k varies, it could mean that different processes structure the diversity of common and rarer species. Complementarity of ant assemblages was calculated for k=1 (identical to the Morisita-Horn index), k=64 and k=128. Because plant assemblages had less occurrences, complementarity of plants was calculated only for k=1 and k=64. Values range from 0, if localities i and j are not complementary (i.e. they host the same species) to 1, if species collected in the two localities are totally different. The software program BiodivR 1.0 (Hardy, 2005) was used to compute the NNESS index.

To study the variation in β-diversity (sensu Tuomisto and Ruokolainen, 2006) of ants and plants, complementarity results were ordinated by non-metric multidimensional scaling (NMDS). This method performs well to reveal gradient structure (Brehm and Fiedler, 2004). Cluster analyses based on the unweighted arithmetic average (UPGMA) clustering method complemented the NMDS ordinations. In addition, complementarity matrices of ants and plants were compared with matrices derived from geographic distances (km) by Mantel tests (10000 permutations) using the shareware Mantel 2.0 (Liedloff, 1999). A Mantel test was also carried out to compare matrices of assemblage complementarity of ants and of plants. For this analysis, the 24 transects for which both plant and ant data were available were used to compute the complementarity indices and ant data from reference locality 7 were restricted to the 3 transects collected in 2004.

RESULTS

Environmental factors.

Measures of edaphic variables are presented in Table 4-1 (mean soil pH and mean chloride quantities) and Figure 4-2 (soil texture). Mean annual rainfall was strongly correlated with soil texture (i.e. with mean sand: r = -0.766, P=0.021; mean silt: r =0.766, P=0.021 and mean clay proportions: r =0.826, P=0.005, Spearman rank order correlations) but neither with soil pH (r = -0.455, P=0.233) nor with chloride concentrations (r =0.371, P=0.321). However, soil pH was correlated with mean sand (r =0.833, P=0.005) and mean silt proportions (r = -0.833, P=0.005).

Ant diversity.

Overall, 48015 ants corresponding to 5462 occurrences and 197 morphospecies were collected. A single transect of 20 pitfall traps contained between 57 and 263 occurrences (median = 140, n=36) and between 24 and 56 ant species (median = 39, n=36). The number of observed ant species per locality ranged from 36 to 74 (Figure 4-3). After three sampling years at reference locality 7, 101 morphospecies (1705 occurrences) were collected. Generally a species frequent in one locality was also largely distributed within the studied area (Figure 4-4; r = 0.553, P<0.0001, Spearman rank order correlation).

Local ant diversity (i.e. α-diversity) was neither related to mean annual rainfall (Chao2: r =0.087, P=0.764; Gini coefficient: r =0.190, P=0.516; rarefied species richness: r =0.064, P=0.821; Spearman rank order correlations) (Table 4-1; Figure 4-5) nor to edaphic variables. Similar results were obtained when analyses were restricted to assemblages collected during a same sampling year.

Ant and plant distribution.

Three faunal complexes of ground-foraging ants were differentiated along the first DCA axis: (1) the assemblage of locality 1, the wettest locality, (2) the assemblage of locality 10, the driest locality, also characterized by pure sandy soils, and (3) the assemblages of all other localities (Figure 4-6). In addition, collections from 2001 were distinguished by the second DCA axis. It should be noted that collections from 2001 were conducted before or during a series of rainfalls whereas all other collections happened during a dry period. Localities with close aridity and soil conditions (i.e. locality collected perpendicularly to the aridity gradient) possessed similar scores along the first DCA axis (Figure 4-6). At the opposite, localities 10 and 11, with close aridity conditions but contrasted soil texture, harboured different ant assemblages. Scores of ant assemblages extracted from the first DCA axis were highly correlated with both mean annual rainfall and soil texture (Table 4-2). This result remains valid even when localities collected in 2001 were discarded from the DCA analysis.

The abundance of 45 dominant plants was censused along the aridity gradient (Appendix 4-2). Based on these data, DCA ordinations suggested that plants responded to soil texture more finely than ants. In particular locality 3, which had soils with the highest silt proportions (Figure 4-2), possessed a distinct vegetation (Figure 4-7A). When data from this locality were discarded, ordination of plant assemblages along the first DCA axis reflected the aridity and soil texture gradients (Figure 4-7B, Table 4-2).

Similar DCA ordinations were obtained for both ant and plant assemblages after having downweighted the influence of rare species.

Assemblage complementarity of ants and plants.

For both ant and plant assemblages, the NMDS ordinations based on the complement of the NNESS index, whatever the *k* value, led to very similar results to those obtained by DCA ordinations and are therefore not shown here. Detailed complementarity values are provided in Appendix 4-3.

Changes among ant assemblages were correlated with the geographic distance separating them (Mantel tests, 10000 iterations, with *k*=1: r = 0.526, P=0.018; with *k*=64: r =0.543, P=0.018; with *k*=128, r =0.587, P=0.012). A similar result was obtained for plant assemblages when the influence of rare species was emphasized (with k=64: r = 0.560, P=0.010) but no correlation was found when the influence of frequent species was accentuated (with *k*=1: r = 0.325, P= 0.116).

Overall, patterns of assemblage complementarity of ants and plants were congruent, showing that these organisms responded globally to the same underlying gradient (Mantel test, 10000 iterations, with *k*=1: r =0.616, P=0.031; with k=64: r=0.859; P=0.0001). Nevertheless, plant and ant assemblages clustered differently (Figure 4-8). As for DCA ordinations, the main difference concerned locality 3, which was very distinctive in terms of vegetation but which had an ant assemblage similar to other localities situted between the extremes of the geographic transect.

Within the study region, β-diversity was higher for plants than for ants when dominant species were emphasized: means of the complementarity indices with *k*=1 were 0.43 and 0.58

for ants and plants respectively (t-test: t=-2.464, *df*=70, P=0.016). However, the difference was not significant when the importance of rarer species was accentuated: with *k*=64, means of the complementarity indices were 0.41 and 0.46 for ants and plants respectively (t= -1.383, *df*=70, P=0.171).

DISCUSSION

Unexpectedly, local species richness (either rarefied or extrapolated) and Gini coefficient did not decrease with aridity. This result does not support the hypothesis predicting that aridity will limit species richness through a restriction of the habitat productivity (Kaspari et al., 2000; Hawkings et al., 2003). It has been previously suggested that rainfall effects on habitat productivity may be balanced by edaphic conditions (Morton and Davidson, 1988). For instance, sandy soils retain little rainfall water and have a low ability to keep chemicals and nutrients in a form available to plants (Brady and Weil, 1999). As a consequence, rainfall may be a poor predictor of the habitat productivity when soil conditions vary substantially (Morton and Davidson, 1988). Here, no relationship was found between soil texture and α-diversity. Moreover in our study, the driest localities were probably also the less productive since rainfall was negatively correlated with the proportion of sand in the mineral soil fraction. Salt excess in the soil is another potential negative factor for plant productivity (Brady and Weil, 1999). In the Chaco biome, past marine intrusions have led to deposits of salty sediments (Spichiger, 2004) and saline soils are therefore prevailing in this area (Pennington, 2000). Nevertheless, quantities of chlorides were not correlated with ant α-diversity.

The independency of ant α-diversity to aridity may be helped by physiological, behavioral and/or anatomical adaptations. For instance, the ability of ground-foraging ants to remain inactive and/or to enter into diapause during harsh environmental conditions (Hölldobler and Wilson, 1990) probably facilitates their existence in arid and semi-arid environments. In this direction, cycles of ant colony activities in the Chihuahua desert are intimately linked to rainfall variations (Whitford, 1978). Ants only forage during seasons of higher primary productivity and higher availability of food resources. Moreover, numerous ant species are able to store nutrients in the form of fats which can be used to overcome periods of food scarcity (Tschinkel, 1987; Yang, 2006). We suspect that some Chacoan ants possess this ability but further studies are necessary to confirm this hypothesis. The fact that, in the Paraguayan dry Chaco, the majority of ground-foraging ants shelter in subterranean nests (Delsinne, pers. obs.) also facilitates to overcome drought periods because variations of soil temperature and humidity are generally less marked than above ground (Délye, 1967; Tschinkel, 1987; Hölldobler and Wilson, 1990). Therefore, the primary effect of aridity through physiological stress may be less pronounced for ground-foraging ants than for other organisms unable to remain inactive for prolonged period and/or to shelter underground.

Moreover, interspecific competition is generally lower at sites with high environmental stress (Andersen, 1995, 1997), facilitating species coexistence (Cerdá et al., 1998; Retana and Cerdá, 2000). For instance, we observed at reference locality 7, a set of trade-offs between species food discovery and food dominance abilities, on the one hand, and between thermal tolerance and competitive dominance, on the other hand (Delsinne et al., 2007). This set of trade-offs makes easier the food partitioning between ant species and thus their coexistence.

Although α-diversity was not related to rainfall, the aridity influence on the ant assemblage composition was globally observed. Changes were not gradual but rather split into three faunal complexes. The first one was found in the most humid locality (locality 1; 1000mm of mean annual rainfall) situated at the border of the wet Chaco (1000-1400mm) (Ramella and Spichiger, 1989; Mereles 2005). It is possible that mesoxeromorphic forests of the wet Chaco shelter a specific ant fauna which influenced the species composition of this locality. A second faunal complex was in the driest locality (locality 10; 350mm), covered by shrubs and with sandy soils. Locality 10 belongs to a relictual dune system indicative of a drier climate in former times in this area (Pennington et al., 2000). The singularity of this ant fauna could be caused by edaphic factors and/or historical events. The last faunal complex was found in localities with a large range of rainfall and soil conditions.

Species frequent at a local scale were also generally widespread. This "abundance-occupancy" relationship is documented for a large set of organisms and is considered as one of the most fundamental in ecology (Gaston et al., 2000). DCA ordinations were similar after having downweighted the influence of rare species or not, and NMDS ordinations were relatively similar for all *k* values of the complementarity NNESS indices studied. These results suggest that, globally, similar processes structured the distribution of both abundant and rarer species.

In the literature, three principal and nonexclusive hypotheses are currently proposed to explain variations in β-diversity (Legendre et al. 2005; Tuomisto and Ruokolainen, 2006). First, species composition may be mainly determined by biological interactions. In this case, assemblage composition is expected to be uniform over large areas. Second, species composition fluctuates in a random, autocorrelated way (neutral theory of Hubbell, 2001) and is thus linked to geographic distance mainly. Third, species composition is under environmental control. Here, ground-foraging ants species were not randomly distributed among the 11 localities studied. Changes in ant assemblage composition were related to geographic distance but it is probably because this factor was strongly collinear with aridity and soil texture. Soil texture appeared particularly important for ants since distant localities with close soil texture but contrasted aridity conditions supported relatively similar ant assemblages (e.g. locality 11 close to localities 5 and 6). At the opposite, close localities with contrasted edaphic conditions supported distinct assemblages (e.g. locality 10 contrasting with localities 9 and 8). Studies investigating the influence of soil texture on ant distribution are scarce but have demonstrated that this factor is particularly important for soil-nesting species (Johnson, 1992; 2000, Bestelmeyer and Wiens, 2001). Soil texture determines physicochemical soil properties, including water retention and thermal conductivity (Johnson, 1992; Brady and Weil, 1999), which are two determinant factors for the survival of underground ant colonies. Mechanical soil properties and ant digging abilities may also determine in which kind of soil nests are established. At last, soil texture may affect ant species composition indirectly through vegetation characteristics.

Within the Paraguayan dry Chaco, assemblage complementarity of ants and dominant plant species were globally correlated but ordinations suggested that plants responded more finely to soil conditions than ants. As a consequence, distinct vegetations can support similar ant assemblages (e.g. localities 3 and 11). Among the localities studied, higher β-diversity values were found for plants than for ants but the difference was not significant when the importance of rare species was emphasized. These results corroborate the findings of Englisch et al. (2005) that for coarse spatial scale studies, ants did not yield much more additional informations than plant assemblages. Moreover, results of reference locality 7 demonstrated that the sampling efficacy to document ant assemblages is influenced by recent precipitation events (Delsinne et al., submitted). Plants appear to be a more reliable taxon to define conservation priorities.

In conclusion, our results did not support the productivity limitation hypothesis but suggested that β-diversity of ground-foraging ant assemblages was affected by environmental conditions, mainly soil texture. Plants seem to constitute a relevant umbrella taxon for ant assemblages since they respond more finely to edaphic conditions.

ACKNOWLEDGMENTS

We thank John Kochalka, Bolivar Garcete-Barrett, Victor Filippi, Jorge Jara, César Bénilez, Carlos Aguilar Julio from the "Museo Nacional de Historia Natural del Paraguay", the guards from Teniente Enciso National Park and Véronique Olivier for their help during fieldwork or administrative procedures. Fatima Mereles and Frieda Billiet contributed to the plant identifications and Wolff Gruber advised during soil analyses. This study was made possible by financial support from the “Fonds pour la Formation à la Recherche dans l’Industrie et l’Agriculture” and the "Fonds de la Recherche Scientifique" (FNRS, Belgium).

REFERENCES

Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. J. Biogeogr. 22: 15-29.

Andersen, A.N., 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. J. Biogeogr. 24: 433-460.

Andersen, A.N., Fisher, A., Hoffmann, B., Read, J.L., Richards, R., 2004. Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecology 29: 87-92.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Anim. Ecol. 69: 998-1009.

Bestelmeyer, B.T., Wiens, J.A., 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. Ecological Applications 11: 1123-1140.

Brady, N.C., Weil, R.R., 1999. The Nature and properties of soils, twelfth edition. Prentice Hall, Upper Saddle River, New Jersey. 881 pp.

Brehm, G., Fiedler, K., 2004. Ordinating tropical moth ensembles from an elevational gradient: a comparison of common methods. Journal of Tropical Ecology 20: 165-172.

Cerdá, X., Retana, J., Cros, S., 1998. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12, 45-55.

Chapman, R.E., Bourke, A.F.G., 2001. The influence of sociality on the conservation biology of social insects. Ecology Letters 4: 650-662.

Colwell, R.K. 2004. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL: <purl.oclc.org/estimates>.

Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. R. Soc. Lond. B 345: 101-118.

Davidson, D.W., 1977. Species diversity and community organization in desert seed-eating ants. Ecology 58: 711-724.

Delsinne, T., Roisin, Y., Leponce, M., 2007. Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage. J. Arid Environ. 71: 29-44.

Delsinne T., Leponce M., Theunis L., Braet Y and Roisin Y. Rainfall influence the ant sampling in dry forests. Biotropica, under revision.

Délye, G., 1967. Physiologie et comportement de quelques fourmis (Hym. Formicidae) du Sahara en rapport avec les principaux facteurs du climat. Insectes Sociaux 4: 323-338.

Dunn, R.R., 2005. Modern insect extinctions, the neglected majority. Conservation Biology 19: 1030-1036.

Engelbrecht, B.M.; Comita, L.S.; Condit, R.; Kursar, T.A.; Tyree, M.T.; Turner, B.L.; Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80-82.

Englisch, T., Steiner, F.M., Schlick-Steiner, B.C., 2005. Fine-scale grassland assemblage analysis in Central Europe: ants tell another story than plants (Hymenoptera: Formicidae; Spermatophyta). Myrmecologische Nachrichten 7: 61-67.

Fariña Sánchez, T., 1973. The climate of Paraguay. pp. 33–38. In: Gorham, J.R. (ed.). Paraguay: ecological essays. Academy of the Arts and Sciences of the Americas, Miami, FL.

Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7: 1221-1244.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405: 220-227.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M., Lawton, J.H., 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37: 39-59.

Gotelli, N. J., Colwell, R. K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Grimaldi, D., Engel, M.S., 2005. Evolution of the insects. Cambridge University Press, Cambridge. 755pp.

Hardy, O. 2005. BiodivR 1.0. A program to compute statistically unbiases indices of species diversity within samples and species similarity between samples using rarefaction principles. Université Libre de Bruxelles.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 24: 3105-3117.

Henderson, P.A., Seaby, R.M.H., 2002. Capacity Analysis Package. Pisces Conservation Ltd. http://www.irchouse.demon.co.uk/

Hölldobler, B., Wilson, E.O., 1990. The Ants. Cambridge: Bellknap Press.732 pp.

Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey. 375pp.

Johnson, R.A., 1992. Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. Oecologia 89:118-124.

Johnson, R.A., 2000. Habitat segregation based on soil texture and body size in the seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus.* Ecological Entomology 25: 403–412.

Kaspari, M., O'Donnell, S., Kercher, J.R., 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. The American Naturalist 155: 280-293.

Legendre, P., Borcard, D., Perres-Neto, P.R., 2005. Analyzing β diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75: 435-450.

Legendre, P., Legendre, L., 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam. 853 pp.

Liedloff, A., 1999. Mantel 2.0. Mantel nonparametric test calculator.

Longino, J.T. 2000. What to do with the data ? Pages 186-203 in D., Agosti, J.D., Majer, L.E., Alonso, and T.R., Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington DC.

Longino, J.T., J., Coddington, and R.K., Colwell. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology 83: 689-702.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell Publishing. 256 pp.

Marsh, A.C.,1986. Ant species richness along a climatic gradient in the Namib Desert. Journal of Arid Environments 11: 235–241.

Mereles, M.F., 2005. Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay. Rojasiana 6: 5-48.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82: 2381-2396.

Morton, S.R., Davidson, D.W., 1988. Comparative structure of harvester ant communities in arid Australia and North America. Ecological Monographs 58: 19-38.

Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26: 867-878.

New, T.R., 1995. An introduction to invertebrate conservation biology. Oxford University Press, Oxford. 194pp.

Oliver, I., Beattie, A.J., York, A., 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. Conservation Biology 12: 822-835.

Panzer, R., Schwartz, M.W., 1998. Effectiveness of a vegetation-based approach to insect conservation. Conservation Biology 12: 693-702.

Pennington, T.R., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27: 261-273.

Pfeiffer, M., Chimedregzen, L., Ulykpan, K., 2003. Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. Journal of Biogeography 30: 1921-1935.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M. 1995. The future of biodiversity. Science 269: 347–350.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639-680.

Retana, J., Cerdá, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123, 436-444.

Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Croves, G., Anderson, H., Caicco, S., D'erchia, F., Edwards Jr., T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123. 41 pp.

Spichiger, R., Calenge, C., Bise, B., 2004. Geographical zonation in the Neotropics of tree species characteristic of the Paraguay-Paraná Basin. Journal of Biogeography 31: 1489-1501.

Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conservation Biology 18: 167-173.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, E., 2004. Extinction risk from climate change. Nature 427: 145-148.

Trueblood, D.D., Gallagher, E.D., Gould, D.M.,. 1994. Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnology and Oceanography 39: 1440-1454.

Tschinkel, W.R., 1987. Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. Insectes Sociaux 34: 143-164.

Tuomisto, H., Ruokolainen, K., 2006. Analyzing or explaining β diversity? Understanding the targets of different methods of analysis. Ecology 87: 2697-2708.

Underwood, E.C., Fisher, B.L., 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132: 166-182.

Vane-Wright, R.I., Humphries, C.J., Williams, P.H., 1991. What to protect?—Systematics and the agony of choice. Biological Conservation 55: 235-254.

Whitford, W.G. 1978. Structure and seasonal activity of Chihuahua Desert ant communities. Insectes Sociaux 25: 79-88.

Wilson, E.O., 1987. The little things that run the world (the importance and conservation of invertebrates). Conservation Biology 1: 344-346.

Yang, A.S., 2006. Seasonality, division of labor, and dynamics of colony-level nutrient storage in the ant *Pheidole morrisi*. Insectes Sociaux 53: 456-462.

Table and figure legends

Table 4-1:
Environmental variables and measures of α-diversity for the 11 localities studied. Locality numbers refer to Figure 4-1. Locality 7 was sampled in 2001, 2002 and 2004.

Table 4-2:
Spearman rank order correlation coefficients (r) between environmental variables and locality scores extracted from the first and second axes of DCA ordinations. Significant correlations ($P<0.05$) are in bold.

Figure 4-1:
Study localities distributed along the aridity gradient of the Paraguayan Chaco plains. Lines are isolines of mean annual rainfall (mm). Localities are: 1: Rio Verde, 2: Cruce de Los Pioneros, 3: Mariscal Estigarribia, 4: Garrapatal, 5: Estancia María Vicenta, 6: Teniente Enciso National Park-Northern side, 7: Teniente Enciso N. P.-Southern side 8: Siracua, 9: Nueva Asunción, 10: Fortín Mister Long, 11: Fortín Mayor Infante Rivarola.

Figure 4-2:
Soil texture along the aridity gradient. Proportions of sand, silt and clay in the soil mineral fraction of 8 localities were measured (n=9 soil samples per locality). See Appendix 4-1 for further protocol details. Number inside triangles correspond to locality numbers on Figure 4-1.

Figure 4-3:
Occurrence-based rarefaction curves (Coleman method) for ground-foraging ants at all 11 localities studied. Locality numbers refer to Figure 4-1. Data from the three sampling years of reference locality 7 were computed separately and are represented by dotted curves. Vertical line correspond to the rarefied number of occurrences used to compare the 13 samplings (204 occurrences).

Figure 4-4:

Relationship between the mean local numerical dominance and the geographic extension of the 197 ground-foraging ants collected in 11 localities of the Paraguayan Chaco. The geographic extension is the number of kilometers separating the two most distant localities where each species was sampled. The mean local numerical dominance is the mean percentage of pitfall traps recording each ant species, counting only localities where the species was present.

Figure 4-5:

Relationship between the rarefied number of ant species and the mean annual rainfall along the aridity gradient. Empty symbols correpond to the three sampling years at reference locality 7.

Figure 4-6:

Detrended correspondence analysis (DCA) of the ant assemblages at 11 localities of the Paraguayan dry Chaco. Locality numbers refer to Figure 4-1. The three sampling years of reference locality 7 were computed separately. Ground-foraging ants were sampled along three 200m-long transects (letters a, b and c), except localities 7-2002 and 5 with 1 and 2 transects respectively. The eigenvalues of the first and second axes are 0.391 and 0.175 respectively. The corresponding lengths of the gradients, expressed in standard deviation units of species turnover (see Legendre and Legendre, 1998), are 3.8 SD and 1.9 SD respectively. Three faunal complexes are distinguished by the first DCA axis. In addition, ants collected during a rainy period are separated by the second DCA axis (see text).

Figure 4-7:

Detrended correspondence analysis (DCA) of the plant assemblages at 9 localities of the Paraguayan dry Chaco. Locality numbers refer to Figure 4-1. Plants were surveyed along three 200m×2m transects per locality (letters a, b and c), except locality 6 with 2 transects. Four plant groups are distinguished. Silty soils of locality 3 possess a distinct vegetation (7A). Data from this locality were subsequently discarded from the analysis in order to reveal the three other groups reflecting the influences of aridity and soil texture (7B) (see text).

The eigenvalues of the first and second axes of the ordinations are 0.603 and 0.338 respectively (7A) [0.557 and 0.201 (7B)]. The corresponding lengths of the gradients are 4.4 SD and 2.2 SD respectively (7A) [3.8 and 2.1 (7B)].

Figure 4-8:

Complementarity of plant (A) and ant (B) assemblages illustrated by cluster analyses (UPGMA clustering) based on the complement of the NNESS index with *k*=1. Locality numbers refer to Figure 4-1.

Table 4-1

Locality	Sampling period	Latitude °S	Longitude °W	Soil pH (mean ± SD)	Chlorides (µg/g of soil) (mean ± SD)	Chao2	Rarefied species richness*	Gini coefficient
1	15-16 Oct. 2003	23.21785	59.20294	6.1 ± 0.4	394.69 ± 287.04	73.2 ± 12.2	47.0 ± 2.4	0.95
2	09-10 Oct. 2003	22.69014	59.77186	5.7 ± 0.4	640.78 ± 481.81	87.3 ± 14.5	54.1 ± 2.9	0.97
3	05-06 Oct. 2003	21.99097	60.63583	5.3 ± 0.2	347.36 ± 151.99	75.7 ± 9.8	48.8 ± 2.8	0.94
4	05-06 Nov. 2001	21.44661	61.48749	-	-	91.2 ± 12.2	53.1 ± 3.1	0.97
5	27-28 Sept. 2004	20.9213	61.39321	6.4 ± 0.8	338.85 ± 110.90	39.6 ± 4.8	35.6 ± 0.6	0.96
6	24-25 Sept. 2003	21.13747	61.50945	5.7 ± 0.4	300.18 ± 235.04	99.3 ± 45.0	44.3 ± 2.6	0.94
7-2001	04-05 Nov. 2001	21.2059	61.65762	-	-	89.6 ± 19.3	45.9 ± 2.8	0.96
7-2002	18-19 Sept. 2002	21.2059	61.65762	-	-	81.3 ± 9.9	50.3 ± 2.9	0.96
7-2004	23-24 Sept. 2004	21.2059	61.65762	-	-	96.2 ± 15.8	49.8 ± 3.2	0.95
8	20-21 Sept. 2003	21.04616	61.75151	5.8 ± 0.7	329.09 ± 128.21	47.7 ± 5.9	39.2 ± 1.5	0.93
9	01-02 Nov. 2001	20.69528	61.92877	-	-	86.2 ± 10.5	57.5 ± 2.8	0.97
10	17-18 Sept. 2003	20.60386	62.05053	7.0 ± 0.3	162.02 ± 175.75	80.9 ± 26.1	45.9 ± 1.6	0.96
11	01-02 Oct. 2004	21.67146	62.41312	6.1 ± 0.4	722.47 ± 618.14	72.2 ± 4.5	52.3 ± 2.9	0.95

* Rarefied to 204 occurrences (Coleman method).

Table 4-2

	Mean annual rainfall (mm)	Mean sand proportion	Mean silt proportion	Mean clay proportion	Mean pH	Mean chloride quantity
<u>Ground-foraging ants:</u>						
DCA axis 1 of Fig. 4-5	r = 0.604	r = -0.784	r = 0.763	r = 0.837	r = -0.3	r = 0.249
	P <0.001 (n=36)	**P <0.001** (n=22)	**P <0.001** (n=22)	**P <0.001** (n=22)	P = 0.172 (n=22)	P = 0.271 (n=21)
DCA axis 2 of Fig. 4-5	r = 0.100	r = -0.220	r = 0.237	r = 0.240	r = 0.313	r = -0.065
	P = 0.559 (n=36)	P = 0.319 (n=22)	P = 0.285 (n=22)	P = 0.278 (n=22)	P = 0.154 (n=22)	P = 0.776 (n=21)
<u>Dominant plant species (locality 3 included)</u>						
DCA axis 1 of Fig. 4-7A	r = -0.554	r = 0.896	r = -0.890	r = -0.684	r = 0.647	r = -0.154
	P = 0.004 (n=26)	**P <0.001** (n=23)	**P <0.001** (n=23)	**P <0.001** (n=23)	**P <0.001** (n=23)	P = 0.488 (n=22)
DCA axis 2 of Fig. 4-7A	r = 0.390	r = -0.227	r = 0.208	r = 0.438	r = 0.261	r = 0.193
	P = 0.049 (n=26)	P = 0.293 (n=23)	P = 0.335 (n=23)	**P = 0.037** (n=23)	P = 0.226 (n=23)	P = 0.383 (n=22)
<u>Dominant plant species (locality 3 discarded):</u>						
DCA axis 1 of Fig. 4-7B	r = -0.662	r = 0.956	r = -0.923	r = -0.902	r = 0.494	r = -0.447
	P <0.001 (n=23)	**P <0.001** (n=20)	**P <0.001** (n=20)	**P <0.001** (n=20)	**P = 0.026** (n=20)	P = 0.054 (n=19)
DCA axis 2 of Fig. 4-7B	r = -0.086	r = -0.073	r = 0.044	r = 0.171	r = 0.190	r = 0.204
	P = 0.692 (n=23)	P = 0.753 (n=20)	P = 0.846 (n=20)	P = 0.464 (n=20)	P = 0.414 (n=20)	P = 0.393 (n=19)

Figure 4-1

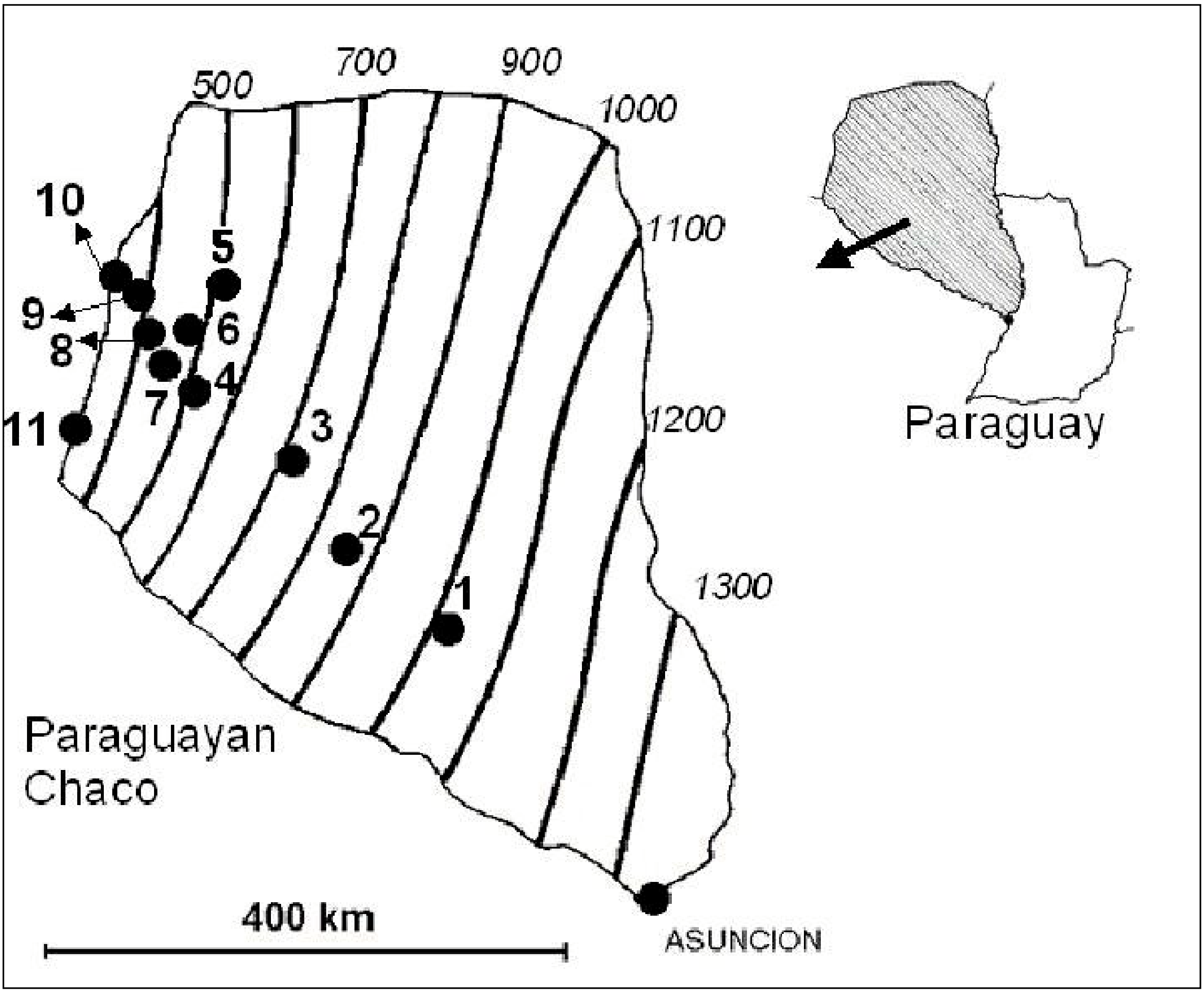

500
700
900
1000
1100
1200
1300
10
9
8
5
6
7
4
11
3
2
1
Paraguay
Paraguayan Chaco
400 km
ASUNCION

Figure 4-2

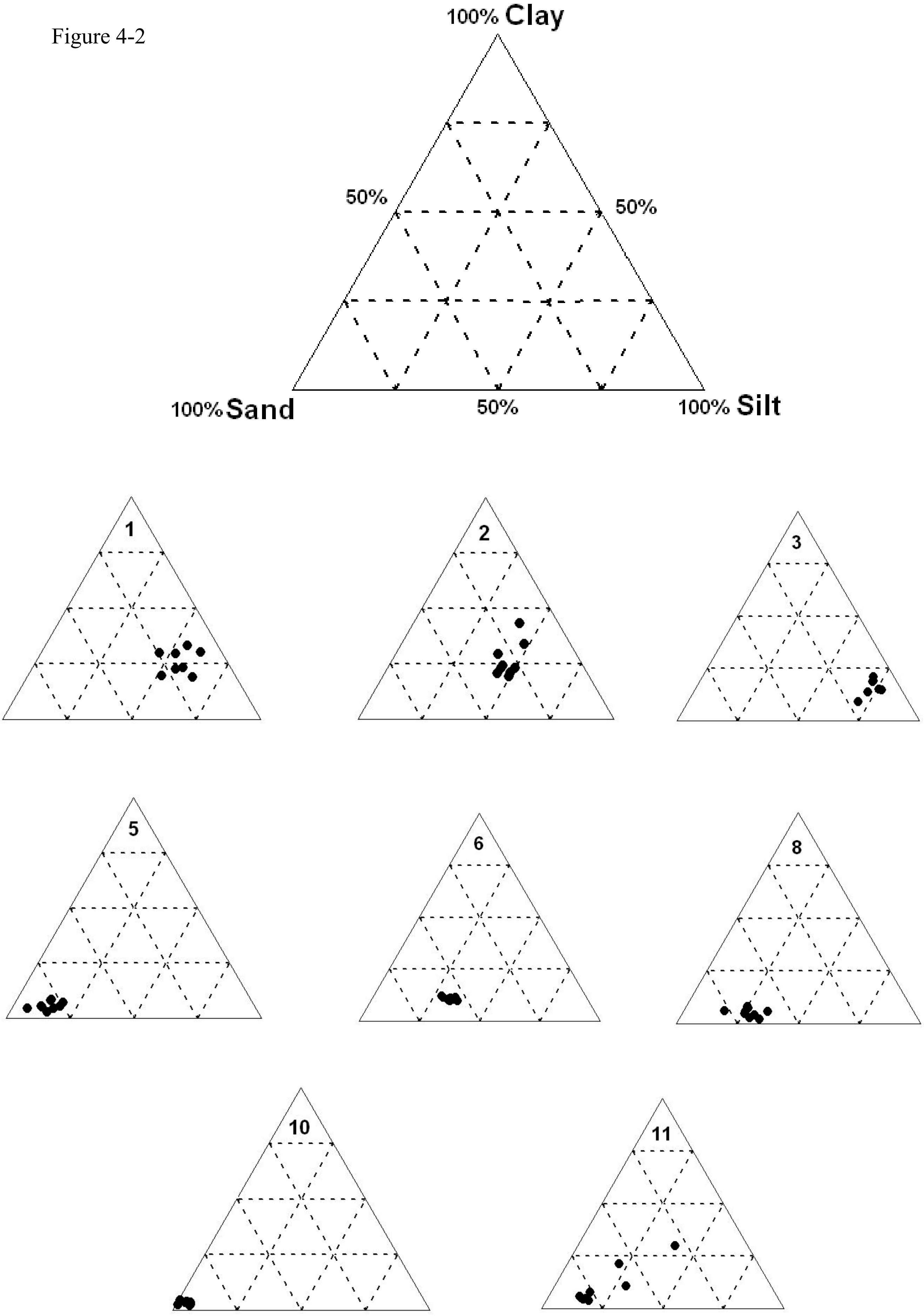


Figure 4-3

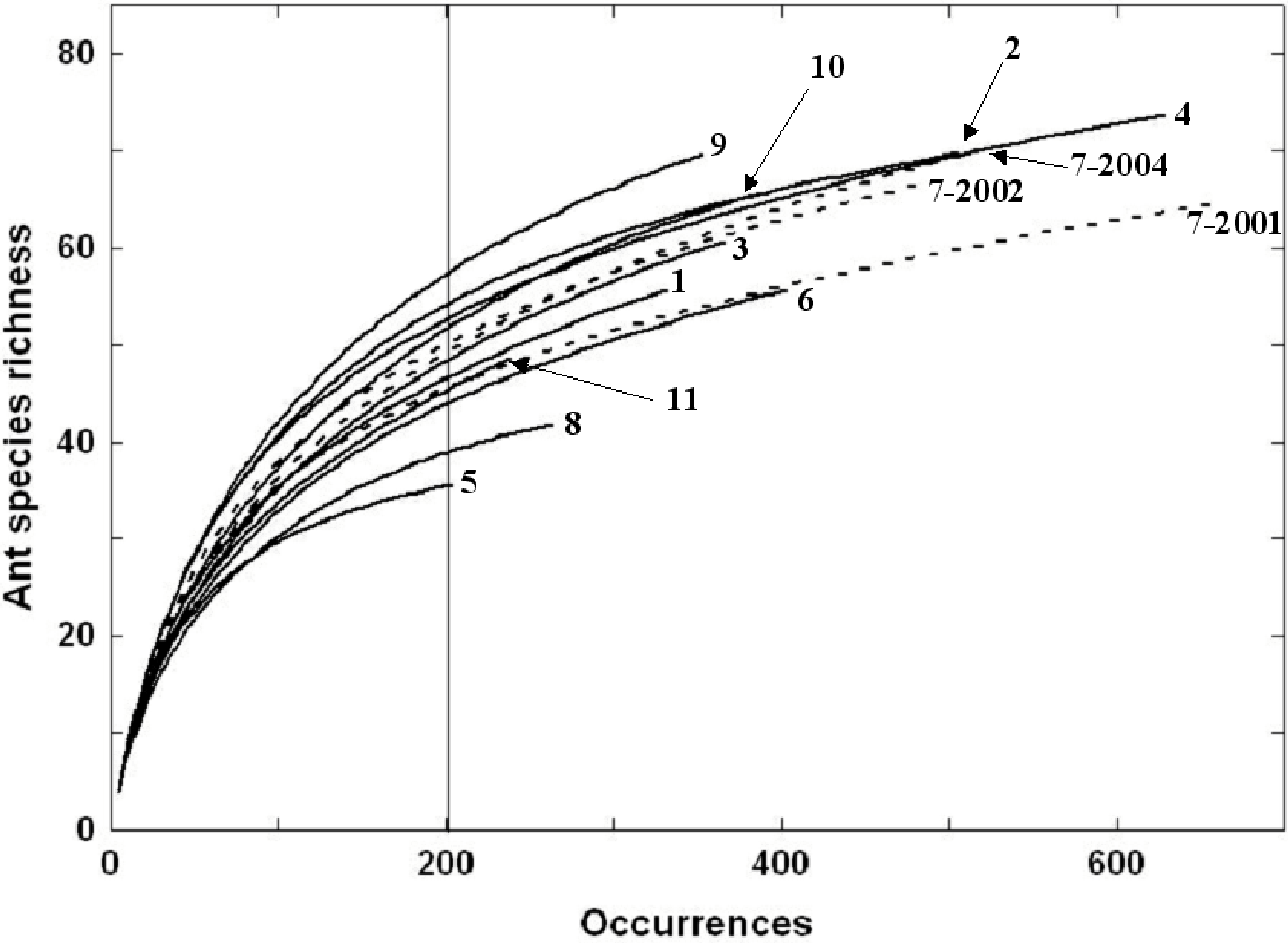

Ant species richness
Occurrences
0
20
40
60
80
0
200
400
600
9
10
2
4
7-2004
7-2002
7-2001
3
1
6
11
8
5

Figure 4-4

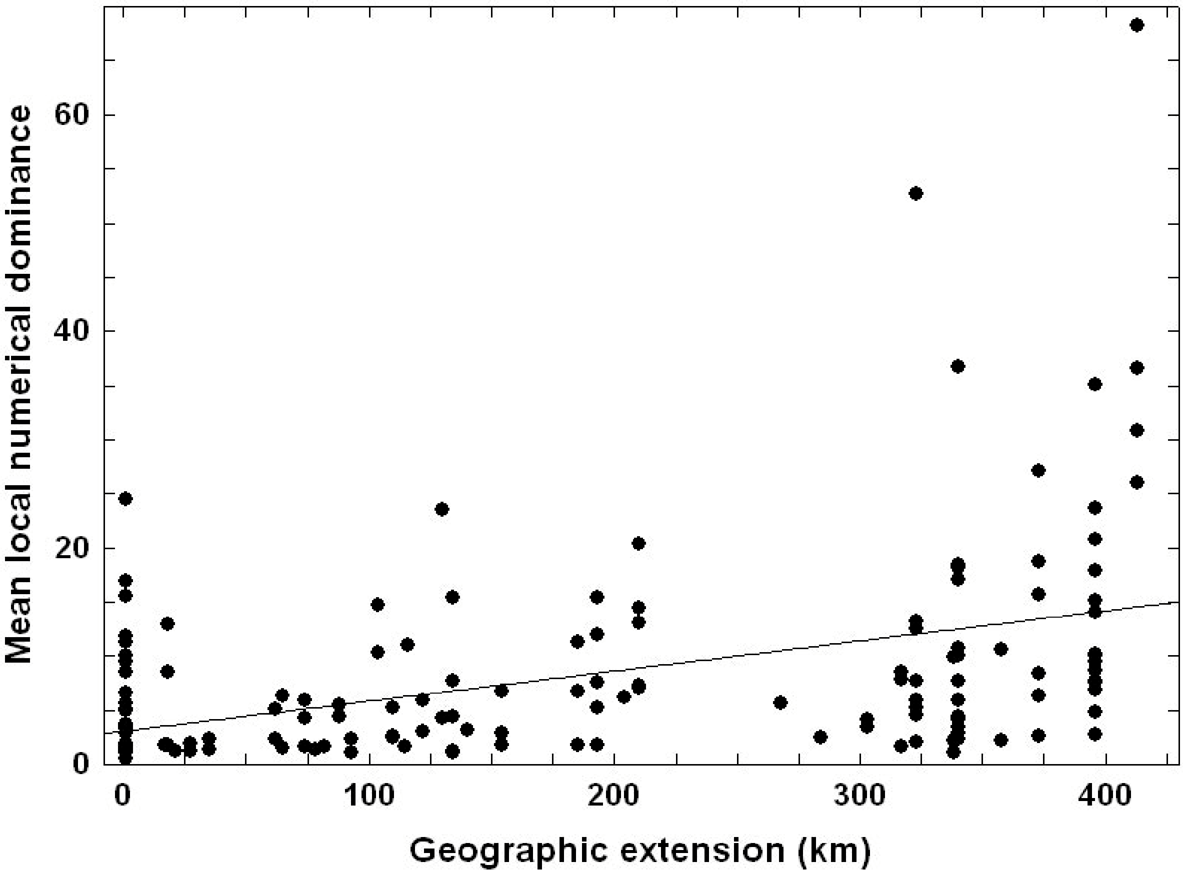

Mean local numerical dominance
60
40
20
0
0
100
200
300
400
Geographic extension (km)

Figure 4-5

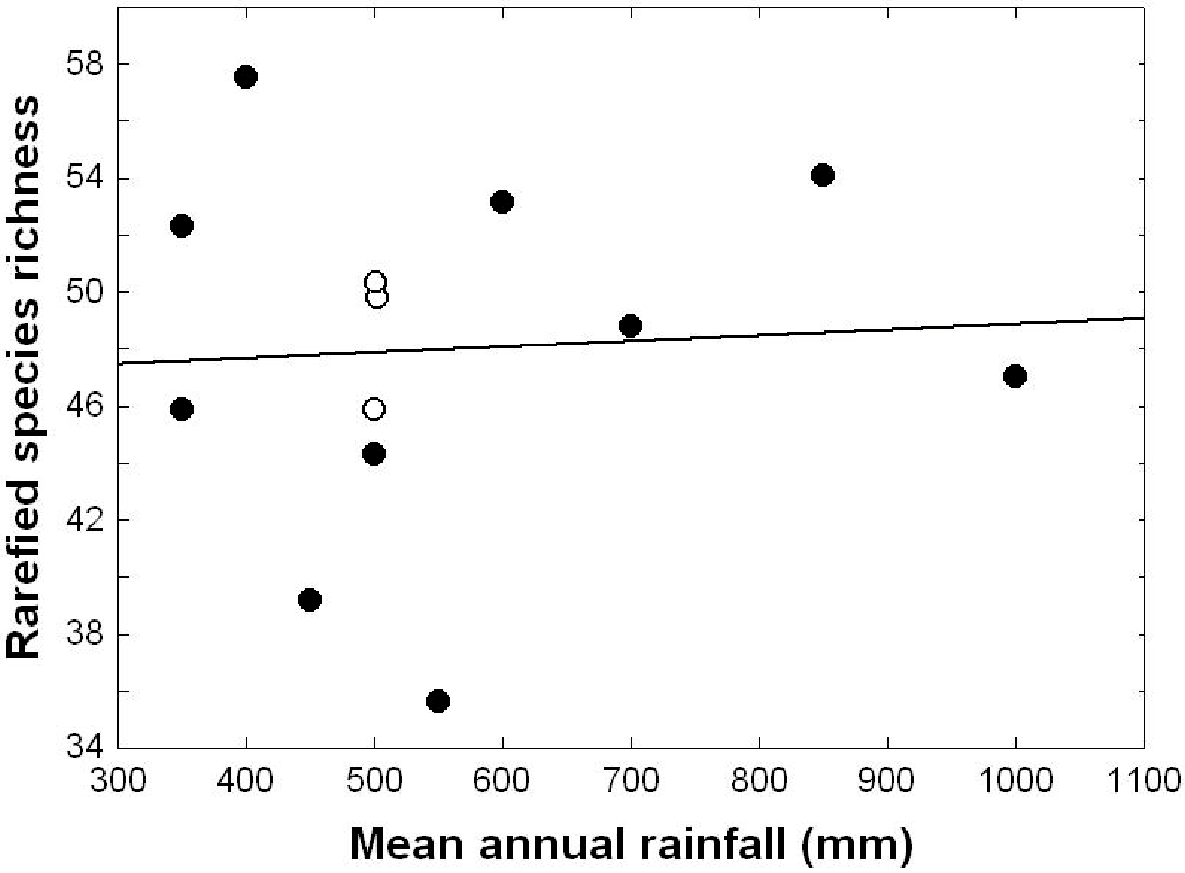

Rarefied species richness
58
54
50
46
42
38
34
300
400
500
600
700
800
900
1000
1100
Mean annual rainfall (mm)

Figure 4-6

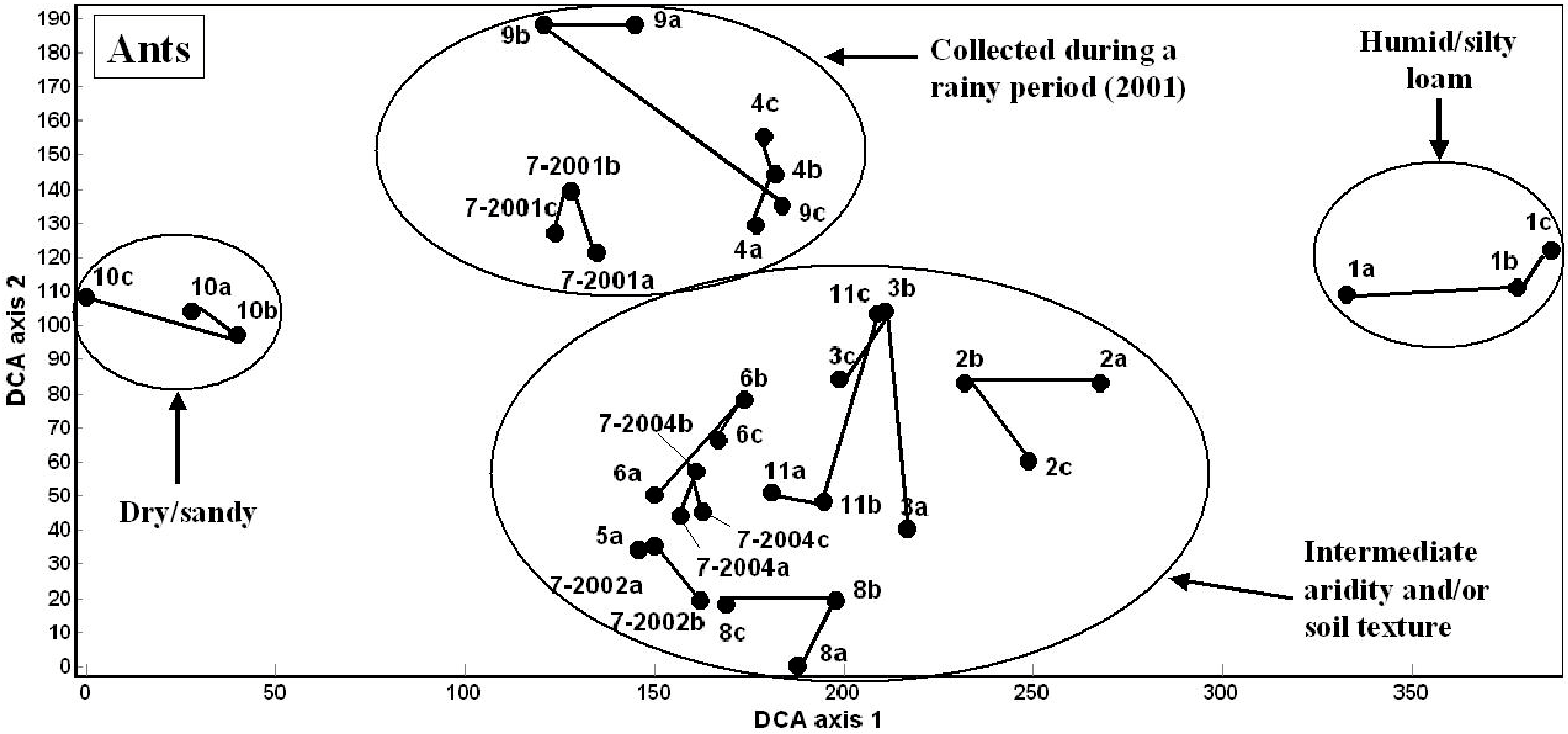

Ants
Collected during a rainy period (2001)
Humid/silty loam
Dry/sandy
Intermediate aridity and/or soil texture
DCA axis 1
DCA axis 2
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
0
50
100
150
200
250
300
350
9a
9b
9c
4a
4b
4c
7-2001a
7-2001b
7-2001c
10a
10b
10c
1a
1b
1c
2a
2b
2c
3a
3b
3c
11a
11b
11c
6a
6b
6c
5a
7-2004a
7-2004b
7-2004c
7-2002a
7-2002b
8a
8b
8c

Figure 4-7

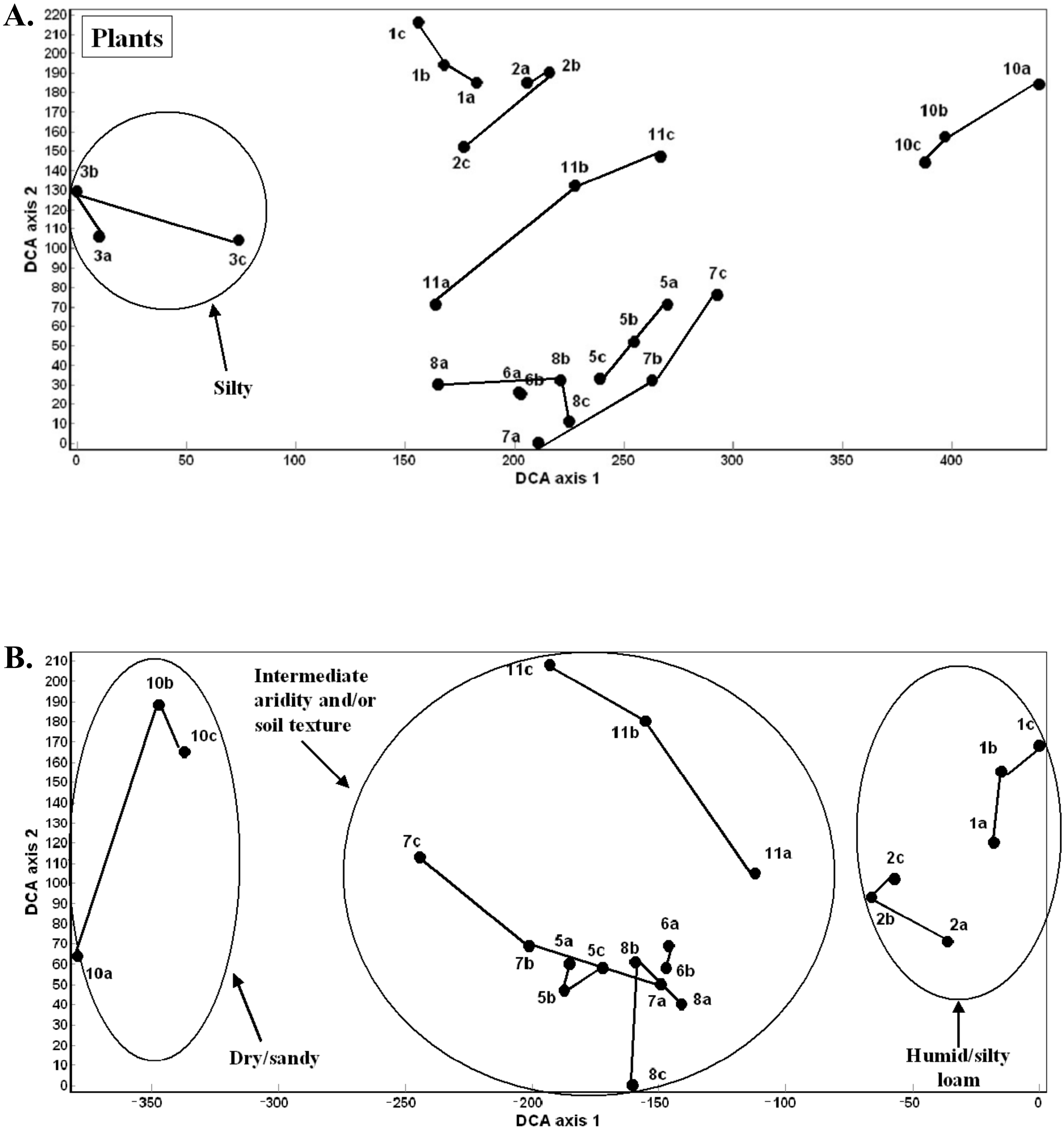
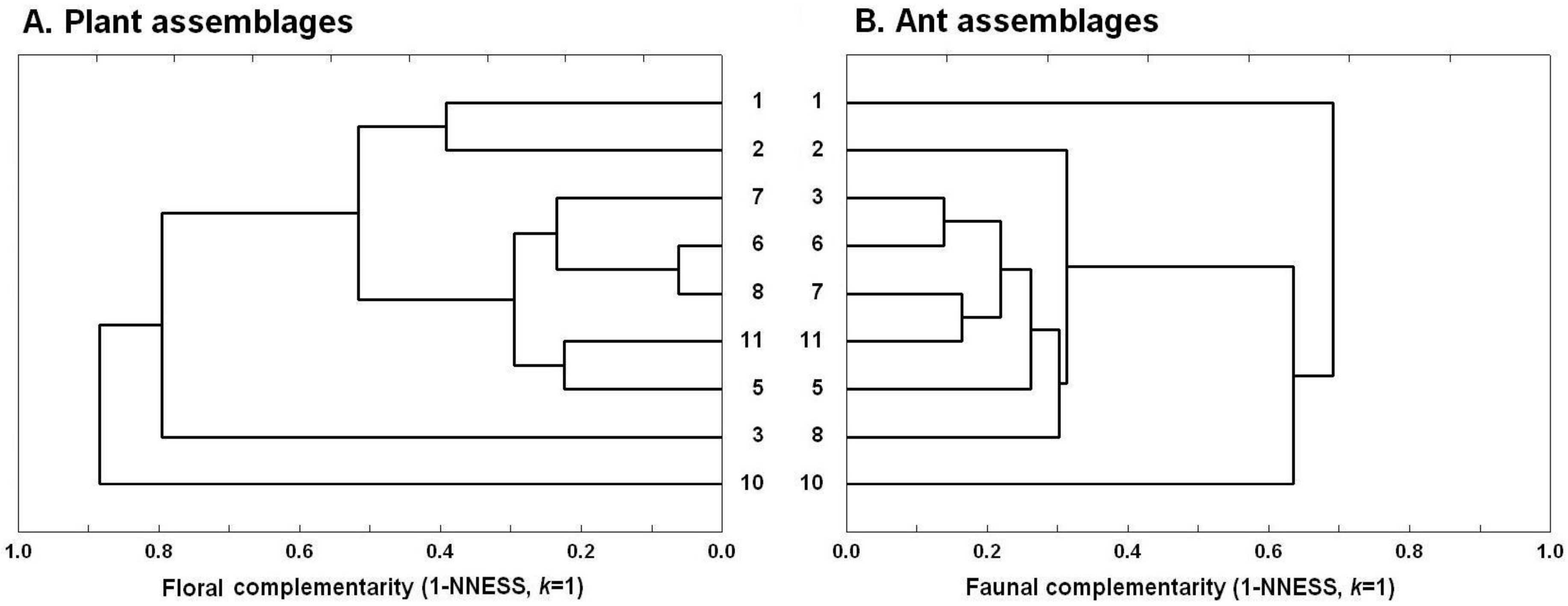

A.
Plants
DCA axis 2
DCA axis 1
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
0
50
100
150
200
250
300
350
400
1c
1b
1a
2a
2b
2c
10a
10b
10c
11c
11b
11a
3b
3a
3c
Silty
5a
5b
5c
7c
7b
7a
8a
8b
8c
6a
6b
B.
DCA axis 2
DCA axis 1
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
-350
-300
-250
-200
-150
-100
-50
0
10b
10c
10a
Dry/sandy
Intermediate aridity and/or soil texture
11c
11b
11a
7c
7b
7a
5a
5b
5c
8b
8a
8c
6a
6b
1c
1b
1a
2c
2b
2a
Humid/silty loam

Figure 4-8


A. Plant assemblages
1
2
7
6
8
11
5
3
10
1.0
0.8
0.6
0.4
0.2
0.0
Floral complementarity (1-NNESS, k=1)
B. Ant assemblages
1
2
3
6
7
11
5
8
10
0.0
0.2
0.4
0.6
0.8
1.0
Faunal complementarity (1-NNESS, k=1)

Appendix 4-1: Protocols of soil analyses.

The 10 first centimeters of soil (~150g) were collected at the beginning, the middle and the end of all elementary 200m-long transects (except at localities 4, 7 and 9). Samples were homogenized and air-dried for physicochemical analyses. Soil texture, pH and concentration of chlorides were measured.

Soil texture.

The soil texture describes the relative proportions of sand (i.e. particles with a size ranging from 50 to 2000µm), silt (2-50µm) and clay (<2µm) in the mineral soil fraction (Baize, 2000).

From every soil samples, a 10g subsample was treated with hydrogen peroxide (H_2O_2) to remove organic matter. A dispersing agent [20ml of sodium citrate ($Na_3C_6H_5O_7$) (40g/l)] was added and the mixture was turned mechanically for 30 minutes. After sieving to isolate sand particles, the mixture was transferred into a 1000ml-settling cylinder. The suspension was mixed thoroughly and then standed undisturbed. The time required for silt and clay particles to reach a given depth into the cylinder was calculated based on the Stoke's law and taken into account the ambient air temperature. At the determined time and at the depth corresponding to either the silt or the clay particles, an aliquot of the suspension was withdrawn with a Robinson's pipet. The aliquots were placed overnight into an oven set at 105°C. The weight and percentage of sand, silt and clay were then calculated.

Soil pH.

A few grams of every soil samples were saturated by deionized water and let stand for about 30 minutes. The immersion of an electrode allowed to determine the soil pH directly.

Concentration of chlorides.

Ten grams of soil were mixed into 50ml of deionized water. The suspension was turned mechanically for 30 minutes before filtration. Between 0.5 and 2ml of the resulting solution was mixed with 2ml of a ferric (III) nitrate nonanhydrate [$Fe(NO_3)_3\bullet 9H_20$]solution and 2ml of saturated mercury (II) thiocyanate [$Hg(SCN)_2$] solution. Dionized water was added to reach a 12.5ml volume. After about 10 minutes, the absorbance of the solution was measured at

460nm by spectrophotometry. The value obtained was compared to a standard curve in order to determine the chloride concentration of the solution.

Reference.

Baize, D., 2000. Guide des analyses en pédologie - 2ème édition. INRA editions, Paris, 257pp.

Appendix 4-2: Geographic distribution and abundance of 45 characteristic trees and shrubs along the aridity gradient. Numbers refer to the number of individuals counted along three 400m² belt transects per locality (except in locality 6 were only two transects were conducted). Locality numbers as in Figure 4-1.

		Locality								
Family	Species	1	2	3	5	6	7	8	10	11
Anacardiaceae	*Schinopsis cornuta*	-	-	-	-	-	-	-	8	-
Anacardiaceae	*Schinopsis quebracho-colorado*	3	4	5	-	18	7	-	-	11
Anacardiaceae	*Schinus fasciculata*	-	8	-	1	1	-	-	1	5
Apocynaceae	*Aspidosperma pyrifolium*	-	-	-	-	-	-	-	1	-
Apocynaceae	*Aspidosperma quebracho-blanco* (height >2m)	6	28	14	-	12	3	10	1	9
Arecaceae	*Copernicia alba* (height >1m)	10	3	-	-	-	-	-	-	-
Bignoniaceae	*Jacaranda mimosifolia*	-	-	-	-	-	-	-	10	-
Bignoniaceae	*Tabebuia nodosa*	13	8	-	-	-	-	-	-	-
Bombacaceae	*Ceiba insignis*	4	2	2	3	2	4	7	-	11
Cactaceae	*Cereus stenogonus*	1	4	9	-	5	7	6	-	7
Cactaceae	*Opuntia* sp. 01	-	-	-	-	-	-	-	-	6
Cactaceae	*Pereskia* cf *sacharosa*	-	-	-	1	2	1	-	-	-
Cactaceae	*Quiabentia verticillata*	-	-	1	9	-	4	5	-	2
Cactaceae	*Stetsonia coryne*	-	1	54	2	15	3	3	-	23
Capparaceae	*Capparis retusa*	42	30	35	7	99	71	86	-	16
Capparaceae	*Capparis salicifolia*	-	25	21	2	61	34	37	3	7
Capparaceae	*Capparis tweediana*	154	43	18	-	-	-	-	-	16
Caricaceae	*Jacaratia* cf *corumbensis*	1	-	-	-	-	1	-	-	1
Celastraceae	*Maytenus* sp. 01	20	115	-	0	-	-	-	-	-
Celastraceae	*Maytenus* sp. 02	1	1	2	3	10	1	-	-	7
Euphorbiaceae	*Cnidoscolus vitifolius*	-	-	-	6	1	5	1	-	-
Euphorbiaceae	*Jatropha excisa*	1	-	-	-	3	-	-	1	2
Euphorbiaceae	*Jatropha excisa* var. *pubescens*	-	-	-	6	-	-	-	-	-

Euphorbiaceae	*Jatropha* sp. 01	-	-	-	10	-	-	32	-	-
Fabaceae	*Acacia* sp. 01	11	3	-	-	-	-	-	-	-
Fabaceae	*Caesalpinia paraguariensis*	9	2	-	8	2	-	2	-	5
Fabaceae	*Caesalpinia stuckertii*	-	-	-	2	-	-	-	-	34
Fabaceae	*Cercidium* cf *praecox*	1	1	47	-	3	5	26	-	2
Fabaceae	*Chloroleucon chacoense*	-	-	-	6	5	18	2	1	27
Fabaceae	*Prosopis* cf *alba*	4	-	-	-	-	-	-	-	2
Fabaceae	*Prosopis kuntzei*	-	5	-	-	-	-	-	-	-
Fabaceae	*Prosopis ruscifolia*	-	5	-	-	-	-	-	-	-
Fabaceae	*Prosopis* sp. 01	-	-	353	-	-	-	-	-	18
Fabaceae	*Prosopis* sp. 02	-	-	22	-	-	-	-	-	-
Fabaceae	*Senna* cf *pendula*	-	-	6	-	-	-	-	-	-
Fabaceae	*Senna chloroclada*	-	-	-	8	-	84	11	86	36
Fabaceae	Undetermined sp. 01	-	-	1	-	-	5	-	-	3
Fabaceae	Undetermined sp. 02	-	-	1	7	29	54	10	-	-
Fabaceae	Undetermined sp. 03	20	-	-	-	-	-	-	-	-
Olacaceae	*Ximenia americana*	8	8	-	-	1	2	1	-	1
Polygonaceae	*Ruprechtia triflora*	76	115	74	28	124	73	101	-	223
Rhamnaceae	*Ziziphus mistol*	23	26	56	1	1	1	-	-	7
Santalaceae	*Acanthosyris spinescens*	11	26	10	3	10	10	11	6	27
Ulmaceae	*Celtis* cf *spinosa*	13	30	-	1	-	-	-	6	-
Zygophyllaceae	*Bulnesia sarmientoi*	-	16	-	-	-	-	-	-	5

Appendix 4-3: Complementarity matrices of ant assemblages based on the complement of the NNESS index with *k*=1 (A. upper part), *k*=64 (A. lower part) and *k*=128 (B. uppert part). To compare complementarity patterns of ant and plant assemblages, only the 24 transects for which both plant and ant data were available were used to compute the complement of the NNESS index. Resulting values of the complementarity index with *k*=1 and *k*=64 are provided in C. upper and lower parts respectively for plant assemblages, and in D. for ants. Numbers from 1 to 11 correspond to the locality number on Figure 4-1. Sampling year is specified for locality 7. Values in **bold** are minimum and maximum of each half matrix.

A	1	2	3	4	5	6	7-2001	7-2002	7-2004	8	9	10	11
1	*0*	0.521	0.721	0.612	0.752	0.725	0.756	0.715	0.670	0.626	0.654	**0.903**	0.599
2	0.336	*0*	0.289	0.334	0.339	0.317	0.541	0.397	0.290	0.368	0.526	0.667	0.280
3	0.524	0.282	*0*	0.354	0.353	0.127	0.537	0.409	0.314	0.366	0.523	0.875	0.210
4	0.456	0.333	0.322	*0*	0.351	0.279	0.233	0.331	0.261	0.481	0.237	0.611	0.281
5	0.589	0.377	0.353	0.353	*0*	0.247	0.409	0.306	0.210	0.317	0.513	0.464	0.252
6	0.574	0.344	0.289	0.295	0.298	*0*	0.447	0.328	0.206	0.329	0.452	0.665	0.159
7-2001	0.591	0.466	0.387	0.185	0.404	0.340	*0*	0.315	0.285	0.527	0.312	0.578	0.430
7-2002	0.610	0.378	0.363	0.330	0.275	0.266	0.257	*0*	**0.099**	0.308	0.510	0.648	0.267
7-2004	0.512	0.329	0.303	0.252	0.218	0.188	0.233	**0.153**	*0*	0.208	0.443	0.519	0.164
8	0.548	0.364	0.366	0.429	0.311	0.344	0.449	0.235	0.269	*0*	0.507	0.655	0.290
9	0.563	0.436	0.438	0.253	0.441	0.400	0.238	0.393	0.359	0.437	*0*	0.584	0.471
10	**0.863**	0.693	0.699	0.556	0.480	0.545	0.552	0.576	0.491	0.625	0.527	*0*	0.622
11	0.413	0.276	0.263	0.254	0.267	0.310	0.386	0.351	0.259	0.338	0.383	0.575	*0*

B	1	2	3	4	5	6	7-2001	7-2002	7-2004	8	9	10	11
1	*0*	0.355	0.549	0.467	0.606	0.592	0.575	0.627	0.533	0.594	0.582	**0.867**	0.457
2		*0*	0.324	0.342	0.424	0.379	0.431	0.375	0.342	0.393	0.418	0.686	0.305
3			*0*	0.330	0.363	0.321	0.336	0.360	0.292	0.358	0.413	0.662	0.303
4				*0*	0.359	0.307	**0.170**	0.322	0.248	0.430	0.254	0.544	0.245
5					*0*	0.342	0.388	0.297	0.249	0.362	0.445	0.511	0.304
6						*0*	0.298	0.273	0.215	0.340	0.383	0.566	0.335
7-2001							*0*	0.251	0.213	0.433	0.227	0.549	0.330
7-2002								*0*	0.191	0.233	0.336	0.565	0.340
7-2004									*0*	0.300	0.314	0.498	0.251
8										*0*	0.419	0.640	0.347
9											*0*	0.521	0.348
10												*0*	0.560
11													*0*

C	1	2	3	5	6	7	8	10	11
1	*0*	0.391	0.837	0.630	0.567	0.681	0.567	0.992	0.521
2	0.210	*0*	0.821	0.458	0.401	0.566	0.414	0.977	0.361
3	0.513	0.395	*0*	0.832	0.770	0.840	0.768	**0.996**	0.707
5	0.623	0.582	0.601	*0*	0.308	0.297	0.253	0.829	0.224
6	0.563	0.434	0.324	0.383	*0*	0.233	**0.061**	0.985	0.254
7	0.617	0.505	0.408	0.312	0.177	*0*	0.237	0.526	0.392
8	0.605	0.500	0.383	0.307	0.258	**0.158**	*0*	0.922	0.269
10	0.776	0.619	**0.792**	0.650	0.663	0.593	0.616	*0*	0.853
11	0.497	0.394	0.303	0.338	0.298	0.287	0.368	0.623	*0*

D	1	2	3	5	6	7-2004	8	10	11
1	*0*	0.521	0.721	0.752	0.735	0.670	0.626	**0.903**	0.599
2	0.334	*0*	0.289	0.338	0.313	0.290	0.369	0.667	0.280
3	0.523	0.281	*0*	0.353	**0.139**	0.314	0.336	0.875	0.210
5	0.589	0.377	0.353	*0*	0.229	0.210	0.317	0.464	0.252
6	0.578	0.338	0.290	0.282	*0*	0.191	0.327	0.641	0.162
7-2004	0.512	0.329	0.303	0.218	**0.180**	*0*	0.208	0.519	0.164
8	0.548	0.365	0.366	0.311	0.334	0.269	*0*	0.655	0.290
10	**0.863**	0.693	0.699	0.480	0.538	0.491	0.625	*0*	0.622
11	0.413	0.276	0.263	0.267	0.305	0.259	0.338	0.575	*0*

Taxonomic structure of ant assemblages along aridity gradients.

DELSINNE Thibaut[1, 2], LEPONCE Maurice[2], ROISIN Yves[1]

[1]: Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, BELGIUM.

[2]: Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral and Evolutionary Ecology - CP 160/12, 1050 Brussels, BELGIUM.

Abstract

Aim. Constraining abiotic factors such as aridity may constitute environmental filters decreasing the taxonomic diversity of assemblages. At continental scale, in Australia, a reduction of the ant genus number is observed from rainforests to deserts. We were interested to verify this trend along aridity gradients at regional scale.

Location. Paraguayan dry Chaco, Mongolia, Namib desert, American deserts.

Methods. First, we investigated the taxonomic structure of ant assemblages along a 400km-long aridity gradient (350-1000mm mean annual rainfall) in Chacoan xeromorphic forests. Ants were collected by pitfall traps along elementary 200m-long transects. Taxonomic distinctness indices (Δ^*, Δ^+, Λ^+) were used to assess the average degree of species relatedness and its variation within local ant assemblages. Second, we analyzed in a similar way the data available from four other studies along bio-climatic gradients.

Results. In the Paraguayan dry Chaco, neither the numbers nor the relative proportions of both ant genera and subfamilies were correlated with aridity. In all regions, taxonomic distinctness indices were not related to aridity and the distribution of ant species among localities was random with respect to taxonomy.

Main conclusions. At regional scale, aridity does not affect the taxonomic structure of ant assemblages. Hence, at this spatial scale, differences in assemblage composition along aridity gradients are more pronounced at species rather than at higher taxa levels.

Keywords: Dry ecosystems, Formicidae, Gran Chaco, niche conservatism, taxonomic distinctness, taxon distribution, taxon proportions.

Aridity is one of the major environmental factors susceptible to play a determinant role in the distribution of taxa either directly through the physiological tolerance of each species or indirectly through the control of habitat productivity (Kaspari et al., 2000; Mittelbach et al., 2001; Hawkings et al., 2003; Evans et al., 2005). It is generally expected that closely related taxa present higher similarities in ecological preferences than distant ones because of niche conservatism in the evolution of lineages (Lord et al., 1995; Webb, 2000; Webb et al., 2002; Wiens and Graham, 2005). Assuming that conservatism dominates in the phylogenetic distribution of arid-adapted traits, assemblages from arid localities should be more taxonomically related than expected by chance. This trend is verified for Australian ant assemblages at continental scale. Arid and tropical Australian regions harbour similar numbers of ant species but the number of ant genera is reduced in arid zones (Shattuck and Barnett, 2001). However, at large spatial scale, the effects of aridity may be confounded by the influence of historical factors and by the contribution of different pools of species (Gotelli and Ellison, 2002). Here, we were interested to verify whether the taxonomic diversity of ant assemblages decreases along aridity gradients at regional scale because, at this spatial scale, distributions of species are suspected to be influenced mainly by ecological factors and because the species pool is likely to be similar at all study localities.

To attain our objective, we first examined the taxonomic structure of ant assemblages along an aridity gradient (350-1000mm mean annual rainfall) in xeromorphic forests of the Paraguayan dry Chaco. In this region, we showed that ground-foraging ants were relatively diverse with up to 76 species expected per locality (Chao2 estimations) but that species richness was not related to aridity (Delsinne et al., in prep.). Nevertheless, this factor influenced the distribution of species, suggesting that changes in taxonomic structure could occur along the aridity gradient. We then expanded our findings by an analysis of the taxonomic structure of ant assemblages distributed along four other bioclimatic gradients found in the literature.

METHODS

Study sites and sampling protocol.

The study was conducted in the plains of the Paraguayan dry Chaco, which appear as ideal for such study because of their wide rainfall range and flat topography allowing to discard altitudinal influences (Fariña Sánchez, 1973; Ramella and Spichiger, 1989). Additionally, the study was carried out between the 24 and 26°C isolines of mean annual temperature in order to minimize the influence of temperature. Eleven localities separated by 20 to 400km and spread along an aridity gradient (Table 5-1) were sampled between 2001 and 2004, at the beginning of the wet season, in September-November, when temperature and rainfall increased. This period was selected in order to avoid the extreme temperatures which may limit the foraging of some Chacoan ant species (Bestelmeyer, 2000; Delsinne et al., 2007), and because at that time the leaf litter depth was maximal. Locality 7 (500 mean annual rainfall) was sampled in 2001, 2002 and 2004 in order to verify the stability of the taxonomic structure and faunal composition of a reference ant assemblage.

Previously we have shown that soil texture, along with aridity, influenced the distribution of ants in the Paraguayan dry Chaco (Delsinne et al., in prep.). In an attempt to control the possible confounding effects of edaphic conditions, soil texture was measured in 8 of the 11 localities studied [see Delsinne et al. (in prep.) for a detailed protocol and description of soil conditions along the study gradient].

Ants were sampled along elementary transects of 20 pitfall traps spaced at 10m intervals. Three elementary transects, spread along a 1km-long line and separated from each other by 200m, were carried out per locality (except in localities 5 and 7-2002 with 1 and 2 transects, respectively). All workers were identified to species or morphospecies. Reproductives were excluded from the analyses because only workers certify the presence of an established colony (Longino et al., 2002). Species occurrences in samples were used as surrogate of abundance because ants are spatially aggregated due to their sociality (Longino, 2000) and because colony sizes may strongly vary among species (Hölldobler and Wilson 1990).

Informations about ant α-diversity (based on species richness and Gini coefficient) and β-diversity are available in Delsinne et al. (in prep.).

Taxonomic distinctness measures.

Recently, Warwick and Clarke defined a taxonomic distinctness index (based on abundance data, Δ^* [Warwick and Clarke, 1995] or on presence/absence data, Δ^+ [Clarke and Warwick, 1998]), as a measure of the average degree of species relatedness in an assemblage (Clarke and Warwick, 1998, 2001). They also introduced a measure of its variation (Λ^+; Clarke and Warwick, 2001) in order to be able to distinguish differences in taxonomic structure for instance in assemblages with some over- or under-represented taxa. These indices were obtained with the equations:

$\Delta^* = [\sum\sum_{i<j} \omega_{ij}\, x_i x_j] / [\sum\sum_{i<j} x_i x_j]$

$\Delta^+ = [\sum\sum_{i<j} \omega_{ij}] / [S(S-1)/2]$

$\Lambda^+ = [\sum\sum_{i<j} (\omega_{ij} - \Delta^+)^2] / [S(S-1)/2]$

where x_i and x_j were the abundance (=total number of occurrences) of species i and j in the study locality; S was the observed number of species and ω_{ij} was the weight given to the path length linking species i and j through a phylogenetic or taxonomic hierarchy. Here, based on the latest taxonomic review (Bolton et al., 2007) a Linnean classification of the ant species collected was compiled. Five taxonomic levels were included: species, genus, tribe, subfamily and family. Following Clarke and Warwick (1999) a simple linear scaling was adopted such that the longest path between two species is set to $\omega = 100$ (i.e. species belong to the same family but to different subfamilies). Consequently, the weights were $\omega = 0$ (same species), $\omega = 25$ (species in the same genus), $\omega = 50$ (same tribe but different genera), $\omega = 75$ (same subfamily but different tribes).

These three biodiversity measures have been developed to evaluate anthropogenic impacts on marine ecosystems (Warwick and Clarke, 1995; Clarke and Warwick, 1998, 2001) and their usefulness in this domain has often been acknowledged (as examples: Rogers et al., 1999; Ceschia et al., 2007). Their performance to detect the effects of natural abiotic factors on the taxonomic structure of terrestrial assemblages has rarely been tested despite the fact that these measures present appealing properties for biodiversity assessments. Indeed they are robust with respect to differences in sample size or sampling methods, are not sensitive to species richness and may better reveal the impact of a disturbance or an abiotic stress than "conventional" indices of diversity such as species richness or evenness indices (Warwick and Clarke, 1995; Clarke and Warwick, 1998, 2001). Also, a significance test can be carried out to examine the departure of both Δ^+ and Λ^+ from the null expectation that each local assemblage contains species randomly selected from the regional pool. Indeed, random subsamples (here, we carried out 10,000 random draws from the regional list) of different numbers of species allowed the expected values of Δ^+ or Λ^+ to be plotted as a probability funnel delimited by the 95% confidence intervals. In this study, the regional list was simply the combined species list of all localities under study (Clarke and Warwick, 1998; Warwick and Clarke, 1998). Observed Δ^+ or Λ^+ values were then added to the plot to allow a simultaneous comparison of the observed values with each other and with the expected limits. Taxonomic distinctness analyses were carried out using the PRIMER 6.1.6 software (PRIMER-E Ltd, Plymouth, U.K., www.primer-e.com).

Local genus richness and taxa proportions.

For each locality, the number of ant genera was evaluated by rarefaction (Coleman method) and by extrapolation (Chao2 estimation) with EstimateS 7.5 (Colwell, 2004). Relative proportions of ant subfamilies were calculated from genus and species numbers and from occurrences. Similarly, relative proportions of ant genera were calculated from occurrences.

Aridity/taxonomic distinctness patterns from published data sets.

With the attempt to reveal some consistent trends of aridity influence on taxonomic structure of ant assemblages, we calculated taxonomic distinctness indices (Δ^+ and Λ^+) for ant assemblages available in the literature. We selected three surveys from different continents and with contrasting results in order to generalize our conclusions. A negative relationship was found between species richness and aridity in the Namib Desert (all ground-foraging ants: Marsh 1986) and for seed-eating ants from American southwestern deserts (Davidson, 1977) but no relationship was found for ground-foraging species in Mongolia (Pfeiffer et al, 2003). Along with these studies, taxonomic distinctness indices were calculated from data of the seminal paper of Andersen (1997). In his study, Andersen presented distribution patterns of ant genera and functional groups along an elevational gradient in Arizona. Although this paper did not aim to document the effect of aridity on ant assemblages, Andersen selected his localities in order to represent a bio-climatic gradient, from desert to forest, rather than an elevation gradient *per se* (Andersen, 1997, p. 435).

Before calculating Δ^+ and Λ^+, the taxonomic status of every species was checked (Bolton, 2007; Agosti and Johnson, 2005) to take into account recent advances in ant taxonomy.

RESULTS

Taxonomic structure of ant assemblages in the Paraguayan dry Chaco.

Overall, 48015 ants corresponding to 5462 occurrences, 197 morphospecies, 36 genera, 17 tribes and 7 subfamilies were collected in the 11 localities studied (Appendix 5-1). The seven ant subfamilies globally occurred throughout the whole gradient (Figure 5-1A and 5-1B). The Myrmicinae was the most species rich subfamily at all localities (Figure 5-1A). Ecitoninae and Ponerinae were rarely collected (Figure 5-1B) and their absence in some localities was probably due to stochastic effects. Only four Pseudomyrmecinae species were collected. Consequently, this subfamily only little contributed to the observed species richness of any locality (Figure 5-1A). Nevertheless, in terms of occurrences, this subfamily was not rare (Figure 5-1B) due to the numerical dominance of *Pseudomyrmex denticollis* (mean proportion of occurrences for this species ± SD = 9.2±4.6%; Figure 5-2). Only the Dolichoderinae significantly decreased in species proportions with mean annual rainfall ($r = -0.570$, $P=0.039$, Spearman rank order correlation) and with silt porportions ($r = -0.738$; $P=0.029$; Appendix 5-2). In terms of occurrences, Dolichoderinae proportions were related to soil texture ($-0.929 \leq r \leq 0.929$; $0.001 \leq P \leq 0.037$) but not to aridity ($r = -0.477$; $P=0.093$; Appendix 5-2).

The number of genera per locality ranged from 15 (locality 3) to 24 (locality 2; Table 5-1) but accumulation curves were still rising for almost all localities, suggesting that some genera were not recorded (Figure 5-3). In terms of occurrences, genus proportions were never related to aridity (Figure 5-2; Appendix 5-3). Only *Pheidole* occurrences were related to soil texture (Spearman rank order correlation: $-0.738 \leq r \leq 0.857$, $0.002 \leq P \leq 0.029$, Appendix 5-3). Rarefied and extrapolated genus richnesses (Table 5-1) were neither related to aridity nor to soil texture ($P>0.05$; Table 5-2). Similarly, Δ^* , Δ^+, and Λ^+ were not related to these factors ($P>0.05$; Table 5-2). In addition, species present at any one locality behaved like a random subsample of the regional species pool since observed Δ^+ values fell within the 95% confidence funnel (Figure 5-4). A surprising exception is locality 3 with a significantly reduced average taxonomic distinctness ($\Delta^+= 81.5$; $P=0.008$; Figure 5-4). The variation in taxonomic distinctness was also larger than expected for this locality ($\Lambda^+ = 608.3$; $P=0.001$; Figure 5-5) as for localities 9 ($\Lambda^+ = 522.9$; $P=0.047$), 6 ($\Lambda^+ = 545.3$; $P=0.032$) and 4 ($\Lambda^+ = 523.7$; $P=0.038$). The singularity of locality 3 seemed linked to the low contribution of dolichoderine species to the total species richness (Figure 5-1A). The absence of *Forelius* species in particular was remarkable (Figure 5-2). Values of Δ^+ and Λ^+ for the three sampling years of locality 7 fell within the 95% confidence funnel (Figures 5-4 and 5-5) indicating that only stochastic changes occurred among years in the taxonomic structure of this ant assemblage.

Taxonomic distinctness of ant assemblages from published data sets.

No correlation was found between Δ^+ and aridity for any published data sets [Pearson product moment correlations: Davidson (1977): $r = -0.544$, $P=0.104$; Marsh (1986): $r = -0.395$, $P= 0.229$; Pfeiffer et al. (2003): $r = -0.305$, $P=0.362$] and between Δ^+ and elevation [Andersen (1997): $r = 0.445$, $P=0.231$]. Similarly, no correlation was found between Λ^+ and aridity [Marsh (1986): $r = -0.445$, $P=0.170$; Pfeiffer et al. (2003): $r = 0.068$, $P=0.843$], except for Davidson (1977) [$r = 0.701$, $P=0.024$]. Also, Λ^+ was not related to elevation for ant assemblages from Andersen (1997) [$r = -0.157$, $P=0.687$].
In addition, whatever the study region and whatever bio-climatic conditions occurring at each locality, ant assemblages did not differ from subsamples of species randomly selected from the respective regional list since all assemblages (but one) fell within the 95% confidence intervals for both Δ^+ and Λ^+ values (Figure 5-6).

DISCUSSION

Our results failed to support the hypothesis that at regional scale aridity constitutes an environmental filter reducing the taxonomic diversity of ant assemblages. Taxonomic distinctness indices (Δ^*, Δ^+ and Λ^+) were never (except once) correlated to aridity and the distribution of ant species among localities was random with respect to taxonomic relatedness. These results were obtained for all regions studied, indicating that it could be a general pattern. In addition, the detailed analysis of genus and subfamily distributions within the Paraguayan dry Chaco confirmed that no ant genus or higher taxa were restricted to the most arid zones and, reciprocally, that the ant fauna of these localities were not depauperate. Also, taxa proportions were not related to aridity, except in the case of Dolichoderinae. For this taxa however, aridity effects may be confounded by edaphic preferences since soil texture and aridity are highly collinear in the Paraguayan dry Chaco (Delsinne et al., in prep.). The fact that proportions of Dolichoderinae were related to soil texture suggested that soil properties may be indeed more determinant for them. It thus appeared that aridity may not be stressful enough to clump phylogenetically related species or that aridity-tolerance traits are widespread in the phylogeny of ants. It is important to stress that phylogenetic and taxonomic structures of assemblages are spatial scale-dependent (Cavender-Bares et al., 2006). Indeed, niche conservatism may be better revealed at large geographic scales since a greater environmental heterogeneity is probably encompassed and thus, taxa specializations more easily noted (Cavender-Bares et al., 2006). For instance, *Forelius* species were present from the driest to the wettest locality of the Paraguayan dry Chaco but, at the continental scale, this genus is restricted to dry habitats (Cuezzo, 2003). At the opposite, Ponerinae in South America are mainly found in humid forests (Lattke, 2003) and, in comparison, the Chacoan fauna appeared depauperate. Nevertheless, at large geographic scales, ecological and historical factors are more likely embedded and it becomes difficult to distinguish their effects on fauna composition (Gotelli and Ellison, 2002). Here, our results emphasized that aridity *per se* did not affect taxonomic structure of ant assemblages at a regional scale.

On average, a high functional diversity is expected for taxonomically diverse assemblages because related species are suspected to share more functional traits than unrelated ones (Hooper et al., 2002). However, taxonomies have a hierarchical, non-overlapping structure, whereas functional groups tend to overlap (von Euler and Svensson, 2001). For instance, a functional trait may be shared by several distantly related ant genera (Andersen, 1995, 1997). Therefore, although a clear non-random distribution pattern of functional groups was observed along the bio-climatic gradients studied either by Andersen (1997; his Figure 12) or by Pfeiffer et al. (2003, their Figure 6), the taxonomic structure of every local assemblages did not differ from a random subset of species extracted from the respective regional species pool. This result indicated that taxonomic distinctness indices can not be used as a substitute for functional diversity studies, at least for ground-foraging ants.

In the Paraguayan dry Chaco, one locality (i.e. locality 3) presented a lower Δ^+ and a higher Λ^+ than expected by chance. This locality was also the less rich in terms of genus number (but not in terms of species number [Delsinne et al., in prep.]). These results were apparently due to the very low presence of dolichoderine ants. In particular, no *Forelius* species were collected. These ants are thermophile (Bestelmeyer, 1997, 2000) and forage mainly when ambient air temperature is higher than 25°C (Jara and Delsinne, unpublished data). *Dorymyrmex* species forage under broader thermal conditions and some species are even cold-tolerant, being the only ants active during cold winter nights in the Chaco (Bestelmeyer, 1997, 2000). However at locality 3 during the sampling period, temperature ranged from 18°C to 37.5°C, rejecting the hypothesis that the absence of these ant genera may be caused by unfavourable temperature conditions. Soils of locality 3 contained a high proportion of silt (>70%) (Delsinne et al., in prep.), which may limit the establishment of Dolichoderinae. Additional samplings and further investigations are needed to understand this result.

In conclusion, at regional scale, it seems that differences in assemblage composition along aridity gradients are more pronounced at species rather than at higher taxa levels whereas at continental scale the reverse is observed.

ACKNOWLEDGMENTS

We thank John Kochalka, Bolivar Garcete-Barrett, Victor Filippi, Jorge Jara, César Bénilez, Carlos Aguilar Julio from the "Museo Nacional de Historia Natural del Paraguay", the guards from Teniente Enciso National Park and Véronique Olivier for their help during fieldwork or administrative procedures. This study was made possible by financial support from the "Fonds pour la Formation à la Recherche dans l'Industrie et l'Agriculture" and the "Fonds de la Recherche Scientifique - FNRS" (Belgium).

REFERENCES

Agosti, D., Johnson, N.F., Eds. 2005. Antbase, www. antbase.org, version (05/2005).

Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. J. Biogeogr. 22: 15-29.

Andersen, A.N., 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. J. Biogeogr. 24: 433-460.

Bestelmeyer, B.T., 1997. Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. Journal of Arid Environments 35: 297-310.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Anim. Ecol. 69: 998-1009.

Bolton, B., Alpert, G., Ward, P.S., Naskrecki, P., 2007. Bolton's catalogue of ants of the world: 1758-2005. Harvard University Press.

Cavender-Bares, J., Keen, A., Miles, B., 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87: S109-S122.

Ceschia, C., Falace, A., Warwick, R., 2007. Biodiversity evaluation of the macroalgal flora of the Gulf of Trieste (Northern Adriatic Sea) using taxonomic distinctness indices. Hydrobiologia 580: 43-56.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35: 523-531.

Clarke, K.R., Warwick, R.M., 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Marine Ecology Progress Series 184: 21-29.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology Progress Series 216: 265-278.

Colwell, R.K. 2004. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL: <purl.oclc.org/estimates>.

Cuezzo, F., 2003. Subfamilia Dolichoderinae. pp. 291-297. In: Fernández, F. (ed.). Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia. XXVI + 398 pp.

Davidson, D.W., 1977. Species diversity and community organization in desert seed-eating ants. Ecology 58: 711-724.

Delsinne, T., Roisin, Y., Leponce, M., 2007. Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage. J. Arid Environ. 71: 29-44.

Evans, K.E., Warren, P.H., Gaston, K.J., 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Review 80: 1-25.

Fariña Sánchez, T., 1973. The climate of Paraguay. pp. 33–38. In: Gorham, J.R. (ed.). Paraguay: ecological essays. Academy of the Arts and Sciences of the Americas, Miami, FL.

Gotelli, N.J., Ellison, A.M., 2002. Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. Ecology 83: 1604-1609.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 24: 3105-3117.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Cambridge: Bellknap Press.732 pp.

Hooper, D.U., Solan, M., Symstad, A., Díaz, S., Gessner, M.O., Buchmann, N., Degrange, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E., van Peer, L., 2002. Species diversity, functional diversity and ecosystem functioning. pp. 195-208 *in* P., Inchausti, Loreau, M., Naeem, S., eds. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, UK.

Kaspari, M., O'Donnell, S., Kercher, J.R., 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. The American Naturalist 155: 280-293.

Lattke, J.E., 2003. Subfamilia Ponerinae. pp. 261-276. In: Fernández, F. (ed.). Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia. XXVI + 398 pp.

Longino, J.T. 2000. What to do with the data ? Pages 186-203 *in* D., Agosti, J.D., Majer, L.E., Alonso, and T.R., Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington DC.

Longino, J.T., J., Coddington, and R.K., Colwell. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology 83: 689-702.

Lord, J., Westoby, M., Leishman, M., 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. American Naturalist 146: 349-364.

Marsh, A.C.,1986. Ant species richness along a climatic gradient in the Namib Desert. Journal of Arid Environments 11: 235–241.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82: 2381-2396.

Pfeiffer, M., Chimedregzen, L., Ulykpan, K., 2003. Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. Journal of Biogeography 30: 1921-1935.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639-680.

Rogers, S.I., Clarke, K.R., Reynolds, J.D., 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-East Atlantic. Journal of Animal Ecology 68: 769-782.

Shattuck, S.O., Barnett, N.J., 2001. Australian ants online. The guide to the Australian ant fauna, CSIRO. http://www.ento.csiro.au/science/ants/default.htm

von Euler, F., Svensson, S., 2001. Taxonomic distinctness and species richness as measures of functional structure in bird assemblages. Oecologia 129: 304-311.

Warwick, R.M., Clarke, K.R., 1995. New "biodiversity" measures reveal a decrease in taxonomic distinctness with increasing stress. Marine Ecology Progress Series 129: 301-305.

Warwick, R.M., Clarke, K.R., 1998. Taxonomic distinctness and environmental assessment. Journal of Applied Ecology 35: 532-543.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist 156: 145-155.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annual Reviews of Ecology, Evolution and Systematics 33: 475-505.

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Reviews of Ecology, Evolution and Systematics 36: 519-539.

Table and figure legends

Table 5-1: Mean annual rainfall, genus numbers and taxonomic distinctness indices of ant assemblages collected in the 11 localities of the Paraguayan dry Chaco. Localities are: 1: Rio Verde, 2: Cruce de Los Pioneros, 3: Mariscal Estigarribia, 4: Garrapatal, 5: Estancia María Vicenta, 6: Teniente Enciso National Park-Northern side, 7: Teniente Enciso N. P.-Southern side 8: Siracua, 9: Nueva Asunción, 10: Fortín Mister Long, 11: Fortín Mayor Infante Rivarola. Locality 7 was sampled in 2001, 2002 and 2004.

Table 5-2: Spearman rank order correlation coefficients (r) between environmental variables (aridity and soil texture) and both genus numbers and taxonomic distinctness indices of ant assemblages collected in the Paraguayan dry Chaco.

Figure 5-1: Proportions of subfamilies of all ant assemblages collected in the Paraguayan dry Chaco, based on (A) species numbers and (B) occurrences. Locality numbers refer to Table 5-1. See Appendix 5-2 for correlation coefficients with environmental factors.

Figure 5-2: Proportions (based on species occurrences) of main genera and other higher taxa level of the 11 assemblages sampled along an aridity gradient in the dry Chaco. Locality numbers refer to Table 5-1. See Appendix 5-3 for correlation coefficients with environmental factors.

Figure 5-3: Occurrence-based rarefaction curves of genus numbers (Coleman method) for ground-foraging ants collected in the 11 localities of the dry Chaco. Locality numbers refer to Table 5-1. Data from the three sampling years of reference locality 7 were computed separately and are represented by dotted curves. Vertical line correspond to the rarefied number of occurrences used to compare the 13 samplings (136 occurrences).

Figure 5-4: Taxonomic distinctness (Δ^+) values for ant assemblages collected in the 11 study localities of the dry Chaco. Locality numbers refer to Table 5-1. The three sampling years at locality 7 were analysed separately. The dotted line is the theoretical mean taxonomic distinctness and lines represent the 95% confidence funnel obtained from 10,000 random draws from the total species list.

Figure 5-5: Variation in taxonomic distinctness (Λ^+) values for ant assemblages collected in the 11 study localities of the dry Chaco. Same legend as in Figure 5-4.

Figure 5-6: Values of average taxonomic distinctness index (Δ^+) and its variation (Λ^+) for ant assemblages collected along aridity or bio-climatic gradients in (A & B) American Soutwestern deserts (Davidson, 1977); (C & D) Namib Desert (Marsh, 1986); (E & F) Mongolia (Pfeiffer et al., 2003) and (G & H) Arizona (Andersen, 1997). The central line is the theoretical mean value of Δ^+ or Λ^+ and the funnel corresponds to the 95% confidence limits obtained from 10,000 random draws from the respective total species list. Numbers correspond to the locality code given by the authors in their original publication. In addition, the mean annual rainfall documented by the authors for each locality is given between brackets. For Andersen (1997), the number between brackets correspond to the locality elevation. For correlation coefficients with environmental factors, see the text.

TABLES

Table 5-1

Locality	Latitude °S	Longitude °W	Mean annual rainfall (mm)	Observed genus richness	Expected number of genera (Chao2)	Rarefied genus richness*	Taxonomic distinctness Δ^*	Taxonomic distinctness Δ^+	Variation in taxonomic distinctness Λ^+
1	23.21785	59.20294	1000	21	22.0±1.5	17.9±1.4	85.7	88.3	464.0
2	22.69014	59.77186	850	24	34.3±9.3	18.8±1.6	86.4	86.0	518.4
3	21.99097	60.63583	700	15	15.0±0.1	13.4±1.0	88.3	81.5	608.3
4	21.44661	61.48749	600	23	24.2±1.8	17.9±1.5	88.3	86.8	523.7
5	20.9213	61.39321	550	15	16.0±1.7	14.8±0.4	89.2	86.6	532.4
6	21.13747	61.50945	500	19	21.3±3.8	14.2±1.4	88.9	85.4	545.3
7-2001	21.2059	61.65762	500	18	27.8±10.1	14.4±1.1	89.1	86.8	521.2
7-2002	21.2059	61.65762	500	22	23.5±2.5	19.2±1.3	88.8	86.0	491.5
7-2004	21.2059	61.65762	500	22	28.9±6.3	16.3±1.5	89.7	87.3	486.7
8	21.04616	61.75151	450	18	25.4±7.3	15.2±1.3	90.8	86.5	506.5
9	20.69528	61.92877	400	20	20.7±1.4	17.8±1.2	87.0	85.3	522.9
10	20.60386	62.05053	350	17	26.8±10.1	15.4±1.1	84.8	85.5	492.6
11	21.67146	62.41312	350	21	27.9±5.9	15.5±1.6	89.4	87.4	507.1

* Rarefied to 136 occurrences (Coleman method).

Table 5-2

	Mean annual rainfall (mm) (n=13)	Mean sand proportion (n=8)	Mean silt proportion (n=8)	Mean clay proportion (n=8)
Rarefied genus richness*	r = 0.165	r = 0.048	r = -0.048	r = 0.310
	P = 0.578	P = 0.885	P = 0.885	P = 0.423
Extrapolated genus richness (Chao2)	r = -0.212	r = 0.286	r = -0.286	r = 0.024
	P = 0.469	P = 0.460	P = 0.460	P = 0.931
Δ^* (with locality 10)	r = -0.296	r = 0.167	r = -0.167	r = -0.286
	P = 0.313	P = 0.662	P = 0.662	P = 0.460
Δ^+	r = 0.100	r = 0.190	r = -0.190	r = 0.0238
	P = 0.737	P = 0.619	P = 0.619	P = 0.931
Λ^+	r = 0.148	r = -0.286	r = 0.286	r = 0.238
	P = 0.616	P = 0.460	P = 0.460	P = 0.537

* Rarefied to 136 occurrences (Coleman method).

Figure 5-1

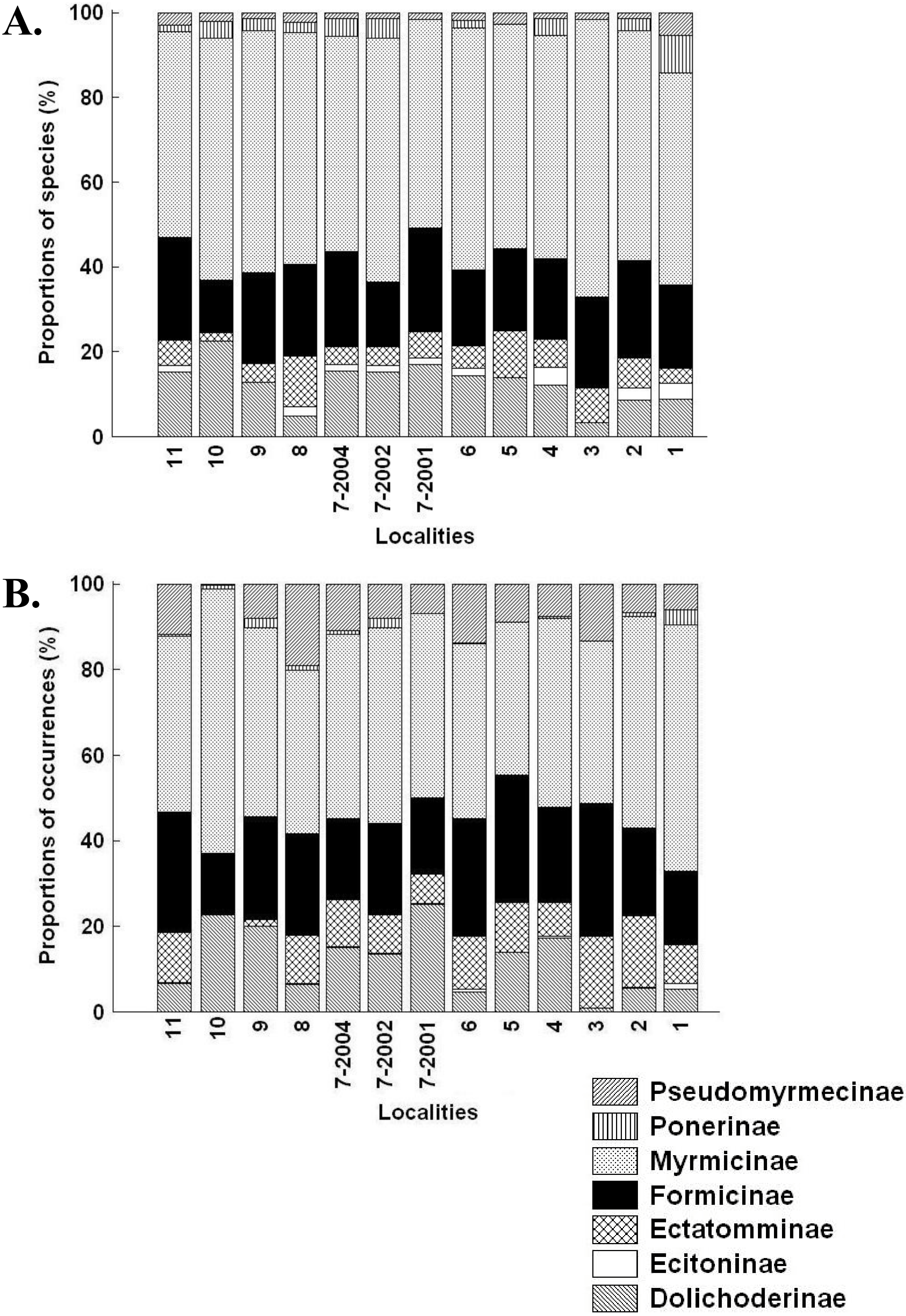

A.
Proportions of species (%)
0
20
40
60
80
100
11
10
9
8
7-2004
7-2002
7-2001
6
5
4
3
2
1
Localities
B.
Proportions of occurrences (%)
0
20
40
60
80
100
11
10
9
8
7-2004
7-2002
7-2001
6
5
4
3
2
1
Localities
Pseudomyrmecinae
Ponerinae
Myrmicinae
Formicinae
Ectatomminae
Ecitoninae
Dolichoderinae

Figure 5-2

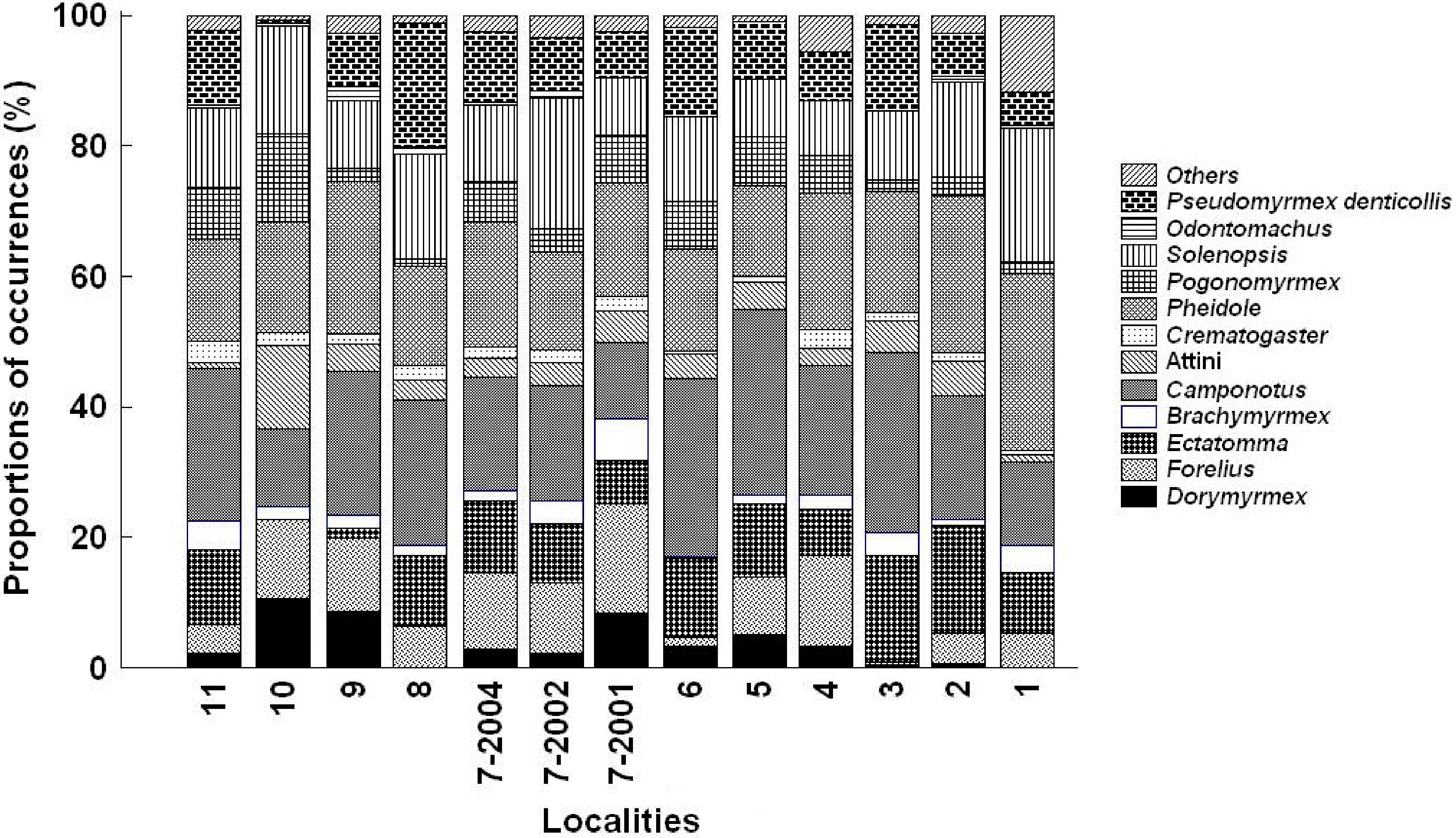

Proportions of occurrences (%)
0
20
40
60
80
100
11
10
9
8
7-2004
7-2002
7-2001
6
5
4
3
2
1
Localities
Others
Pseudomyrmex denticollis
Odontomachus
Solenopsis
Pogonomyrmex
Pheidole
Crematogaster
Attini
Camponotus
Brachymyrmex
Ectatomma
Forelius
Dorymyrmex

Figure 5-3

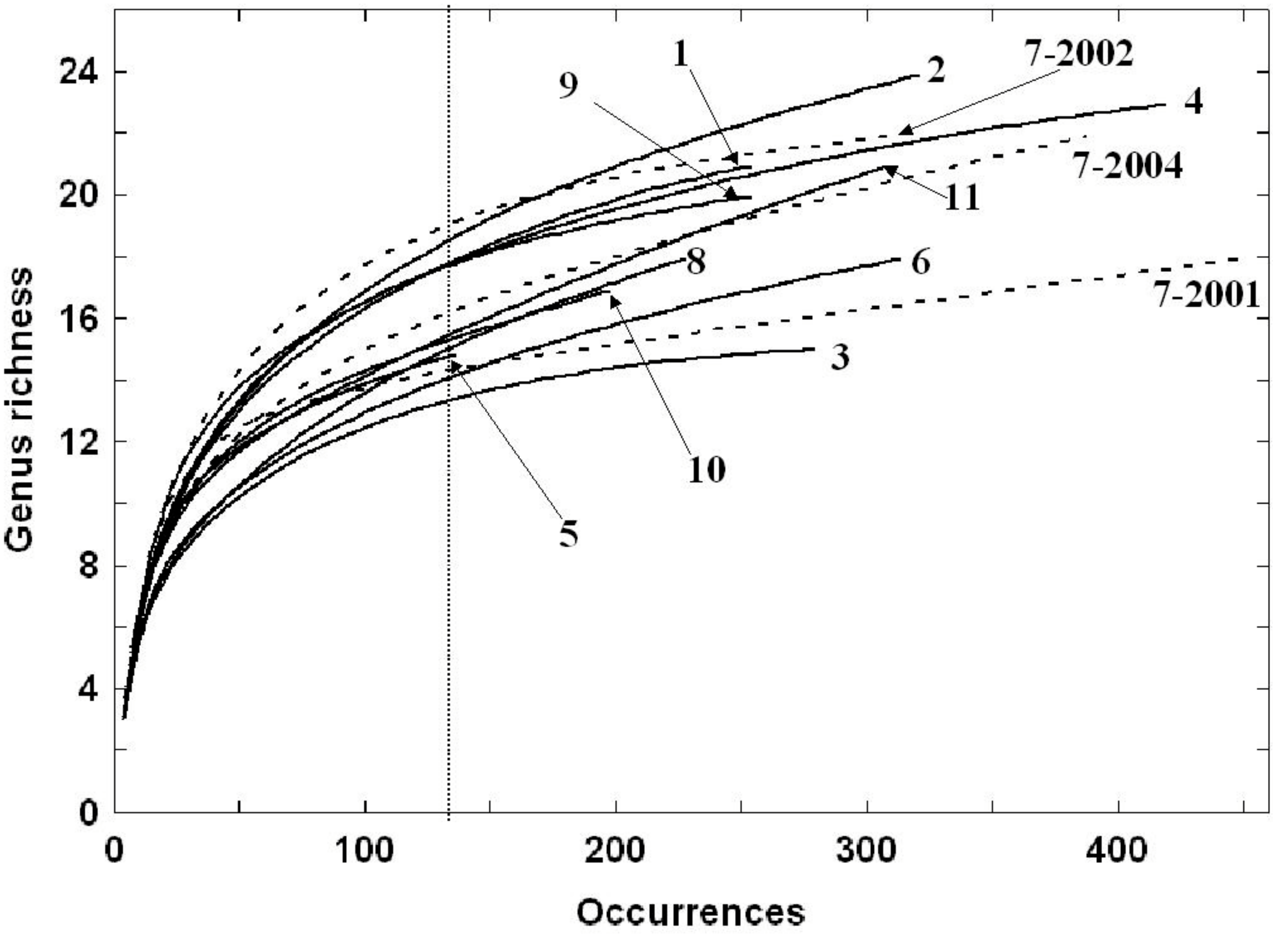

Genus richness
0
4
8
12
16
20
24
Occurrences
0
100
200
300
400
1
2
3
4
5
6
8
9
10
11
7-2001
7-2002
7-2004

Figure 5-4

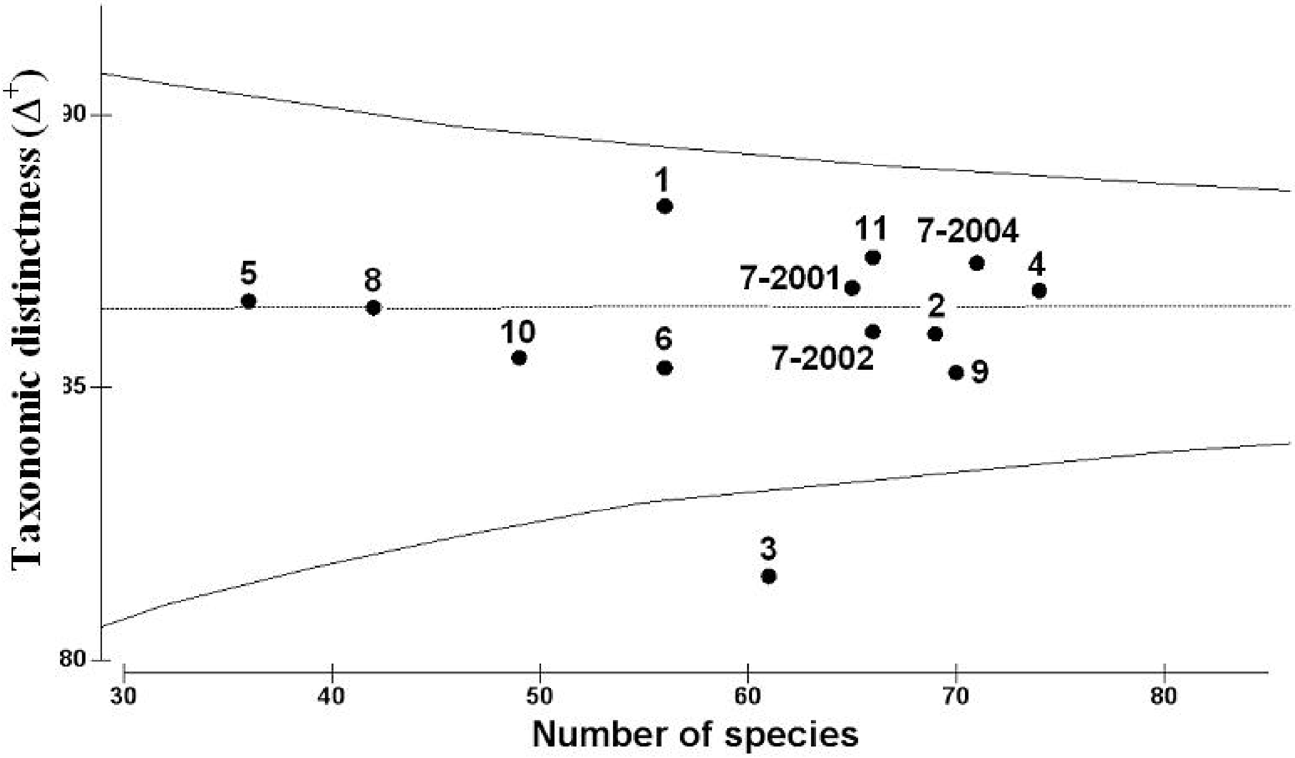

Taxonomic distinctness (Δ^+)
90
85
80
1
11
7-2004
5
8
7-2001
4
2
10
6
7-2002
9
3
30
40
50
60
70
80
Number of species

Figure 5-5

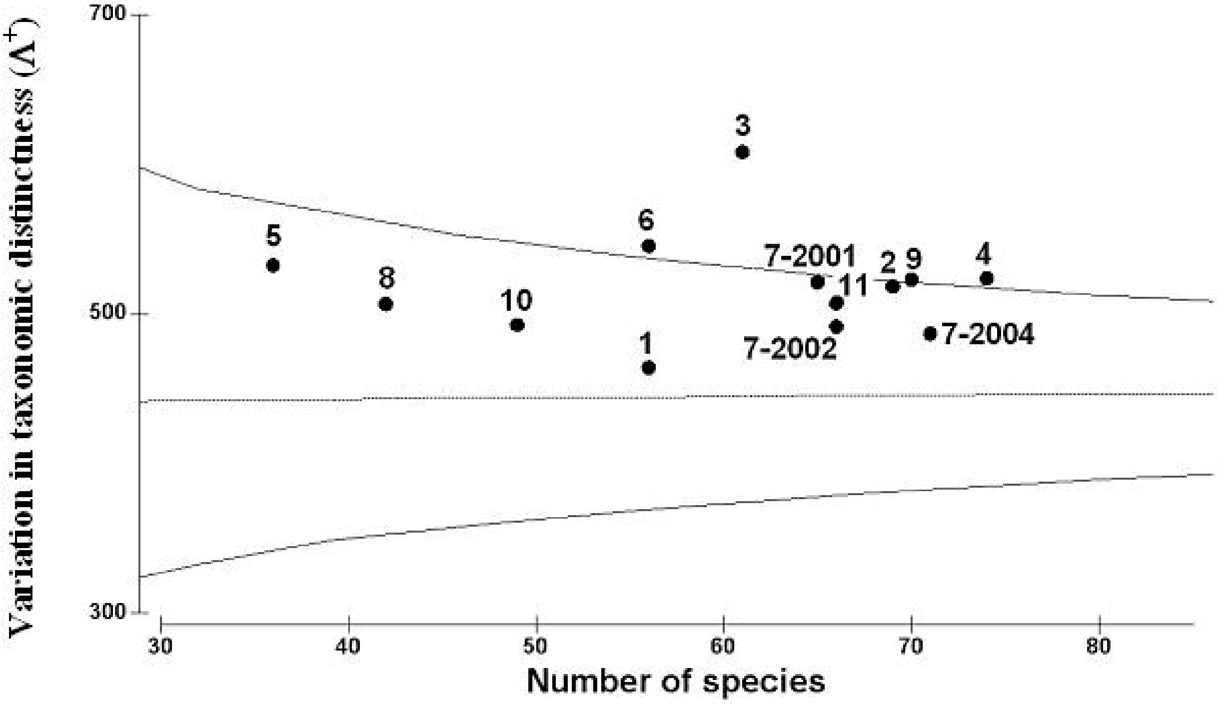
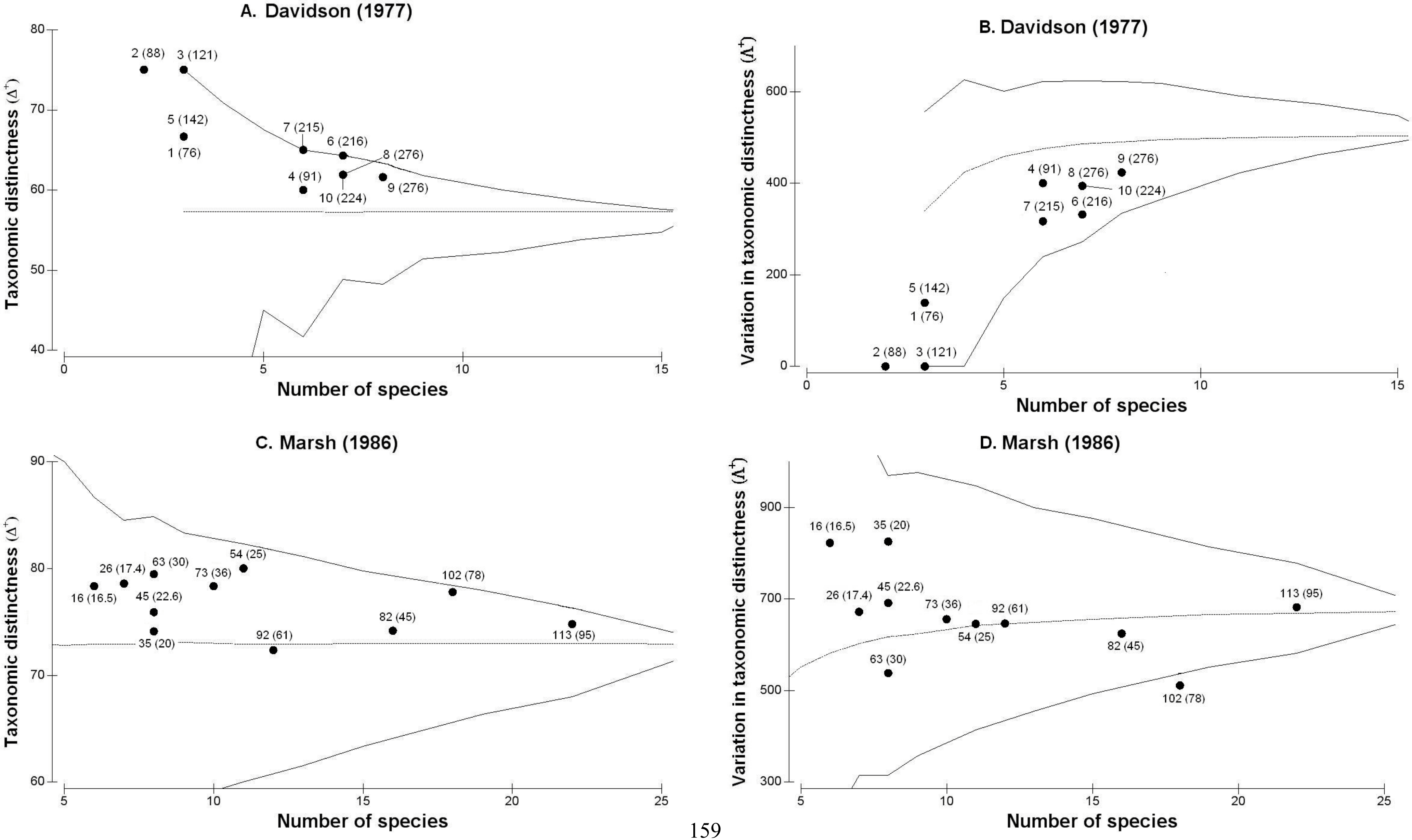
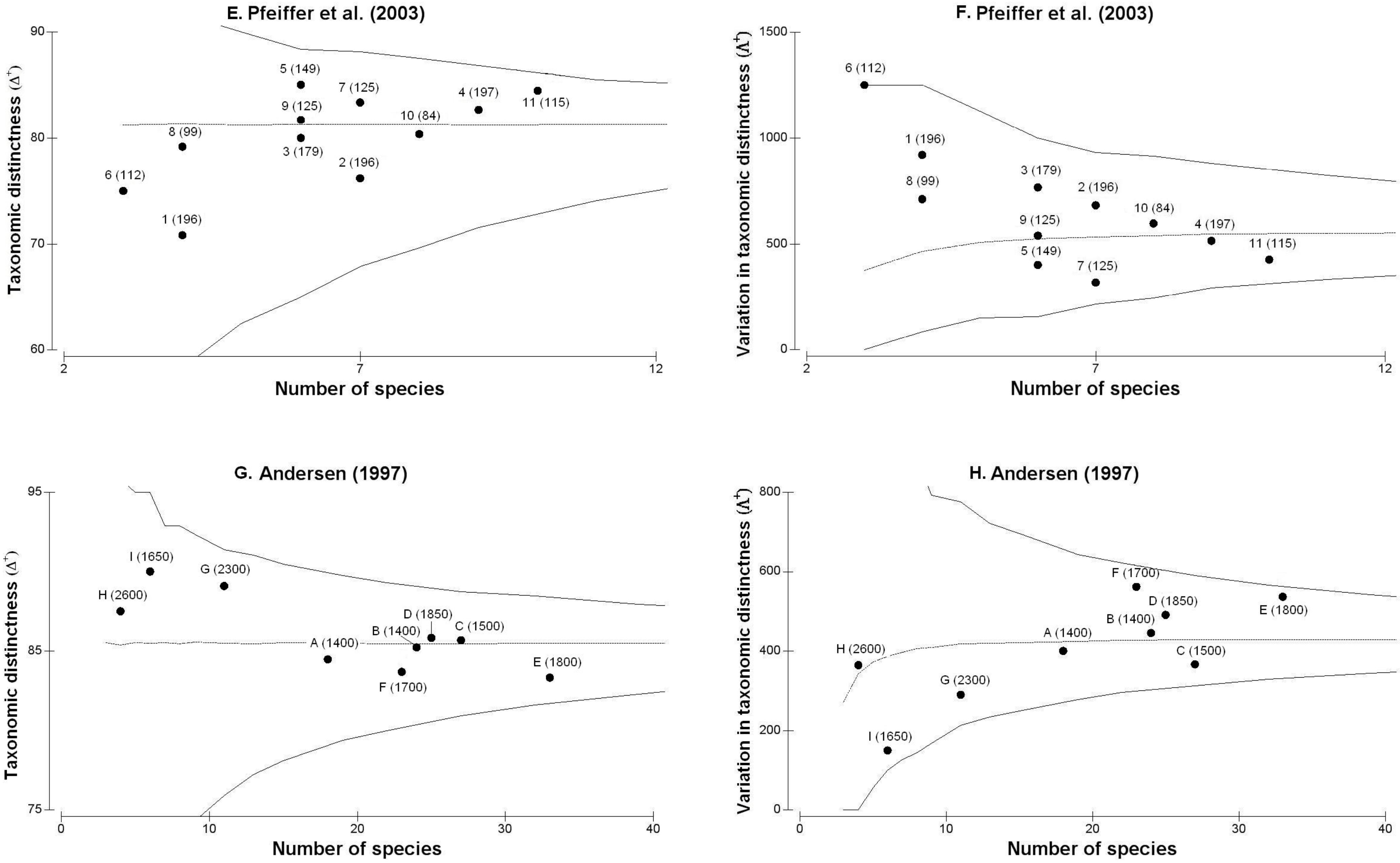

Variation in taxonomic distinctness (Λ^+)
700
500
300
30
40
50
60
70
80
Number of species
3
6
5
8
10
1
7-2001
2
9
4
11
7-2002
7-2004

Figure 5-6


A. Davidson (1977)
Taxonomic distinctness (Δ^+)
80
70
60
50
40
0
5
10
15
Number of species
2 (88)
3 (121)
5 (142)
1 (76)
7 (215)
6 (216)
8 (276)
4 (91)
10 (224)
9 (276)
B. Davidson (1977)
Variation in taxonomic distinctness (Λ^+)
600
400
200
0
0
5
10
15
Number of species
9 (276)
4 (91)
8 (276)
10 (224)
7 (215)
6 (216)
5 (142)
1 (76)
2 (88)
3 (121)
C. Marsh (1986)
Taxonomic distinctness (Δ^+)
90
80
70
60
5
10
15
20
25
Number of species
26 (17.4)
63 (30)
54 (25)
73 (36)
102 (78)
16 (16.5)
45 (22.6)
82 (45)
92 (61)
35 (20)
113 (95)
D. Marsh (1986)
Variation in taxonomic distinctness (Λ^+)
900
700
500
300
5
10
15
20
25
Number of species
16 (16.5)
35 (20)
26 (17.4)
45 (22.6)
73 (36)
92 (61)
113 (95)
54 (25)
82 (45)
63 (30)
102 (78)


E. Pfeiffer et al. (2003)
Taxonomic distinctness (Δ^+)
90
80
70
60
2
7
12
Number of species
5 (149)
7 (125)
4 (197)
11 (115)
9 (125)
10 (84)
8 (99)
3 (179)
2 (196)
6 (112)
1 (196)
F. Pfeiffer et al. (2003)
Variation in taxonomic distinctness (Λ^+)
1500
1000
500
0
2
7
12
Number of species
6 (112)
1 (196)
8 (99)
3 (179)
2 (196)
10 (84)
9 (125)
4 (197)
11 (115)
5 (149)
7 (125)
G. Andersen (1997)
Taxonomic distinctness (Δ^+)
95
85
75
0
10
20
30
40
Number of species
I (1650)
G (2300)
H (2600)
D (1850)
B (1400)
C (1500)
A (1400)
E (1800)
F (1700)
H. Andersen (1997)
Variation in taxonomic distinctness (Λ^+)
800
600
400
200
0
0
10
20
30
40
Number of species
F (1700)
D (1850)
B (1400)
E (1800)
A (1400)
H (2600)
C (1500)
G (2300)
I (1650)

Appendix 5-1

Taxonomy relationship and species number of each ground-foraging ant genus collected in the Paraguayan dry Chaco.

Subfamily	Tribe	Genus	Number of species
Dolichoderinae	Dolichoderini	*Azteca*	1
-	-	*Dorymyrmex*	11
-	-	*Forelius*	10
-	-	*Gracilidris*	1
-	-	*Linepithema*	1
-	-	*Tapinoma*	1
Ecitoninae	Ecitonini	*Labidus*	1
-	-	*Neivamyrmex*	5
Ectatomminae	Ectatommini	*Ectatomma*	4
-	-	*Gnamptogenys*	4
Formicinae	Plagiolepidini	*Brachymyrmex*	8
-	-	*Myrmelachista*	1
-	-	*Paratrechina*	1
-	Camponotini	*Camponotus*	23
Myrmicinae	Attini	*Acromyrmex*	5
-	-	*Atta*	5
-	-	*Cyphomyrmex*	7
-	-	*Mycetophylax*	4
-	-	*Mycetosoritis*	1
-	-	*Trachymyrmex*	5
-	Cephalotini	*Cephalotes*	6
-	Crematogastrini	*Crematogaster*	8
-	Formicoxenini	*Leptothorax*	1
-	Solenopsidini	*Oxyepoecus*	3
-	-	*Solenopsis*	29
-	Pheidolini	*Pheidole*	28
-	Myrmici	*Pogonomyrmex*	3
-	Stenammini	*Rogeria*	2
-	Dacetini	*Strumigenys*	3
-	Blepharidattini	*Wasmannia*	2
Ponerinae	Ponerini	*Anochetus*	1
-	-	*Dinoponera*	1
-	-	*Hypoponera*	2
-	-	*Odontomachus*	3
-	-	*Pachycondyla*	2
Pseudomyrmecinae	Pseudomyrmecini	*Pseudomyrmex*	4

Appendix 5-2: Spearman rank order correlation coefficients (r) between environmental variables and subfamily proportions (based on genus, species and occurrence numbers) of ants collected in the Paraguayan dry Chaco. Significant correlations (P<0.05) are written in **bold**.

	Mean annual rainfall (mm) (n=13)	Mean sand proportion (n=8)	Mean silt proportion (n=8)	Mean clay proportion (n=8)
In terms of genus numbers				
Dolichoderinae	r = -0.112; P = 0.709	r = 0.048; P = 0.885	r = -0.048; P = 0.885	r = 0.036; P = 0.885
Ecitoninae	r = 0.448; P = 0.116	r = -0.464; P = 0.233	r = 0.464; P = 0.233	r = 0.561; P = 0.120
Ectatomminae	r = 0.071; P = 0.806	r = 0.096; P = 0.794	r = -0.096; P = 0.794	r = -0.252; P = 0.498
Formicinae	r = 0.241; P = 0.414	r = -0.289; P = 0.460	r = 0.289; P = 0.460	r = 0.627; P = 0.086
Myrmicinae	r = -0.480; P = 0.093	r = 0.168; P = 0.662	r = -0.168; P = 0.662	r = -0.467; P = 0.207
Ponerinae	r = -0.006; P = 0.978	r = 0.120; P = 0.749	r = -0.120; P = 0.749	r = -0.204; P = 0.578
Pseudomyrmecinae	r = -0.227; P = 0.447	r = 0.241; P = 0.537	r = -0.241; P = 0.537	r = -0.554; P = 0.139
In terms of species numbers				
Dolichoderinae	r = -0.570; **P = 0.039**	r = 0.738; **P = 0.029**	r = -0.738; **P = 0.029**	r = -0.452; P = 0.233
Ecitoninae	r = 0.438; P = 0.126	r = -0.464; P = 0.233	r = 0.464; P = 0.233	r = 0.561; P = 0.120
Ectatomminae	r = 0.262; P = 0.372	r = -0.095; P = 0.794	r = 0.095; P = 0.794	r = -0.071; P = 0.839
Formicinae	r = -0.022; P = 0.935	r = -0.310; P = 0.423	r = 0.310; P = 0.423	r = 0.381; P = 0.321
Myrmicinae	r = -0.037; P = 0.892	r = -0.192; P = 0.619	r = 0.192; P = 0.619	r = -0.144; P = 0.705
Ponerinae	r = 0.082; P = 0.778	r = -0.024; P = 0.931	r = 0.024; P = 0.931	r = 0.108; P = 0.749
Pseudomyrmecinae	r = -0.120; P = 0.682	r = 0.286; P = 0.460	r = -0.286; P = 0.460	r = -0.262; P = 0.498
In terms of occurrences				
Dolichoderinae	r = -0.477; P = 0.093	r = 0.929; **P < 0.001**	r = -0.929; **P <0.001**	r = -0.714; **P = 0.037**
Ecitoninae	r = 0.375; P = 0.199	r = -0.464; P = 0.233	r = 0.464; P = 0.233	r = 0.561; P = 0.120
Ectatomminae	r = 0.405; P = 0.160	r = -0.571; P = 0.120	r = 0.571; P = 0.120	r = 0.595; P = 0.102
Formicinae	r = -0.020; P = 0.935	r = -0.190; P = 0.619	r = 0.190; P = 0.619	r = 0.071; P = 0.839
Myrmicinae	r = 0.087; P = 0.764	r = 0.048; P = 0.885	r = -0.048; P = 0.885	r = 0.119; P = 0.749
Ponerinae	r = -0.048; P = 0.863	r = -0.120; P = 0.749	r = 0.120; P = 0.749	r = 0.132; P = 0.705
Pseudomyrmecinae	r = -0.209; P = 0.481	r = -0.214; P = 0.578	r = 0.214; P = 0.578	r = -0.095; P = 0.794

Appendix 5-3: Spearman rank order correlation coefficients (r) between environmental variables and genus (or other taxa) occurrence proportions of ants collected in the Paraguayan dry Chaco. Significant correlations (P<0.05) are written in **bold**.

	Mean annual rainfall (mm) (n=13)	Mean sand proportion (n=8)	Mean silt proportion (n=8)	Mean clay proportion (n=8)
Dorymyrmex	r = -0.477; P = 0.093	r = 0.587; P = 0.102	r = -0.587; P = 0.102	r = -0.252; P = 0.498
Forelius	r = -0.204; P= 0.493	r = 0.357; P = 0.353	r = -0.357; P = 0.353	r = -0.167; P = 0.662
Ectatomma	r = 0.364; P = 0.214	r = -0.167; P = 0.662	r = 0.167; P = 0.662	r = 0.214; P = 0.578
Brachymyrmex	r = 0.010; P = 0.964	r = 0.012; P = 0.931	r = -0.012; P = 0.931	r = -0.252; P = 0.498
Camponotus	r = 0.002; P = 0.978	r = 0.190; P = 0.619	r = -0.190; P = 0.619	r = -0.357; P = 0.353
Attini	r = 0.047; P = 0.863	r = -0.190; P = 0.619	r = 0.190; P = 0.619	r = 0.357; P = 0.353
Crematogaster	r = -0.493; P = 0.081	r = 0.571; P = 0.120	r = -0.571; P = 0.120	r = -0.667; P = 0.059
Pheidole	r = 0.413; P = 0.154	r = -0.738; **P = 0.029**	r = 0.738; **P = 0.029**	r = 0.857; **P = 0.002**
Pogonomyrmex	r = -0.471; P = 0.098	r = 0.667; P = 0.059	r = -0.667; P = 0.059	r = -0.333; P = 0.387
Solenopsis	r = -0.022; P = 0.935	r = -0.143; P = 0.705	r = 0.143; P = 0.705	r = 0.190; P = 0.619
Odontomachus	r = -0.388; P = 0.179	r = 0.263; P = 0.498	r = -0.263; P = 0.498	r = -0.228; P = 0.537
Pseudomyrmex denticollis	r = -0.268; P = 0.362	r = 0.0; P = 0.977	r = 0.0; P = 0.977	r = -0.452; P = 0.233

Discussion générale - Perspectives

1. Structure des assemblages de fourmis, distribution et coexistence des espèces.

1.1. Synthèse des principaux résultats.

Au sein du Chaco sec paraguayen, nous avons mis en évidence que:

1. la diversité α des assemblages de fourmis n'est corrélée ni à l'aridité, ni aux conditions édaphiques (Chapitres 4 et 5; Tableau 6-1);
2. la distribution des espèces est influencée par ces deux facteurs, en particulier par la texture du sol (Chapitre 4);
3. des ségrégations spatiales d'espèces existent à l'échelle du gradient étudié (Chapitre 3). Trois complexes fauniques sont distingués: le premier dans la localité la plus sèche (pluviométrie moyenne annuelle: 350mm) et la plus sableuse (>90% de sable dans la fraction minérale du sol), le second au niveau de la localité la plus humide (1000mm; sol argilo-limoneux) et le dernier dans des localités présentant de larges conditions de pluviométrie (350-850mm) et de sol (limoneux à sablo-limoneux) (Chapitre 4);
4. les différences de composition faunique des assemblages sont plus prononcées au niveau spécifique qu'au niveau des taxons supérieurs (Chapitres 4 et 5);
5. l'un des mécanismes limitant la compétition interspécifique (et donc qui facilite la coexistence des espèces à l'échelle locale) est l'établissement d'une ségrégation spatio-temporelle fine des espèces lors de l'exploitation des ressources alimentaires en raison de l'existence de deux compromis ("trade-offs"): l'un entre les capacités de dominance et de découverte des ressources, l'autre entre la capacité de dominance et la tolérance aux températures élevées (Chapitre 2).

1.2. Discussion et perspectives de recherche.

L'absence de relation entre la richesse spécifique et l'aridité est peut-être le résultat le plus inattendu de notre étude. L'aridité traduit la différence existant entre les précipitations moyennes annuelles et l'évapotranspiration potentielle (ETP). Cette dernière étant définie comme la quantité d'eau transférée vers l'atmosphère par l'évaporation du sol et par la transpiration des plantes. Dans le cadre de cette thèse, nous avons utilisé la pluviométrie annuelle moyenne comme une approximation du niveau d'aridité. Il serait cependant nécessaire de mesurer l'ETP à chacune des localités étudiées afin d'avoir des données plus précises concernant leur niveau d'aridité et donc d'évaluer ce facteur *per se* sur la structure et la distribution des assemblages de fourmis.

La pluviométrie étant une mesure indirecte de la productivité primaire nette (P.P.N.) d'un habitat (Kaspari *et al.*, 2000), nos résultats suggèrent que la richesse spécifique des assemblages de fourmis n'est pas influencée par ce facteur à l'échelle du gradient étudié. Il est possible que même dans les localités les moins productives, la P.P.N. de l'habitat ne soit pas limitante pour les fourmis. Il est toutefois envisageable qu'elle ait un impact sur des paramètres non mesurés dans le cadre de cette thèse, comme par exemple sur la taille des colonies ou sur la densité des nids (Kaspari *et al.*, 2000). Il serait nécessaire de mesurer directement la P.P.N. et d'établir comment la biomasse végétale produite est transférée aux fourmis via les chaînes trophiques.

Après s'être demandé pourquoi une diminution de la richesse spécifique n'a pas été observée dans les localités les moins productives, on peut se poser la question inverse: pourquoi n'y a-t-il pas plus d'espèces dans les localités les plus productives? Le Gran Chaco et plus généralement les forêts tropicales sèches sont caractérisés par un régime des pluies erratique (Gorham, 1973; Ramella et Spichiger, 1989; Murphy et Lugo, 1995). L'irrégularité des précipitations (durée, quantité et fréquence) engendre probablement des variations spatio-temporelles de P.P.N. (Knapp *et al.*, 2002; Schwinning et Sala, 2004; Haper *et al.*, 2005) dont l'imprédictibilité peut constituer un facteur limitant la diversité α des assemblages de fourmis. Il serait intéressant de mettre au point un système expérimental permettant de manipuler la quantité et la fréquence des pluies sur différentes parcelles du Chaco paraguayen afin de mesurer l'influence de ces variables sur la structure des assemblages de fourmis.

L'aridité était également susceptible de limiter directement la diversité α des assemblages de fourmis en exerçant un stress physiologique sur les espèces (Hawkings *et al.*, 2003).

L'absence de relation entre la richesse spécifique et l'aridité amène à s'interroger sur les mécanismes et les adaptations physiologiques, anatomiques et/ou comportementales potentiellement développés par les espèces de fourmis afin de persister dans les localités les plus sèches du Chaco paraguayen.

Dans le Chapitre 4, nous émettions l'hypothèse selon laquelle les capacités à s'abriter dans un nid souterrain et/ou à rester inactives pendant les périodes défavorables permettaient aux fourmis de tolérer les effets négatifs de l'aridité. Il est possible que l'architecture du nid de certaines espèces permette en outre une régulation de la température et de l'hygrométrie des galeries (Cole, 1994; Kleineidam *et al.*, 2001). Par exemple, plusieurs espèces de *Pheidole* appartenant au groupe *fallax* construisent des nids souterrains dont l'entrée est un large trou au diamètre pouvant dépasser 7 centimètres (Figure 6-1A). Cette structure semblable à une vaste "cheminée" a-t-elle une signification adaptative? Il serait intéressant de le vérifier. D'autres architectures ont été observées (Figure 6-1). Les nids avec dôme de *Mycetophylax emeryi* (Figure 6-1B) sont peut-être une adaptation aux amples variations nycthémérales et saisonnières de températures rencontrées dans le Gran Chaco (Prado, 1993; Pennington *et al.*, 2000; Chapitre 2) car cette structure permet d'augmenter la surface du nid exposée aux rayons du soleil et donc facilite le réchauffement de la colonie (Cole, 1994). Les *Forelius* sont des espèces thermophiles qui installent leurs colonies dans des zones découvertes exposées en plein soleil. L'orifice de leurs nids est un simple trou dont le faible diamètre permet peut-être d'éviter les pertes en eau (Figure 6-1D). Les structures décrites ci-dessus sont les parties visibles du nid. Quelle est l'architecture du nid des différentes espèces sous le sol? Varie-t-elle en fonction des conditions édaphiques et climatiques? Les études concernant l'architecture des nids de fourmis sont encore principalement dans une phase descriptive (Moreira *et al.*, 2004; Tschinkel, 2004; 2005; Verza *et al.*, 2007) dont le développement permettra de mieux comprendre la signification adaptative des structures observées.

D'autres adaptations à l'aridité sont envisageables. Certaines espèces ont pu évoluer vers un mode de vie principalement hypogé. C'est apparemment le cas de *Linepithema cryptobioticum* dont la morphologie très particulière pour ce genre (petits yeux, corps robuste, couleur jaune) semble indiquer une vie essentiellement souterraine (Wild, 2007; Figure 6-2).

Dans les milieux secs, les espèces de petite taille sont généralement défavorisées car elles présentent un rapport surface sur volume élevé ce qui diminue leur résistance à la dessication (Délye, 1967; Hood et Tschinkel, 1990; Kaspari, 1993). Ce désavantage est toutefois compensé par le fait qu'elles possèdent souvent une cuticule plus imperméable que celle des grandes espèces (Délye, 1967). Des résultats préliminaires montrent que la majorité des espèces chaquéennes sont de petite taille (Annexe 1). *Dinoponera mutica* est toutefois une exception remarquable puisqu'il s'agit de l'une des plus grandes fourmis du monde, avec une longueur corporelle d'environ 3cm (Lattke, 2003). Des analyses plus approfondies permettront de déterminer si l'aridité influence la distribution des fourmis en fonction de leur taille dans le Chaco sec paraguayen.

Nos résultats montrent que la distribution des espèces de fourmis au sein du Chaco sec paraguayen est particulièrement influencée par les conditions édaphiques (Chapitre 4). On peut se demander si des adaptations particulières ont été développées de la part des fourmis en réponse à la texture du sol. Les "remparts" présents autour de l'orifice de certains nids (Figure 6-1C) seraient une adaptation aux milieux sableux car ils permettraient de limiter l'entrée dans le nid de particules de sable transportées par le vent (Diehl-Fleig et Diehl, 2007). D'autre part, de nombreuses espèces des milieux arides possèdent de longs poils disposés sur le bord antérieur du clypéus, sur les mandibules et/ou en dessous de la tête (Wheeler, 1907; Figure 6-3). Santschi (1909) a montré qu'ils facilitaient le transport des grains de sable et a donc nommé ces franges de poils "psammophore". Délye (1971) décrit de façon détaillée comment la fourmi saharienne *Messor arenarius* transporte des amas de sable à l'aide de cette structure. Dans le Chaco paraguayen, plusieurs espèces de *Dorymyrmex* possèdent un psammophore (Figure 6-3A) ce qui contribue à expliquer pourquoi la localité la plus sableuse est celle où ce genre était le plus diversifié (7 espèces collectées à Fortín Mister Long; Annexe 2; Figure 3-2 du Chapitre 3).

Il est nécessaire de ne pas oublier que la perception de la relation entre la richesse spécifique et un stress abiotique dépend de l'étendue du gradient échantillonné (Andersen, 1997; Figure 6-4). La relation positive observée par Davidson (1977) et Marsh (1986) entre la richesse spécifique des assemblages de fourmis et l'aridité est probablement due au fait que ces auteurs ont travaillé dans des conditions plus arides que celles du Chaco paraguayen. Bien que l'étendue du gradient de pluviométrie considérée dans le cadre de cette thèse soit déjà importante (350 à 1000mm/an soit la plus large gamme abordée jusqu'à présent) il serait intéressant d'inclure dans de futures analyses des assemblages provenant du Chaco humide afin d'accroître l'amplitude des pluviométries étudiées (jusqu'à 1400mm). Ceci permettrait également de vérifier si la singularité de la myrmécofaune de la localité la moins aride est due à la présence d'espèces du Chaco humide comme nous l'avions supposé dans le Chapitre 4. [Une analyse préliminaire ayant pour but d'identifier les espèces caractéristiques des trois complexes fauniques mis en évidence par notre étude est présentée en Annexe 3]. De même, il est important de souligner que les résultats obtenus et présentés dans cette thèse concernent les espèces de fourmis actives dans le Chaco sec paraguayen au début de la saison humide. Il serait intéressant de réaliser des échantillonnages à différentes saisons et/ou sur des échelles temporelles plus étendues afin d’avoir une meilleure représentation de la myrmécofaune présente au niveau de chaque localité.

L'existence d'un complexe faunique présent dans des milieux aux conditions de pluviométrie (350-850mm) et de sol (limoneux à sablo-limoneux) très larges est surprenante. Cela contredit l'idée générale selon laquelle les fourmis répondent de façon fine aux conditions du milieu (Andersen *et al.*, 2004). D'autre part, le long du gradient environnemental étudié, les espèces semblent se distribuer indépendamment les unes des autres, sans former d'associations d'espèces bien délimitées spatialement (Annexe 3). Ceci reste valable lorsque l'on ne compare que des espèces congénériques. Ces dernières sont supposées présenter entre elles plus de similarités morphologiques et/ou écologiques qu'entre des espèces phylogénétiquement éloignées en raison de la conservation des traits écologiques lors de l'évolution des lignées ("niche conservatism") (Lord *et al.*, 1995; Webb, 2000; Webb *et al.*, 2002). On pouvait donc s'attendre à observer soit des associations étroites entre espèces congénériques, soit au contraire des ségrégations spatiales abruptes en raison d'une forte compétition entre espèces aux exigences écologiques proches. Dans le Chapitre 2 nous avons montré que les variations nycthémérales de températures limitaient la compétition interspécifique et donc facilitaient la coexistence spatiale des espèces. Les résultats des Chapitres 4 et 5 suggèrent en outre que la tolérance à l'aridité est largement répandue au sein des Formicidae.

Puisque cette étude est la première à s'intéresser à l'influence de l'aridité sur les assemblages de fourmis au sein d'une forêt tropicale sèche, il est légitime de se demander jusqu'à quel point nos résultats sont représentatifs. Il serait nécessaire de reproduire notre travail dans d'autres formations sclérophylles. Ceci améliorerait l'interprétation des patrons de distribution obtenus et permettrait de les placer dans un contexte biogéographique plus large. En Amérique du Sud, la Caatinga brésilienne semble pertinente pour une telle étude car s'y présente une gamme de pluviométrie comparable à celle du Chaco sec paraguayen (300 à 1000mm/an [Sampaio, 1995]).

Il serait également important de déterminer les origines et de retracer la mise en place de la myrmécofaune chaquéenne afin de mieux appréhender le rôle de l'histoire dans les distributions observées. Quelles sont les affinités phylogénétiques des fourmis du Gran Chaco et des espèces présentes au sein d'autres formations sèches néotropicales comme le Cerrado ou la Caatinga? La flore du Gran Chaco a évolué à partir d'une formation tempérée de moyenne latitude (Noss *et al.*, 2002) et possède peu d'affinités avec la végétation des autres forêts tropicales sèches d'Amérique du Sud (Pennington *et al.*, 2000; Spichiger *et al.*, 2004). La myrmécofaune chaquéenne a-t-elle connu une histoire évolutive parallèle à celle de la végétation?

Cette étude nécessite un développement préalable des connaissances concernant la taxonomie des fourmis du Chaco paraguayen.

2. Avancées taxonomiques et valorisation des données.

Au total, plus de 50.000 spécimens correspondant à 206 espèces ou morpho-espèces de fourmis ont été collectés au sein des 11 localités du Chaco sec paraguayen étudiées (Annexe 2). A titre de comparaison, la myrmécofaune de la région néotropicale comprend plus de 3100 espèces (Fernández, 2003) dont 544 étaient répertoriées sur l'ensemble du territoire paraguayen avant notre étude (Wild, in prep.). Toujours pour donner un ordre de grandeur, 82 espèces sont recensées en Belgique (Dekoninck *et al.*, 2006), 524 ont été collectées au niveau du sol et de la canopée dans 4km² d'une forêt primaire de Bornéo (Brühl *et al.*, 1998) et 61 au sein de 70 parcelles de 0,1ha réparties dans une zone de 2500km² de la Caatinga brésilienne (Leal, 2003; Leal *et al.*, 2007).

Notre collection est, pour l'instant, la plus importante pour le Chaco sec paraguayen. Une collection de référence est disponible à l'I.R.Sc.N.B., une seconde sera envoyée au "Museo Nacional del Historia Natural del Paraguay". L'identification des morpho-espèces n'est pas achevée et s'effectue en collaboration avec le Dr. William MacKay[1] et le Dr. Alex Wild[2]. De nombreuses espèces sont nouvelles pour la science (peut-être 20%). Par exemple, *Linepithema cryptobioticum* a été décrite à partir de nos échantillons (Wild, 2007; Figure 6-2) et une nouvelle espèce de *Camponotus* est également en cours de description (MacKay et Delsinne, in prep.).

---

[1] "Laboratory for Environmental Biology, The University of Texas, El Paso".

[2] "Department of Entomology, University of Arizona, Tucson."

L'identification des morpho-espèces est une activité laborieuse mais fondamentale car, d'une part, la diversité des taxons supérieurs (genre par exemple) ne peut pas être utilisée comme indicatrice de la diversité spécifique des assemblages de fourmis dans le Chaco sec paraguayen (Annexe 4) et, d'autre part, elle permettra d'utiliser notre collection comme base de référence pour de futures études consacrées aux fourmis de cette région néotropicale.

En collaboration avec Julien Cillis (I.R.Sc.N.B., microscopie à balayage), un projet de documentation, à l'aide de photographies prises en microscopie électronique, de toutes les espèces dont la taille est inférieure au centimètre est actuellement en cours. Jusqu'à présent, plus de 100 spécimens appartenant à 60 morpho-espèces ont ainsi été photographiés. Les espèces plus larges seront documentées à l'aide de photographies à haute résolution et profondeur de champ intégrale réalisées en microscopie optique. Afin d'accélérer l'identification des spécimens et de favoriser l'intégration des fourmis dans des programmes d'évaluations biologiques ou de suivi de la diversité des assemblages dans le Chaco paraguayen, un site internet interactif présentant les images de ce "musée virtuel" sera créé avec l'aide du "Belgian Biodiversity Information Facility" (Be.B.I.F.). Ce site sera en lien avec le "AntWeb" de "the California Academy of Science" (http://www.antweb.org) qui constitue un outil de référence pour les myrmécologistes. Ce dernier dispose pour l'instant de données issues principalement des régions néarctique, eurasienne et malgache. Nos données permettront donc d'accroître l'aire géographique couverte par "AntWeb".

3. Apports de cette étude en biologie de la conservation.

3.1. Calibrage d'un protocole d'échantillonnage de la myrmécofaune en forêt tropicale sèche.

L'un des objectifs du travail de thèse était de vérifier l'applicabilité du protocole "Ants of the Leaf Litter" (Agosti et Alonso, 2000) dans les forêts tropicales sèches. Nous avons clairement montré que l'aridité et la saisonnalité des précipitations influencent la capacité de collecte des pièges à fosse et des Winkler, les deux principales méthodes d'échantillonnage du protocole A.L.L. (Chapitre 1).

Lors de périodes sèches, un échantillonnage basé sur les Winkler peut entraîner une sévère sous-estimation de la diversité d'un assemblage. La méthode des pièges à fosse est donc à conseiller, en particulier lorsque l'objectif est d'effectuer une estimation rapide de la diversité myrmécofaunique d'une localité. Il est toutefois nécessaire de rappeler que les pièges à fosse collectent principalement les espèces qui fourragent au niveau du sol. Des espèces cryptiques, potentiellement intéressantes en biologie de la conservation [comme par exemple les espèces du genre *Oxyepoecus* (Annexe 5)], peuvent ne pas être documentées.

Un transect A.L.L. basé sur les pièges à fosse (c'est-à-dire 20 pièges alignés et espacés de 10m les uns des autres) permet de déterminer les espèces numériquement dominantes d'un assemblage. Cependant, ces espèces sont en général celles dont la répartition est la plus large (Chapitre 4) et l'information apportée est donc limitée. Selon les objectifs visés par les futures études s'intéressant aux assemblages de fourmis en forêt sèche, il sera probablement souvent préférable d'échantillonner le long de deux ou trois transects afin de mieux caractériser l'assemblage.

La disposition spatiale des transects choisie dans le cadre de cette thèse est discutable. Notre but était d'effectuer un inventaire le plus complet possible de la myrmécofaune des différentes localités. Nous avons donc opté pour une disposition linéaire des transects car celle-ci augmente la probabilité de collecter au sein de plusieurs microhabitats et donc d'inventorier des espèces aux exigences écologiques diverses. Si l'objectif est au contraire de caractériser l'assemblage d'un habitat le plus homogène possible, il est alors probablement préférable de disposer les transects parallèlement les uns aux autres.

3.2. Congruence des patrons de distribution des assemblages de fourmis et de végétaux.

Dans le Chaco sec paraguayen, à l'échelle du gradient étudié, les plantes dominantes répondent aux conditions de sol et de pluviométrie plus finement que les assemblages de fourmis (Chapitre 4). Nos résultats vont dans le sens de ceux obtenus par Majer et Delabie (1994) et par Vasconcelos et Vilhena (2006). Les premiers ont comparé la myrmécofaune de formations forestières du Bassin Amazonien brésilien soumises ou non à des inondations périodiques. Ils ont montré qu'environ 50% des espèces de fourmis de l'habitat le plus pauvre (celui périodiquement inondé) étaient présentes au sein de l'habitat le plus riche alors que seulement 5 à 10% des espèces d'arbres étaient communes aux deux types forestiers. Les seconds ont étudié la myrmécofaune d'une parcelle de 256km² du Cerrado brésilien et ont trouvé que 64% des espèces de fourmis collectées dans les savanes étaient présentes dans les forêts.

Ces résultats suggèrent que, dans ces habitats, les plantes dominantes peuvent constituer un groupe "parapluie" ("umbrella species") pour la conservation de la diversité biologique des fourmis. Ainsi, une sélection des sites à protéger basée sur une maximisation de la complémentarité des assemblages de plantes est susceptible de maximiser la conservation de la diversité biologique globale des fourmis.

Nos résultats n'excluent pas l'existence de relations plantes/fourmis au sein du Chaco sec paraguayen et il serait intéressant de détailler ces interactions biotiques car elles peuvent avoir un impact sur les patrons de distributions spatiales de ces deux types d'organismes. La myrmécochorie est un mécanisme de dispersion souvent employé chez les plantes des milieux sclérophylles (Andersen *et al.*, 2000; Botes *et al.*, 2006; Leal *et al.*, 2007). Par exemple, dans 70 parcelles de 0,1ha de Caatinga, les graines de 26,7% des espèces d'arbres et d'arbustes (soit 27 espèces) sont transportées par 18 espèces de fourmis (soit 30% des espèces documentées au sein de ces parcelles) (Leal *et al.*, 2007). Les genres de certaines plantes (*Cereus*, *Opuntia*, *Capparis*, *Jatropha*, *Ziziphus*) et tous ceux de fourmis (*Dorymyrmex, Ectatomma, Camponotus, Crematogaster, Cyphomyrmex, Pheidole, Solenopsis, Trachymyrmex, Odontomachus, Dinoponera*) sont présents dans le Chaco sec paraguayen, ce qui permet de supposer que la myrmécochorie y est également répandue. Quelle est son importance et quel est son impact sur la distribution spatiale des espèces de plantes chaquéennes?

3.3. Perspectives en biologie de la conservation.

L'importance écologique des fourmis à titre de taxon clé de voûte justifie des actions de conservation les visant spécifiquement (Underwood et Fisher, 2006). Trois complexes myrmécofauniques ont été mis en évidence par notre étude (Chapitre 4). Deux d'entre eux sont représentés à l'intérieur du réseau actuel de sites protégés du Chaco paraguayen (Figure 6-5). Le complexe faunique non représenté est celui de la localité la plus humide (Río Verde) et il serait donc souhaitable de mettre en place des actions visant à sa conservation. Ceci est d'autant plus important que la partie orientale du Chaco paraguayen reste peu protégée bien qu'elle subisse une forte pression anthropique.

D'autre part, nous avons montré que la texture du sol influence de façon importante la distribution des espèces de fourmis et de plantes dans le Chaco sec paraguayen (Chapitre 4).

Une zone non prospectée mais susceptible de recéler une forte diversité biologique est celle correspondant au réseau de drainage fossile du Río Pilcomayo (Figure 6-6). La plaine du Gran Chaco ayant une déclivité très faible, les fleuves et les rivières qui la traversent ont, à l'échelle des temps géologiques, un cours instable (Prado, 1993; Figure 6-6A). Les propriétés physico-chimiques des sols actuels varient fortement en fonction de l'âge de ces anciens lits et ces variations se reflètent au niveau des formations végétales qui s'y développent (Mereles, 2005; Figure 6-6B). Il serait intéressant d'étudier la myrmécofaune de cette zone car la variété des conditions édaphiques rencontrées permettrait d'étudier de façon plus approfondie l'impact du sol sur la structure et la distribution des assemblages de fourmis. D'autre part, si la diversité biologique de cette aire géographique se révèle importante et exige une protection, sa mise en défens pourrait être relativement aisée car cette zone est l'une des moins peuplées du Chaco paraguayen.

3.4. Impact potentiel des changements climatiques globaux sur les assemblages de fourmis dans le Chaco sec paraguayen.

Les activités anthropiques, via la combustion des énergies fossiles et l'émission de gaz à effet de serre, sont responsables des "changements climatiques globaux" (I.P.C.C., 2007). Les modèles climatologiques prévoient une augmentation globale de la température ainsi que des pluies (quantité, intensité, fréquence) dans les régions tropicales et de hautes latitudes. En revanche, dans les régions de moyennes latitudes et subtropicales, une diminution de la pluviométrie moyenne est attendue, accompagnée cependant d'une augmentation de l'intensité des précipitations et de la durée des périodes sèches (I.P.C.C., 2007).

Nos résultats indiquent que les distributions des assemblages de fourmis dans le Chaco sec paraguayen sont conditionnées spécialement par la texture du sol. Ces organismes semblent tolérer une large amplitude de pluviométries moyennes (Chapitre 4). Un accroissement de l'aridité lié aux changements climatiques globaux ne devrait donc pas affecter de façon importante la distribution des fourmis dans cette région. Toutefois, nous n'avons étudié ni l'impact de la température ni celui de la fréquence et de l'intensité des pluies sur la structure et la distribution des assemblages de ces organismes. Il serait donc hasardeux d'effectuer de plus amples projections et imprudent d'être trop optimiste. Cette thèse pourrait constituer le point de départ d'un suivi des assemblages de fourmis du Chaco sec paraguayen dans le but d'investiguer l'impact des changements climatiques globaux sur ces insectes.

Références bibliographiques.

Agosti, D., Alonso, L.E., 2000. The ALL protocol: a standard protocol for the collection of ground-dwelling ants. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (eds). Ants: standard methods for measuring and monitoring biodiversity, pp. 204-206. Smithsonian Institution Press, Washington, D.C.

Andersen, A.N., 1997. Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology [online] 1: 8. http:// www.consecol.org/vol1/iss1/art8/

Andersen, A.N., Azcarate, F.M., Cowie, I.D., 2000. Seed selection by an exceptionally rich community of harvester ants in the Australian seasonal tropics. Journal of Animal Ecology 69: 975-984.

Andersen, A.N., Fisher, A., Hoffmann, B.D., Read, J.L., Richards, R., 2004. Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecology 29: 87-92.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P., Chown, S.L., 2006. Ants, altitude and change in the northern Cape Floristic Region. Journal of Biogeography 33: 71-90.

Brühl, C.A., Gunsalam, G. Linsenmair, K.E., 1998. Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. Journal of Tropical Ecology 14: 285-297.

Cole, B.J., 1994. Nest architecture in the western harvester ant, *Pogonomyrmex occidentalis* (Cresson). Insectes Sociaux 41: 401-410.

Davidson, D.W., 1977. Species diversity and community organization in desert seed-eating ants. Ecology 58: 711-724.

Dekoninck, W., Maelfait, J.-P., Vankerkhoven, F., Baugnée, J.-Y., Grootaert, P., 2006. An update of the checklist of the Belgian ant fauna with comments on new species for the country (Hymenoptera, Formicidae). Belgian Journal of Entomology 8: 27-41.

Délye, G., 1967. Physiologie et comportement de quelques fourmis (Hym. Formicidae) du Sahara en rapport avec les principaux facteurs du climat. Insectes Sociaux 4: 323-338.

Délye, G., 1971. Observations sur le nid et le comportement constructeur de *Messor arenarius* (Hyménoptères Formicidae). Insectes Sociaux 18: 15-20.

Diehl-Fleig, Ed., Diehl, E., 2007. Nest architecture and colony size of the fungus-growing ant *Mycetophylax simplex* Emery, 1888 (Formicidae, Attini). Insectes Sociaux. *In press.*

Fernández, F., 2003. Listado de las especies de hormigas de la región Neotropical. pp. 379-411. In: Fernández, F. (ed.). Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia. XXVI + 398 pp.

Gorham, J.R., 1973. The Paraguayan Chaco and its rainfall. In: Gorham, J.R. (ed.). Paraguay: ecological essays, pp. 39-60. Academy of the Arts and Sciences of the Americas, Miami, FL.

Harper, C.W., Blair, J.M., Fay, P.A., Knapp, A.K., Carlisle, J.D., 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem. Global Change Biology 11: 322-334.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 24: 3105-3117.

Hood, G.W., Tschinkel, W.R., 1990. Dessication resistance in arboreal and terrestrial ants. Physiological Entomology 15: 23-35.

I.P.C.C. (Intergovernmental Panel on Climate Change), 2007. Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., (eds.)] Cambridge University Press, United Kingdom and Ne York, NY, USA.

Kaspari, M., 1993. Body size and microclimate use in Neotropical granivorous ants. Oecologia 96: 500-507.

Kaspari, M., O'Donnell, S., Kercher, J.R., 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. American Naturalist 155: 280-293.

Kleineidam, C., Ernst, R., Roces, F., 2001. Wind-induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*. Naturwissenschaften 88: 301-305.

Klingenberg, C., 2006. Brasilianische Pilzzüchter-Ameisen der Gattung *Mycetophylax* - Lebensweise und Taxonomie. Dissertation der Fakultät für Biologie der Eberhard Karls Universität Tübingen. 138pp.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298: 2202-2205.

Lattke, J.E., 2003. Subfamilia Ponerinae. pp. 261-276. In: Fernández, F. (ed.). Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia. XXVI + 398 pp.

Leal, I.R., 2003. Diversidade de formigas em diferentes unidades de paisagem da caatinga. pp. 435-461. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. eds. Ecologia e conservação da caatinga. Recife: Editoria Universitária da U.F.P.E.

Leal, I.R., Wirth, R., Tabarelli, M., 2007. Seed dispersal by ants in the semi-arid caatinga of north-east Brazil. Annals of Botany 99: 885-894.

Lord, J., Westoby, M., Leishman, M., 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. American Naturalist 146: 349-364.

Majer, J.D., Delabie, J.H.C., 1994. Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazon. Insectes Sociaux 41: 343-359.

Marsh, A.C.,1986. Ant species richness along a climatic gradient in the Namib Desert. Journal of Arid Environments 11: 235–241.

Mereles, M.F., 2005. Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay. Rojasiana 6: 5-48.

Moreira, A.A., Forti, L.C., Boaretto, M.A.C., Andrade, A.P.P., Lopes, J.F.S., Ramos, V.M., 2004. External and internal structure of *Atta bisphaerica* Forel (Hymenoptera: Formicidae) nests. Journal of Applied Entomology 128: 204-211.

Murphy, P.G., Lugo, A.E., 1995. Dry forests of Central America and the Caribbean. In: Bullock, S.H, Mooney, H.A, Medina, E., 1995. Seasonally dry tropical forests, pp. 9-34. Cambridge University Press, Cambridge.

Noss, A., Mares, M.A., Diaz, M.M., 2002. The Chaco. In: Mittermeier, R.A., Mittermeier, C.G., Robles-Gil, P., Pilgrim, J.D., Fonseca, G., Brooks, T.M., Konstant, W.R. (eds): Wilderness. Earth's last wild places, pp. 165-172. Cemex, Mexico City.

Pennington, T.R., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27: 261-273.

Prado, D.E., 1993. What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco. V. Candollea 48: 145-172.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639-680.

Sampaio, E.V.S.B., 1995. Overview of the Brazilian caatinga. In: Bullock, S.H, Mooney, H.A, Medina, E., 1995. Seasonally dry tropical forests, pp. 35-63. Cambridge University Press, Cambridge.

Santschi, F., 1909. Sur la signification de la barbe des fourmis arénicoles. Annales de la Société Zoologique Suisse et du Muséum d'Histoire Naturelle de Genève (Revue Suisse de Zoologie) 17: 449-458.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141: 211-220.

Spichiger, R., Calenge, C., Bise, B., 2004. Geographical zonation in the Neotropics of tree species characteristic of the Paraguay-Paraná Basin. Journal of Biogeography 31: 1489-1501.

Tschinkel, W.R., 2004. The nest architecture of the Florida harvester ant, *Pogonomyrmex badius*. 19pp. Journal of Insect Science 4: 21. Available on line: insectscience.org/4.21

Tschinkel, W.R., 2005. The nest architecture of the ant, *Camponotus socius*. 18pp. Journal of Insect Science 5: 9. Available on line: insectscience.org/5.9

Underwood, E.C., Fisher, B.L., 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132: 166-182.

Vasconcelos, H.L., Vilhena, J.M.S., 2006. Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas. Biotropica 38: 100-106.

Verza, S.S., Forti, L.C., Lopes, J.F.S., Hughes, W.O.H., 2007. Nest architecture of the leaf-cutting ant *Acromyrmex rugosus rugosus*. Insectes Sociaux. *In press.*

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist 156: 145-155.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annual Reviews of Ecology, Evolution and Systematics 33: 475-505.

Wheeler, W.M., 1907. On certain modified hairs peculiar to the ants of arid regions. Biological Bulletin 13: 185-202.

Wild, A.L., 2007. Taxonomic revision of the ant genus *Linepithema* (Hymenoptera: Formicidae). University of California Publications in Entomology 126. Available on line at: http://repositories.cdlib.org/ucpress/ucpe/vol_126

Tableau 6-1: Influence de l'aridité et de la texture du sol sur les diversités α et β des assemblages de fourmis dans le Chaco sec paraguayen: synthèse des principaux résultats.

	Influencé par:		Chapitre
	l'aridité?	la texture du sol?	
Diversité α			
• Richesse spécifique	non	non	4
• Coefficient de Gini (mesure basée sur les fréquences relatives des différentes espèces d'un assemblage)	non	non	4
• Richesse générique	non	non	5
• Indices intégrant la diversité taxonomique des espèces d'un assemblage (Δ^*, Δ^+, Λ^+)	non	non	5
• Proportions relatives des différentes sous-familles collectées	non	non(1)	5
• Proportions relatives des différents genres collectés	non	non(2)	5
Diversité β			
• Variations de la diversité β (complémentarité des assemblages)	oui	oui	4

(1) Hormis les Dolichoderinae.

(2) Hormis les *Pheidole.*

Figure 6-1: Entrées du nid de différentes fourmis du Chaco sec paraguayen.
(A) *Pheidole* spp. (groupe *fallax*): large ouverture dont le diamètre peut dépasser 7cm.
(B) *Mycetophylax emeryi*: nid surmonté d'un petit dôme.
(C) *Dorymyrmex* cf *flavescens*: orifices cernés de remparts. La longueur de la structure mesure environ 15cm.
(D) *Forelius nigriventris*: simple trou de faible diamètre (<1cm).

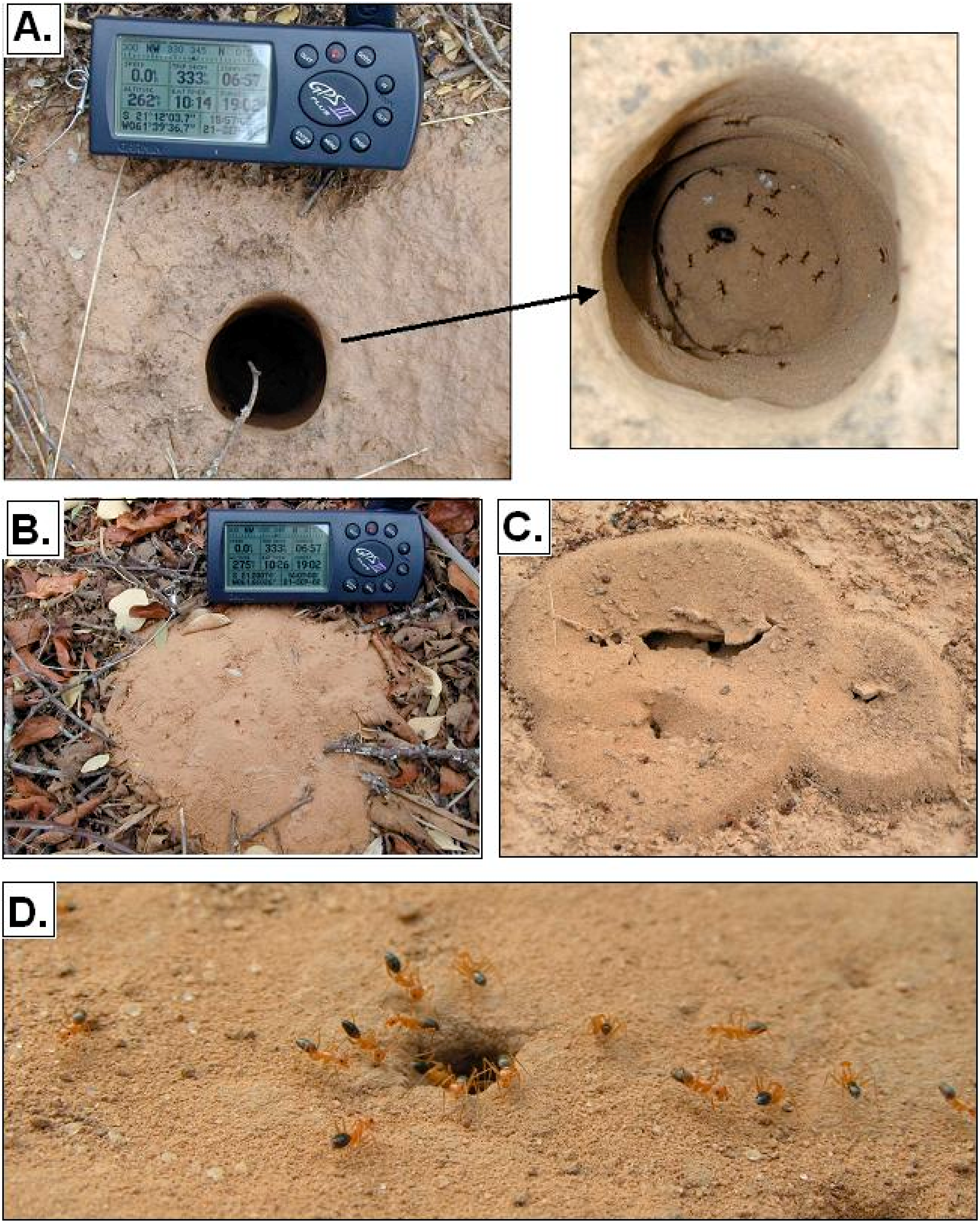


Figure 6-2: *Linepithema cryptobioticum* Wild 2007 (A) Vue dorsale. (B) Vue frontale. (C) Vue latérale. Cette espèce est suspectée être principalement hypogée. Elle a été décrite à partir des échantillons provenant de la localité de référence, le Parc National Teniente Enciso. Jusqu'à présent, elle n'a été collectée qu'au niveau de cette localité et sa biologie est inconnue (Wild, 2007).

-

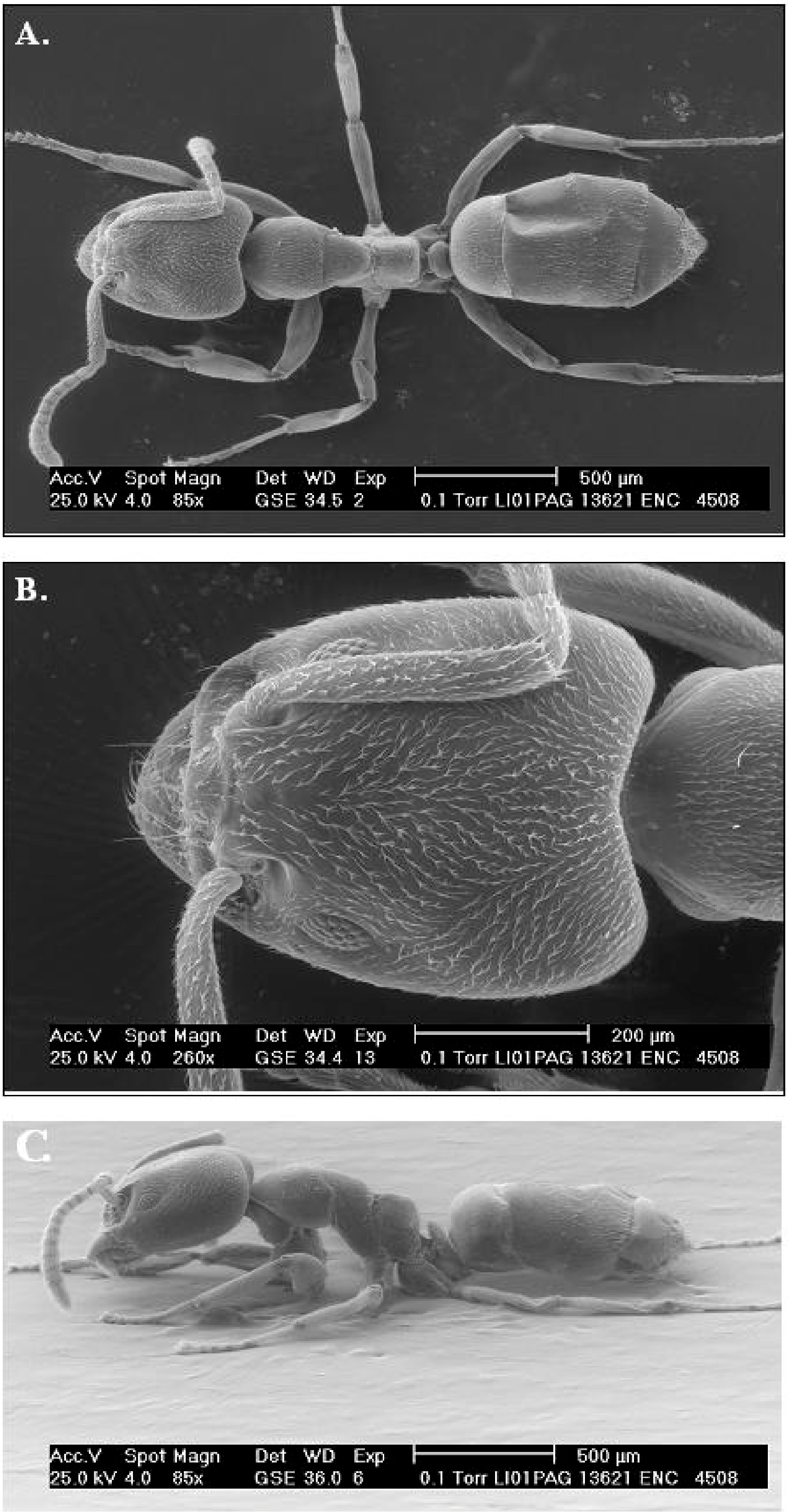
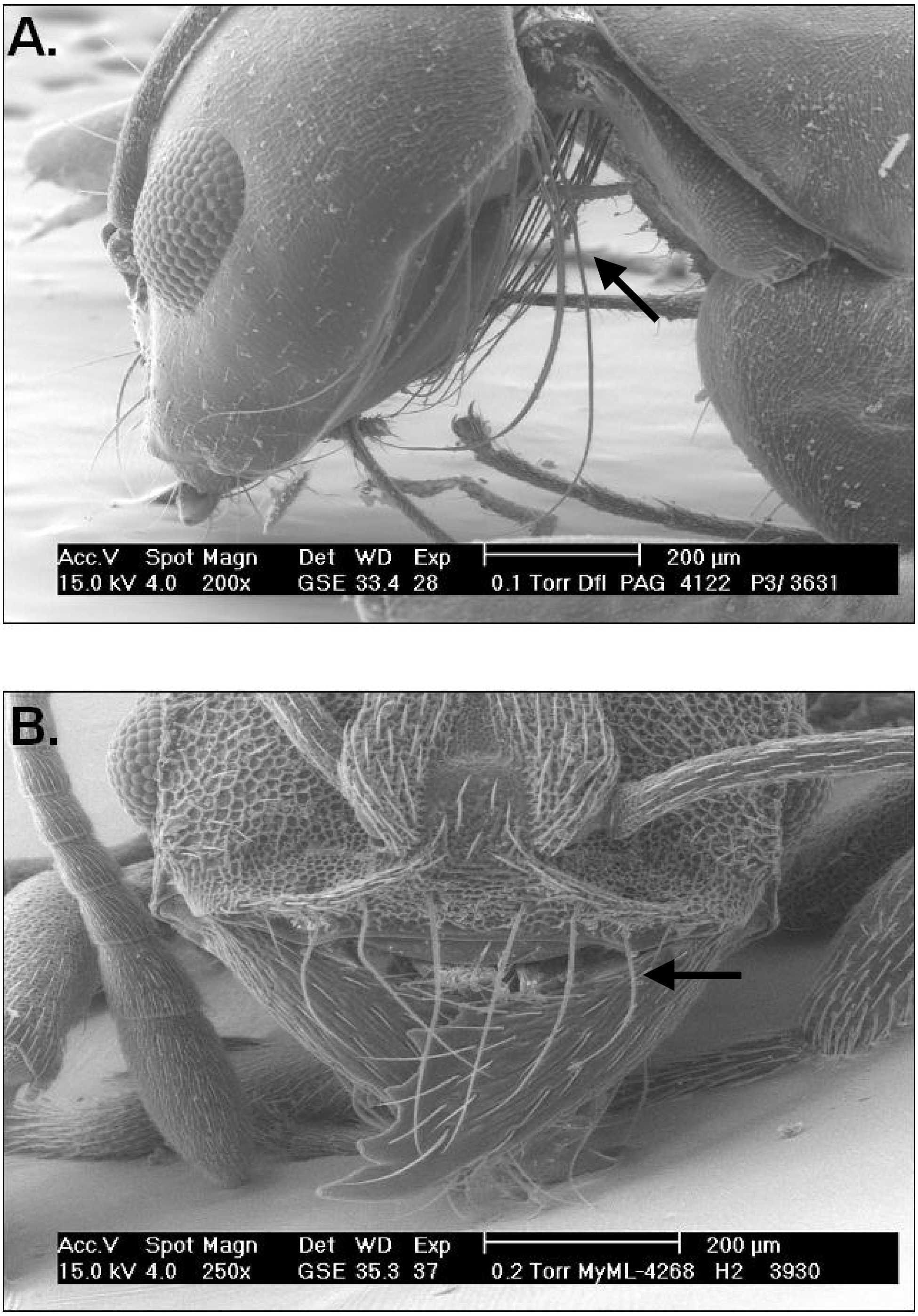


Figure 6-3: Une adaptation aux sols sableux: le psammophore. (A) *Dorymyrmex* cf *flavescens*: le psammophore est situé sous la tête (flèche). (B) *Mycetophylax emeryi*: les portions latérales du clypéus sont applaties dorso-ventralement et forment ainsi une plateforme surélevées. De longs poils sont insérées sur la marge inférieure du clypéus. Les *Mycetophylax* sont des Attini rencontrées principalement dans les milieux arides et sableux (Klingenberg, 2006; Diehl-Fleig et Diehl, 2007)[3].



---

[3] Les *Mycetophylax* collectées dans le Chaco paraguayen appartiendraient en fait au genre *Paramycetophylax* stat. rev. (Klingenberg et Brandão, in prep.). Cependant, puisque cette révision n'est pas encore parue, nous continuons à utiliser le nom *Mycetophylax*.

Figure 6-4: Relation unimodale ("hump-shaped") hypothétique entre la quantité de précipitations et la richesse spécifique des assemblages de fourmis. Selon la portion du gradient échantillonnée, la relation peut apparaître (A) positive, (B) absente ou (C) négative. Modifié d'après Andersen (1997).

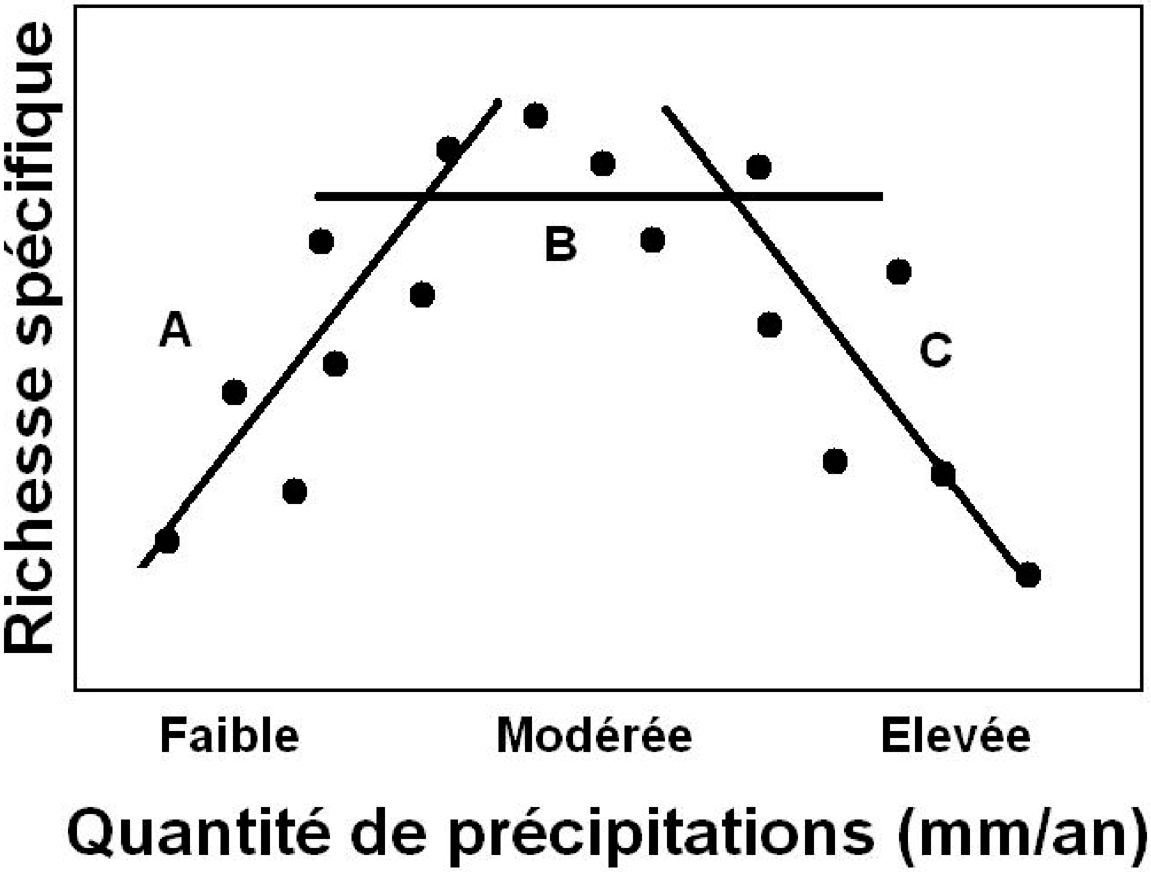


Figure 6-5: Localités échantillonnées (numéros) et sites protégés (lettres) du Chaco paraguayen. 1: Río Verde; 2: Cruce de Los Pioneros; 3: Mariscal Estigarribia; 4: Garrapatal; 5: Estancia María Vicenta; 6: Teniente Enciso-Nord; 7: Teniente Enciso-Sud; 8: Siracua; 9: Nueva Asunción; 10: Fortín Mister Long; 11: Fortín Mayor Infante Rivarola. A: Parc National Tinfunqué (2.413km²); B: P.N. Teniente Enciso (400km²); C: P.N. Médanos del Chaco (5.142km²); D: P.N. Defensores del Chaco (7.200km²); E: "Monumento Natural Cerro Cabrera - Timané" (1.258km²), F: P.N. Chovoreca (1.010km²); G: P.N. Río Negro (1.238km²).

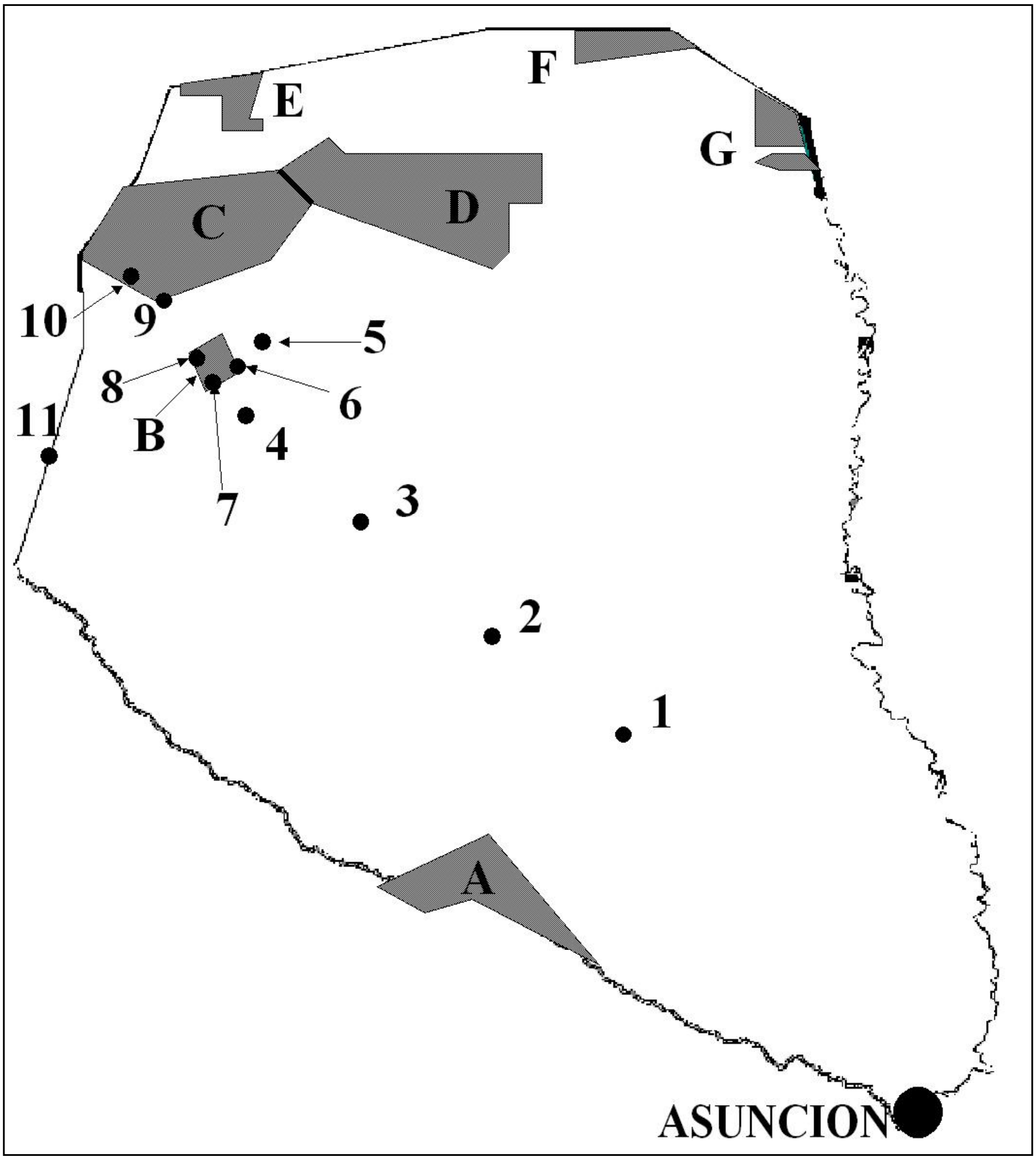
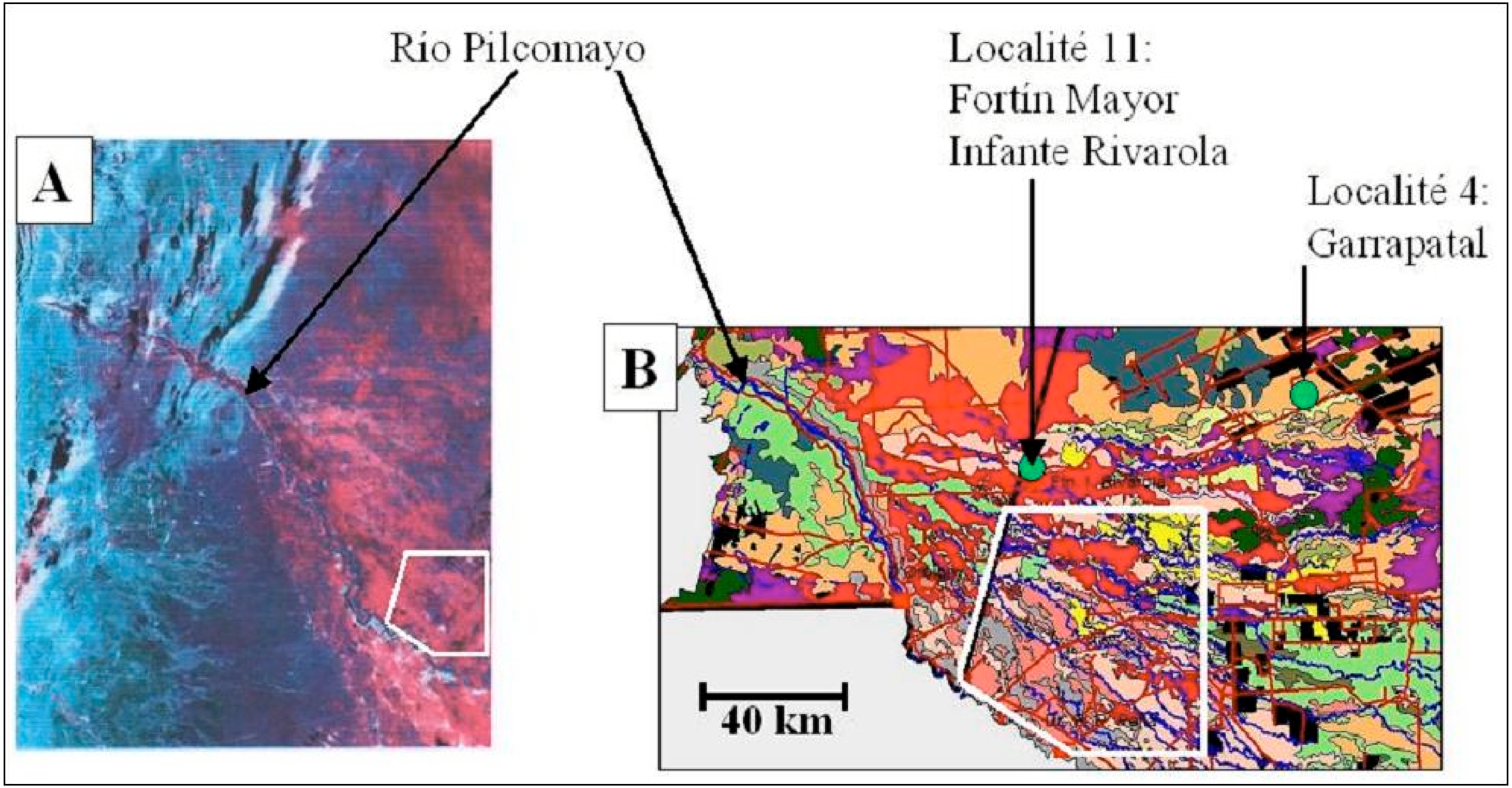


Figure 6-6: Aire du Chaco paraguayen où il serait intéressant d'étudier la structure et la distribution des assemblages de fourmis en raison de la grande hétérogénéité des conditions édaphiques. (A) Image satellite du Río Pilcomayo. Le réseau des anciens lits du fleuve apparaît en rouge. (B) Végétation dévéloppée sur les sols de ces anciens lits (extrait de la Figure 0-5 présentée dans l'introduction de la thèse).
La figure blanche délimite en (A) et en (B) la zone du Chaco paraguayen où une étude de la myrmécofaune est proposée.



ANNEXES

Annexe 1
Résultats préliminaires concernant la distribution des tailles des espèces de fourmis en fonction de l'aridité.

Afin de déterminer si l'aridité influence la distribution des tailles des espèces de fourmis, nous avons mesuré la longueur de Weber (LW) sur 1 à 4 individus de chacune des espèces collectées par piège à fosse. Cette mesure s'effectue en vue latérale et correspond à la longueur située entre la face antérieure du pronotum et l'extension postérieure maximale du métapleuron (Wild, 2002; Figure A1-1). Pour chaque espèce la LW moyenne est calculée. Chez les espèces polymorphiques, la caste la plus petite est celle prise en considération car c'est généralement la caste la plus représentée au sein de la colonie.

Résultats préliminaires

La majorité des espèces collectées sur l'ensemble du gradient d'aridité sont de petite taille: 56% des espèces ont une LW inférieure à 1mm (Figure A1-2). *Dinoponera mutica* est une exception notable puisque sa LW est d'environ 8,5mm. La seconde plus grande espèce est *Odontomachus bauri* avec une LW valant 4,8mm. La distribution des tailles suit une distribution log-normale (test du Chi-carré d'adéquation à la loi log-normale; Chi-carré=6,135; df (ajusté)=3; P= 0,105).

A partir de la liste des espèces collectées, une valeur médiane de la LW est calculée pour chaque assemblage échantillonné. Aucune corrélation n'est observée entre la LW médiane et l'aridité (Pearson Product Moment Correlation; r = -0.147; P= 0.631; Figure A1-3).

Référence bibliographique

Wild, A.L., 2002. The genus *Pachycondyla* (Hymenoptera: Formicidae) in Paraguay. Boletín del Museo Nacional de Historia Natural del Paraguay 14: 1-18.

Figure A1-1: Longueur de Weber. Cette mesure s'effectue en vue latérale et correspond à la longueur située entre la face antérieure du pronotum et l'extension postérieure maximale du métapleuron.

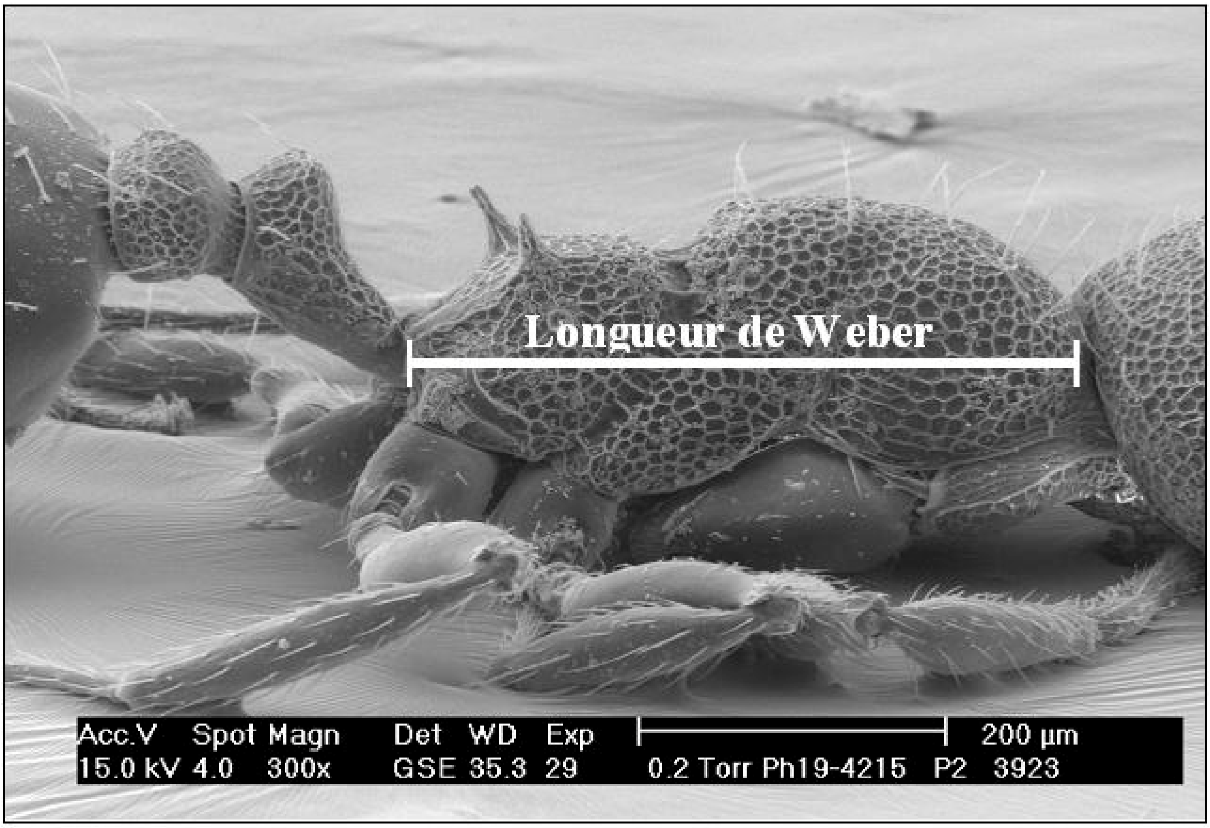


Figure A1-2: Distribution des tailles des espèces de fourmis collectées à l'aide de pièges à fosse au niveau des 11 localités étudiées. La distribution suit celle attendue pour une distribution log-normale (courbe).

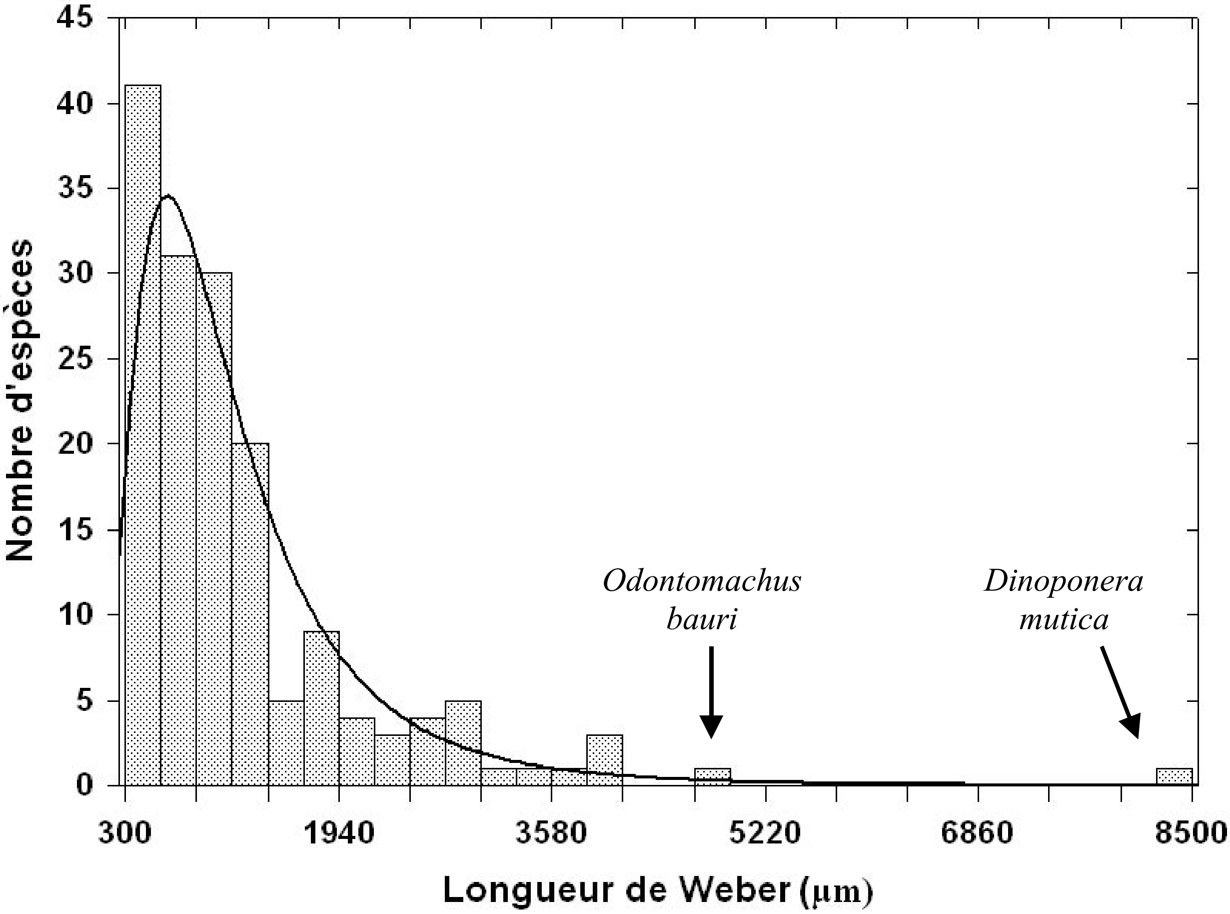
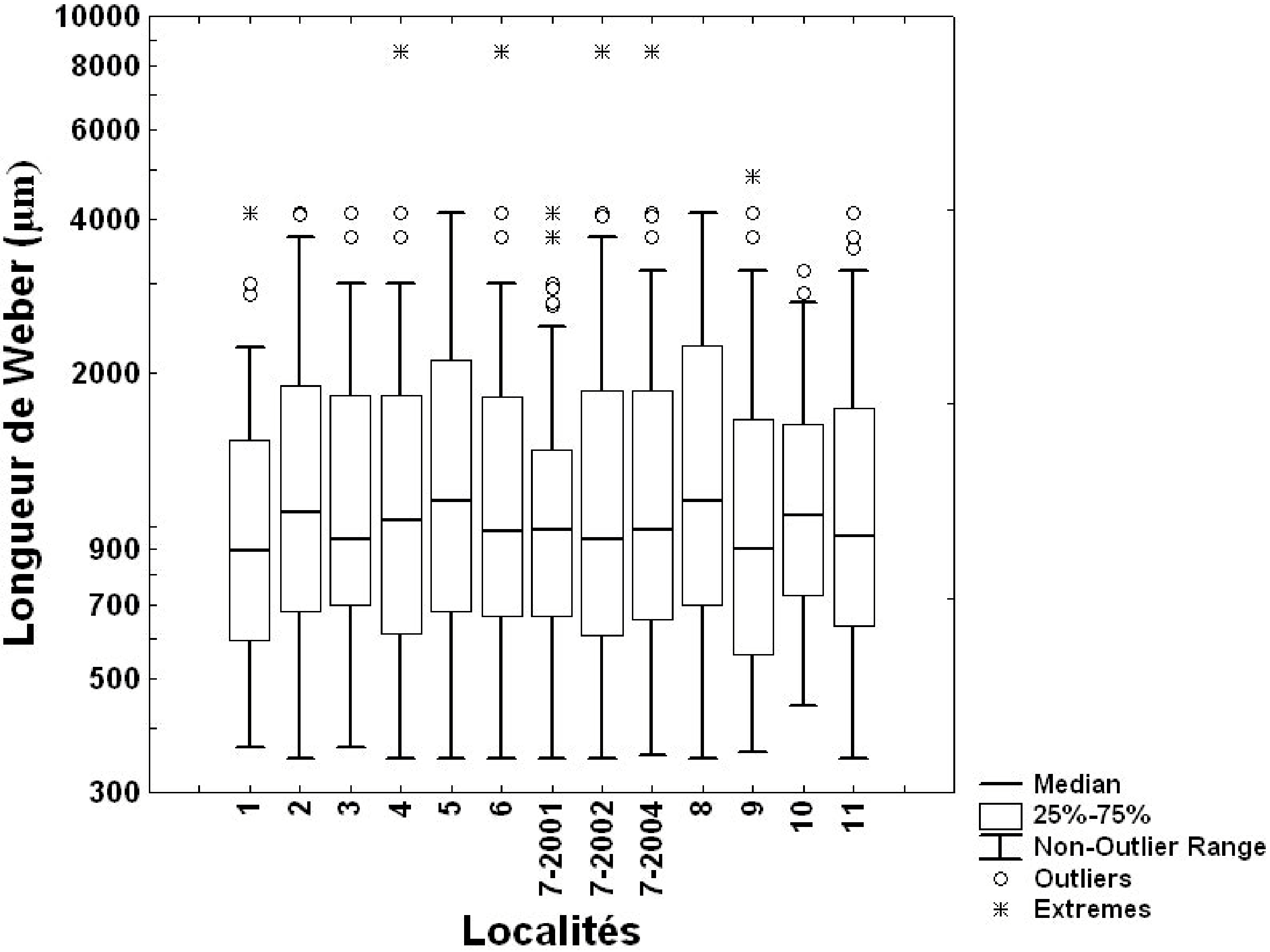


Figure A1-3: Distribution des tailles des espèces de fourmis le long d'un gradient d'aridité dans le Chaco sec paraguayen.

1: Río Verde (pluviométrie moyenne annuelle: 1000mm); 2: Cruce de Los Pioneros (850mm); 3: Mariscal Estigarribia (700mm); 4: Garrapatal (600mm); 5: Estancia María Vicenta (550mm); 6: Teniente Enciso-Nord (500mm); 7: Teniente Enciso-Sud (500mm); 8: Siracua (450mm); 9: Nueva Asunción (400mm); 10: Fortín Mister Long (350mm); 11: Fortín Mayor Infante Rivarola (350mm).Les trois échantillonnages effectués au niveau de la localité de référence (localité 7) sont analysés séparemment. L'échelle de l'axe des ordonnées est logarithmique.



Annexe 2
Liste des espèces de fourmis collectées.

Distribution et occurrences des espèces de fourmis collectées le long d'un gradient d'aridité dans le Chaco sec paraguayen. Les numéros de la première ligne correspondent aux 11 localités étudiées:

1: Río Verde; 2: Cruce de Los Pioneros; 3: Mariscal Estigarribia; 4: Garrapatal; 5: Estancia María Vicenta; 6: Teniente Enciso-Nord; 7: Teniente Enciso-Sud (localité de référence échantillonnée en 2001, 2002 et 2004); 8: Siracua; 9: Nueva Asunción; 10: Fortín Mister Long; 11: Fortín Mayor Infante Rivarola.

Les entrées de la matrice sont les occurrences des espèces dans les pièges à fosse. Trois transects de 20 pièges ont été réalisés par localité, sauf au niveau de la localité 5 (un seul transect) et de la localité 7 en 2002 (2 transects).

Une croix (X) signifie que l'espèce n'a jamais été documentée par les pièges à fosse mais qu'elle a été collectée dans la localité correspondante à l'aide d'une autre méthode d'échantillonnage (Winkler, appâts ou chasse à vue).

Espèces	1	2	3	4	5	6	7-01	7-02	7-04	8	9	10	11
Amblyoponinae													
Amblyopone armigera							X						
Dolichoderinae													
Azteca sp. 01	0	0	0	0	0	0	0	0	0	0	1	0	0
Dorymyrmex flavescens (ou *exanguis?)*	0	0	2	4	11	2	18	4	4	0	3	1	0
Dorymyrmex thoracicus	0	2	0	16	0	9	32	2	6	0	25	13	2
Dorymyrmex sp. 01	0	1	0	0	0	1	0	0	4	0	0	3	2
Dorymyrmex sp. 02	0	0	0	0	0	0	0	0	0	0	1	1	0
Dorymyrmex sp. 03	0	0	0	0	0	1	0	0	0	0	0	0	2
Dorymyrmex sp. 04	0	0	0	0	0	0	0	4	0	0	0	0	1
Dorymyrmex sp. 05	0	0	0	0	0	0	0	0	0	0	0	2	0
Dorymyrmex sp. 06	0	0	0	0	0	0	0	0	0	0	0	5	0
Dorymyrmex sp. 07	0	0	0	2	0	1	4	1	2	0	2	1	2
Dorymyrmex sp. 09	0	0	0	0	0	0	1	0	0	0	0	0	0
Dorymyrmex sp. 10	0	0	0	0	0	0	1	0	0	0	0	0	0
Forelius brasiliensis	0	0	1	7	6	0	39	21	16	4	4	4	2
Forelius nigriventris	2	4	0	40	10	3	47	27	34	13	26	18	3

Forelius sp. 02	9	19	0	16	0	1	1	1	5	0	0	0	8
Forelius sp. 03	0	0	0	10	2	1	23	2	6	0	8	4	2
Forelius sp. 04	5	1	0	11	1	0	1	0	0	0	0	0	2
Forelius sp. 07	0	0	0	4	0	0	2	2	0	0	2	0	0
Forelius sp. 08	0	0	0	0	0	0	0	0	2	0	0	0	0
Forelius sp. 09	1	0	0	0	0	0	0	0	0	0	0	0	0
Forelius sp. 10	1	0	0	0	0	0	0	0	0	0	0	0	0
Forelius sp. 11	0	0	0	0	0	0	0	0	0	0	0	3	0
Gracilidris pombero	0	1	0	0	0	0	0	0	0	0	0	0	0
Linepithema cryptobioticum	0	0	0	0	0	0	0	3	1	0	0	0	0
Tapinoma sp. 01	0	0	0	0	0	0	0	0	1	0	0	0	0
Ecitoninae													
Labidus coecus	2	1	0	1	0	0	1	1	1	0	0	0	0
Neivamyrmex sp. 01	2	0	0	1	0	0	0	0	0	1	0	0	0
Neivamyrmex sp. 02	0	0	0	1	0	0	0	0	0	0	0	0	0
Neivamyrmex sp. 03	0	1	0	0	0	0	0	0	0	0	0	0	0
Neivamyrmex sp. 04	0	0	0	0	0	3	0	0	0	0	0	0	0
Neivamyrmex sp. 05	0	0	0	0	0	0	0	0	0	0	0	0	1
Ectatomminae													
Ectatomma brunneum	0	37	56	26	16	42	31	23	36	9	2	0	29
Ectatomma edentatum	11	13	1	2	4	5	4	2	2	1	1	0	7
Ectatomma permagnum	20	34	4	17	4	3	10	20	21	17	3	0	10
Ectatomma tuberculatum	0	1	0	0	0	0	0	0	0	2	0	0	0
Gnamptogenys moelleri	0	0	1	2	0	0	1	0	0	1	0	0	1
Gnamptogenys sp. 02	0	1	0	4	0	0	0	0	0	0	0	1	0
Gnamptogenys sp. 03	0	0	1	0	0	0	0	0	0	0	0	0	0
Gnamptogenys sp. 04	0	0	0	0	1	0	0	0	0	0	0	0	0
Formicinae													
Brachymyrmex aphidicola	10	3	8	6	3	1	5	9	4	4	1	0	10
Brachymyrmex leuderwaldti	0	0	0	1	0	0	33	9	2	0	4	0	5
Brachymyrmex termitophilus	0	0	0	8	0	0	2	0	0	0	1	5	2
Brachymyrmex sp. 01	0	2	0	0	0	0	1	0	1	0	1	0	1
Brachymyrmex sp. 03	0	0	5	0	0	0	0	0	1	0	0	0	0
Brachymyrmex sp. 04	2	0	0	0	0	0	0	0	0	0	0	0	0
Brachymyrmex sp. 05	2	0	0	0	0	0	0	0	0	0	0	0	0
Brachymyrmex sp. 06	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus atriceps	2	3	0	0	0	0	0	0	0	0	0	0	0
Camponotus blandus	0	4	10	21	0	1	11	6	6	2	10	0	2
Camponotus borelli	0	5	8	10	14	0	1	10	3	12	5	1	9
Camponotus crassus	0	8	2	3	14	3	0	5	2	5	3	0	2
Camponotus crispulus	4	3	3	8	0	0	7	0	4	0	5	0	4
Camponotus leydigi	0	7	3	0	2	7	1	4	11	2	1	0	0
Camponotus mus													X

Camponotus rosariensis	23	10	8	17	0	7	10	0	3	0	23	0	17
Camponotus rusticus		X											
Camponotus substitutus	0	23	18	6	12	22	8	33	41	31	2	13	34
Camponotus tenuiscapus	1	5	1	3	0	4	26	15	6	1	4	0	0
Camponotus termitarius	0	1	1	14	12	22	11	13	12	3	5	9	2
Camponotus sp. 01	4	22	37	37	7	42	0	1	3	4	20	0	18
Camponotus sp. 06	0	0	0	0	0	0	0	0	0	0	0	1	0
Camponotus sp. 08 (nr. *blandus*)	0	0	0	0	0	0	0	0	0	0	0	5	0
Camponotus sp. 09	4	6	12	5	0	4	2	0	0	0	0	0	3
Camponotus sp. 15	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp. 16 (nr. *blandus*)	0	0	0	3	0	0	0	0	0	0	0	0	0
Camponotus sp. 17	0	0	0	0	0	0	0	0	0	0	0	0	1
Camponotus sp. 18	0	0	0	0	0	0	0	0	1	0	0	0	1
Camponotus sp. 19	5	0	0	0	0	0	0	0	0	0	0	0	0
Camponotus sp. 21	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp. 22	0	0	0	0	0	0	0	0	0	0	1	0	0
Camponotus sp. 23 (nr. *blandus*)	0	0	0	0	0	0	0	0	2	0	0	0	0
Myrmelachista sp. 01	1	1	0	0	0	0	0	0	0	0	0	0	0
Paratrechina sp. 02	0	2	0	0	0	0	0	0	0	0	0	0	2
Myrmicinae													
Acromyrmex sp. 01	0	0	1	1	1	0	0	4	0	2	0	0	0
Acromyrmex sp. 02	0	0	0	0	0	0	0	0	0	0	0	5	0
Acromyrmex sp. 03	0	0	1	0	0	0	0	0	0	0	0	0	0
Acromyrmex sp. 04	4	9	0	1	0	0	0	0	0	0	0	0	0
Acromyrmex sp. 05	0	7	0	0	0	0	0	0	0	0	0	0	0
Atta sp. 01	0	0	0	0	0	0	0	0	0	0	0	0	1
Atta sp. 02	0	0	0	0	0	0	0	0	0	0	0	6	0
Atta sp. 03	0	0	0	0	0	0	0	0	0	0	1	0	0
Atta sp. 04	0	1	0	0	0	0	0	0	0	0	4	0	0
Atta sp. 05	0	0	0	0	2	0	0	0	0	0	0	0	0
Cephalotes atratus	0	0	0	0	0	0	0	1	1	0	0	0	0
Cephalotes borgmeieri	0	0	2	0	1	0	0	1	1	0	0	0	0
Cephalotes minutus	1	3	0	3	0	1	1	1	2	0	1	0	1
Cephalotes persimilis	0	0	1	0	0	0	0	1	0	0	0	0	0
Cephalotes sp. 02	0	0	0	0	0	0	0	0	1	0	0	0	0
Cephalotes sp. 03	1	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster brevispinosa	0	0	1	0	0	0	0	0	1	0	0	0	0
Crematogaster quadriformis	1	3	2	10	2	0	1	0	6	0	1	1	10
Crematogaster sp. 01	0	2	1	1	0	0	3	6	0	4	2	3	2
Crematogaster sp. 03	0	1	0	8	0	0	11	0	1	0	3	0	1
Crematogaster sp. 06	0	0	0	0	0	1	0	2	0	1	0	1	0
Crematogaster sp. 07	0	0	0	0	0	1	0	0	0	0	0	0	0
Crematogaster sp. 08	0	0	1	0	0	0	0	1	2	1	0	0	0
Crematogaster sp. 09	1	1	0	0	0	0	0	0	0	0	0	0	0

Cyphomyrmex transversus	0	4	6	6	6	8	6	7	8	1	1	6	1
Cyphomyrmex cf *rimosus*	0	0	0	0	0	0	0	0	0	0	0	1	0
Cyphomyrmex sp. 03	0	0	0	0	0	0	0	0	0	0	1	8	0
Cyphomyrmex sp. 04	0	0	1	1	0	0	0	0	0	0	0	0	0
Cyphomyrmex sp. 05	0	0	2	0	0	0	0	0	0	0	0	0	0
Cyphomyrmex sp. 06	0	0	1	0	0	0	0	0	0	0	0	0	0
Cyphomyrmex sp. 07	0	0	0	0	0	0	1	0	0	0	0	0	0
Leptothorax sp. 01							X		X				
Leptothorax sp. 02	1	0	0	0	0	0	0	0	0	0	0	0	2
Mycetophylax emeryi	0	0	6	6	0	4	22	2	6	3	1	0	1
Mycetophylax prox emeryi sp. 01	0	0	0	0	0	1	2	0	0	0	1	0	0
Mycetophylax sp. 02	0	0	0	0	0	0	0	0	0	0	0	3	0
Mycetophylax sp. 03	0	0	0	0	0	0	0	0	0	0	0	1	0
Mycetosoritis explicata	0	0	0	0	0	0	0	1	0	1	0	0	0
Oxyepoecus cf *bruchi*	1	0	0	0	0	0	0	0	0	0	0	0	0
Oxyepoecus cf *inquilinus*	0	0	0	0	0	0	0	0	0	0	2	0	0
Oxyepoecus cf *rastratus*				X			X						
Oxyepoecus cf *vezenyii*	3	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole jelskii	6	6	2	11	0	4	18	9	17	15	12	0	2
Pheidole radoszkowskii	6	5	15	22	3	17	11	37	28	0	0	0	25
Pheidole scapulata	0	0	3	2	0	1	10	2	0	0	5	0	0
Pheidole spininodis	0	0	2	3	0	3	4	0	3	0	10	4	0
Pheidole vafra	9	12	7	2	4	0	5	3	9	2	2	3	7
Pheidole vallifica	0	0	1	14	0	0	35	0	0	0	9	0	0
Pheidole sp. 06	7	32	3	6	13	12	3	6	22	18	3	28	7
Pheidole sp. 08	0	0	0	2	0	1	0	0	0	2	0	0	1
Pheidole sp. 11	0	21	11	26	1	4	20	7	0	0	11	2	2
Pheidole sp. 13	0	0	0	0	0	0	0	0	0	0	13	1	0
Pheidole sp. 14	7	0	0	0	0	0	0	0	0	0	3	0	0
Pheidole sp. 18	32	4	0	7	0	0	0	0	0	0	0	0	1
Pheidole sp. 19	0	0	0	3	0	0	0	0	0	0	2	0	0
Pheidole sp. 20	0	0	0	2	0	0	0	0	0	0	0	0	0
Pheidole sp. 21	1	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp. 24	4	5	2	0	0	0	0	0	0	0	0	0	0
Pheidole sp. 25	1	0	0	1	0	0	0	0	0	0	0	0	0
Pheidole sp. 27	0	4	1	0	0	0	0	0	0	0	0	0	0
Pheidole sp. 32	0	0	0	0	0	0	1	0	1	0	0	0	0
Pheidole sp. 33	13	23	13	18	5	11	6	5	15	4	8	0	8
Pheidole sp. 34	0	0	3	0	0	0	0	0	0	0	0	0	5
Pheidole sp. 35	0	0	2	0	4	5	4	1	3	0	0	2	1
Pheidole sp. 36	1	3	1	0	0	0	0	0	1	0	0	0	0
Pheidole sp. 37	0	1	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp. 38	0	0	0	1	0	0	0	1	0	0	0	0	0
Pheidole sp. 40	0	0	1	0	0	0	0	0	0	0	1	0	0
Pheidole sp. 41	5	2	0	0	0	0	0	2	1	0	3	0	0
Pheidole sp. 43							X						

Pheidole sp. 45	0	6	2	14	0	6	0	2	3	0	2	1	3
Pogonomyrmex cunicularius	6	14	5	37	16	30	49	17	33	3	7	19	32
Pogonomyrmex naegelii	0	0	0	0	0	0	0	0	0	0	0	13	0
Pogonomyrmex uruguayensis	0	1	2	0	0	0	0	0	0	0	0	1	0
Pyramica tanymastax							X						
Rogeria sp. 01 (nr. *germaini*)	0	1	0	0	0	0	0	0	0	0	0	0	0
Rogeria sp. 02	0	0	0	0	0	1	0	0	0	0	0	0	0
Rogeria sp. 04							X						
Solenopsis prox geminata sp. 01	0	2	4	10	3	4	8	1	5	4	2	14	8
Solenopsis sp. 01	0	3	1	0	1	1	0	14	6	3	1	1	2
Solenopsis sp. 02	0	0	7	0	0	12	3	13	11	2	0	0	2
Solenopsis sp. 03	0	0	0	1	5	2	0	0	1	0	13	19	10
Solenopsis sp. 04	0	0	3	20	0	0	18	2	0	0	3	0	2
Solenopsis sp. 06	0	0	0	1	0	1	0	1	0	0	0	0	0
Solenopsis sp. 07	0	0	0	1	0	6	0	6	0	4	0	0	2
Solenopsis sp. 08	0	0	1	0	0	3	0	0	0	8	0	0	0
Solenopsis sp. 09	0	0	0	0	0	0	0	0	0	0	0	0	9
Solenopsis sp. 10	0	0	0	1	0	0	0	0	0	0	5	0	0
Solenopsis sp. 12	0	0	0	0	0	0	6	1	1	0	3	0	0
Solenopsis sp. 13	0	3	0	0	0	4	2	8	1	3	1	0	0
Solenopsis sp. 14	14	8	0	1	0	0	1	0	0	0	0	0	0
Solenopsis sp. 17	9	10	7	3	4	6	12	24	16	11	6	0	5
Solenopsis sp. 18	42	5	2	0	0	0	0	0	0	8	2	0	4
Solenopsis sp. 19	0	0	0	0	0	0	0	0	0	0	0	2	0
Solenopsis sp. 20	0	0	0	0	3	0	0	1	1	0	0	0	4
Solenopsis sp. 21	0	5	0	1	1	0	2	8	0	0	0	0	0
Solenopsis sp. 22	0	0	0	14	2	11	8	20	19	0	1	2	0
Solenopsis sp. 23	0	18	10	0	0	0	0	0	0	0	0	0	0
Solenopsis sp. 24	0	10	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp. 25	0	0	0	0	0	3	0	0	0	0	0	0	0
Solenopsis sp. 26	0	5	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp. 27	0	0	0	0	0	0	0	0	0	0	0	1	0
Solenopsis sp. 28	0	0	0	0	0	0	0	0	0	0	0	1	0
Solenopsis sp. 29	0	0	0	0	0	0	0	0	2	0	0	0	0
Solenopsis sp. 31	2	5	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp. 32	2	0	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp. 33	0	0	4	0	0	0	0	0	0	0	0	0	0
Strumigenys silvestrii	0	0	0	0	0	0	0	0	0	0	1	0	0
Strumigenys sp. 01	0	0	0	0	0	0	0	0	1	0	0	0	0
Strumigenys sp. 02	0	0	0	2	0	0	1	0	0	0	0	0	0
Thaumatomyrmex cf *ferox*							X						
Trachymyrmex sp. 01	0	0	0	0	0	0	0	4	1	1	1	0	0
Trachymyrmex sp. 02	0	0	0	0	0	2	0	0	0	0	5	0	0
Trachymyrmex sp. 03	0	6	0	0	0	0	1	0	0	0	0	0	1
Trachymyrmex sp. 04	0	0	0	1	0	0	0	0	0	0	0	0	0

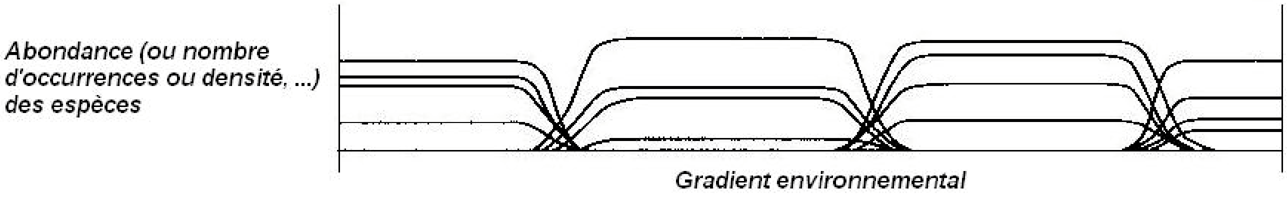
Trachymyrmex sp. 05	0	0	0	0	0	0	0	0	0	0	0	1	0
Wasmannia auropunctata	13	3	0	18	0	1	13	2	1	1	5	0	1
Wasmannia sp. 01	0	0	0	0	0	1	0	2	1	0	0	0	0
Wasmannia sp. 02	X												
Ponerinae													
Anochetus neglectus	1	0	0	1	0	0	0	0	0	0	0	0	0
Dinoponera mutica	0	0	0	1	0	1	0	4	1	0	0	0	0
Hypoponera sp. 01	1	0	0	0	0	0	0	0	1	0	0	0	0
Hypoponera sp. 02	1	0	0	0	0	0	0	0	0	0	0	0	0
Odontomachus bauri	0	0	0	0	0	0	0	0	0	0	2	0	0
Odontomachus chelifer	0	5	0	0	0	0	0	6	2	3	6	1	2
Odontomachus sp. 03	1	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla harpax	8	0	0	2	0	0	0	0	0	0	0	0	0
Pachycondyla marginata	0	0	0	0	0	0	0	1	0	0	0	1	0
Pseudomyrmecinae													
Pseudomyrmex acanthobius (ou *duckei?)*	2	0	0	0	0	0	0	0	0	0	0	0	0
Pseudomyrmex denticollis	17	34	50	48	19	56	47	40	59	51	29	1	46
Pseudomyrmex sp. 01	0	0	0	0	0	0	0	0	0	0	0	0	1
Pseudomyrmex sp. 03	1	0	0	0	0	0	0	0	0	0	0	0	0
Nombre total d'espèces: * 206 (toutes méthodes) * 197 (dans pièges à fosse uniquement)	56	69	61	74	36	56	65	66	71	42	70	49	66
Nombre total d'occurrences dans les pièges à fosse: 5462	336	514	373	640	215	410	672	495	538	268	359	243	399

Annexe 3
Distribution des espèces de fourmis le long d'un gradient d'aridité dans le Chaco sec paraguayen - Espèces indicatrices.

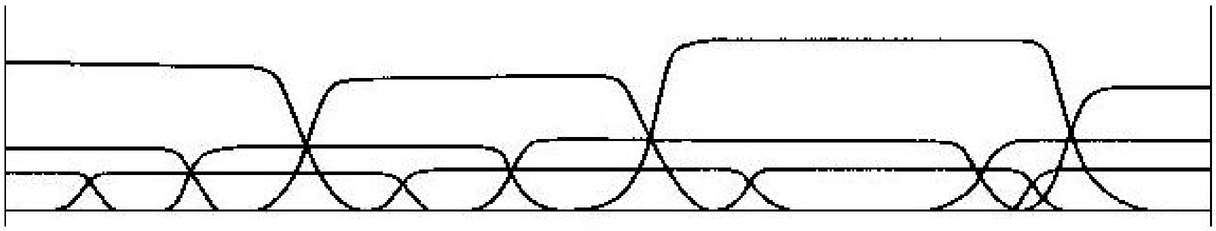
1. Distribution des espèces de fourmis le long d'un gradient d'aridité dans le Chaco sec paraguayen.

Le long d'un gradient environnemental, au moins cinq patrons de distribution des espèces animales ou végétales peuvent être attendus (Whittaker, 1975 *in* Brown et Lomolino, 1998).

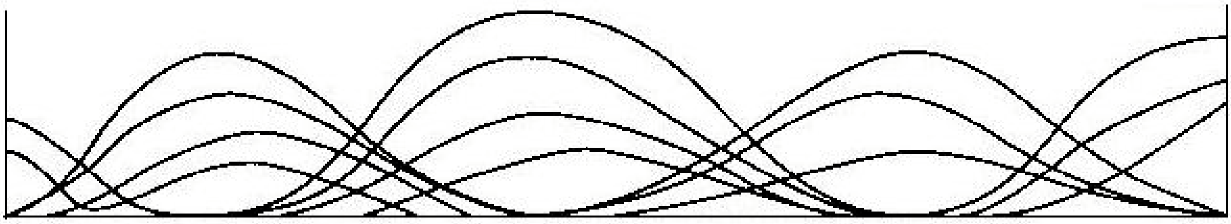
1. Les espèces présentent des exigences écologiques similaires et forment des assemblages bien délimités spatialement. Une forte compétition interspécifique engendre des ségrégations spatiales[1].



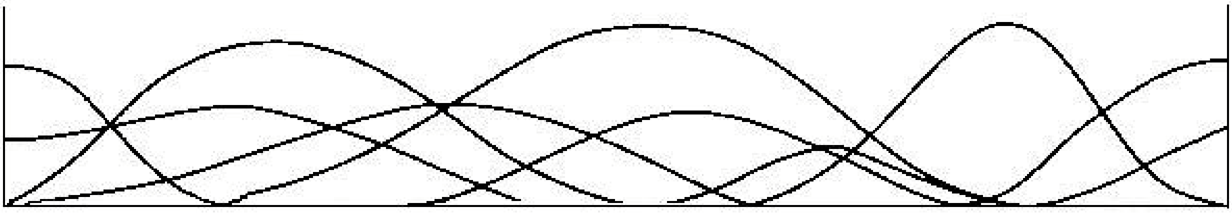
2. Des ségrégations spatiales sont observées mais les espèces ne forment pas d'assemblages bien définis.



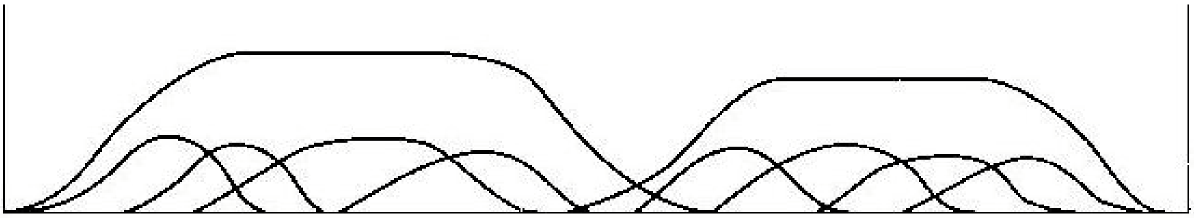
3. Les espèces sont regroupées dans des assemblages bien définis mais les espèces se remplacent de façon graduelle le long du gradient environnemental en raison, par exemple, d'une compétition interspécifique peu intense.



4. Les espèces sont distribuées aléatoirement les unes par rapport aux autres. Aucune association ou exclusion d'espèces n'est observée. Les espèces se comportent comme des entités indépendantes les unes des autres.



5. Les distributions de la plupart des espèces sont intégrées dans des distributions plus larges d'espèces dominantes qui s'excluent mutuellement. Ce patron, en rappelant qu'une distribution aléatoire peut apparaître structurée à une échelle spatiale plus vaste, souligne l'importance de préciser l'échelle à laquelle s'effectue les observations.



---

[1] Les figures sont modifiées d'après Brown et Lomolino (1998).

Dans le Chaco sec paraguayen, les espèces de fourmis du sol semblent se distribuer selon le quatrième patron de Whittaker, c'est-à-dire indépendamment les unes des autres, sans former d'associations d'espèces bien délimitées spatialement (Figure A3-1). Ceci reste valable lorsque l'on restreint la comparaison à des espèces congénériques (Figure A3-2). Ces dernières sont supposées présenter entre elles plus de similarités morphologiques et/ou écologiques qu'entre des espèces phylogénétiquement éloignées en raison de la conservation des traits écologiques lors de l'évolution des lignées ("niche conservatism") (Lord *et al.*, 1995; Webb, 2000; Webb *et al.*, 2002). On pouvait donc s'attendre à observer soit des associations étroites entre espèces congénériques, soit au contraire, des ségrégations spatiales abruptes en raison d'une forte compétition entre espèces aux exigences écologiques proches. Nos résultats suggèrent que dans le Chaco sec paraguayen, la compétition entre espèces de fourmis est faible ou du moins qu'elle influence peu la distribution des espèces à l'échelle régionale (voir aussi le Chapitre 3). Ils suggèrent également que la tolérance à l'aridité est largement répandue au sein des Formicidae (voir aussi les Chapitres 4 et 5).

2. Espèces indicatrices des complexes myrmécofauniques.

2.1. Méthode.

Trois complexes myrmécofauniques ont été mis en évidence le long du gradient étudié (Chapitre 4). Afin de déterminer les espèces caractéristiques de ces trois ensembles, nous avons utilisé la méthode "Indicator Value" (IndVal) développée par Dufrêne et Legendre (1997). Pour réaliser cette étude, il est nécessaire d'obtenir au préalable une classification des assemblages échantillonnés. Pour cela, une analyse de classification ("complete linkage clustering") basée sur l'indice de complémentarité 1-NNESS, k=1 (Chapitre 4) a été réalisée. L'approche "complete linkage" a été choisie car elle permet d'augmenter le contraste entre les groupes formés par l'analyse de classification (Legendre et Legendre, 1998).

Ensuite, l'objectif est d'identifier les espèces indicatrices des différents groupes obtenus. Une espèce est considérée comme une indicatrice parfaite lorsqu'elle n'est collectée que dans un seul groupe de localités (i.e. spécificité de l'espèce vis-à-vis du groupe) et lorsqu'elle est présente dans tous les transects des localités de ce groupe (i.e. fidélité de l'espèce pour ce groupe). L'indice IndVal combine ces deux facettes. Il est défini ainsi:

Spécificité = A_{ij} = $\text{Nindividus}_{ij}/\text{Nindividus}_{i.}$

Fidélité = B_{ij} = $\text{Nsites}_{ij}/\text{Nsites}_{.j}$

$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$

où IndVal_{ij} est la valeur indicatrice de l'espèce *i* dans le groupe de localités *j,* Nindividus_{ij} est le nombre moyen d'individus de *i* dans *j*, $\text{Nindividus}_{i.}$ est la somme des nombres moyens d'individus de *i* sur l'ensemble des groupes, Nsites_{ij} est le nombre de localités dans le groupe *j* où l'espèce *i* est présente, $\text{Nsites}_{.j}$ est le nombre total de localités dans le groupe *j*.

Ici, plutôt que le nombre d'individus par transect, nous utilisons le nombre d'occurrences/transect car les fourmis sont spatialement agrégées du fait de leur socialité (Longino, 2000) et car la taille des colonies varie fortement entre les espèces (Hölldobler et Wilson, 1990).

La spécificité A_{ij} est maximale lorsque l'espèce *i* est présente uniquement dans le groupe de localités ou dans la localité *j*. La fidélité B_{ij} est maximale lorsque *i* est présente dans toutes les les transects du groupe de localités ou de la localité *j*. La valeur indicatrice de l'espèce *i* est maximale (100%) lorsque la spécificité et la fidélité sont maximales.

Afin de tester la significativité de la plus haute valeur IndVal obtenue pour chaque espèce et pour un niveau hiérarchique donné, 5000 permutations aléatoires des données sont effectuées. L'indice IndVal observé est ensuite comparé directement à la distribution des valeurs générées aléatoirement ("Monte Carlo randomization tests").

L'analyse IndVal peut être effectuée pour chacun des différents niveaux de la hiérarchie des localités afin de déterminer le niveau pour lequel l'espèce est la plus indicatrice. Ici, nous avons d'abord mesuré l'IndVal de chaque espèce à l'échelle des trois complexes fauniques (Figure A3-3; Tableau A3-1) puis à un niveau plus fin de la hiérarchie (Figure A3-4; Tableau A3-2) et enfin au niveau de chaque localité (Figure A3-5; Tableau A3-3). Seules les espèces dont l'IndVal était différent de celui attendu sous l'effet du hasard ($P<0{,}05$) sont présentées. Une espèce est considérée être une bonne indicatrice du groupe de localités ou de la localité considéré lorsque la valeur de son indice IndVal est supérieure à 70% (McGeoch *et al.*, 2002). Les analyses ont été réalisées avec PC-ORD 5.0 (McCune et Mefford, 1999).

2.2.Principaux résultats.

- *Pachycondyla harpax, Pheidole* sp. 18 et *Pheidole* sp. 14 sont les trois espèces les plus caractéristiques du complexe faunique présent au sein de la localité la plus humide (localité 1; pluviométrie moyenne annuelle: 1000mm; sol argilo-limoneux) (Tableaux A3-1 à A3-3).
- *Atta* sp. 02, *Camponotus* sp. 08, *Dorymyrmex* sp. 06 et *Pogonomyrmex naegelii* sont les espèces caractéristiques du complexe faunique présent au niveau de la localité 10, c'est-à-dire celle qui est la plus sèche (350mm) et la plus sableuse (>90% de sable dans la fraction minérale du sol) (Tableaux A3-1 à A3-3).
- *Ectatomma brunneum, Camponotus blandus* et *Pseudomyrmex denticollis* sont caractéristiques du troisième complexe faunique (Tableau A3-1).
- Quelques espèces ont une aire de distribution très restreinte. C'est par exemple le cas de *Pheidole* sp. 13 qui est caractéristique de l'assemblage présent au sein de la localité 9 (Nueva Asunción) (Tableau A3-3).
- *Pheidole vallifica* et *Solenopsis* sp. 04 sont deux espèces qui caractérisent les assemblages collectés en 2001 (Tableau A3-2). Il faut noter que quelques épisodes pluvieux ont précédé cette période d'échantillonnage. Ces espèces sont peut-être principalement actives lors de la saison des pluies.

Références bibliographiques.

Brown, J.H., Lomolino, M.V. 1998. Biogeography, second edition. Sinauer Associates, INC. Publishers, Sunderland, Massachusetts. 692 pp.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Cambridge: Bellknap Press.732 pp.

Legendre, P., Legendre, L., 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam. 853 pp.

Leponce, M., Theunis, L., Delabie, J.H.C., Roisin, Y., 2004. Scale dependence of diversity measures in a leaf-litter ant assemblage. Ecography 27: 253-267.

Longino, J.T. 2000. What to do with the data ? Pages 186-203 in D., Agosti, J.D., Majer, L.E., Alonso, and T.R., Schultz. (eds): Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington DC.

Lord, J., Westoby, M., Leishman, M., 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. American Naturalist 146: 349-364.

McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate analysis for ecological data. Version 5.0. MjM Software, Gleneden Beach, Oregon, U.S.A.

McGeoch, M.A., van Rensburg, B.J., Botes, A., 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39: 661-672.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist 156: 145-155.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annual Reviews of Ecology, Evolution and Systematics 33: 475-505.

Tableau A3-1: Espèces caractéristiques des trois complexes fauniques. Les groupes pour lesquels le caractère indicateur des espèces est testé sont ceux de la Figure A3-3. Seules les espèces dont l'IndVal (IndVal obs.) était différent de celui attendu (IndVal att.) sous l'effet du hasard (*P*<0,05) sont présentées. Les espèces présentant une valeur de l'indice IndVal supérieure à 70% sont écrites **en gras**. La déviation standard des valeurs attendues est donnée (S.D.)

Groupe	**Espèce indicatrice**	**Spécificité (%)**	**Fidélité (%)**	**IndVal obs.**	**IndVal att.**	**S.D.**	***P***
1	***Pachycondyla harpax***	97	100	**97.5**	21.4	11.26	0.0012
-	***Pheidole* sp. 18**	96	100	**96.3**	27.9	13.21	0.0006
-	***Pheidole* sp. 14**	96	100	**95.8**	21.5	11.29	0.0008
-	***Solenopsis* sp. 18**	95	100	**95.1**	33.8	14.28	0.0004
-	***Solenopsis* sp. 14**	93	100	**93.1**	26.8	13.57	0.0008
-	***Pheidole* sp. 41**	86	100	**85.8**	25.7	13.13	0.0076
-	***Ectatomma edentatum***	74	100	**73.7**	38.3	12.54	0.0122
-	***Wasmannia auropunctata***	74	100	**73.6**	39	13.78	0.0224
-	***Camponotus rosariensis***	70	100	**70.1**	37.5	12.53	0.0152
-	*Brachymyrmex* sp. 05	100	67	66.7	14.6	12.04	0.0122
-	*Camponotus* sp. 09	100	67	66.7	14.6	12	0.0122
-	*Oxyepoecus* cf *rastratus*	100	67	66.7	14.6	11.91	0.0122
-	*Solenopsis* sp. 32	100	67	66.7	14.6	11.78	0.0098
-	*Brachymyrmex aphidicola*	65	100	65.5	38	11.7	0.026
-	*Forelius* sp. 02	63	100	63	33.7	14.01	0.046
-	*Camponotus borelli*	87	67	57.7	21.2	10.67	0.0474
-	*Pheidole* sp. 24	85	67	56.4	21	10.77	0.0468
-	*Pheidole* sp. 33	53	100	53.1	41.4	6.06	0.0382
A	***Ectatomma brunneum***	100	90	**89.7**	40.1	8.96	0.0002
-	***Camponotus blandus***	100	79	**79.3**	40.6	11.6	0.0012
-	***Pseudomyrmex denticollis***	73	100	**72.6**	39.5	3.68	0.0002
10	***Atta* sp. 02**	100	100	**100**	17.5	10.42	0.0006
-	***Camponotus* sp. 08 (nr. *blandus*)**	100	100	**100**	18.1	10.68	0.0006
-	***Dorymyrmex* sp. 06**	100	100	**100**	17.8	10.48	0.0006
-	***Pogonomyrmex naegelii***	100	100	**100**	17.1	10.55	0.0006
-	***Brachymyrmex termitophilus***	79	100	**78.8**	26.7	13.56	0.0092
-	***Solenopsis prox geminata* sp. 01**	74	100	**73.8**	40.9	10.76	0.005
-	*Acromyrmex* sp. 02	100	67	66.7	14.1	11.51	0.0088
-	*Dorymyrmex* sp. 05	100	67	66.7	14.3	11.57	0.0084
-	*Mycetophylax* sp. 02	100	67	66.7	14.2	11.43	0.0084
-	*Solenopsis* sp. 19	100	67	66.7	14.1	11.54	0.0088
-	*Solenopsis* sp. 03	87	67	58.1	29.9	13.56	0.0348

Tableau A3-2: Espèces caractéristiques des groupes de localités de la Figure A3-4 correspondant à un niveau hiérarchique intermédiaire entre les trois complexes fauniques et les localités.

Groupe	**Espèce indicatrice**	**Spécificité (%)**	**Fidélité (%)**	**IndVal obs.**	**IndVal att.**	**S.D.**	***P***
1	***Pachycondyla harpax***	92	100	**92.3**	18.2	10.36	0.0012
-	***Pheidole* sp. 18**	89	100	**88.9**	21.8	11.33	0.0006
-	***Pheidole* sp. 14**	88	100	**87.5**	18.2	10.35	0.0008
-	***Solenopsis* sp. 18**	87	100	**86.6**	25.7	11.51	0.0004
-	***Solenopsis* sp. 14**	81	100	**80.8**	20.9	11.16	0.0008
-	*Pheidole* sp. 41	67	100	66.8	19.6	10.99	0.008
-	*Brachymyrmex* sp. 05	100	67	66.7	15.8	10.45	0.0122
-	*Camponotus* sp. 19	100	67	66.7	16	10.36	0.0122
-	*Oxyepoecus* cf *rastratus*	100	67	66.7	16.2	10.13	0.0122
-	*Solenopsis* sp. 32	100	67	66.7	15.6	10.15	0.0098
-	*Ectatomma edentatum*	48	100	47.7	26.8	8.67	0.0362
10	***Atta* sp. 02**	100	100	**100**	16.7	9.89	0.0006
-	***Camponotus* sp. 08 (nr. *blandus*)**	100	100	**100**	16.9	9.26	0.0006
-	***Dorymyrmex* sp. 06**	100	100	**100**	16.7	9.55	0.0006
-	***Pogonomyrmex naegelii***	100	100	**100**	16.8	10.25	0.006
-	*Acromyrmex* sp. 02	100	67	66.7	15.3	9.99	0.0088
-	*Dorymyrmex* sp. 05	100	67	66.7	15.3	9.99	0.0084
-	*Mycetophylax* sp. 02	100	67	66.7	15.6	9.65	0.0084
-	*Solenopsis* sp. 19	100	67	66.7	15.1	10.05	0.0088
-	*Cyphomyrmex* sp. 03	96	67	64	16.8	9.72	0.0078
-	*Brachymyrmex termitophilus*	54	100	53.6	20.1	10.22	0.0128
-	*Solenopsis prox geminata* sp. 01	48	100	48	28.1	7.32	0.02
-	*Solenopsis* sp. 03	68	67	45.5	22.6	10.9	0.0384
-	*Dorymyrmex* sp. 01	56	67	37.3	20.4	10.46	0.0468
B	***Pheidole vallifica***	98	89	**87.4**	21.6	11.13	0.0002
-	***Solenopsis* sp. 04**	86	100	**86.1**	23.7	10.11	0.0002
-	*Crematogaster* sp. 03	89	78	68.9	21.6	10.75	0.0034
-	*Pheidole scapulata*	76	78	58.9	23.6	10.59	0.0138
-	*Forelius* sp. 03	66	89	58.4	25.2	9.6	0.0058
-	*Dorymyrmex thoracicus*	56	100	56.2	29.3	8.34	0.0058
-	*Dorymyrmex flavescens* (ou *exanguis?)*	65	78	50.9	25	10.05	0.0282
-	*Brachymyrmex leuderwaldti*	73	67	48.7	24.7	11.66	0.041
-	*Pheidole* sp. 11	54	89	47.8	26.7	8	0.0148
-	*Solenopsis* sp. 12	85	56	47	19.7	11.02	0.0454
-	*Mycetophylax emeryi*	60	78	46.7	26.9	8.95	0.0422
-	*Camponotus blandus*	60	78	46.5	27.6	7.56	0.0202
-	*Forelius nigriventris*	47	100	46.5	27.7	5.82	0.0018
-	*Solenopsis* sp. 10	100	44	44.4	17.7	10.25	0.0366
C	*Solenopsis* sp. 02	72	91	65.6	25.6	9.15	0.0008
-	*Solenopsis* sp. 01	66	82	54.2	25.6	10.64	0.0262
-	*Solenopsis* sp. 07	81	64	51.8	21.8	10.6	0.0226
-	*Solenopsis* sp. 13	69	73	49.9	25	10.82	0.0266
-	*Camponotus borelli*	62	73	45.1	23.9	9.83	0.0466
-	*Camponotus substitutus*	44	89	44.4	27.8	4.92	0.0008
-	*Pseudomyrmex denticollis*	35	100	35.4	24.6	1.85	0.0002
D	*Ectatomma brunneum*	45	100	45	26.4	5.03	0.0004
-	*Solenopsis* sp. 23	100	44	44.4	18.1	10.99	0.0474

Tableau A3-3: Espèces caractéristiques de chaque localité. Les groupes correspondent à ceux de la Figure A3-5. Le transect unique de la localité 5 n'a pas été intégré à cette analyse.

Groupe	**Espèce indicatrice**	**Spécificité (%)**	**Fidélité (%)**	**IndVal obs.**	**IndVal att.**	**S.D.**	***P***
1	***Pachycondyla harpax***	80	100	**80**	21	11.85	0.0036
-	***Pheidole* sp. 18**	73	100	**72.7**	21.8	10.59	0.001
-	***Pheidole* sp. 14**	70	100	**70**	21.2	11.95	0.006
-	*Solenopsis* sp. 18	67	100	66.7	23.1	9.32	0.0006
-	*Solenopsis* sp. 14	58	100	58.3	21.2	10.23	0.0094
10	***Atta* sp. 02**	100	100	**100**	26.7	11.46	0.0016
-	***Camponotus* sp. 08 (nr. *blandus*)**	100	100	**100**	20	12.71	0.0016
-	***Dorymyrmex* sp. 06**	100	100	**100**	25	11.59	0.0016
-	***Pogonomyrmex naegelii***	100	100	**100**	27.6	11.6	0.0016
-	*Cyphomyrmex* sp. 03	89	67	59.3	23.6	11.64	0.0536
2	***Solenopsis* sp. 26**	100	100	**100**	24.9	11.77	0.002
-	*Acromyrmex* sp. 04	64	100	64.3	21.4	10.97	0.007
-	*Solenopsis* sp. 23	64	100	64.3	23.9	12.27	0.0102
-	*Pheidole* sp. 33	18	100	18.2	14.2	1.8	0.027
3	*Brachymyrmex* sp. 03	83	100	83.3	19.5	12.07	0.0018
-	*Camponotus* sp. 09	33	100	33.3	18.3	6.45	0.0198
-	*Ectatomma brunneum*	19	100	18.5	14.9	1.77	0.0128
4	*Brachymyrmex termitophilus*	44	100	44.4	19.1	8	0.0112
-	*Solenopsis* sp. 04	41	100	40.8	19.8	7.42	0.012
-	*Pheidole* sp. 45	35	100	35	20.1	6.68	0.031
-	*Camponotus blandus*	28	100	27.6	18.4	4.23	0.0206
7-01	*Pheidole vallifica*	59	100	59.3	21.1	9.58	0.0046
-	*Brachymyrmex leuderwaldti*	56	100	56.4	23.3	9.8	0.0094
-	*Solenopsis* sp. 12	52	100	52.2	21.1	10.64	0.0312
-	*Dorymyrmex flavescens* (*ou exanguis?)*	45	100	45	20	7.05	0.0018
-	*Crematogaster* sp. 03	44	100	44	19.9	8.25	0.0122
-	*Mycetophylax emeryi*	42	100	42.3	19.8	6.03	0.0014
-	*Forelius* sp. 03	40	100	40.4	19.6	6.51	0.003
-	*Forelius brasiliensis*	36	100	35.9	20.7	6.18	0.0192
-	*Camponotus tenuiscapus*	35	100	35.4	20.2	6.62	0.028
-	*Pogonomyrmex cunicularius*	19	100	18.8	14.6	1.79	0.017
7-02	***Dorymyrmex* sp. 04**	86	100	**85.7**	20.1	12.94	0.0044
-	*Dinoponera mutica*	67	100	66.7	21.8	11.38	0.0184
-	*Trachymyrmex* sp. 01	67	100	66.7	21.9	11.4	0.0182
-	*Solenopsis* sp. 21	60	100	60	20.1	10.94	0.0032
-	*Solenopsis* sp. 01	54	100	53.8	22.6	8.87	0.001
-	*Crematogaster* sp. 06	50	100	50	18.3	11.12	0.0326
-	*Solenopsis* sp. 13	46	100	46.2	23	9.64	0.02
-	*Solenopsis* sp. 07	41	100	40.9	19.6	8.1	0.0338
-	*Solenopsis* sp. 22	35	100	35.3	18.9	6.06	0.0116
-	*Solenopsis* sp. 02	35	100	34.5	19.4	6.04	0.0168
-	*Crematogaster* sp. 01	33	100	33.3	18.8	6.3	0.0260
-	*Pheidole radoszkowskii*	30	100	30.1	18.1	4.11	0.0036
-	*Solenopsis* sp. 17	30	100	29.8	17.8	3.72	0.0012
-	*Camponotus substitutus*	20	100	20	15.6	2.09	0.0086
9	***Pheidole* sp. 13**	93	100	**92.9**	21.5	11.88	0.001
-	***Solenopsis* sp. 10**	83	100	**83.3**	23.1	11.5	0.0042
-	***Trachymyrmex* sp. 02**	71	100	**71.4**	19.5	11.24	0.0036

Figure A3-1: Distribution des espèces de fourmis le long d'un gradient d'aridité dans le Chaco sec paraguayen. Seules les 8 localités alignées le long du gradient d'aridité sont considérées. Il s'agit de Río Verde (pluviométrie moyenne annuelle: 1000mm); Cruce de Los Pioneros (850mm); Mariscal Estigarribia (700mm); Garrapatal (600mm); Teniente Enciso-Sud, collecté en 2004 (500mm); Siracua (450mm); Nueva Asunción (400mm); Fortín Mister Long (350mm). Les trois complexes myrmécofauniques mis en évidence dans le Chaco sec paraguayen (Chapitre 4) sont donc inclus.

Au niveau de chaque localité, les fourmis du sol ont été collectées à l'aide de 60 pièges a fosse. Classiquement, une espèce est considérée numériquement dominantes lorsqu'elle est présente dans au moins 10% des échantillons (voir par exemple Leponce *et al.*, 2004). Seules les espèces numériquement dominantes au niveau d'au moins une localité sont retenues pour cette analyse (68 espèces). Les espèces sont groupées en fonction de leur ubiquité (i.e. celles échantillonnées au niveau des 8 localités sont représentées ensemble, etc.) Ceci non seulement afin d'accroître la lisibilité des figures mais également afin d'illustrer d'une manière nouvelle la relation positive liant la répartition et la dominance numérique des espèces de fourmis chaquéennes (Chapitre 4). Globalement, plus une espèce a une distribution large, plus elle est numériquement dominante localement.

Les espèces de fourmis semblent se distribuer indépendamment les unes des autres, sans former d'associations d'espèces bien délimitées spatialement. Les courbes sont lissées selon l'algorithme d'Excel.

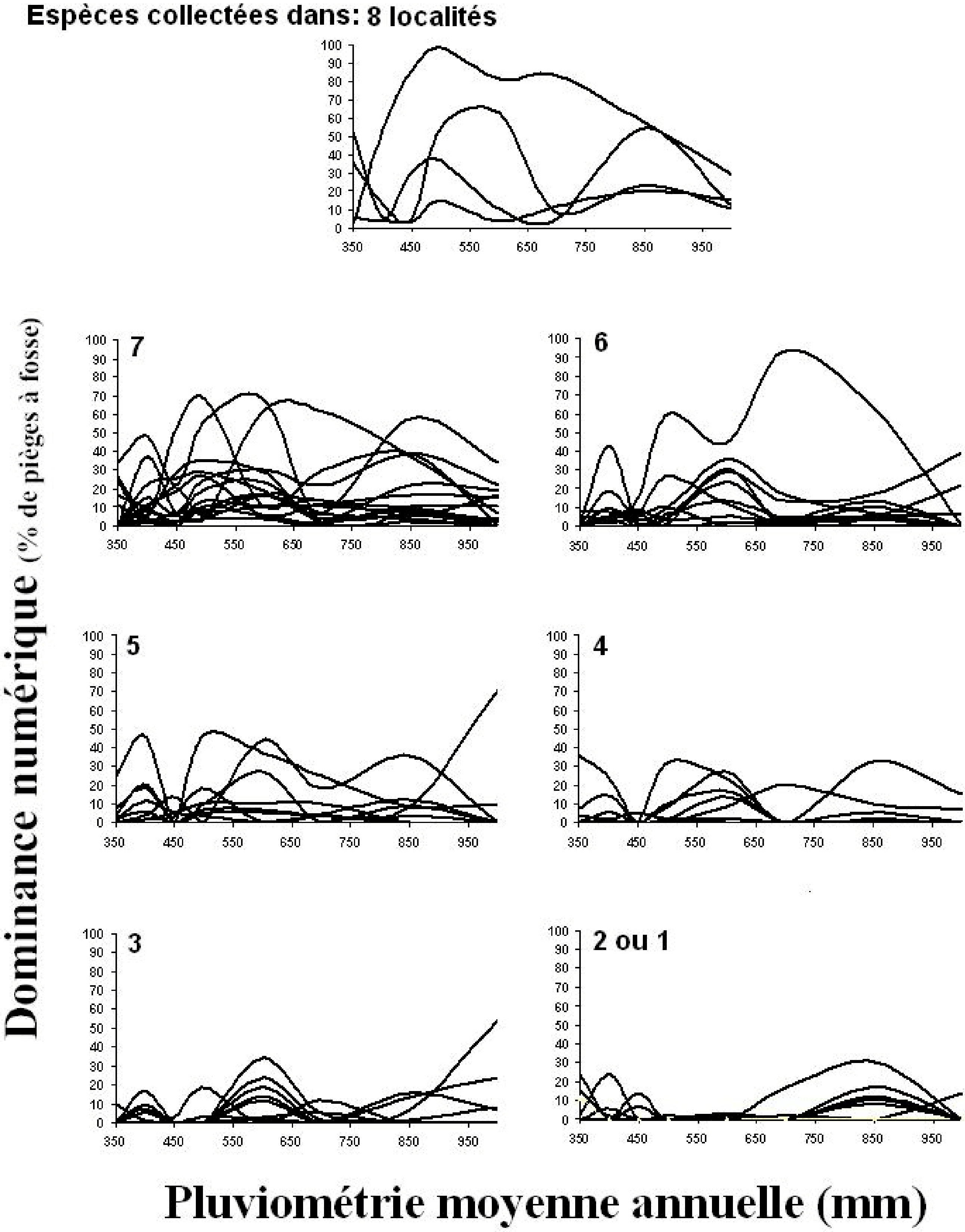

Espèces collectées dans: 8 localités
7
6
5
4
3
2 ou 1
0
10
20
30
40
50
60
70
80
90
100
350
450
550
650
750
850
950
Dominance numérique (% de pièges à fosse)
Pluviométrie moyenne annuelle (mm)

Figure A3-2: Distribution des espèces de fourmis appartenant aux principaux genres collectés le long d'un gradient d'aridité dans le Chaco sec paraguayen. Le principe est identique à celui décrit dans la légende de la Figure A3-1 sauf que les espèces congénériques sont regroupées.

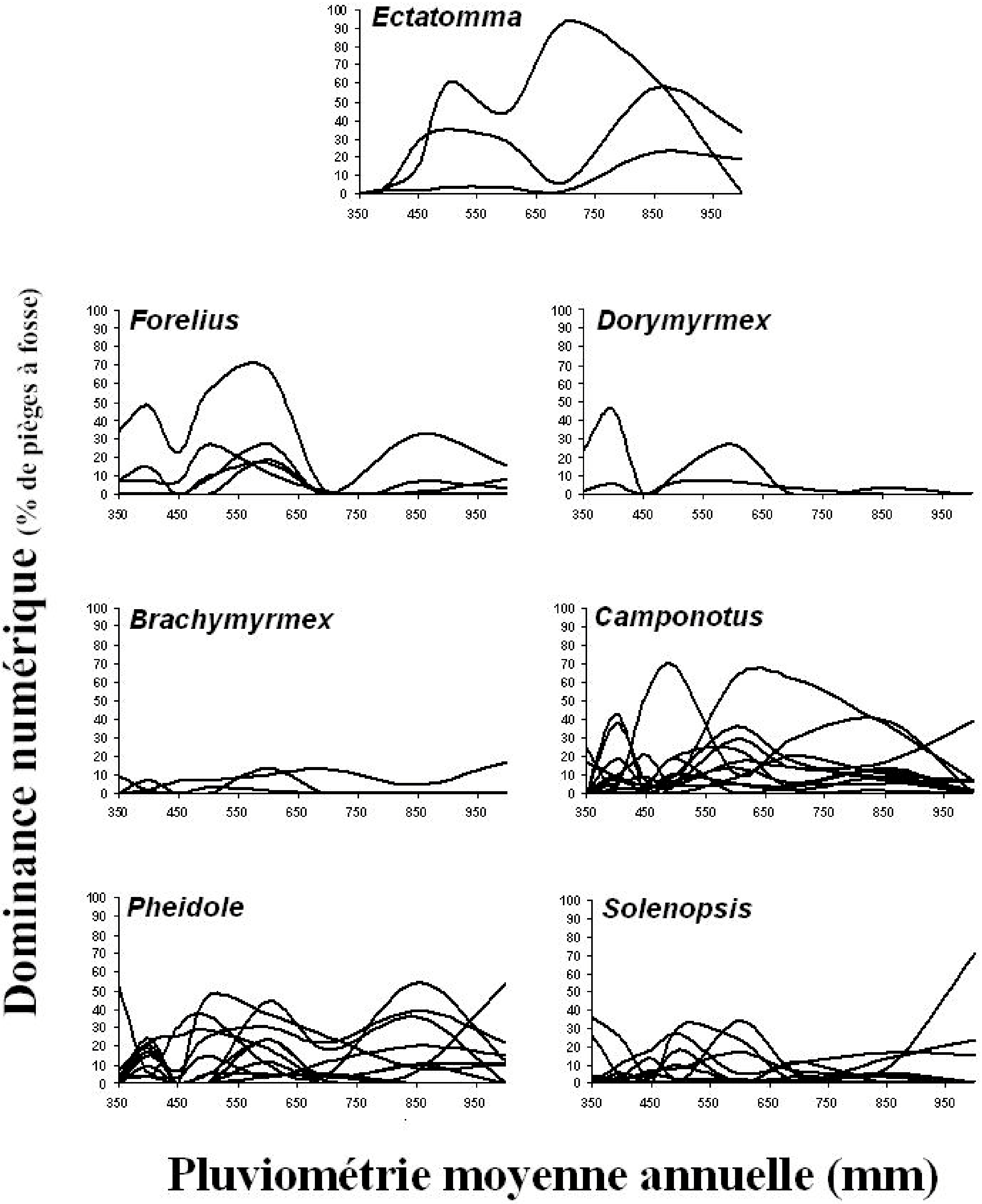


Figure A3-3: Groupes retenus pour l'analyse IndVal dont les résultats sont présentés dans le Tableau A3-1. Une classification des localités est effectuée ("complete linkage clustering"). Les numéros des localités sont: 1: Río Verde; 2: Cruce de Los Pioneros; 3: Mariscal Estigarribia; 4: Garrapatal; 5: Estancia María Vicenta; 6: Teniente Enciso-Nord; 7: Teniente Enciso-Sud; 8: Siracua; 9: Nueva Asunción; 10: Fortín Mister Long; 11: Fortín Mayor Infante Rivarola. Les trois échantillonnages réalisés au niveau de la localité de référence (localité 7) sont analysés séparemment.

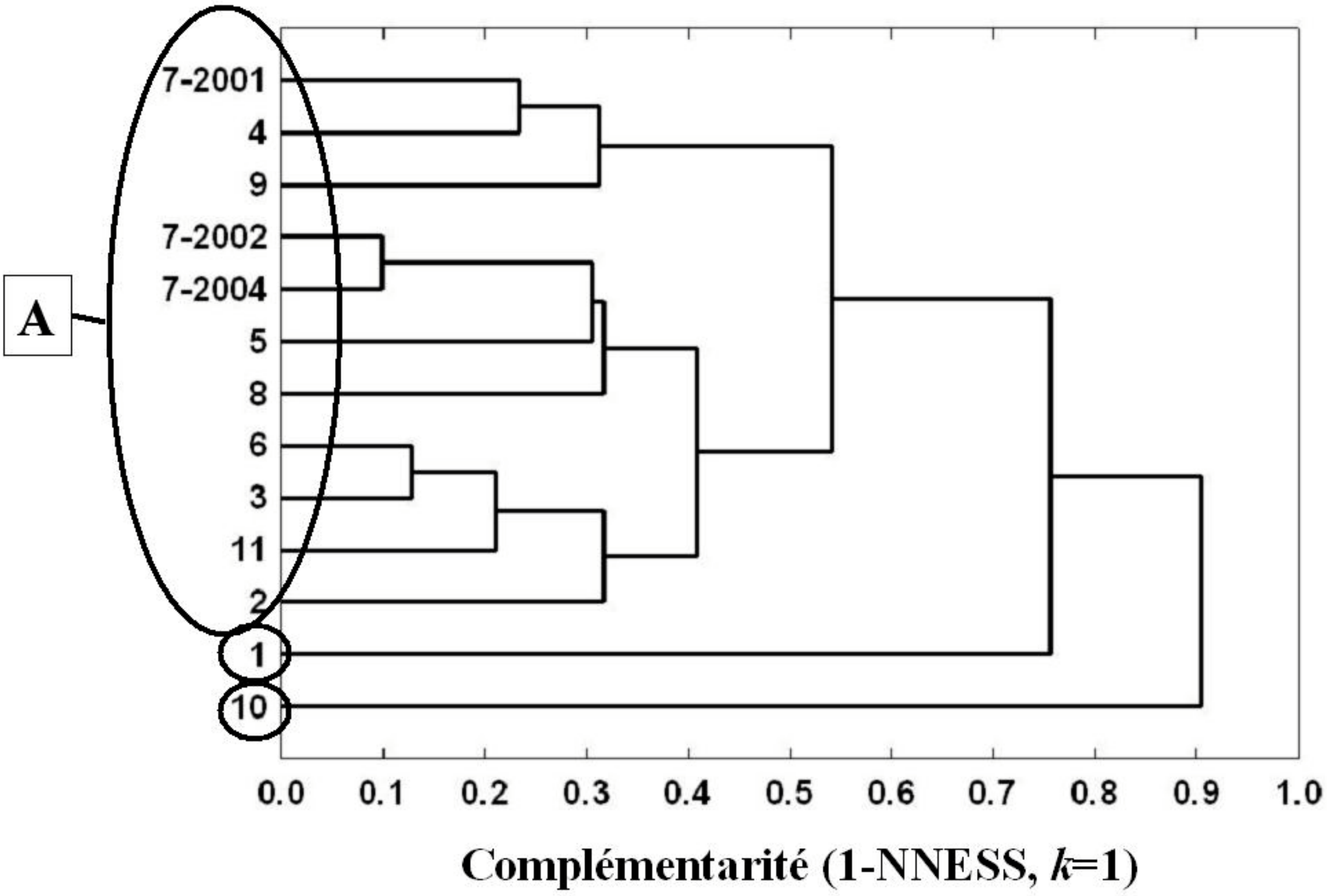


Figure A3-4: Groupes retenus pour l'analyse IndVal dont les résultats sont présentés dans le Tableau A3-2.

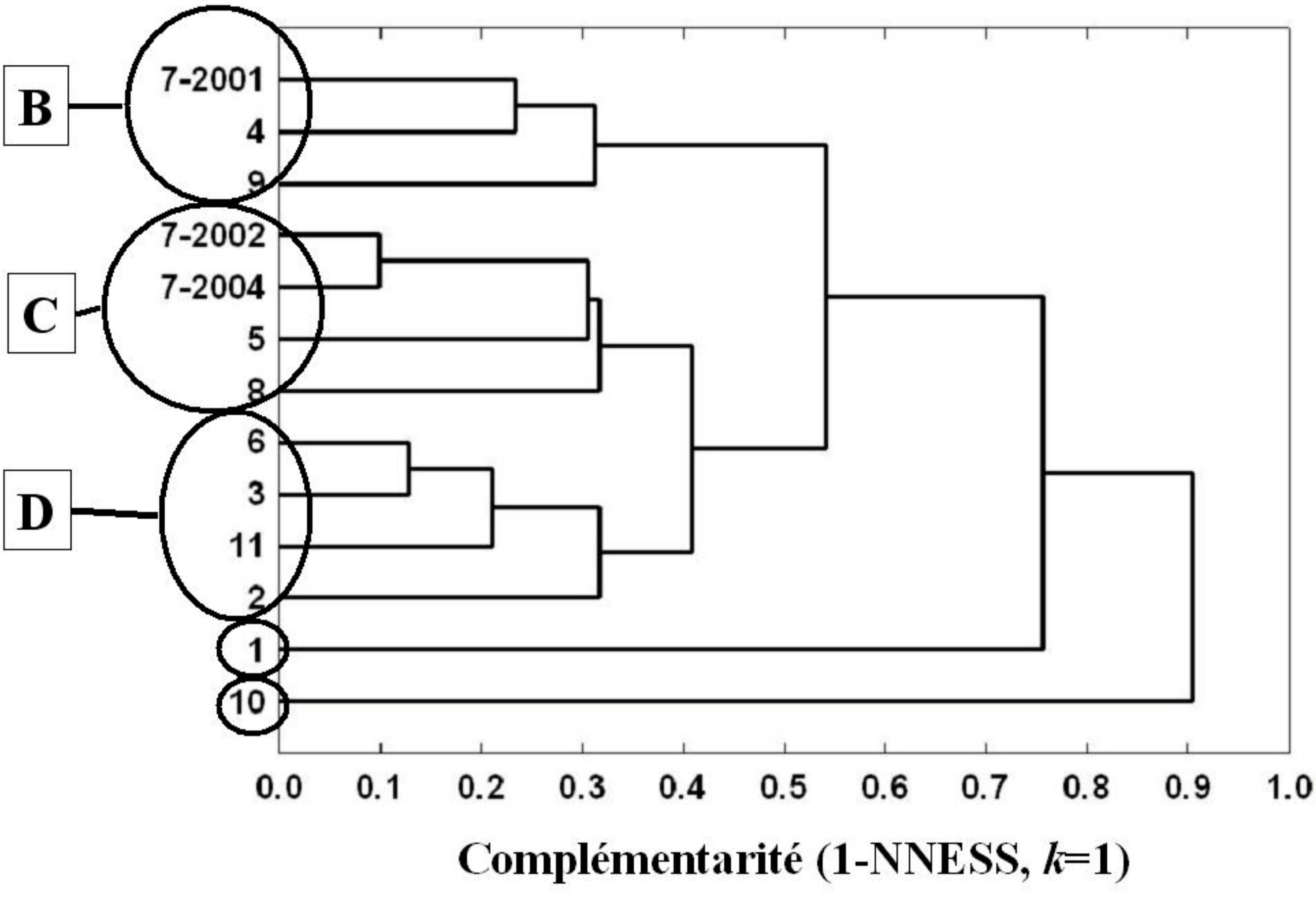
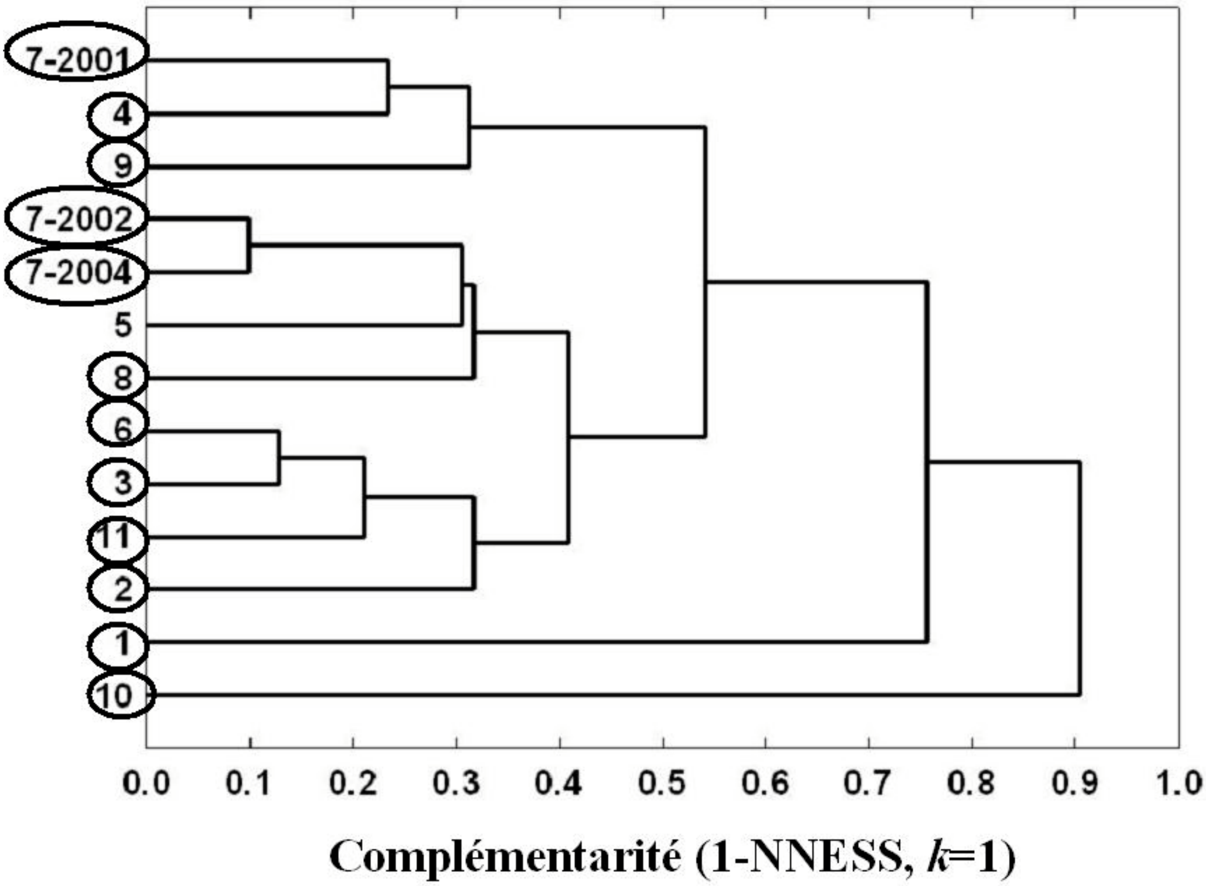


Figure A3-5: Groupes retenus pour l'analyse IndVal dont les résultats sont présentés dans le Tableau A3-3.



Annexe 4
Peut-on utiliser la richesse générique pour estimer la richesse spécifique d'un assemblage de fourmis dans le Chaco sec paraguayen?

Introduction

L'utilisation des taxons supérieurs comme indicateurs de la diversité spécifique ("higher-taxon surrogacy") est une idée séduisante dans le contexte actuel d'érosion croissante de la diversité biologique (Gaston et Williams, 1993; Báldi, 2003). Le but visé est de permettre d'effectuer une sélection des sites à conserver et/ou un suivi ("monitoring") de la qualité des écosystèmes de façon rapide et efficace avec des moyens financiers et humains limités.

La validité et l'efficacité de cette approche dépendent du degré de corrélation qui existe entre la richesse générique (ou d'un niveau taxonomique supérieur) et la richesse spécifique d'un assemblage (Andersen, 1995).

Andersen (1995) a montré que l'application de cette méthode pour les assemblages de fourmis n'était pas envisageable à l'échelle continentale car la relation genres/espèces présente des variations interrégionales liées à la diversité des habitats étudiés. Par contre, à l'échelle régionale, une forte corrélation est généralement trouvée (Andersen, 1995, 1997; Pik *et al.*, 1999; Negi et Gadgil, 2002).

Ici, je propose de mesurer le degré de corrélation existant entre la richesse spécifique et la richesse générique des assemblages de fourmis du Chaco sec paraguayen afin de déterminer si une évaluation rapide de la diversité des fourmis peut être envisageable au sein de cette région.

Méthode

Le long d'un gradient d'aridité 11 localités furent échantillonnées à l'aide de pièges à fosse. En outre, une localité de référence fut échantillonnée à trois reprises (se référer à la Figure 0-1 de l'introduction de la thèse pour une description détaillée du protocole et à la Figure 0-5 pour la situation géographique des localités étudiées; se référer au chapitre 4 pour les données relatives à la richesse spécifique et au chapitre 5 pour celles concernant la richesse générique).

Résultats et conclusion

Le nombre d'espèces observées était corrélé au nombre de genres observés (r =0,723; P=0,005; n=13; Pearson Product Moment Correlation; Figure A4-1A). La corrélation est cependant plus faible lorsqu'elle est calculée pour les richesses raréfiées (r =0,571; P=0,041, n=13; Figure A4-1B) et elle disparaît lorsqu'elle est réalisée à partir des richesses extrapolées (Chao2; r =0,382; P=0,198, n=13; Figure A4-1C).

Ces résultats montrent que la méthode utilisant la richesse générique comme indicateur de la richesse spécifique a un intérêt réduit voire nul au sein de la région étudiée dès lors que l'on tient compte des biais d'échantillonnages éventuels.

Références bibliographiques:

Andersen, A.N., 1995. Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. Biological Conservation 73: 39-43.

Andersen, A.N., 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24: 433-460.

Báldi, A., 2003. Using higher taxa as surrogates of species richness: a study based on 3700 Coleoptera, Diptera, and Acari species in Central-Hungarian reserves. Basic and Applied Ecology 4: 589-593.

Gaston, K.J., Williams, P.H., 1993. Mapping the world's species - the higher taxon approach. Biodiversity Letters 1: 2-8.

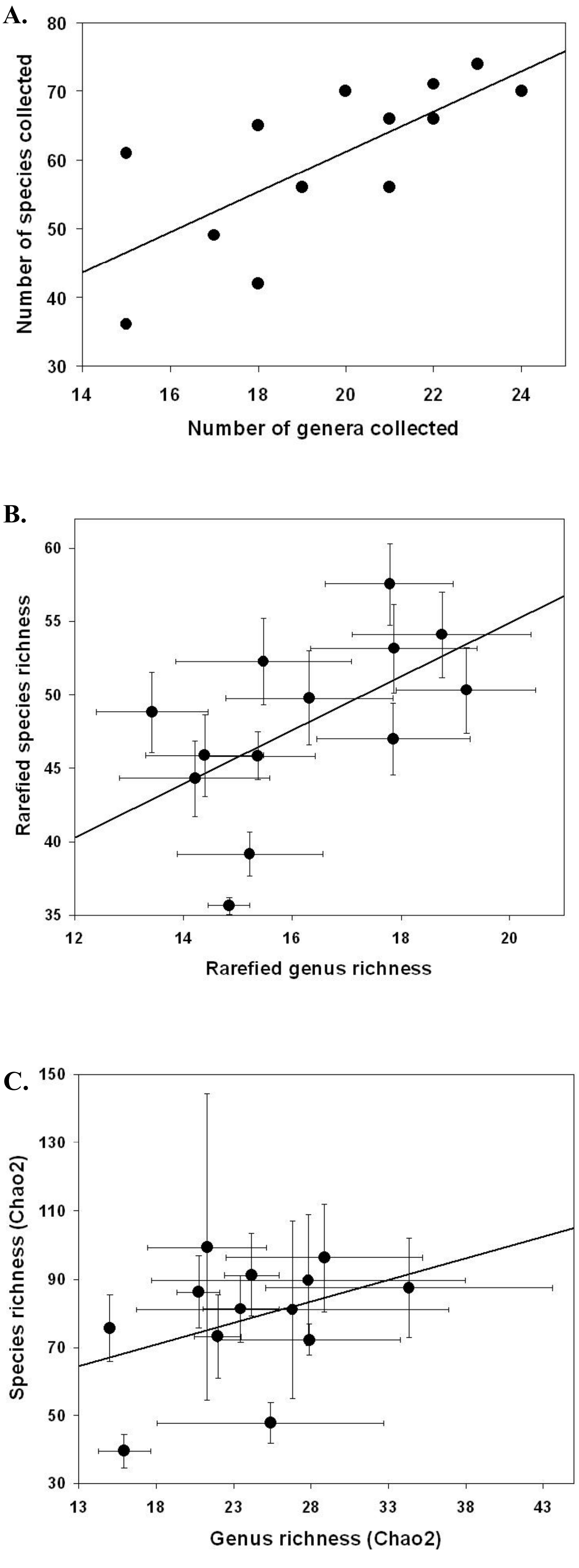
Negi, H.R., Gadgil, M., 2002. Cross-taxon surrogacy of biodiversity in the Indian Garhwal Himalaya. Biological Conservation 105: 143-155.

Pik, A.J., Oliver, I, Beattie, A.J., 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Australian Journal of Ecology 24: 555-562.

Figure A4-1:

Relation entre la richesse spécifique et la richesse générique (A) observées, (B) raréfiées (méthode de Coleman; richesses spécifiques et génériques des localités raréfiées à 204 et 136 occurrences respectivement), (C) extrapolées (Chao 2). Les barres des figures A4-1B et A4-1C correspondent aux déviations standards des valeurs calculées.

Figure A4-1:


A.
Number of species collected
80
70
60
50
40
30
14
16
18
20
22
24
Number of genera collected
B.
Rarefied species richness
60
55
50
45
40
35
12
14
16
18
20
Rarefied genus richness
C.
Species richness (Chao2)
150
130
110
90
70
50
30
13
18
23
28
33
38
43
Genus richness (Chao2)

Distribution and diversity of the cryptic ant genus *Oxyepoecus* (Formicidae: Myrmicinae) in Paraguay[1].

DELSINNE T. (1,2)**, MACKAY W.** (3)**, WILD A.** (4)**, ROISIN Y.** (2), **LEPONCE M.** (1)

(1): Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, Belgium.
Thibaut.Delsinne@naturalsciences.be;

(2): Université Libre de Bruxelles, 50 avenue Roosevelt, Department of Evolutive Eco-Ethology, 1050 Brussels, Belgium.

(3): Laboratory for Environmental Biology, The University of Texas, El Paso 79968, USA.

(4): Department of entomology, University of Arizona, Tucson, az 85721, USA.

---

[1] Les résultats présentés dans cette annexe sont préliminaires. Une comparaison des spécimens collectés avec les types des différentes espèces sera réalisée par le Dr. William MacKay en septembre 2007 afin de confirmer les identifications.

ABSTRACT

Oxyepoecus cf *inquilinus, O.* cf *bruchi* and *O.* cf *rastratus* are recorded for the first time in Paraguay and new distribution data are provided for *O.* cf *vezenyii*. An illustrated key to the workers of these species is provided. At Teniente Enciso National Park, the four species co-occurred. This locality appears as a promising site to undertake studies documenting the biology of the poorly known *Oxyepoecus* genus and, because *O. inquilinus* and *O. bruchi* are classified as vulnerable in the IUCN Red list 2006, the park value for biological conservation is underlined.

INTRODUCTION

The genus *Oxyepoecus* Santschi 1926 is a group of cryptobiotic species, sparsely and rarely collected from Colombia to Argentina (Fernández, 2002a; De Albuquerque and Brandão, 2004). It is placed in the Myrmicinae subfamily and in the Solenopsidini tribe (Bolton, 2003) and is currently represented by 16 species (Kempf, 1974; De Albuquerque and Brandão, 2004). In Paraguay, only *O. vezenyii* (Forel, 1907) was recorded from a single locality [Concepción: Puerto Max, locality 5 on Figure A5-1] (Forel, 1907).

The biology of the genus is poorly known, but three species (*O. inquilinus* (Kusnezov, 1952), *O. bruchi* Santschi, 1926 and *O. daguerrei* [Santschi, 1933]) are suspected to be inquiline of *Pheidole* or *Solenopsis* species (Santschi, 1926; Kusnezov, 1952; Kempf, 1974) although the exact nature of the relationship is still unclear (De Albuquerque and Brandão, 2004). These three species are considered as vulnerable D2 (IUCN, 2006), which means that they are suspected to be "facing a high risk of extinction in the wild in the medium-term future" because "their populations are characterised by an acute restriction in their area of occupancy (typically less than 100 km^2) or in the number of locations (typically less than five)." Under the present context of rapid biodiversity loss and uncertainty concerning the conservation status of social insects (Chapman and Bourke, 2001), data increasing our knowledge on threatened species are needed.

Here, the sampling of *O. inquilinus, O. bruchi* and *O. rastratus* is reported for the first time in Paraguay and new distribution data are provided for *O. vezenyii*.

METHODS

In the Paraguayan dry Chaco, 11 localities were inventoried along a 400km transect from locality 1 to locality 4 (Figure A5-1). Ants were sampled between 2001 and 2004 at the end of the dry season (September-November). Ants living in elementary quadrats of 1m² of leaf-litter were extracted with Winkler eclectors (n= 560). Ants running on the ground surface were catched with pitfall traps consisting in 70mm-diameter drinking cups, filled with water and a drop of detergent, and operated during 24 hours.

Voucher specimens were deposited in 5 collections: the Royal Belgian Institute of Natural Sciences (RBINS); the University of Texas at El Paso (UTEP); the Alexander L. Wild collection (ALWC), the Los Angeles County Museum, Los Angeles, California, USA (LACM); and at the "Museo Nacional del Historial Natural del Paraguay", San Lorenzo, Paraguay (INBP).

RESULTS

Oxyepoecus species collected in Paraguay:

***Oxyepoecus rastratus* (Mayr, 1887)** / Figure A5-2**:**

Canindeyú: Reserva Natural del Bosque Mbaracayú, 05.II.1996, A. Wild (#AW0129). [7 workers and 1 gyne, ALWC, IBNP, LACM]. Nest in red rotting log; wood was too hard for a full excavation. One chamber uncovered with queen and brood (locality 6 on Figure A5-1).

Boquerón: Teniente Enciso National Park, 03-05.XI.2001, Leponce, M. [29 workers and 1 gyne in 8 Winkler samples, RBINS, UTEP]. Boquerón: Garrapatal, Lat: S 21.45°; Long: W 61.49° (locality 3 on Figure A5-1), 05-06.XI.2001, Leponce, M. [1 worker in a Winkler sample, RBINS].

***Oxyepoecus bruchi* Santschi, 1926** / Figure A5-3:

Boquerón: T. Enciso N.P., 03-05.XI.2001, Leponce, M. [5 workers in 3 Winkler samples, RBINS, UTEP]. Boquerón: Garrapatal, 05-06.XI.2001, Leponce, M. [1 worker in a Winkler sample, RBINS]. Presidente Hayes: Río Verde, Lat: S 23.22°; Long: W 59.20° (locality 4 on Figure A5-1), 15-16.X.2003, Delsinne, T. [2 workers in a single 24h-pitfall sample, RBINS].

***Oxyepoecus inquilinus* (Kusnezov, 1952)** / Figures A5-4**:**

Boquerón: T. Enciso N.P., Lat: S 21.21°; Long: W 61.66° (locality 2 on Figure A5-1), 03-05.XI.2001, Leponce, M. [2 workers from a single Winkler sample, RBINS]. Boquerón: Nueva Asunción, Lat: S 20.70°; Long: W 61.93° (locality 1 on Figure A5-1), 02-06.XI.2001, Leponce, M. [2 workers in two 4-day pitfall traps, RBINS].

***Oxyepoecus vezenyii* (Forel, 1907)** / Figure A5-5**:**

Boquerón: T. Enciso N.P., 03-05.XI.2001, Leponce, M. [16 workers and 5 gynes in 9 Winkler samples, RBINS, UTEP]. Boquerón: Garrapatal, 05-06.XI.2001, Leponce, M. [1 worker in a Winkler sample, RBINS]. Presidente Hayes: R.Verde, 15-16.X.2003, Delsinne, T. [4 workers in three 24h-pitfall samples, RBINS, UTEP].

Localities 1, 2 and 3 are xeromorphic forests (mean annual rainfall: 400-500mm; mean annual temperature: 26°C; elevation: 200-250m) and locality 4 is a mesoxeromorphic forest (1000 mm, 26°C, 100m) of the dry Chaco. Locality 6 belongs to the Alto Parana formation of the Atlantic rainforest (1800mm).

Key to the workers of *Oxyepoecus* in Paraguay:

1. - Cephalic dorsum entirely sculptured (Figures A5-2C and A5-3D): 2
   - Cephalic dorsum totally smooth and shinny (Figures A5-4C and A5-5C), or with at least a smooth median frontal stripe: 3

2. - Subpostpetiolar process prominent and bidentate (Figure A5-3B): *bruchi*
   - Subpostpetiolar without bidentate process: *rastratus*

3. - Eyes large with more than 40 ommatidies (Figures A5-4A and A5-4C): *inquilinus*
   - Eyes small with around 20 ommatidies (Figures A5-5A and A5-5C): *vezenyii*

DISCUSSION

Three *Oxyepoecus* species are recorded for the first time in Paraguay and new records are provided for *O. vezenyii*. The four species co-occur in the dry Chaco, in particular at Teniente Enciso National Park (locality 2 on Figure A5-1) where 58 individuals were collected. To our knowledge, it is the first observation of at least four *Oxyepoecus* species co-occurring in a same locality.

Specimens were mainly collected with Winkler extractors. This method is highly effective to sample minute and cryptic ant species, which were suspected rare before its wider use (Fernández, 2002b). The variability in catch success of *Oxyepoecus* species could be a methodological artefact. In dry areas the Winkler efficiency (both in terms of species collected and species occurrences) is very low during drought period probably because most ants do not forage in the leaf litter, at least during daytime (Delsinne *et al.*, submitted). Our sampling campaigns occurred at the end of the dry season/beginning of the wet season. Only the 2001 campaign could be conducted during a rainfall period, possibly explaining the success of our Winkler catches in the localities sampled during this period (localities 1, 2, 3). Before to conclude for the absence of occurrence of *Oxyepoecus* species in the other localities, new Winkler extracts should be performed during a rainfall period.

Except for the type specimen of *Oxyepoecus vezenyii* collected from Paraguay (Forel, 1907), this species was exclusively known from Brazil where it was sampled in different ecosystems over a large spatial scale (De Albuquerque and Brandão, 2004). The presence of this species in the Paraguayan Chaco increases its range of 400km to the West.

O. rastratus was only documented from South and South-East Brazil. Its presence at T. Enciso N.P. increases its range of nearly 1000km to the West. In addition, its occurrence in the dry Chaco and in the Parana forest suggests that this species may be present in a large variety of biomes.

O. inquilinus was sampled in two localities of the Paraguayan dry Chaco. In the literature, *O. inquilinus* was reported from two savanna localities of the Brazilian Cerrado (Kempf, 1974), one anthropic area (i.e. the "Jardin del Instituto Miguel Lillo") from the Argentinean Tucumán province (Kusnezov, 1952) and one locality in the Bolivian Beni Department (Kempf, 1974). Recently a worker of a species very close to *O. inquilinus* was collected in a savanna-morichal habitat from Colombia but its specific status awaits more investigation (Fernández, 2002a). Although data are insufficient to determine the exact requirements of this species, *O. inquilinus* seems to be present in both open and closed habitats and in both dry and wet areas. The distribution of this species seems large but discontinuous and *O. inquilinus* is always locally rare, justifying its vulnerable status (IUCN, 2006).

Inside the genus, *O. bruchi* is the species exhibiting the most southern distribution since it was collected in three Chacoan localities of Argentina (2 in Córdoba and 1 in Tucumán provinces) (De Albuquerque and Brandão, 2004). To our knowledge, this species was not collected since 1948 (De Albuquerque and Brandão, 2004). Its presence in the Paraguayan Chaco increases its range of 650km to the North and of near 600km to the East.

O. inquilinus is suspected to be inquiline of *Pheidole radozskowskii* (Kusnezov, 1952). At T. Enciso N.P., two workers of *O. inquilinus* and 11 workers of *Ph. radozskowskii* were collected in the same Winkler sample. However, at Nueva Asunción the latter was not recorded in our 60 Winkler and 60 pitfall samples, suggesting that *O. inquilinus* is not restricted to this host species. In the same direction, *O. bruchi* is suspected to be inquiline of *Ph. rosae* (*silvestrii*) and *Ph. obtusopilosa* (Santschi, 1926; Kusnezov, 1952; Kempf, 1974) but these species were not present in our samples.

Oxyepoecus ants appeared diversified and well established at T. Enciso N.P., which may hence constitute a promising reference locality to undertake studies concerning these poorly known myrmicines. Moreover, the presence of *O. inquilinus* and *O. bruchi* at T. Enciso N.P. emphasizes the importance of this park for the conservation of the Chacoan fauna.

ACKNOWLEDGMENTS

This study was made possible by the financial support of the “Fonds pour la Formation à la Recherche dans l’Industrie et l’Agriculture -FRIA” (Belgium) and the "Fonds National de la Recherche Scientifique - FNRS" (Belgium). We thank Dr. J. Kochalka, B. Garcete-Barrett, V. Filippi, J. Jara, C. Bénilez and C. Aguilar Julio from the Museo Nacional de Historia Natural del Paraguay, Asunción. The guards of T. Enciso National Park. and V. Olivier provided help during fieldwork. J. Cillis, RBINS took the electron microscope photographs. T. Arias Penna and D. Arias Penna commented on the manuscript.

REFERENCES

Bolton B., 2003: Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute* 71: 1-370.

Chapman R.E. and Bourke F.E., 2001: The influence of sociality on the conservation biology of social insects. *Ecology Letters* 4: 650-662.

De Albuquerque N.L. and Brandão C.R.F., 2004: A revision of the neotropical Solenopsidini ant genus *Oxyepoecus* Santschi 1926 (Hymenoptera: Formicidae: Myrmycinae). 1. The Vezenyii species-group. *Papéis Avulsos de Zoologia* 44: 55-80.

Delsinne T., Leponce M., Theunis L., Braet Y and Roisin Y. Rainfall influence the ant sampling in dry forests. *Biotropica, under revision.*

Fernández F., 2002a: New ant records for Colombia and South America (Hymenoptera: Formicidae) *Revista Colombiana de Entomología* 28: 215.

Fernández F., 2002b: First record of the myrmicine ant genus *Paedalgus* Forel, 1911 (Hymenoptera: Formicidae) from the Western Hemisphere. *Entomotropica* 17: 181-182.

Forel A., 1907: Formicides du Musée National Hongrois. *Annales Historico-Naturales Musei Nationalis Hungarici* 5: 1-42.

I.U.C.N. (Species Survival Commission of the World Conservation Union) 2006**:** 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 24 February 2007.

Kempf W.W., 1974: A review of the neotropical ant genus *Oxyepoecus* Santschi (Hym, Formicidae). *Studia Entomologica* 17: 471-512.

Kusnezov N., 1952: Acerca de las hormigas simbióticas del género *Martia* Forel (Hymenoptera, Formicidae). *Acta Zoologica Lilloana* 10: 717-722.

Santschi F., 1926: Deux nouvelles fourmis parasites de l'Argentine. *Folia Myrmecologica and Termitologica* 1: 6-8.

Figure A5-1: Distribution of *Oxyepoecus* species in Paraguay: *O. rastratus* (localities 2, 3 and 6), *O. vezenyii* (2, 3, 4 and 5), *O. inquilinus* (1 and 2) and *O. bruchi* (2, 3 and 4). Localities where *Oxyepoecus* species were collected are (1) Nueva Asunción, (2) Teniente Enciso National Park-Southern side, (3) Garrapatal, (4) Río Verde, (5) Puerto Max, (6) Reserva Natural del Bosque Mbaracayú. Localities where no *Oxyepoecus* were collected are: (a) Cruce de Los Pioneros, (b) Mariscal Estigarribia, (c): Teniente Enciso-Northern side, (d) Estancia María Vicenta, (e) Siracua, (g) Fortín Mayor Infante Rivarola, (f) Fortín Mister Long.

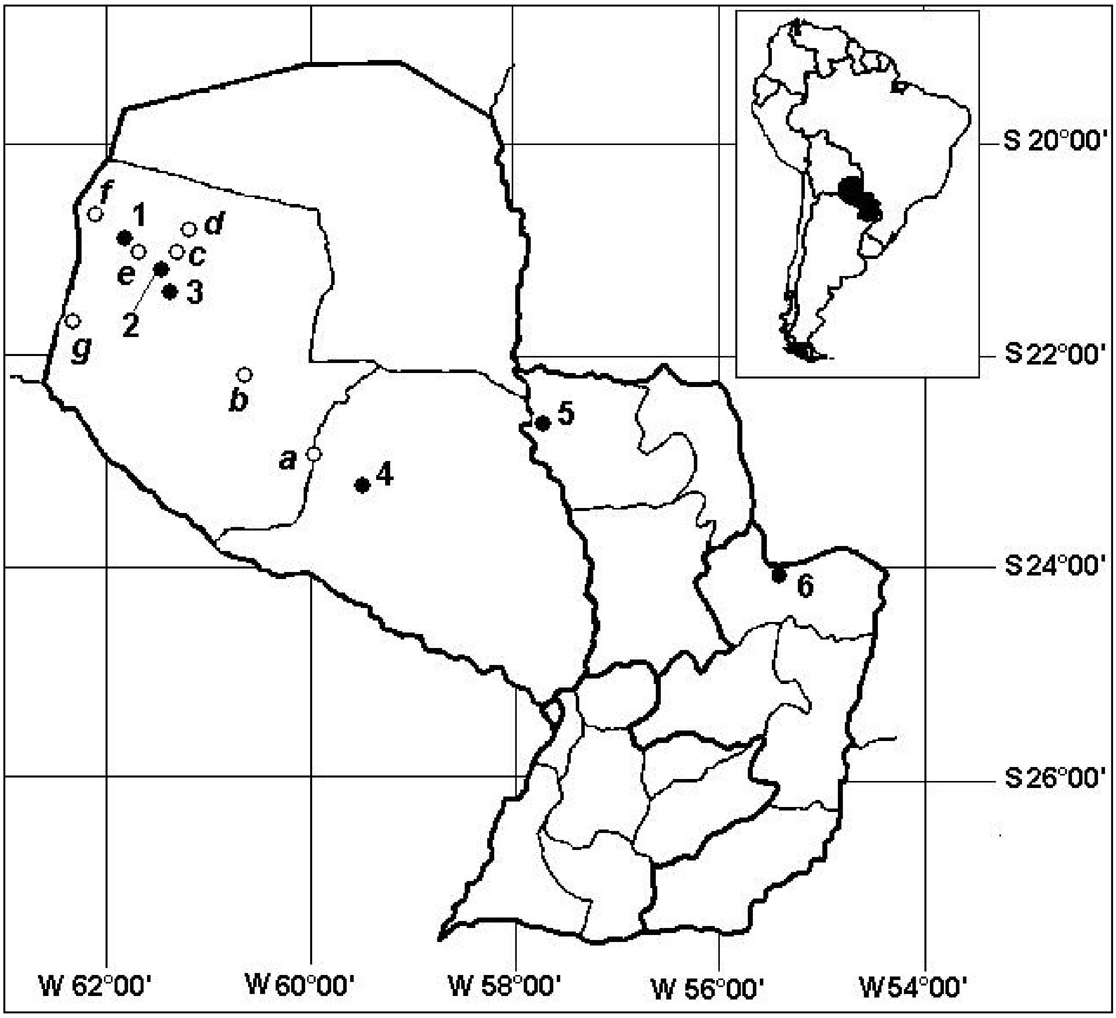


Figure A5-2: Worker of *Oxyepoecus rastratus*. A) lateral view, B) mesosoma, petiole and postpetiole, dorsal view, C) head, frontal view.

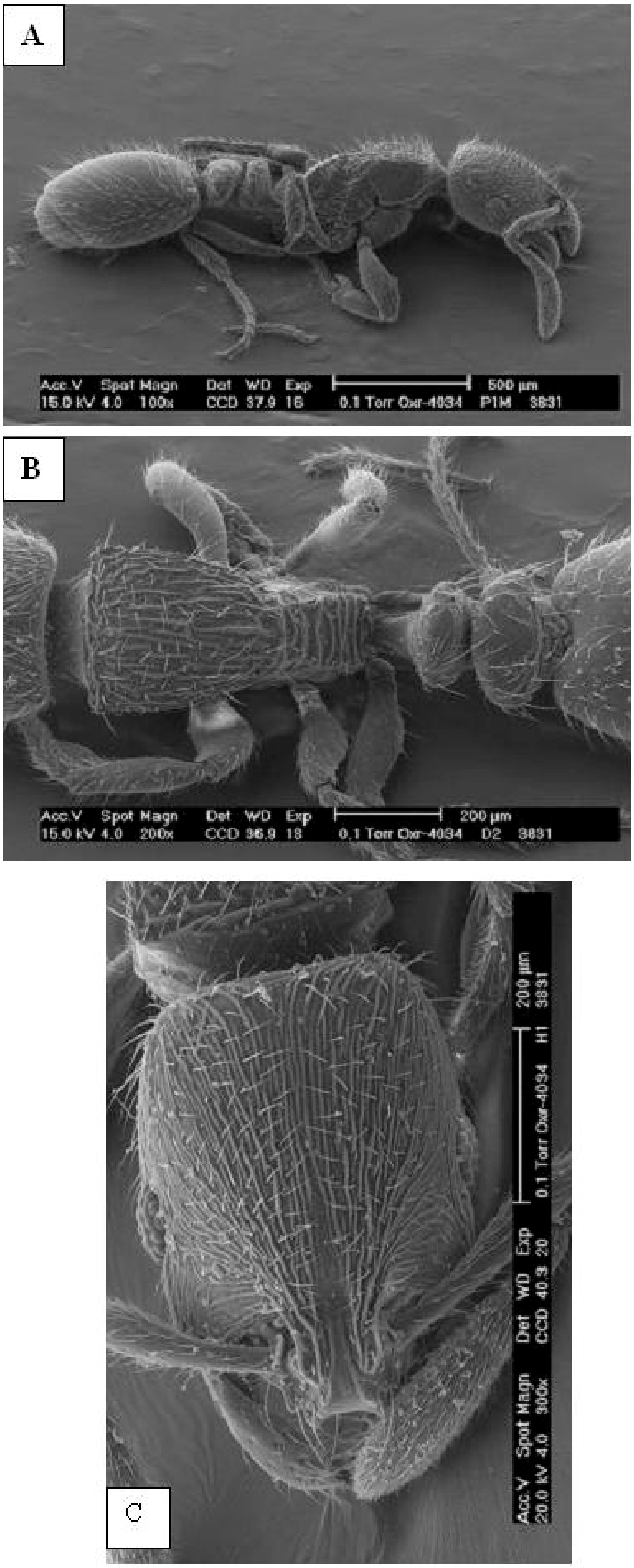


Figure A5-3: *Oxyepoecus bruchi* worker. A) lateral view, B) petiole and postpetiole, lateral view, C) mesosoma, petiole and postpetiole, dorsal view, D) head, frontal view.

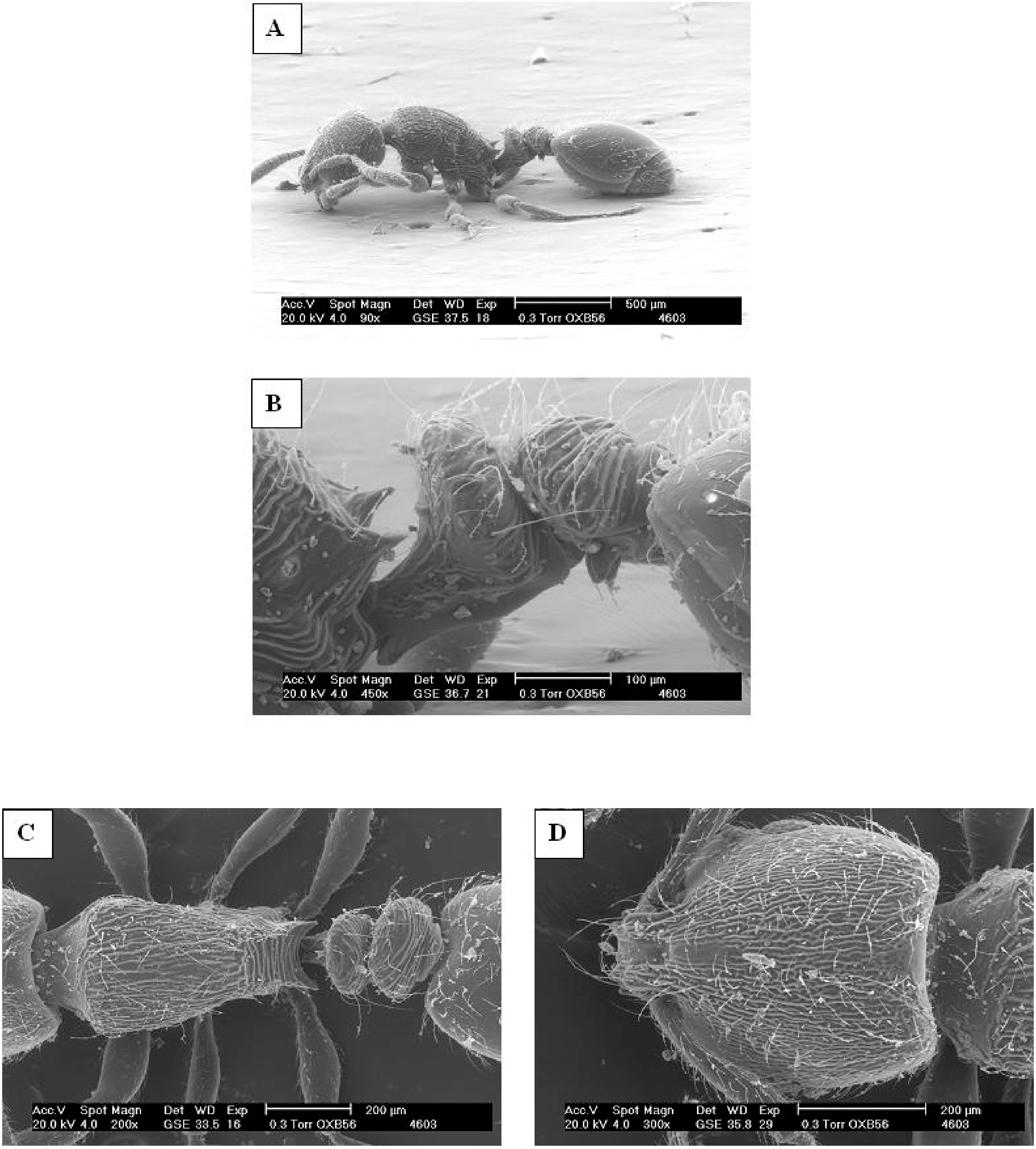


Figure A5-4: Worker of *Oxyepoecus inquilinus*. A) lateral view, B) mesosoma, petiole and postpetiole, dorsal view, C) head, frontal view.

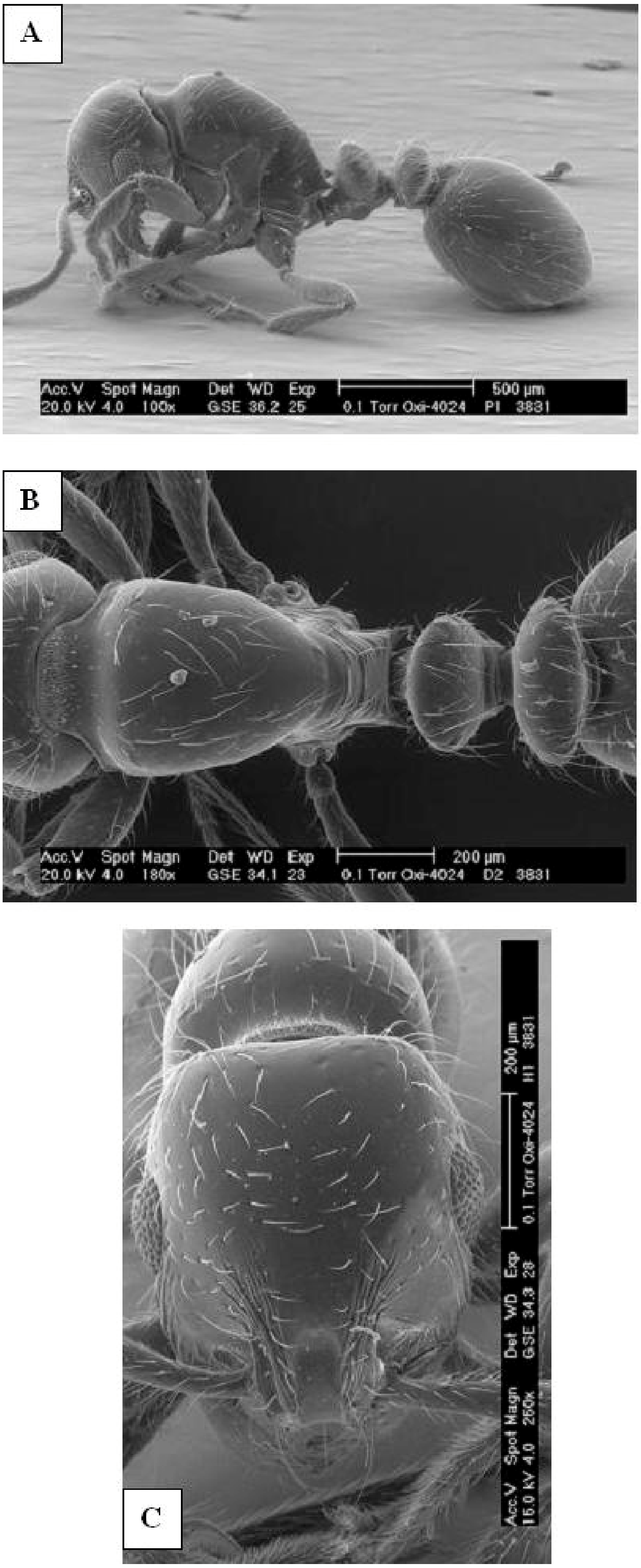


Figure A5-5: Worker of *Oxyepoecus vezenyii*. A) lateral view, B) mesosoma, petiole and postpetiole, dorsal view, C) head, frontal view.