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Thèse pour le doctorat en Sciences de la Vie

Communautés natives des fourmis de la litière en forêts naturelles de Guyane française et impact de la conversion forestière en plantations monospécifiques

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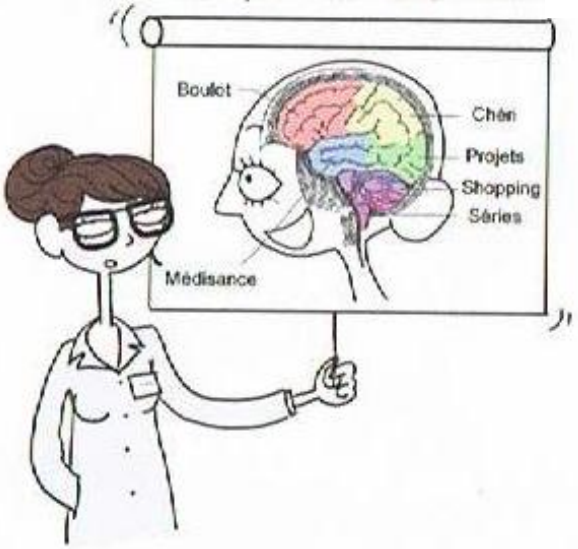
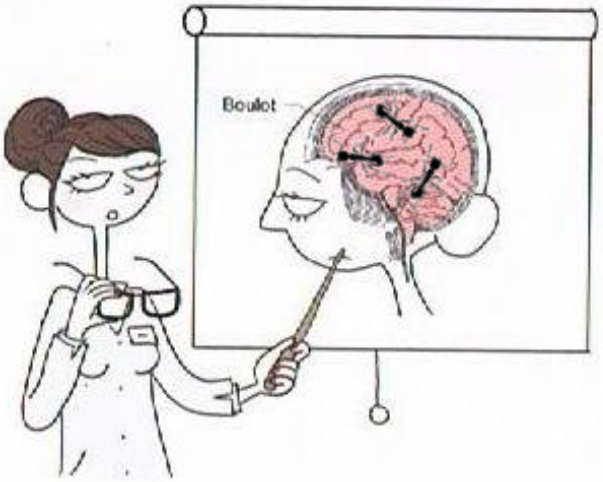
Bonjour.
Voici une vue en coupe de ma tête avant la thèse...



Bon, eh bien ces derniers temps, ça ressemble plutôt à ça :



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Le présent manuscrit a été rédigé sous la forme d'une thèse sur articles. Il est composé d'une introduction et d'une conclusion générales, écrites en français ; le corps du manuscrit comporte deux chapitres. Ces deux chapitres se composent d'une brève introduction et des principaux résultats en français, et se terminent par des articles scientifiques rédigés en anglais.

TABLE DES MATIÈRES

TABLE DES FIGURES

LISTE DES TABLEAUX

INTRODUCTION GÉNÉRALE

Nous sommes actuellement au cœur d'une ère dominée par une certaine inquiétude quant au devenir de la biodiversité dans son ensemble (Wilson, 1988). Les objectifs pour 2010 fixés par les leaders mondiaux lors de la Convention sur la Diversité Biologique (CBD ; www.cbd.int/2010-target/; Secrétariat de la Convention sur la Diversité Biologique, 2003), en 2002, et ceux résultant de leur incorporation dans d'autres programmes à l'échelle planétaire (Nations Unies, 2008), sont loin d'avoir été atteints. En effet, nous assistons à une perte continue de biodiversité globale sans précédent (Wilson, 1988, laquelle est significativement aggravée par l'augmentation constante des pressions anthropiques (Pimm et al., 1995 ; Tilman et al., 2001 ; Millenium Ecosystem Assessment [MEA], 2005 ; Butchart et al., 2010). L'intérêt de la protection de la biodiversité, notamment en termes de ressources et services écologiques (régulation du climat, qualité de l'air et de l'eau, formation et maintien de la fertilité des sols, etc.) a déjà été largement développé (Wilson, 2003 ; Tscharntke et al., 2005 ; Barlow et al., 2007 ; Sapijanskas and Loreau, 2010). Dans l'état actuel de notre connaissance écologique, il est quasiment impossible de prévoir les conséquences à long terme de l'élimination ne serait-ce que de quelques espèces.

1. Préservation des forêts tropicales humides et leur extraordinaire biodiversité, en particulier en Amazonie

1.1. Extinctions de masse et tentatives de conservation

Les forêts tropicales humides (FTH) sont remarquables par leur extraordinaire biodiversité (Tuomisto et al., 1995 ; Tilman, 1999) : 50 à 75% de la totalité des espèces terrestres de la planète s'y trouvent (Terborgh, 1993 ; Myers et al., 2000). Les invertébrés, en particulier les insectes, y représentent 94% de la biomasse animale (Fittkau et Klinge, 1973) et la grande majorité de la diversité (Stork, 1998). Une bonne compréhension de la distribution spatio-temporelle des communautés d'insectes dans les forêts est donc une information fondamentale nécessaire pour guider les actions futures de conservation et de gestion des territoires sous les tropiques (Basset et al., 1998). Mais jusqu'à présent, les communautés d'arthropodes tropicaux n'ont fait l'objet que de quelques d'études relativement récentes (Samways, 2007 ; Basset et al., 2008a ; Condon et al., 2008 ; Diniz-Filho et al., 2010 ; Hamilton et al., 2010). De plus, la majorité de ces organismes est caractérisée par une absence d'information biologique et écologique de base (Godfray et al., 1999). Par rapport à toutes les espèces à ce jour décrites, il en resterait entre 75 et 90% à découvrir, la grande majorité vivant dans les FTH (Wilson, 1988 ; Hammond, 1995 ; Stork, 1999; Ødegaard, 2000 ; Stork et al., 2008). Malheureusement, compte tenu du rythme d'extinctions des espèces, de nombreux taxons tropicaux, en particulier d'insectes (Mawdsley and Stork, 1995 ; Dunn, 2005), se seront éteints avant même d'être connus de la science (Lawton et May, 1995 ; McKinney, 1999 ; Pimm and Raven, 2000 ; Thomas et al., 2004).

Bien que des efforts considérables aient été faits pour établir et mettre en œuvre une exploitation plus durable des FTH durant ces deux dernières décennies, leur situation continue de se dégrader à un rythme inquiétant (Wardle, 1999 ; Singh, et al., 2001 ; Achard et al., 2007 ; Hansen et al., 2008). L'altération, la fragmentation et la destruction des habitats en forêt tropicale sont plus intenses que dans presque tous les autres biomes (Bradshaw et al., 2009 ; Asner et al., 2010), à tel point que presque la moitié des forêts tropicales à canopée fermée de la planète a déjà été convertie à d'autres fins (Wright, 2005). Ainsi, chaque année, environ 5,8 millions d'hectares de forêts tropicales sont totalement détruits suite à la conversion en plantations ou en pâturages, ces habitats ne pouvant héberger, par exemple, qu'une fraction de l'entomofaune présente auparavant (Lewis et Basset, 2007). La pression démographique croissante et plus généralement les changements globaux (García-Barrios,

2003 ; Thomas et al., 2004 ; Mace et al., 2005 ; Betts et al., 2008) sont les principales causes du taux impressionant d'extinction d'espèces de ces dernières décennies (Laurance et al., 1997). En effet, la population des pays tropicaux, qui a presque triplé depuis 1950, devrait continuer à croître de plus de 2 milliards d'êtres humains d'ici 2030. Cette pression anthropique croissante signifie inévitablement que seule une petite fraction des forêts tropicales de la planète pourra être maintenue dans des réserves ou des parcs ; ainsi, le nombre d'espèces menacées d'extinction dépasse largement le potentiel de conservation des réserves disponibles (Rodrigues et al., 2004). De plus, bien qu'à l'abri de toute altération, ces zones protégées resteront inévitablement soumises à des intensités variables de perturbation (Wright, 2005), et leur intégrité sera souvent menacée dans les zones où la déforestation est généralisée (Pedlowski et al., 2005).

1.2. La forêt amazonienne en danger

La forêt amazonienne est l'un des plus précieux trésors biologiques de la planète, ainsi qu'une composante majeure du système terrestre, et ce depuis le Crétacé (Maslin et al., 2005 ; Betts et al., 2008). Le cycle hydrologique de l'Amazone (Salati et Vose, 1984), en particulier l'évaporation et la condensation au-dessus de l'Amazonie, sont des moteurs de la circulation atmosphérique globale qui influencent les précipitations à travers l'Amérique du Sud, mais également au-dessus de l'Hémisphère Nord (Gedney et Valdes, 2000 ; Werth et Avissar, 2002). Le changement climatique menace d'affecter substantiellement la région amazonienne (Mitchell et al., 1995 ; Quintana-Gomez, 1999), notamment en accentuant ses périodes de sécheresse (Lewis et al., 2011), ce qui risque certainement d'altérer le climat régional et global (Phillips et al., 2009), contribuant ainsi à une accélération du rythme d'appauvrissement de la biodiversité (Chagnon et al., 2004 ; Miles et al., 2004 ; Chagnon et Bras, 2005 ; WWF, 2007 ; Petit, 2008).

Le bassin amazonien rassemble plus de la moitié des FTH restantes de la planète (Instituto Nacional de Pesquisas Espaciais, 2000 ; Laurance et al., 2001a) et couvre neuf pays sud-américains (Bolivie, Brésil, Colombie, Équateur, Guyana, Guyane française, Pérou, Surinam et Venezuela). En 2001, cette immense forêt couvrait environ 5,4 millions de km², soit approximativement 87% de son étendue d'origine (Soares-Filho et al., 2006). Le bassin amazonien abrite les communautés les plus riches (des milliers d'espèces de plantes – au moins 12% de toutes les plantes à fleurs de la planète (Gentry, 1982) –, plus d'un million

d'espèces d'insectes, plus de 700 espèces de poissons, environ 1000 espèces d'oiseaux, et plus de 300 espèces de mammifères ; WWF, 2007), rassemblant un quart des espèces terrestres (Dirzo et Raven, 2003 ; Betts et al., 2008). Ces communautés se composent d'espèces animales et végétales spécialisées dont la distribution géographique est parfois très limitée. Pour les fourmis, dont la biomasse y est quatre fois supérieure à celle de l'ensemble des vertébrés (Fittkau et Klinge, 1973), les raisons et les mécanismes de maintien de cette richesse hors du commun (Lapolla, 2007 ; Ryder Wilkie et al., 2009 ; Vasconcelos et al., 2009 ; Ryder Wilkie et al., 2010) ne sont pas encore élucidés, mais il semble que l'hétérogénéité environnementale naturelle joue un rôle prépondérant (Wilson, 1987 ; Benson and Harada, 1988 ; Byrne, 1994).

Le bassin amazonien subit le taux de déforestation le plus important au monde (Instituto Nacional de Pesquisas Espaciais, 2000 ; Laurance et al., 2001a). Depuis le début du siècle, la forêt amazonienne fait face à un grand nombre de menaces anthropiques interconnectées de manière complexe : la coupe-rase, la dégradation et la fragmentation forestières, le réchauffement climatique global qui va de pair avec l'augmentation de la concentration atmosphérique de CO_2, les feux de forêts, et les augmentations de sécheresses extrêmes (Laurance et al., 2002 ; Malhi et al., 2008 ; Nobre and Borma, 2009). La sécheresse (Lewis et al., 2011), en plus d'accroître la vulnérabilité de la forêt aux incendies, augmenterait la disponibilité de zones appropriées pour l'élevage ou la culture intensive de soja ou de canne à sucre. L'intensification de la conversion des forêts en terres cultivées et pâturages (Malhi et al., 2008) s'accélèrerait ainsi, situation qui semble quasiment inévitable dans le contexte actuel de développement économique et démographique des pays amazoniens (Soares-Filho et al., 2006 ; Killeen, 2007). Ainsi, en 2001, près de 837000 km² de forêt amazonienne ont été détruits (Soares-Filho et al., 2006), dont 80% au Brésil (Malhi et al., 2008). Au total, approximativement 6% des terres amazoniennes défrichées demeurent des terres cultivées, 62% forment des pâturages, alors que seulement 32% sont finalement abandonnées et peuvent se régénérer (Ramankutty et al., 2007). De plus, l'interaction entre le changement climatique et l'utilisation des terres, accélèrera la disparition des forêts amazoniennes (IPCC, 2001), et induira inexorablement de grands changements au sein des écosystèmes concomitants à des pertes importantes d'espèces dans de nombreuses régions (Miles et al., 2004 ; Phillips et al., 2009). Dans le pire des scénarios, les impacts cumulés de ce changement global pourraient être dévastateurs, incluant l'accélération de l'érosion, la dégradation des réserves d'eau douce, la disparition de sols précieux et une diminution des rendements agricoles, l'augmentation des infestations par les insectes ou encore la propagation de maladies infectieuses (WWF, 2007).

2. Potentiel des agrosystèmes pour la préservation de la diversité et le bon fonctionnement des écosystèmes

2.1. Changement d'utilisation des terres à des fins agricoles en zone tropicale

L'agriculture est un des principaux agents responsables de la fragmentation des écosystèmes tropicaux, induisant de profonds changements locaux à l'échelle du paysage et affectant la biodiversité, la composition et la structure des communautés (Benhin, 2006). En milieu tropical, l'anthropisation conduit généralement à un réseau de fragments forestiers résiduels relativement intacts, séparés par une matrice allant de la forêt secondaire en régénération, en apparence assez similaire à l'état du système avant la perturbation, aux monocultures ou pâturages dépourvus de végétation ligneuse (Seidler et Bawa, 2001). Les altérations de la faune native forestière sont susceptibles d'avoir des répercussions négatives sur les mécanismes de maintien et de régénération de la forêt après exploitation, donc sur les principales fonctions écosystémiques comme par exemple la pollinisation, la dispersion des graines, la prédation, l'herbivorie et son contrôle (Redford, 1992), ou encore la décomposition et le recyclage de la matière organique (Lavelle et al., 1992).

Les écologues connaissent depuis longtemps l'importance de l'agrodiversité pour la santé des écosystèmes, notamment au niveau du contrôle des pestes (Altieri et al., 1977 ; Letourneau, 1987 ; Swift and Anderson, 1993 ; Philpott and Armbrecht, 2006 ; Philpott et al., 2009). Dans le cas des études sur les communautés de fourmis, certains agrosystèmes, de type agroforêts rustiques traditionnelles, se développant sous une canopée forestière native et caractérisées par une structure végétale complexe (*e.g.* les plantations de cacaoyers ou de caféiers), pourraient (1) fournir un refuge suffisant pour préserver et maintenir des niveaux de diversité similaires à ceux des forêts natives proches (Majer et al., 1994 ; Perfecto et al., 1997 ; Rappole et al., 2003 ; Schulze et al., 2004 ; Tylianakis et al., 2006), (2) faciliter la dispersion des organismes entre les fragments forestiers (Vandermeer and Carvajal, 2001 ; Steffan-Dewenter, 2002), et (3) maintenir une dynamique de métapopulation ainsi que la survie de certaines espèces forestières natives à long terme (Vandermeer and Carvajal, 2001 ; Perfecto and Vandermeer, 2002), à condition que la nature de la matrice forestière les entourant soit intacte (Barlow et al., 2007). De plus, à l'instar des zones abandonnées se régénérant naturellement, ces agrosystèmes pourraient fournir d'importants bénéfices en termes de biens et services écologiques à l'échelle écosystémique (Myers, 1997 ; Schroth et

al., 2004 ; Tscharntke et al., 2005 ; Philpott and Armbrecht, 2006 ; Philpott et al., 2009). La gestion durable, permettant une exploitation humaine à long terme, devrait donc impliquer, dans les agrosystèmes, la préservation d'un niveau approprié de diversité biologique, garant du maintien de la productivité et du bon fonctionnement écologique. Bien que la perte d'une certaine proportion d'espèces au sein de tous les taxons pourrait avoir des conséquences fonctionnelles inconnues à long terme (Brook et al., 2006), ces agroforêts sont donc de précieux moyens potentiels de conservation d'espèces forestières natives contrairement aux exploitations agricoles alternatives plus intensives (Lindenmayer et Franklin, 2002 ; Barlow et al., 2007).

L'intensification et l'industrialisation agricoles, dont l'extrême correspond au système monocultural sans ombrage, ont conduit à la création de systèmes instables non-durables hautement dépendants d'apports externes en eau et en substances agrochimiques (Matson et al., 1997 ; Shriar, 2000 ; Schulze et al., 2004). Comme le niveau de richesse spécifique dépend de la complexité de l'habitat agroforestier (Armbrecht et al., 2004 ; Steffan-Dewenter et al., 2007), le système monocultural induit généralement une diminution de la biodiversité, résultat de l'exclusion d'espèces natives, laquelle s'accompagne dans la majorité des cas d'une altération profonde voire irréversible des communautés animales et végétales (en termes de composition et de structure fonctionnelle), souvent due à l'introduction d'espèces exotiques, parfois envahissantes (Schmidt and Diehl, 2008). En dépit de cela, le système monocultural est souvent favorisé par rapport aux autres pratiques agricoles car il est relativement facile à gérer et apporte une productivité économique rentable à court terme.

2.2. Importance de l'agrodiversité pour la conservation des écosystèmes

Les conséquences de la destruction intensive des forêts tropicales ainsi que les limitations des zones protégées, ont donc suscité un intérêt grandissant pour le potentiel de conservation de l'agrodiversité (Rice and Greenberg, 2000 ; Daily, 2001 ; Schroth et al., 2004 ; Dudley et al., 2005 ; Tscharntke et al., 2005 ; Vandermeer et Perfecto, 2007). Ainsi, un appel récurrent relativement récent de la part des communautés scientifique, gouvernementale et publique, a mis l'accent sur la nécessité d'intensifier les études comparatives documentant les effets de l'altération des forêts tropicales en particulier sur la faune (Rice and Greenberg, 2000 ; Schroth et al., 2004). Dans un contexte où les écologues et les gestionnaires sont confrontés à

des écosystèmes dégradés dont il faut évaluer la reconstruction, cette demande a pour but d'aider à concevoir des programmes viables d'aménagement durable (Mittermeier et al., 2003 ; Dudley et al., 2005). Mais à ce jour, trop peu d'études ont porté sur les conséquences de ces altérations ou contribué à clarifier dans quelle mesure les systèmes tropicaux altérés sont capables d'assurer les mêmes fonctions et de délivrer les mêmes services écosystémiques que les systèmes naturels (Laurance, 1998 ; Chapin, et al. 2000).

Il est donc urgent de comprendre comment la structure des communautés tropicales est altérée par l'homme, de déterminer quel degré de perturbation est compatible avec le maintien de niveaux acceptables de biodiversité dans les forêts tropicales, et quels groupes d'organismes sont les plus sérieusement affectés (Lewis et Basset, 2007).

3. Choix du taxon cible et fiabilité des paramètres reflétant l'altération des communautés en écologie terrestre

3.1. Les fourmis, organismes cibles appropriés aux études environnementales

Dans un contexte où il est impossible de mesurer et de surveiller les effets des diverses pratiques de gestion des terres sur toutes les espèces vivantes, choisir des organismes cibles performants reflétant l'état des systèmes écologiques naturels est un pré-requis essentiel à l'identification d'indicateurs biologiques (ou bioindicateurs) pertinents et fiables (Noss, 1990 ; McKenzie et al., 1995 ; Gardner et al., 2007). A terme, ces bioindicateurs pourront être utilisés comme des outils permettant d'identifier des zones de conservation prioritaires ou d'évaluer le succès ou l'échec des pratiques de gestion dans la préservation de la biodiversité et des écosystèmes (Noss, 1990 ; McKenzie et al., 1995 ; Gardner et al., 2007). Cependant, un travail considérable est nécessaire avant que des candidats fiables puissent être identifiés et systématiquement inclus dans les programmes de gestion écologique durable (Lindenmayer et al., 2000).

Contrairement aux insectes aquatiques ayant une longue histoire couronnée de succès en bioindication (James et Evison, 1979 ; Jones, 2008), la littérature concernant les insectes terrestres est loin d'être abondante (Dunn, 2004a). Il existe cependant une exception : les Formicidés, qui font partie des invertébrés terrestres les plus étudiés et donc les mieux connus (Jenkins et al., 2011), font de plus en plus l'objet d'études s'intéressant à la dynamique de leurs communautés (Fitzpatrick et al., 2011). Les Formicidés ont de nombreux avantages par rapport aux autres organismes terrestres –notamment les autre arthropodes – qui en font d'excellents organismes cibles. En effet, ils répondent parfaitement aux deux grandes catégories de sélection incontournables que sont l'aptitude économique et logistique – incluant le coût financier, le temps d'efficacité et la mobilisation de personnel – et la compétence biologique – incluant les critères taxonomiques, de distribution, de fiabilité, de représentation et de sensibilité –, lesquelles se déclinent en quelques critères (Noss, 1990 ; McGeoch, 1998) :

1) une large distribution, une abondance et une richesse spécifique importantes ainsi qu'une bonne stabilité et résolution de leur taxonomie :

La distribution globale des fourmis est de mieux en mieux documentée (www.antweb.org; http://www.antmacroecology.org/ant_genera/index.html°; Bolton et al., 2006). Elles sont très diversifiées (plus de 14700 espèces décrites à ce jour ; www.antweb.org), ubiquistes et abondamment présentes dans presque tous les écosystèmes terrestres de la planète (Hölldobler et Wilson, 1990). Dans les forêts tropicales, elles dominent en termes de biomasse et de richesse spécifique (Fittkau et Klinge, 1973 ; Wilson, 1987), d'où leurs diversité et abondance locales très élevées (Pisarski, 1978 ; Hölldobler et Wilson, 1990).

Leur taxonomie, de mieux en mieux résolue (Astruc et al., 2004 ; Wilson and Hölldobler, 2005 ; Ward, 2007, 2011), est robuste et facilement accessible au niveau du genre (Bolton, 1994). De plus, de bonnes ressources pour leur identification taxonomique (clés d'identification de sous-familles, genres, espèces, base de données photographiques, etc.) sont maintenant disponibles (http://academic.evergreen.edu/projects/ants/AntsofCostaRica.html; www.antweb.org; Bolton, 1994 ; Fernández, 2003).

2) une haute fidélité écologique, un rôle écosystémique majeur dont l'importance fonctionnelle est bien connue :

La plupart des espèces ont des nids stationnaires pérennes et utilisent des aires de fourragement assez restreintes (moins d'un mètre à quelques centaines de mètres), témoignant de leur présence relativement constante dans un site donné ; elles peuvent ainsi être échantillonnées et surveillées de façon fiable au cours du temps – contrairement à d'autres insectes qui se déplacent fréquemment entre les habitats en quête de nourriture, de partenaire sexuel, ou de sites de nidification (Kaspari et Majer, 2000).

Les fourmis affichent des comportements très divers et jouent un rôle fondamental dans le fonctionnement des écosystèmes dont elles affectent les processus et les propriétés (Hölldobler et Wilson, 1990) : effets directs sur la fertilité, la structure du sol, et indirects sur les flux d'énergie et de matière (Petal, 1978 ; Dauber et Wolters, 2000 ; Jouquet et al., 2006). Elles peuvent donc être considérées comme des ingénieurs de l'écosystème (Folgarait, 1998), où elles exercent un rôle structurant sur les communautés animales et végétales avec lesquelles elles interagissent (Bronstein et al., 2006 ; Dejean et al. 2007).

3) une facilité d'échantillonnage, tri et identification, notamment grâce à des protocoles standardisés :

Les fourmis sont aisément observables et échantillonnables tout au long de l'année par diverses techniques (Bestelmeyer et al., 2000), aisément séparables des autres organismes collectés (Andersen, 1990)**,** et il est relativement facile de les identifier soit au niveau du genre, soit en morphoespèces, et même par des non spécialistes (Oliver et Beattie, 1993). Depuis plus d'une décennie, il existe des méthodes quantitatives standardisées pour leur échantillonnage, comme par exemple le « protocole ALL » (*Ants of the Leaf Litter*), spécifiquement adapté pour les études comparatives s'intéressant aux fourmis de la litière (Agosti et Alonso, 2000).

4) une sensibilité aux changements environnementaux dont la réponse doit pouvoir être interprétée de manière fiable :

Comme tous les insectes, les fourmis répondent rapidement au stress environnemental (faible résilience à la perturbation de l'habitat) du fait de leur cycle de vie court (Noss, 1990), mais également de leur petite taille et leur dépendance aux températures relativement élevées qui les rend particulièrement sensibles aux changements climatiques et microclimatiques (Kremen et al., 1993). Elles sont ainsi suffisamment sensibles pour alarmer précocement d'une altération écosystémique discrète, et capables de fournir une évaluation continue sur une large gamme de stress (Noss, 1990) ou de facteurs environnementaux comme le climat, le sol ou encore la végétation (Andersen, 1990 ; Peck et al., 1998 ; Mitchell et al., 2002). Leur sensibilité aux changements environnementaux est relativement bien documentée et la réponse des assemblages aux perturbations environnementales, via les changements dans l'abondance, la richesse ou la composition, est généralement claire, rapide, et similaire à d'autres taxons (Andersen, 2000 ; Kaspari et Majer, 2000 ; Andersen et Majer, 2004).

Pour toutes ces raisons, les fourmis sont fréquemment utilisées pour évaluer les réponses biotiques et écosystémiques face aux changements environnementaux (Andersen et Majer, 2004 ; Underwood et Fisher, 2006 ; Majer et al., 2007), mais aussi particulièrement appropriées pour les programmes d'inventaire, d'évaluation ou de suivi de l'état des écosystèmes (Kaspari et Majer, 2000 ; Underwood et Fisher, 2006). C'est notamment le cas en Australie, où elles sont couramment utilisées par les gestionnaires du territoire pour évaluer les réponses biotiques face à un large éventail d'altérations environnementales (pour

une synthèse voir Andersen et Majer, 2004 ; Underwood et Fisher, 2006) comme l'exploitation ou la réhabilitation de zones minières (Hoffmann et al., 2000 ; Andersen et al., 2003), la restauration de zones d'activité militaire (Graham et al., 2004 ; Graham et al., 2008), l'impact des feux sur les écosystèmes (Andersen, 1991b), l'exploitation forestière et la déforestation (Carvalho and Vasconcelos, 1999 ; Vasconcelos, 1999 ; Vasconcelos and Delabie, 2000 ; Vasconcelos et al., 2000b, 2001, 2006), l'impact des pratiques agricoles – défrichement, labour, utilisation de pesticides, surpâturage – (Peck et al., 1998 ; Read et Andersen, 2000 ; Calcaterra et al., 2010 ; Philpott et al., 2010). De plus, en Amérique du Sud également, elles ont fait l'objet d'études relatives à la fragmentation des habitats (Carvalho et Vasconcelos, 1999 ; Ribas et al., 2005), et la santé des agrosystèmes (Bestelmeyer et Wiens, 1996 ; Armbrecht et al., 2004 ; Delabie et al., 2006 ; Stephens and Wagner, 2006).

3.2. Pertinence des paramètres reflétant l'altération des entomofaunes terrestres

En général, les décisions pratiques de conservation ou de gestion du territoire considèrent davantage les arguments basés sur l'identité des espèces et les informations écologiques précises, mais cela semble impossible pour les organismes peu connus des FTH, comme la majorité des arthropodes (Lewis et Basset, 2007). Ceci impose une pression, notamment sur les biologistes de la conservation et les écologues, pour qu'ils fournissent des solutions simples permettant d'évaluer les changements fauniques, lesquels incluent souvent les estimations de richesse spécifique et de perte d'espèces (Basset et al., 2008b). Néanmoins, la richesse spécifique est une variable qui retient peu d'information biologique, et ne serait donc pas le choix le plus pertinent pour quantifier, à elle seule, l'effet de l'altération sur les communautés d'arthropodes (Barlow et al., 2007 ; Basset et al., 2008a). En effet, ce type de variable est très sensible à l'effort d'échantillonnage (Gotelli et Colwell, 2001 ; Leponce et al., 2004) ainsi qu'à l'invasion des zones dégradées par les espèces tolérantes à la perturbation (Brown Jr, 1997), et des conclusions erronées pourraient être tirées, même en considérant plusieurs taxons simultanément (Basset et al., 2008a).

Malgré cela, il existe un parti pris évident pour les changements observés au niveau de la richesse spécifique plutôt que de la similarité, la composition en espèces ou la structure fonctionnelle des assemblages, particulièrement dans les études s'intéressant aux patrons de réponses en écologie des communautés (Schulze et al., 2004 ; Wolters et al., 2006). Pourtant,

par rapport à une gamme de variables testées, l'abondance, la richesse spécifique estimée, le pourcentage de taxons spécifiques par habitat, et le renouvellement des espèces, par exemple, possèdent parfois un pouvoir discriminant supérieur à celui de la richesse spécifique observée (Barlow et al., 2007 ; Basset et al., 2008a). Les études de conservation, d'impact ou de bioindication devraient donc, prioritairement, utiliser le renouvellement des espèces associé à la richesse spécifique comme une évaluation plus précise des effets des perturbations sur les assemblages fauniques (Barlow et al., 2007 ; Basset et al., 2008a). De plus, Basset et al. (2008b) ont clairement montré qu'il est impératif d'abandonner l'usage exclusif des variables décrivant uniquement la structure de la communauté pour inclure des variables plus discriminantes basées sur l'identité des espèces. En effet, ces dernières reflètent une haute sensibilité à la perturbation des assemblages d'arthropodes.

A l'instar de la structure taxonomique des communautés, il semble également pertinent de considérer la diversité fonctionnelle des communautés. En écologie des communautés, la classification des insectes, basée sur leur type fonctionnel, est une approche prometteuse qui permet d'aborder les questions écologiques relatives à la santé écosystémique que ce soit à l'échelle des biomes, des paysages ou des écosystèmes (Koricheva et al., 2000 ; Niemelä et al., 2000). C'est un moyen d'identifier les règles générales basées sur la biologie plutôt que sur l'identité de certaines espèces. Il permet de transcender les frontières taxonomiques en réduisant la complexité apparente des systèmes écologiques (Andersen, 1997b). Cependant, l'approche habituellement basée sur les « guildes » (ensembles d'espèces exploitant un pool commun de ressources ; Terborgh et Robinson, 1986) donc sur les relations trophiques, est d'une utilité limitée dans les études sur la myrmécofaune (Andersen, 1991a ; Delabie et al . 2000a) car la plupart des espèces de fourmis ont des exigences de fourragement similaires. Par contre, les classifications de groupes fonctionnels des plantes sont des modèles davantage appropriés pour les études concernant les communautés de fourmis (Andersen, 1991a, 1995a). En effet,ils sont basés sur un large éventail de caractères écologiques, incluant la forme de vie, la morphologie, le comportement trophique et reproducteur et la capacité de colonisation (Brandão et al., 2009 ; Silva et Brandão, 2010).

4. Site d'étude : la Guyane française

Située au Nord-Est de l'Amérique du sud, la Guyane française fait partie de ce que l'on appelle « le Bouclier des Guyanes» qui couvre la partie nord amazonienne du Brésil, la pointe orientale du Venezuela et de la Colombie, ainsi que le plateau des Guyanes (Barret, 2008). 83% du territoire est compris entre le niveau de la mer et 200 mètres d'altitude et seulement 0,32% du territoire a une altitude supérieure à 500 mètres. La densité de population y est faible (2 habitants au km²), en revanche le taux de croissance démographique de 3,8% y est très important – 5 à 6 fois supérieur qu'en métropole selon l'Insee ; http://www.insee.fr/fr/regions/guyane/default.asp?page=publications/publications.htm – (Petit, 2008).

4.1. Contexte climatique

Le climat guyanais, de type équatorial humide, est relativement stable du fait à la fois de la proximité de l'équateur et de l'influence océanique. Les vents sont modérés et les cyclones absents de la région. La température, d'une moyenne de 26°C tout au long de l'année, est soumise à de faibles amplitudes thermiques mensuelles (inférieures à 2°C). L'humidité atmosphérique relative est très élevée (80 à 90%), et, en Guyane française, comme dans toute la zone intertropicale, la pluviométrie et ses variations constituent le facteur déterminant du climat (Aubréville, 1938). Ces variations sont liées aux déplacements saisonniers de la Zone Intertropicale de Convergence (ZIC), où se rencontrent les alizés Nord-Est et Sud-Est. En se déplaçant entre 3° de latitude Sud et 15° de latitude Nord, cet « équateur météorologique » détermine l'existence de quatre saisons : une petite saison des pluies de mi-novembre à fin janvier; une petite saison sèche ou « petit été de mars » qui a lieu entre début février et mi-mars ; une grande saison des pluies, de fin mars à mi-juillet; une grande saison sèche de mi-juillet à mi-novembre ; les mois les plus secs étant septembre et octobre avec une pluviométrie générale inférieure à 50 mm.

Les précipitations annuelles sont de l'ordre de 3.000 mm par an mais varient fortement selon un gradient pluviométrique décroissant vers l'ouest et vers le sud (Figure 1). Ainsi, la région de Régina, Kaw et Cacao reçoit en général plus de 4000 mm par an tandis que celle de Saint-Laurent du Maroni ne recueille que 2000 mm par an. À Paracou (un des sites échantillonné pour cette étude), la pluviosité est de 3041 mm (moyenne de 1977 à 2001 ;

Gourlet-Fleury et al., 2004). Mais ces moyennes masquent de fortes variations interannuelles, et les limites entre saisons peuvent couramment varier de plusieurs semaines ; ainsi, la petite saison sèche n'est pas observée certaines années. La Guyane est en effet soumise aux alternances d'épisodes « El Niño », qui se traduisent par des années plus sèches, suivis

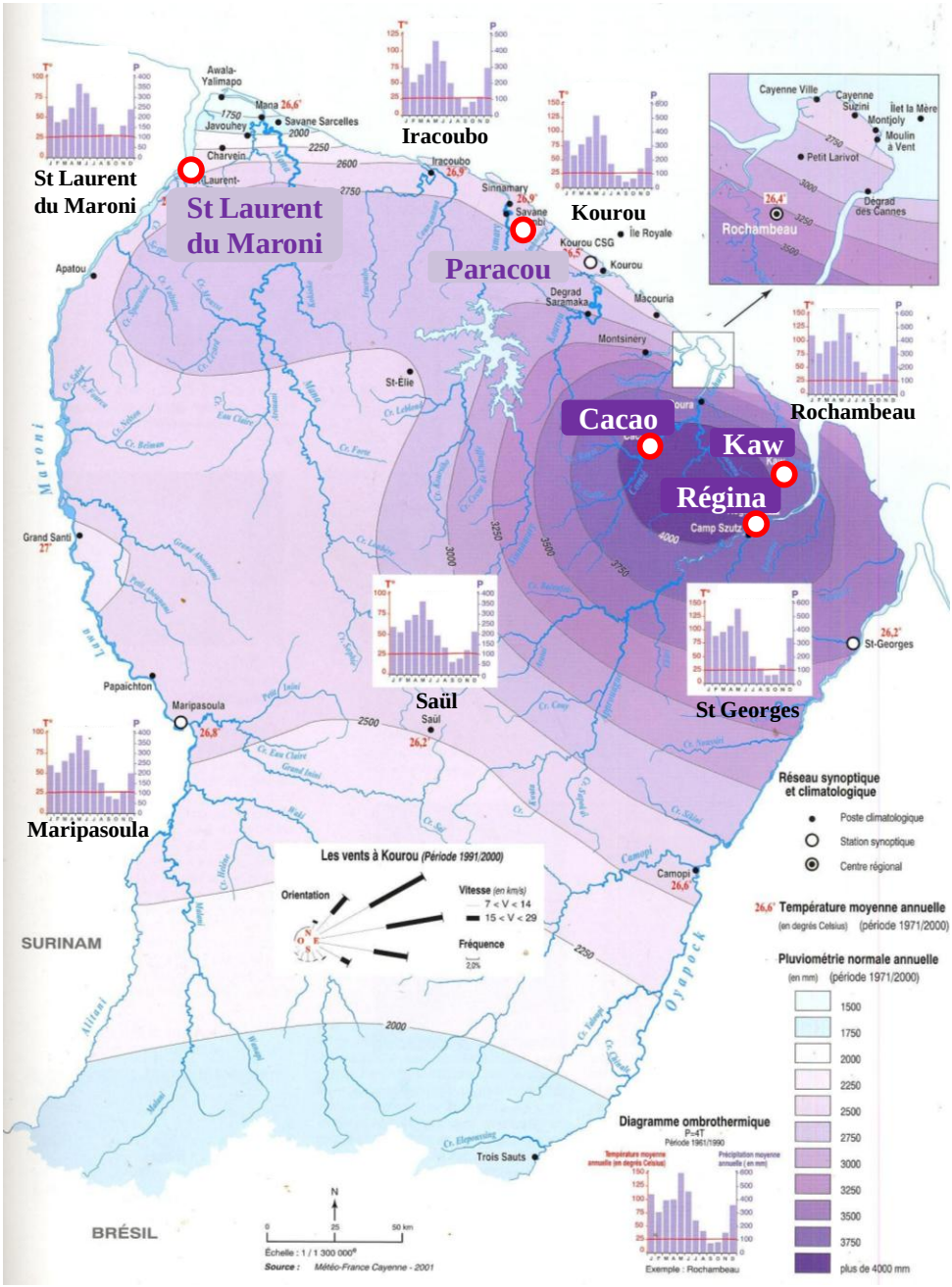

Figure 1°: Carte de la pluviométrie et rose des vents (Barret, 2008).

d'épisodes « La Niña » où, au contraire, les précipitations sont plus abondantes.

4.2. Contexte géomorphologique

Sur toutes les Terres Hautes de Guyane, les conditions climatiques anciennes à actuelles ont favorisé une altération poussée de tous les minéraux primaires et entrainé la formation de sols ferralitiques (Gourlet-Fleury et al., 2004). La plupart des horizons supérieurs ont ainsi les caractéristiques générales des vieilles couvertures ferralitiques : de bonnes propriétés physiques (macro et microporosité importantes), dues à une structure microagrégée des constituants élémentaires (kaolinite, gibbsite, hématite, goethite, quartz), et une fertilité chimique en revanche très limitée : acidité marquée ($4 < pH < 4,5$), faible capacité d'échange cationique (Freycon et al., 2003), etc. Les sols sur socle au Nord de la Guyane sont relativement uniformes par leur fertilité chimique faible, mais présentent en revanche des variations importantes de propriétés physiques, ayant des impacts majeurs sur le drainage et l'alimentation en eau des arbres (Boulet et al., 1979).

4.3. La forêt guyanaise

Actuellement en Amérique du Sud, 85 millions d'hectares de forêts sont entièrement dédiés à la conservation de la diversité biologique (FAO, 2010). Le bouclier des Guyanes, encore largement préservé, comprend approximativement 25% des FTH primaires intactes de la planète (Guayana Shield Conservation Priority Setting Workshp, 2002 ; Higgins, 2007). Mais, bien que la forêt guyanaise ait la réputation d'être une des mieux protégées d'Amérique du Sud (faible pression anthropique actuelle, peu d'intérêt de la part des compagnies d'exploitation forestière, et majeure partie du territoire constituant une réserve indigène ; Kohler, 2000) 91.720 ha de forêts tropicales (mangroves comprises) ont été déforestés entre 1990 et 2006 (pour le logement, l'agriculture, l'activité minière et la production de bois ; IFN, 2008). Ceci correspond à une moyenne de déforestation supérieure à 5.700 ha par an.

Cette région du globe a toujours été préservée des effets des glaciations, ce qui explique son énorme diversité biologique (Haffer and Prance). Paradoxalement la forêt guyanaise s'est développée sur un des sols les plus pauvres du monde en termes de nutriments et de matière organique (Petit, 2008). Le massif forestier guyanais occupe 96,7% du territoire (source : DAF, 1999, http://www.cr-guyane.fr). Bien qu'étant en continuité avec l'immense bloc amazonien, il s'en différencie par l'appartenance à un système hydrologique différent, la nature des sols et la répartition des espèces arborescentes (Groene, 1990). Le niveau de

diversité végétale y est néanmoins tout aussi élevé (ter Steege et al., 2000) : sa grande richesse floristique est représentée par 68 familles d'arbres réparties en un peu plus d'un millier d'espèces (Sabatier et Prévost, 1990).

En fonction des variations spatiales liées aux conditions édaphiques, plusieurs types forestiers peuvent être distingués : la forêt sur podzol ou sable blanc, la forêt ripicole marécageuse, la forêt sommitale à partir de 400 m d'altitude et la forêt de sol ferralitique qui représente l'essentiel des surfaces boisées (90%) et procure l'essentiel de la ressource en bois. Dans ce dernier type de forêt typiquement mixte, aucune espèce n'est réellement dominante et 250 à 300 espèces peuvent être présentes sur un seul hectare. Sabatier et Prévost (1990) distinguent deux faciès principaux de la forêt sur sol ferralitique : le faciès a Burséracées et celui à Césalpiniacées en fonction de la prépondérance relative de ces deux familles végétales. De manière générale, les arbres ont un enracinement superficiel et une taille relativement modeste par rapport aux forêts équatoriales africaines : la hauteur de la voûte forestière oscille entre 30 et 40 m, certains arbres émergents pouvant atteindre 50 m (Oldeman, 1974).

4.4. La myrmécofaune guyanaise

La diversité des fourmis néotropicales, particulièrement en Amazonie, attise la curiosité des entomologistes depuis de nombreuses années. Des inventaires de fourmis des pays limitrophes ou proches de la Guyane Française ont ainsi été publiés depuis le début du 20ème siècle ; Brésil (Mann, 1916), Guyana (Wheeler, 1916a), Surinam (Borgmeier, 1934), Trinidad (Wheeler, 1916b). Depuis la fin des années 1990, ces inventaires se sont multipliés dans les projets promouvant une meilleure compréhension de la biodiversité en Amérique du Sud et Centrale : Argentine, Brésil, Colombie, Costa Rica, le Plateau des Guyanes (notamment Guyana et Venezuela) et Pérou (Jaffé et al., 1993 ; Armbrecht et al. 2001 ; Longino et al., 2002 ; Lapolla et al., 2007 ; Ryder Wilkie et al., 2009 ; Vasconcelos et al., 2009 ; Ryder Wilkie et al., 2010). Par ailleurs, une grande quantité d'informations concernant le bassin amazonien et le littoral de forêt atlantique au Brésil ont été obtenues depuis la mise au point du Protocole « ALL » (*Ants of the Leaf Litter*) pour la récolte des fourmis de la litière (Agosti et Alonso, 2000). Paradoxalement, la myrmécofaune guyanaise est encore très peu connue, largement inexplorée et la littérature la concernant quasiment inexistante.

La Guyane française représente un contexte idéal pour les études environnementales de conservation, de contrôle et de suivi de la santé des écosystèmes naturels et altérés car elle

possède à la fois des milieux naturels abritant une incroyable biodiversité (comme la station de recherche des Nouragues ou la réserve naturelle Trésor de Kaw par exemple) mais aussi des zones soumises à une anthropisation récente plus ou moins intense (utilisation traditionnelle des terres par les Amérindiens, station de recherche de Paracou où la matrice forestière naturelle entoure des plantations agricoles monospécifiques expérimentales de différentes essences natives d'Amazonie et exotiques).

5. Objectifs et structure de l'étude

Après cette introduction générale replaçant le contexte général de cette thèse et la présentation du site d'étude (la Guyane française), sont maintenant développés les objectifs que nous nous sommes fixés dans ce travail et la façon dont le manuscrit se structure. Ensuite, la méthodologie générale utilisée dans cette étude sera développée, à laquelle succèderont les deux chapitres présentés sous forme d'articles scientifiques.

Afin de pouvoir analyser, dans un premier temps, puis anticiper dans un second temps les changements écosystémiques induits par l'homme lors de la conversion des FTH en terres cultivées, il est avant tout fondamental de comprendre les patrons selon lesquels la diversité s'établit, se structure et se maintient dans les forêts naturelles. Ensuite, en sachant quelles communautés d'organismes devraient être présentes dans une zone géographique donnée, il est possible d'estimer le degré auquel l'activité humaine les a altérées : n'importe quel biote d'un site donné peut être comparé à celui d'un site de référence, la moindre variation dans les assemblages attendus pouvant refléter les changements environnementaux. Par conséquent, dans le contexte de changement d'utilisation des terres, le principal défi réside dans la distinction des réponses face à la perturbation anthropique (« signal » écologiquement significatif) par rapport à la variabilité naturelle (« bruit de fond »), principalement induite par l'hétérogénéité des habitats (Andersen, 1999).

Ainsi, cette étude est centrée autour de deux objectifs principaux :

- Analyser et comprendre comment les communautés de fourmis se structurent localement dans les forêts naturelles, c'est-à-dire de quelle façon elles répondent à l'hétérogénéité et aux perturbations environnementales naturelles.
- Déterminer et analyser comment une perturbation naturelle ou d'origine anthropique, qui simplifie la structure végétale ou des sols, par exemple, peut localement influencer les communautés de fourmis, et si la réponse de la myrmécofaune est du même ordre que lors d'une perturbation naturelle.

Plutôt que de considérer les communautés de fourmis dans leur intégralité (espèces arboricoles, de la litière, du sous-sol, etc.) pour lesquelles il n'existe toujours pas de protocole d'échantillonnage standard, j'ai choisi de me focaliser sur les communautés de la litière pour lesquelles le protocole ALL (*Ants of Leaf Litter* ; Agosti et Alonso, 2000) garantit la récolte d'une part représentative de la communauté, permettant ainsi une standardisation de l'échantillonnage et facilite les études comparatives.

Les deux axes de recherche présentés ci-dessus ont donc été traités à travers les quatre questions suivantes :

1) Comment l'hétérogénéité environnementale, via le type de formation végétale (conditionnant la qualité, la nature et la structure de la litière) influence-t-elle localement les communautés de fourmis de la litière ?
2) Comment une formation végétale stable dans le temps issue d'une perturbation naturelle passée influence la communauté des fourmis de la litière?
3) Comment se traduit l'impact sur les communautés de fourmis de la litière de la simplification de la structure végétale via la conversion de la forêt en monocultures, dans un contexte d'utilisation traditionnelle des terres ou d'agriculture intensive?
4) Une perturbation d'origine anthropique va-t-elle affecter la communauté de fourmis de la litière de la même manière qu'une perturbation naturelle ?

Dans ce contexte d'impact de l'anthropisation sur la myrmécofaune forestière native, les résultats présentés dans ce manuscrit, sous la forme d'articles scientifiques, ne concernent que les stations de recherche des Nouragues et de Paracou et certaines collectes faites auparavant près de Maripasoula (Durou et al., données non publiées ; Delabie et al., 2009 : Article 3 présenté dans le chapitre 2). Ceux issus des échantillonnages faits au sein de la forêt des Chutes Voltaire et de Kaw n'ont été traités, pour l'instant, que de façon préliminaire. Le présent mémoire décline ces quatre questions sous forme de deux chapitres :

Le chapitre 1 rassemble deux articles illustrant l'effet de l'hétérogénéité naturelle environnementale sur les communautés de fourmis de la litière le long d'un gradient altitudinal de végétation en zone de forêt primaire. L'influence d'une perturbation naturelle permanente sur ces communautés est aussi analysée et comparée à celle de la variabilité environnementale naturelle. Ces deux articles s'intitulent :

- Article 1 : "*Baseline study of the leaf-litter ant fauna in a French Guianese forest*"
- Article 2 : "*The outstanding diversity and heterogeneous functional structure of leaf-litter ant assemblages in a Guianese pristine rainforest*"

Le chapitre 2 rassemble deux articles illustrant l'effet du changement de l'utilisation des terres via la conversion de la forêt primaire en terres agricoles. Le premier article documente l'influence d'un gradient d'anthropisation à travers l'utilisation traditionnelle des terres par les Amérindiens, alors que le second traite de l'altération des communautés lors de la conversion forestière en plantations monospécifiques et compare ses effets à une perturbation naturelle de type formation de chablis :

- Article 3 : "*Ants as biological indicators of Wayana Amerindian land use in French Guiana*"
- Article 4 : "*Plantations make a contribution to leaf-litter ant diversity in Neotropical agrosystems*"

Les résultats présentés dans ces deux chapitres sont ensuite réunis dans une discussion générale composée de deux parties : (1) une synthèse replaçant nos résultats majeurs dans la littérature actuelle concernant les facteurs structurant les assemblages de fourmis de la litière en forêts naturelles et converties en zones agricoles, et (2) les perspectives à court et à long terme qui en découlent.

6. Méthodologie expérimentale, obtention et traitement des données

6.1. Sites d'échantillonnage

6.1.1. Localités et types d'habitats

La plupart des zones échantillonnées sont localisées au niveau de la bande côtière guyanaise (d'Est en Ouest : montagnes de Kaw, station de Paracou[1], zone forestière des Chutes Voltaire), exceptée la forêt entourant la station des Nouragues[2] et celle aux alentours du village amérindien Tidamali près de Maripasoula, plus à l'intérieur des terres (Figure 2). Différents types d'habitats forestiers naturels (perturbés ou non) ou anthropisés ont été échantillonnés (Tableau 1) :

- Chutes Voltaire : zone forestière naturelle
- Kaw : cinq zones forestières dont la situation topographique varie (exposition ou non aux alizés), dont une perturbée par la présence d'une importante colonie de Chiroptères (très forte accumulation et concentration de guano donc disponibilité de nutriments, notamment l'azote, extrêmement accrue par rapport à la matrice forestière environnante)
- Nouragues : quatre habitats forestiers naturels se succédant selon un gradient de végétation lié à la présence d'un « inselberg », dont un issu d'une perturbation ancienne (forêt de lianes)
- Maripasoula : échantillonnages selon un gradient d'anthropisation :
    - Village
    - plantation de manioc récente (plantes hautes de plus de 3 m)
    - plantation de manioc abandonnée depuis 6 ans
    - fragment forestier de type *terra firme* préservé par les villageois et isolé au centre d'une zone de terres cultivées
    - zone forestière ripicole naturelle adjacente au fleuve Maroni
    - matrice forestière mature

[1] La station de recherche de Paracou (http://www.cirad.fr/guyane/le_cirad_en_guyane/station_de_paracou) est gérée par le CIRAD et regroupe plusieurs parcelles de forêt naturelle dont certaines sont soumises à des traitements forestiers particuliers, ainsi que des plantations monospécifiques d'essences ayant un intérêt économique (acacias, cacaoyers, caféiers, eucalyptus, hévéas, pins caraïbes, etc.).

[2] La station de recherche du CNRS des Nouragues (*http://www.nouragues.cnrs.fr/*) est une station de terrain implantée au cœur de la forêt tropicale, dans la Réserve Naturelle des Nouragues.

- Paracou :
    - zones de forêt naturelle non perturbée et perturbée récemment par la formation d'un chablis conséquent
    - quatre types de plantations monospécifiques d'essences originaire de la Région

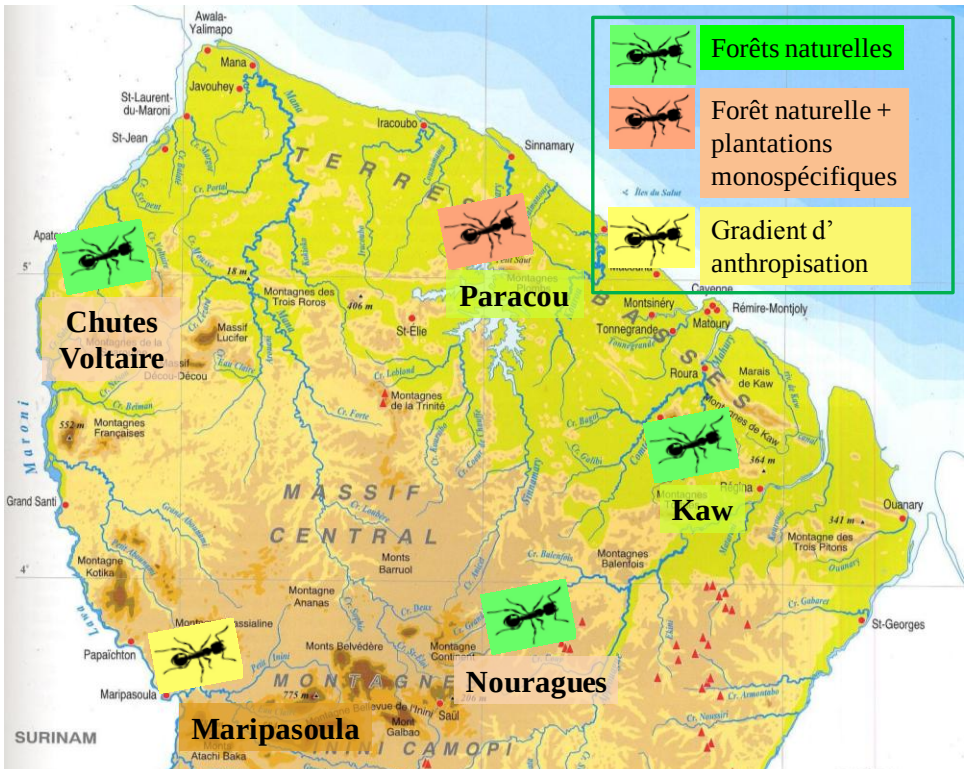

Figure 2°: Localisation des différents sites échantillonnés (fond de carte : Barret, 2008).

Néotropicale ou exotiques

Tableau 1°: Localisation des sites de récolte et types d'habitats échantillonnés.

	Localités échantillonnées				
	Chutes Voltaire	**Kaw**	**Nouragues**	**Maripasoula**	**Paracou**
Coordonnées GPS	N5°27'51", W54°03'07"	N4°32'34", W52°09'14"	N4°00'88", W52°67'72"	N3°60'00", W54°00'00"	N05°16'12", W052°55'40"
Type d'habitats	Forêt naturelle (*terra firme*)	Forêt naturelle (*terra firme*): – versants exposés aux alizés – versants protégés des alizés – zone abritant une colonie populeuse de Chiroptères très localisée	– Forêt naturelle du grand plateau (*terra firme*) – Forêt de lianes – Forêt de transition – Forêt sommitale d'inselberg	Village amérindien Plantation de manioc Plantation de manioc abandonnée Fragment forestier isolé Zone forestière ripicole Forêt naturelle (*terra firme*)	Forêt naturelle (*terra firme*) Plantations monospécifiques: acacias, cacaos hévéas, pins caraïbes

6.1.2. Types de monocultures sur le site de Paracou

En zone néotropicale, différentes essences sont cultivées selon un système monocultural : (1) des essences natives d'Amazonie, comme l'hévéa (*Hevea brasiliensis* Müll. Arg.), qui, bien que parfois difficile à entretenir, possède une importante valeur économique en raison de sa productivité en latex utilisé pour la fabrication de caoutchouc (Silva et al., 1998), ou encore le cacaoyer (*Theobroma cacao* Linn.) et le caféier, souvent cultivés en agroforêts sous ombrage et considérés comme les meilleurs candidats à la conservation d'espèces natives forestières (comme c'est le cas pour les fourmis : Philpott and Armbrecht, 2006 ; Delabie et al., 2007) ; et (2) des espèces d'arbres exotiques à croissance rapide comme l'acacia (*e.g. Acacia mangium* Willd.), le pin caraïbe (*Pinus caribaea* Mor.) ou des espèces du genre *Eucalyptus*, largement plantés pour la production de bois ou encore la protection des sols contre l'érosion. *Acacia mangium* est aussi utilisé pour réhabiliter les sols dégradés (par exemple après des exploitations minières ; Le Roux, 2002) du fait de son association symbiotique avec des bactéries fixatrices d'azote et son importante capacité à accumuler de la matière organique au niveau du sol (Bernhard-Reversat et al., 1993).

6.2. Méthodologie

6.2.1. Période et effort d'échantillonnage

Six campagnes d'échantillonnage ont été réalisées hors saison des pluies (« grande saison sèche » et « petite saison sèche » ; Tableau 2) afin de maximiser le nombre d'espèces récoltées.

Tableau 2°: Périodes et méthodes d'échantillonnage, ainsi que nombre d'échantillons récoltés dans chacun des habitats selon leur localisation géographique.

	Caractéristique de l'échantillonnage			
	Période	**Méthode**	**Habitats**	**Nombre d'échantillons**
Chutes Voltaire	Avril 2010	Winklers	Forêt naturelle	49
		Pièges à fosse		49
Kaw	Octobre 2008	Winkler	2 versants exposés, 2 versants protégés, 1 zone perturbée	50 × 5
Nouragues[3]	Octobre 2009	Winklers	Forêt de grand plateau, lianes et transition	50
			Forêt d'inselberg	20
		Pièges à fosse	Forêt de grand plateau, lianes et transition	50
			Forêt d'inselberg	20
Maripasoula	2000-2002	Pièges à fosse	Village amérindien	20
			Plantations de manioc (récente, abandonnée)	20 × 2
			Forêt mature (matrice, fragment, zone ripicole)	20 × 3
Paracou	Avril 2009	Winklers	Forêt naturelle, Acacias, hévéas	50 × 3
	Mars 2010		Chablis	49
			Cacaos	42
			Pins	50
	Septembre 2009	Pièges à fosse	Chablis	49
	Octobre 2009		Cacaos	42
	Novembre 2009		Forêt naturelle,	50
	Février 2010		Acacias, hévéas	50 × 2
	Mars 2010		Pins	50

[3] les données de mon Master 2 (Groc, 2007) ont été cumulées à celles collectées au cours de ma thèse grâce à un projet financé par un appel d'offres Nouragues en 2009 intitulé « L'étonnante myrmécofaune de la litière de la forêt de lianes des Nouragues » (3900€).là, il faut peut-être juste ajouter le nom de l'organisme financeur

6.2.2. Méthodes d'échantillonnage

Au cours de ma thèse, les fourmis de la litière ont été récoltées à l'aide de deux méthodes d'échantillonnage très complémentaires : la méthode Winkler (Figure 3) et les pièges à fosse. Ces deux méthodes d'échantillonnage sont fréquemment couplées dans les études de diversité concernant les fourmis du sol ; en effet, Agosti et Alonso (2000) ont montré que le tamisage d'1m² de litière de 20 points d'échantillonnage par la méthode Winkler associés à 20 pièges à fosse garantissent la récolte d'au moins 70% des espèces de fourmis de litière (quelque soit le contexte géorgraphique). De plus, dans une étude massive menée dans une région de forêt atlantique au Brésil, dont le but était de comparer l'efficacité en capture d'espèces de 17 méthodes d'échantillonnage de fourmis, Delabie et al. (2000b) ont montré que cette combinaison de méthodes capturait 50 % de la richesse spécifique totale trouvée.

Figure 3°: Illustration des différentes étapes de l'extraction des organismes de la litière par la méthode Winkler.

La méthode Winkler

Les extracteurs de litière permettent d'avoir accès, pour chaque échantillon de litière collecté, aux données de richesse, composition, abondance relative et fréquence d'occurrences (Bestelmeyer et al., 2000). La méthode Winkler est hautement recommandée pour la réalisation des inventaires d'entomofaune du sol des habitats forestiers où la litière est abondante (Fisher, 1999 ; Bestelmeyer et al., 2000), donc incontournable en forêts tropicales. Elle est l'une des seules méthodes permettant d'extraire les fourmis minuscules, cryptiques et peu mobiles nichant dans la litière, et parfois même dans le sol (Ward, 2000).

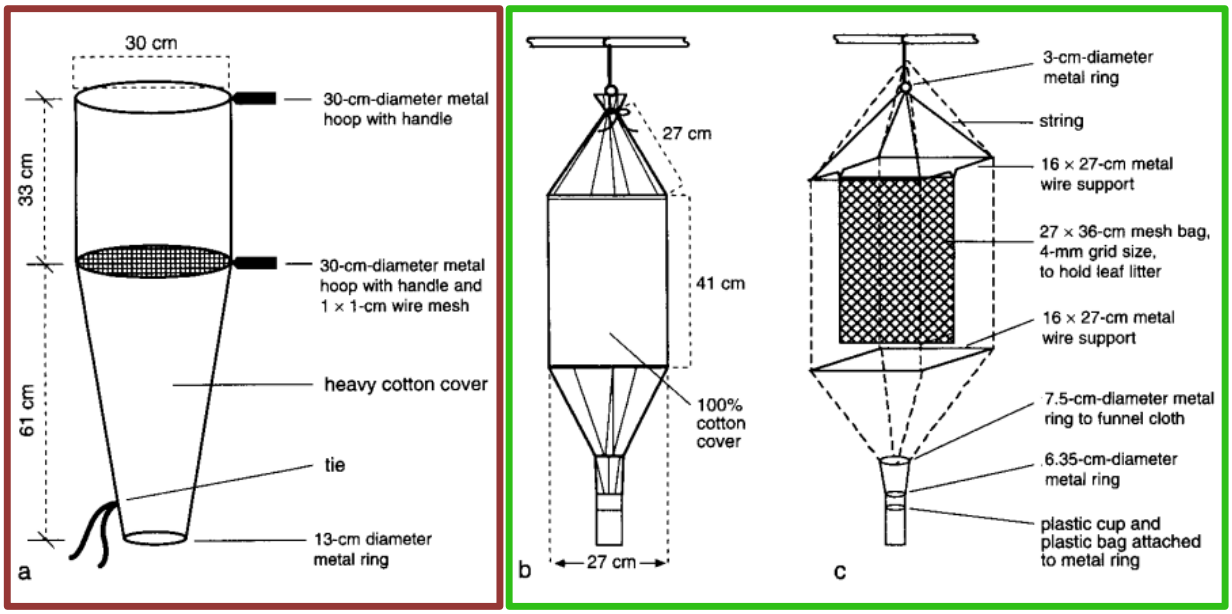

Figure 4°: Détail de l'appareillage Winkler : a. Schéma d'un tamis à litière, b. Enceinte de coton dans laquelle la litière est déposée, c. Sac de litière suspendu dans l'enceinte de coton pendant 48h (Fisher, 1999 ; Bestelmeyer et al., 2000) ; phase de terrain avec le tamisage et la récolte de la litière (encadré en marron), phase de laboratoire où la litière récupérée est suspendue pendant 48h dans des enceintes de coton immobiles à l'abri du vent (encadré en vert).

Nous avons utilisé l'extracteur de litière Winkler selon la méthode préconisée par Bestelmeyer et al. (2000). Ainsi, dans chaque parcelle, la litière d'un quadrat de 1m² a été passée au tamis et récupérée dans un sac numéroté pour une extraction ultérieure en laboratoire (Figure 3a). Dans le laboratoire, chaque échantillon de litière a été placé dans un sac maillé suspendu pendant 48 heures dans une enceinte de coton, afin de séparer les fourmis du matériel végétal (Figure 3b, c). Très rapidement, les fourmis du sol commencent à migrer dans la litière et à se déplacer dans tout le compartiment (comportement en réponse à la perturbation de leur habitat). Elles sont finalement collectées dans un petit récipient partiellement rempli d'alcool suspendu en bas du sac, dont le principe est assez similaire à celui du piège à fosse (voir ci-dessous). Il est important de préciser que chaque sachet de litière tamisée a été pesé avant d'être vidé dans le sac maillé et mis à déposer dans l'enceinte de coton.

Figure 5°: Illustration du principe du piège à fosse.

Les pièges à fosse

Des gobelets en plastique, enfoncés dans la litière et enterrés dans le sol jusqu'à la surface, ont fait office de pièges à fosse (Figure 5). Ce sont majoritairement des fourmis fourrageuses mobiles à la surface du sol qui sont ainsi piégées. Le diamètre des gobelets utilisés était de 70mm (très proche du diamètre recommandé -75mm- par Bestelmeyer et al. (2000) pour optimiser l'efficacité du piège). La végétation autour des pièges a seulement été dégagée lorsqu'elle était en contact avec le gobelet. Chaque piège était rempli à 25% d'eau savonneuse salée, qui, en principe, n'est ni attractive, ni répulsive pour les fourmis, contrairement à l'alcool même très dilué. Le détergent permet de diminuer la tension superficielle des organismes qui vont donc couler, et le sel retarde leur décomposition. Après 48h d'échantillonnage ininterrompu, les pièges ont été enlevés et les fourmis récoltées. Cette méthode est simple à mettre en œuvre et à appliquer. Peu onéreuse, elle échantillonne en continu (piégeant ainsi tous les types de fourrageuses, indépendamment de leur période journalière de prospection), et permet d'avoir, dans un court laps de temps, des résultats comparables et représentatifs de la composition des assemblages d'espèces de fourmis au sol. De plus, la plupart des fourmis épigées y sont généralement bien représentées Bestelmeyer et al. (2000). Cette technique est donc idéale, dans le cadre de l'étude préliminaire des assemblages d'espèces de fourmis des chablis, pour détecter rapidement s'il y a une différence de composition de ces assemblages avec ceux vivant dans la forêt hors du chablis. L'échantillonnage par les pièges à fosse conduit à l'obtention de données comme la richesse et la composition, l'abondance relative des ouvrières fourrageuses pour chaque piège ou pour un ensemble de pièges pour un milieu donné, ainsi que la fréquence d'occurrence des espèces (Bestelmeyer et al., 2000).

6.2.3. Protocole d'échantillonnage: le protocole ALL (*Ants of the Leaf Litter*)

La standardisation des protocoles d'échantillonnage est primordiale car elle permet des approches comparatives entre les communautés dans l'espace et dans le temps (Bonar et al., 2009). Les méthodes d'échantillonnage utilisées pour la récolte des fourmis de la litière ont été utilisées selon le protocole ALL (Agosti et Alonso, 2000 ; Fisher et al., 2000). Ce protocole suggère un minimum de 20 points d'échantillonnage séparés de 10m pour capturer entre 45 et 70% de la myrmécofaune d'un site. Selon Leponce et al. (2004), un seul transect (i.e. ligne d'échantillonnage) réalisé selon le protocole ALL apparaît comme l'effort d'échantillonnage minimal pour la caractérisation de l'assemblage de fourmis de litière étudié.

Pour chaque zone échantillonnée (lorsque la surface et la topographie du milieu le permettaient ; voir Tableau 2), 50 points d'échantillonnage ont été réalisés le long de transects, dont le nombre et la longueur dépendaient de la physionomie de l'habitat. Dans le cas de la méthode Winkler, 50m² de litière tamisée ont été collectés. Des transects séparés d'au moins 10m les uns des autres ainsi que des bordures de forêt ou de parcelles ont été réalisés. Il est préconisé de laisser au moins 10m d'écart avec la bordure pour éviter de biaiser les résultats par l'effet de « lisière », particulièrement dans les zones naturelles ou dans les zones anthropisées entourées de forêt naturelle. En effet, les bordures sont des milieux très perturbés abritant des espèces caractéristiques, souvent généralistes ou opportunistes, qui pourraient biaiser les résultats de capture lors de l'échantillonnage (Terayama and Murata 1990 ; Majer et al., 1997 ; Vasconcelos et al., 2001).

6.2.4. Processus d'identification

Au total, 1440 échantillons ont été récoltés, entre Octobre 2009 et Mars 2010. Le travail de laboratoire, consistant (1) à séparer les fourmis des autres organismes de la litière, (2) monter un individu par morphoespèce par échantillon pour réaliser une collection de référence, et (3) séparer les différentes morphoespèces, s'est échelonné d'Octobre 2009 à Octobre 2010. Les identifications des espèces ont finalement été faites avec l'aide de deux taxonomistes – le Pr. Jacques Delabie (Centro de Pesquisas do Cacau, Bahia, Brésil) et le Dr. Fernando Fernández (Institut des Sciences Naturelles de Bogotá, Colombie) –, d'Août à Mars 2011. Les premières matrices complètes de présence-absence ont donc été obtenues à la fin de la deuxième année

de thèse (Novembre-décembre 2010) pour les sites des Nouragues et de Paracou, les matrices restantes (sites de Kaw et des Chutes Voltaire) au début de la troisième année de thèse (février-mars 2011).

Des collections de référence (complètes ou partielles) ont finalement été déposées à l'UMR EcoFoG (Kourou, Guyane française), au Laboratoire de Myrmécologie du Centro de Pesquisas do Cacau d'Itabuna (CEPLAC, Bahia, Brésil), à l'Institut des Sciences Naturelles de l'Université Nationale de Colombie (ICN, Bogotá, Colombie), ainsi qu'à l'Institut Royal des Sciences Naturelles de Belgique (IRSNB ; Bruxelles). La réalisation de la collection de référence à l'IRSNB, sous la direction du Dr. Maurice Leponce, a été financée par un projet SYNTHESYS(1)[4], et a donné lieu à la numérisation de 150 espèces de fourmis guyanaises (exemples p.40-42) qui, à terme, seront disponibles dans une base d'images mise en ligne (http://projects.biodiversity.be/ants) destinée à l'aide à l'identification d'espèces néotropicales. Toutes les espèces récoltées au cours de ma thèse et au cours de missions précédentes (Durou et al., données non publiées) ont également été intégrées à la base de données SID (Leponce et Vander Linden, 1999).

[4] Janvier-Février 2011: bourse SYNTHESYS (European Union Synthesis of Systematic Resources - (BE-TAF-1205) 2011, Diversity of French Guianese ants (1660 €).


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6.3. Outils statistiques

L'ensemble des calculs, des analyses statistiques et des graphiques présentés dans ce mémoire ont été réalisés grâce aux logiciels suivants :

- Calculs des indices de diversité spécifique et des valeurs nécessaires pour la construction des courbes de raréfaction : EstimateS, version 7.5 (Colwell, 2005).
- Courbes et graphiques : SIGMAPLOT, version 8.0 (Brannan et al., 2002).
- Analyses et comparaisons de diversité et de similarité, analyses statistiques univariées : PAST, version 2.0 (Hammer et al., 2001).
- Analyse des réseaux de neurones : MATLAB Version 7.2.0.232 (The Mathworks Inc., 2006)

Les différentes méthodes d'analyse utilisées seront présentées en détail dans les chapitres concernés.

<u>CHAPITRE 1 :</u> INFLUENCE DE L'HÉTÉROGÉNÉITÉ ENVIRONNEMENTALE NATURELLE SUR LES COMMUNAUTÉS NÉOTROPICALES DES FOURMIS DE LA LITIÈRE À L'ÉCHELLE LOCALE

1. Contexte phytogéographique

La couverture végétale est influencée, à l'échelle régionale, par le climat et la géomorphologie et, à l'échelle locale, par les variations dans la fertilité des terres,, la profondeur des sols et de la nappe phréatique, la topographie, ou encore l'occurrence de feux. De cette façon il est possible d'identifier une grande variété de formations végétales, même à distances relativement faibles (de l'ordre de centaines de mètres), comme par exemple, dans les zones d'inselbergs en Guyane (Barthlott et al., 1997). Les inselbergs sont des formations géologiques d'origine métamorphique, particulièrement fréquentes en zone intertropicale (Bornhardt, 1900 ; Barthlott et al., 1997). Ils accueillent une végétation spécifique. Ils forment généralement des refuges pour des écosystèmes non perturbés ; ainsi, à l'échelle du Nord de l'Amérique du Sud et particulièrement en Guyane, ils concourent à la biodiversité régionale par la spécificité de leur flore, de leur faune et de leur fonctionnement écologique. En plus de leur morphologie particulière – qui justifie leur nom (« montagne-île » en allemand) –, d'un point de vue écologique, ils hébergent des milieux fortement contrastés par comparaison avec ceux de la forêt tropicale humide mature dont ils émergent (Poncy et al., 1998). Bien que l'évolution vers un stade forestier soit freinée et limitée par certains facteurs physiques du milieu (*e.g.* le lessivage intense des sols par les eaux de ruissellement accentué par l'effet de pente qui défavorise l'installation d'une végétation arborée; Gasc et al., 1998), il semble que ces milieux soient actuellement en phase d'envahissement par la forêt. C'est ainsi qu'on trouve à la périphérie des inselbergs des forêts dites de transition (Larpin, 1993). De plus, aux Nouragues la grande partie sud de la forêt de grand plateau est dominée par des lianes (on parlera de forêt de lianes par la suite), constituant une formation végétale homogène considérée comme un type de forêt distinct. Cette forêt de lianes est composée d'une dense couche de végétation avec une faible densité d'arbres (Chave et al., 2001).

2. Conclusion

Les résultats des deux études composant ce chapitre (Articles 1 et 2) indiquent que la forêt entourant la station de recherche des Nouragues abrite une myrmécofaune hautement diversifiée, incluant probablement des espèces endémiques, rares et/ou peu connues, mais potentiellement exposées à des invasions biologiques futures (premier registre pour *Technomyrmex vitiensis* en Amérique du Sud continentale ; Delabie et al., 2011 : Annexe 1). Bien que ces études montrent un changement dans la composition taxonomique des communautés de fourmis de la litière entre les différentes formations végétales, le recouvrement d'espèces entre celles-ci est apparu très faible. Comme le préconise Andersen (1997b), dans ce cas l'approche des groupes fonctionnels est particulièrement bien adaptée. Elle nous a permis de montrer que les communautés de fourmis de la litière sont fonctionnellement spécifiques au type de formation végétale, donc d'habitat dans lequel elles vivent. En effet, la diversité et l'abondance des espèces au sein de chaque groupe fonctionnel reflètent de façon claire les caractéristiques de chaque habitat. De plus, le site de la station de recherche des Nouragues s'est révélé être un endroit idéal pour tester l'hypothèse de l'hétérogénéité de l'habitat sur les communautés de fourmis, les cas opposés des forêts de lianes et de transition illustrant parfaitement ce phénomène écologique.

3. Articles

3.1. Article 1 : Baseline study of the leaf-litter ant fauna in a French Guianese forest

Insect Conservation and Diversity (2009) 2, 183–193

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Baseline study of the leaf-litter ant fauna in a French Guianese forest

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Abstract. 1. Leaf-litter ants represent a major component of biodiversity and are excellent bioindicators reflecting the health of terrestrial ecosystems. This study, conducted in an unspoiled forest near the Nouragues Research Station, represents the first inventory of leaf-litter ant diversity conducted in French Guiana, and so can be considered as the baseline dataset for ants in this country.

2. Ants were extracted from the leaf-litter using the Ants of the Leaf Litter Protocol, along an altitudinal gradient at four forest sites, including an inselberg.

3. A total of 196 ant species representing 46 genera distributed over eight subfamilies were collected. Four distinct communities spread over a gradient of diversity were thus identified: the liana forest was the most species-rich (140 species) followed by the forested plateau (102 species), the transition forest (87 species) and the forest at the top of the inselberg (71 species).

4. The discovery of species new to science plus several species recorded for the first time in French Guiana, coupled with the particular context of this area, suggests that the Nouragues Research Station might represent a centre of endemism. Once completed, this leaf-litter ant dataset will contribute greatly to the knowledge of ant biodiversity in French Guiana, and has the potential to progressively become an indispensable tool for country-wide conservation planning programmes.

Key words. Ants of the Leaf Litter Protocol, baseline study, leaf-litter ants, Nouragues, Winkler method

Introduction

It is commonly acknowledged that invertebrates are essential to the processes shaping ecosystems because they are major components of biodiversity and good biological indicators of biota diversity and environmental quality. Consequently, they have more and more often been the focus of environmental studies (Hites *et al*., 2005; Rohr *et al*., 2006; Grimbacher *et al*., 2008). Among terrestrial invertebrates, ants have many attributes making them indispensable tools for conservation projects. Indeed, by their ecological dominance in most terrestrial ecosystems – especially in the tropics, their diversity, the relative ease of sampling them, and their sensitivity to environmental changes, they are relevant bioindicators reflecting the health of ecosystems (Kaspari & Majer, 2000; Andersen *et al*., 2002; Lapolla *et al*., 2006; Rohr *et al*., 2006). Ground- and litter-dwelling ants, for example, have commonly been used as bioindicators in numerous biodiversity studies conducted in tropical regions (Brühl *et al*., 1999; Delabie *et al*., 2000b, 2006; Fisher, 2000; Longino *et al*., 2002; Leponce *et al*., 2004). These ants form a particularly promising group because a standard protocol to sample them was developed: the Ants of the Leaf Litter Protocol (ALL Protocol; Agosti & Alonso, 2000; Fisher *et al*., 2000). This protocol provides a quantitative methodology for comparing species richness between sites. This is of major importance because there are only a few standardised methods for

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sampling invertebrates despite a growing call for their use in conservation biology (New, 1995; Samways, 2005).

The Neotropics undoubtedly possess one of the richest ant faunas in the world, with about 3100 known species (Fernández & Sendoya, 2004). For example, La Selva Biological Reserve (1500 ha in Costa Rica) has at least 437 ant species (Longino *et al*., 2002), and at Ilheus (1750 km^2 in Bahia, Brazil) 442 species have been identified (Delabie *et al*., 1998). Since the late 1990s, ant fauna inventories have multiplied in projects promoting a greater understanding of biodiversity in South and Central America: Argentina (Leponce *et al*., 2004), Brazil (Delabie *et al*., 2000a; Marinho *et al*., 2002; Vasconcelos *et al*., 2003; Hites *et al*., 2005), Colombia (Jiménez *et al*., 2007), Costa Rica (Longino & Colwell, 1997), and Guyana (Lapolla *et al*., 2006). In comparison, the French Guianese ant fauna is still poorly known, largely unexplored, and taxonomic literature on it scarce.

In addition to the absence of studies on the ground-dwelling ant fauna of French Guiana justifying the choice of and interest in creating just such an inventory, it also has relevance for clarifying the role of vegetal cover in the diversity of leaf-litter ants. Because of its preservation from relatively recent anthropisation, the biodiversity at the 'inselberg site' of the Nouragues Research Station, a totally preserved area situated in the Nouragues Nature Reserve, French Guiana, is commonly used as a reference point for monitoring programmes (for plants see Bongers *et al*., 2001). With the aim of expanding knowledge of the ground- and litter-dwelling ant communities of this area and establishing a reference collection, we conducted an analysis of the litter-dwelling ant diversity.

Material and methods

Study sites

The Nouragues Research Station is located in the Balenfois Mountains, southeast of Regina. Mainly dominated by hills, it is covered by an expanse of dense forest that has remained uninhabited for over two centuries. This site is particularly interesting for its granitic inselberg, a tabular rocky outcropping rising abruptly from the surrounding rainforest to 430 m above sea level (Bremer & Sander, 2000). The geology of this area is dominated by two types of substrates: Caribbean granite, and metavolcanic rocks from the Paramaca series (Grimaldi & Riéra, 2001). Consequently, the soil is acidic, and the vegetation is particularly heterogeneous.

In March 2006, four different forested environments were sampled along an altitudinal gradient: a liana forest (4°04′58″N, 52°40′28″O; 120 m altitude); a wide, forested plateau (4°05′20″N, 52°40′28″O; 140 m altitude); a low transition forest (4°05′30″N, 52°40′38″O; 200 m altitude) and the inselberg's summit (4°05′47″N, 52°40′51″O; 430 m altitude). The liana forest is separated from the wide, forested plateau by 700 m; the same is true for the distance between the transition forest and the summit of the inselberg, while only 400 m separate the transition forest and the plateau.

The liana and the plateau forests, although different, have high tree species richness where Leguminosae and Lecythidaceae dominate (Larpin, 2001). The transition forest, a patch of shrubby forest characterised by the absence of large trees, is much less diverse than the previous two. Finally, the inselberg summit, characterised by a specific type of rock savannah vegetation adapted to drought, is dominated by evergreen shrubs belonging to the Clusiaceae, Myrtaceae and Bombacaceae families (Sarthou *et al*., 2003).

The litter layer, varying from one environment to another, depending on the altitude, soil type and vegetation, was thick in the liana forest, on the plateau (classical primary rainforest) and at the summit of the inselberg, whereas it was minimal in the transition forest.

Experimental protocol

Because it is highly recommended for invertebrate inventories in forested habitats where litter abounds (Fisher, 1999; Delabie *et al*., 2000b), the Winkler method was used (see Bestelmeyer *et al*., 2000). We collected ant workers from a series of 1 m^2 leaf-litter samples that were weighed, and their weight considered as a proxy of the leaf-litter thickness.

The ALL Protocol (Agosti & Alonso, 2000; Fisher *et al*., 2000) suggests using a minimum of 20 sampling points separated by 10 m intervals to collect at least 70% of the ant fauna at a given site. We thus selected 50 sampling points separated by 10 m in the forested plateau (one 500 m-long transect), liana forest (two 250 m-long transects), and the transition forest (five 100 m-long transects). Given the relatively small size of the inselberg forest, only 20 sampling points, separated by 10 m, were set up.

All ant samples were preserved in 70% ethanol; for each sample at least one individual per morphospecies was kept in order to constitute a reference collection. The ants were identified to species (whenever possible), according to the key developed by Bolton (1994, 1995) and Bolton *et al*. (2006). Voucher specimens were deposited in the *Laboratório de Mirmecologia*, Cocoa Research Centre CEPEC/CEPLAC (Ilhéus, Bahia, Brazil).

Data analysis

For each sample, the number of worker morphospecies was recorded. Thus, the specific richness (number of species captured) and species occurrences (number of times that a given species was collected in a sampled site) were compared between the four forests.

To estimate and compare the efficiency of the sampling of the ant fauna, species accumulation curves (cumulated numbers of species according to the number of samples) were plotted for each environment, and the Chao 2 non-parametric estimator of total species richness was used (Chao, 1987). Because the number of individuals is not a reliable parameter in ant studies (data can be distorted when ants are collected close to a nest, an ant trail or a site where ants recruit nestmates), only species occurrences were taken into account. EstimateS 7.5 software was employed to build these curves with a confidence interval of 95%; because the order in which each sample is added influences

the shape of these curves, the matrices of species occurrences (presence/absence) were treated with 500 randomisations of the sampling order without replacement (see Colwell *et al.*, 2004; Colwell, 2005).

We aimed to compare the number of species in each sampled site, taking into account the effect of leaf-litter thickness (through its weight), using a Generalised Linear Model (GLM, McCullagh & Nelder, 1989). We used the canonical link function, so that the model is:

$$\ln(E(Y_{ij})) = \mu + \alpha_i + \beta x_{ij} + \gamma_i x_{ij}$$

where Y_{ij} is the number of species (assumed to be independent and distributed according to a Poisson distribution for parameter λ_{ij}; see Vincent & Haworth, 1983), i stands for the site, α_i the effect of site i for sample j, β the effect of leaf-litter weight, and γ_i the difference in slopes between sites (i.e. the interaction between the site and leaf-litter weight). The formula corresponds to an ANCOVA in a linear model context. We performed a pairwise comparison between environments using the Bonferroni correction (Shaffer, 1995). These analyses were conducted using the R statistical software (R Development Core Team, 2003).

The similarity among the ant assemblages at the different sites was assessed using a cluster analysis (Jaccard coefficient of similarity). The resulting similarity matrix was analysed through a sequential, agglomerative, hierarchical and nested clustering algorithm described by Sneath and Sokal (1973). The option used was the Unweighted Pair-Group Method, arithmetic average (UPGMA). This analysis was conducted using the MVSP programme (Kovach, 2001).

Results

Taxonomic structure of the entire litter-dwelling ant fauna

A total of 196 species representing 46 genera and eight subfamilies were collected from 170 m^2 of leaf-litter from all sites (Appendix 1).

The species accumulation curve for all environments combined as well as those for the different sites sampled tended to slow down, but they did not reach a horizontal asymptote corresponding to the total estimated number of species for the environment considered (Fig. 1). Yet, the Chao 2 estimator, providing a theoretical species number, showed that a reasonable part of the community of litter-dwelling ants was inventoried: more than 74% of the species were recorded for all environments combined, and 81%, 67%, 66% and 73% for the liana, plateau, transition and inselberg forests respectively (Table 1).

The GLM analysis resulted in a significant difference ($P < 0.001$) showing the combined effect of leaf-litter weight and sites on species number with a significant difference between the liana forest and both the plateau and the inselberg forests, but non-significant differences between the three other forest types (Table 2).

The most diverse subfamilies were the Myrmicinae with 27 genera and 129 species, followed by the Ponerinae, the Formicinae, the Ectatomminae and the less speciose ones (Amblyoponinae, Dolichoderinae, Proceratiinae and Pseudomyrmicinae) (Table 3). The most speciose genera were *Pheidole* (42 sp.),

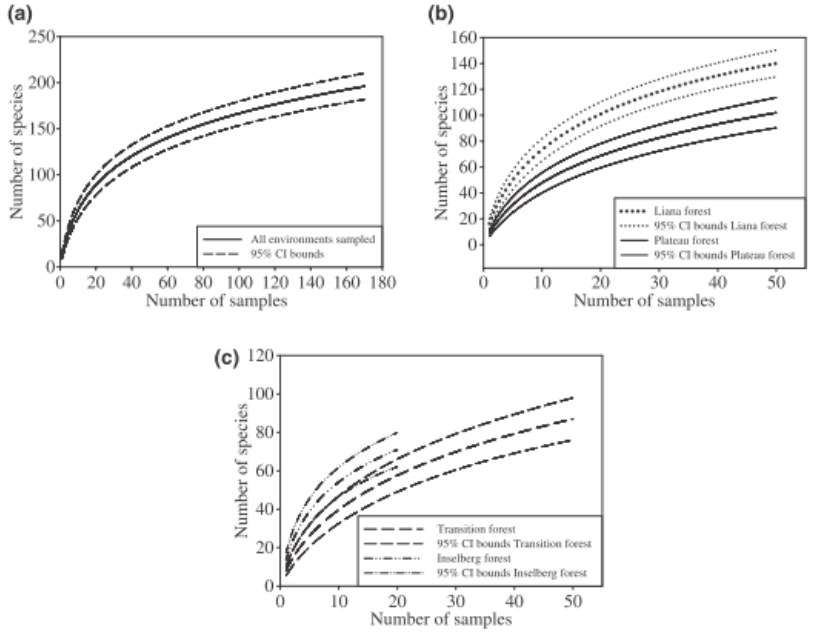

Fig. 1. Species accumulation curves representing the total cumulated number of species depending on the number of samples (with 95% confidence intervals) for (a) all studied environments pooled ($N = 170$ samples), and (b, c) for each environment studied ($N = 50$ samples for the liana, plateau and transition forests; $N = 20$ samples from the inselberg forest).

Table 1. Number and percentage of species collected, and number of estimated species for all environments and each site sampled (Chao 2) with its standard deviation.

	Number of species collected	% of species collected	Chao 2	Chao 2 SD
All environments	196	74.1	264.47	24.18
Liana forest	140	81.2	172.45	13.20
Plateau forest	102	67	152.23	21.22
Transition forest	87	66.4	131.1	19.88
Inselberg forest	71	73.4	96.73	13.50

Table 2. *P*-values associated with the pairwise comparison of the ANCOVA coefficient slopes.

	Liana forest	Forested plateau	Transition forest	Inselberg forest
Liana forest	×	0.441	0.004	0.008
Forested plateau	×	×	0.071	0.093
Transition forest	×	×	×	0.881
Inselberg forest	×	×	×	×

The multi-comparison test resulted in *P*-values, which based on the Bonferroni correction, had to be inferior to 0.0083 to be considered as significant in our analysis.

Table 3. Number and proportion of genera and species for each subfamily of ants collected.

Subfamilies	Number of genera	%	Number of species	%
Myrmicinae	27	58.7	129	65.8
Ponerinae	6	13	31	15.8
Formicinae	4	8.8	13	6.6
Ectatomminae	3	6.5	13	6.6
Amblyoponinae	2	4.3	3	1.5
Dolichoderinae	2	4.3	3	1.5
Proceratiinae	1	2.2	2	1.1
Pseudomyrmecinae	1	2.2	2	1.1

Solenopsis (13 sp.), *Pyramica* (12 sp.), *Hypoponera* and, unexpectedly, *Gnamptogenys* (10 sp.) (Appendix 1).

Of the 196 species collected, 108 (55%) were identified to species level. The remaining 45% were (1) species new to science (at least 11 species), (2) species awaiting description, (3) species belonging to genera awaiting revision (e.g. *Hypoponera*, *Paratrechina*), and (4) species belonging to the most speciose genera and thus difficult to identify (*Pheidole* and *Solenopsis*). Indeed, the current state of taxonomy may imply that we have overlooked cryptic species in these problematic genera. Furthermore, 37 species (nearly 20%) were recorded for the first time in French Guiana, most of them Myrmicinae (including the genera *Cryptomyrmex* and *Stegomyrmex*) plus one species of Amblyoponinae, Ectatomminae and Proceratiinae (Appendix 1).

Ant communities in the forests studied

The most species-rich site was the liana forest (140 species; 71.4% of all species); the poorest, the inselberg forest (71 species; 36.2%), and the diversity of the two other sites somewhere in-between (plateau forest 102 species, 52%; transition forest 87 species, 44.4%). In addition to the ubiquitous presence of Myrmicinae, Formicinae and Ectatomminae, the transition and inselberg forests are distinct from the other sites due to the lower species number of Ponerinae, more occurrences of Dolichoderinae and the presence of Pseudomyrmecinae. Therefore, each forest has its own ant fauna resulting largely from different geological conditions influencing the type of dominant vegetal formation, itself influencing the microclimatic conditions, something illustrated by the low similarity coefficients (Fig. 2).

The proportion of subfamilies, in terms of number of species, remained broadly constant for the most frequently represented subfamilies (Myrmicinae, Formicinae and Ectatomminae; Table 3). The Amblyoponinae and Proceratiinae were found on occasion in three out of the four sampled forests. It is noteworthy that the Ponerinae, predators of litter-dwelling arthropods, were better represented in the liana and plateau forests. Because they are mostly represented by arboreal species, the Dolichoderinae and Pseudomyrmecinae are not very diverse in this study and present almost only in the transition and inselberg forests, both with low vegetation (Appendix 1).

The ant fauna at a given site consists of generalist (i.e. found in all sampled environments) and specific species (only found at one site, they are 'indicator species' characterising each environment), the whole forming a species assemblage. The frequency of the 34 ubiquitous species varied between sites, three species being the most frequent at all sites: *Pyramica denticulata*, *Solenopsis* (*Diplorhoptrum*) sp.4 and *Solenopsis* (*Diplorhoptrum*) sp.5 (Appendix 1). Indicator species represent 29% of all species in the liana forest compared to 24%, 17% and 11% for the plateau, transition and inselberg forests respectively.

The number of species new to science and species still being described followed a gradient from the liana to the inselberg forests (Appendix 1). Moreover, among the 37 species recorded for the first time in French Guiana, 21 (57%) are specific to one forest: ten, seven, three and one for the liana, plateau, transition and inselberg forests, respectively (Appendix 1).

Discussion

Sampling the leaf-litter ant fauna

Although conducted over a limited period of time and through only one extraction method, our inventory indicates a great diversity in the litter-dwelling ant fauna at the Nouragues Research Station, demonstrating that there is still much to learn about the Guianese ant fauna, particularly if we keep in mind the very small surface of the areas sampled.

Even though it is probably impossible to reach a horizontal asymptote in a very diverse Neotropical site in a single survey and with one sampling method, we captured a reasonable part of the community of leaf-litter ants, creating an acceptable first

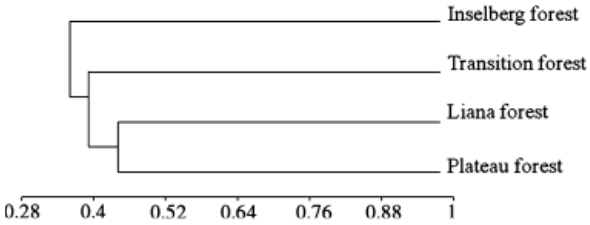

Fig. 2. Dendrogram of the similarities (Jaccard coefficient, UPGMA cluster analysis) of the leaf-litter ant fauna among the four sites sampled. The scale illustrates the low similarity coefficients (< 0.5 in all cases).

inventory. Numerous studies have shown that a 50 m^2 litter sample enables reliable estimations to be made with the first-order Jackknife and Chao 2 estimators (Delabie *et al*., 2000b; Fisher, 2000; but see Leponce *et al*., 2004). However, it is essential to combine several sampling methods to obtain an exhaustive inventory of the litter-dwelling ant fauna (Bestelmeyer *et al*., 2000; Delabie *et al*., 2000b; Fisher *et al*., 2000). Indeed, this would increase the number of Guianese ant species recorded.

Because the litter is dependent on the nature of vegetal cover at each sampling site, we showed a positive relationship between leaf-litter thickness (weight) and ant species diversity, as noted by Kaspari (1996), Soares and Shoereder (2001), Theunis *et al*. (2005). Litter quantity is related to a structural complexity due to a vertical layering (Vasconcelos, 1990); however, the leaf-litter quantity did not influence ant species abundance, density or composition in two other studies (Delabie & Fowler, 1995; Soares & Shoereder, 2001).

The litter-dwelling ant diversity in the sites studied

The liana forest, by far the most species-rich site and with the largest number of indicator species, is very likely anthropized, developing from forests that Amerindians felled and burned for shifting cultivation at least once in the past. After the fields were abandoned, a succession of trees developing and then decaying all at once favoured the formation of the liana forest, stopping the development of new trees (see Balee & Campbell, 1990). Liana forests are formed after numerous large trees of about the same age fall, providing an abundant vegetal biomass for litter- and wood-degrading arthropods, their predators and parasites, resulting in the development of a very diverse fauna. Ants, which are present in a wide range of trophic levels, are particularly diverse in this context.

Among the 37 newly recorded species, at least five were until now considered to be endemic to one country or region: *Carebara elongata* in Colombia; *Crematogaster wardi*, *Mycocepurus tardus* and *Pheidole carinata* in Central America; and *Rogeria alzatei* in Central America and the Caribbean islands. On the contrary, *Wasmannia scrobifera*, *Carebara urichi* and *Strumigenys elongata* have already been reported in Suriname and in much of tropical South America (Bolton *et al*., 2006).

Because we found at least 11 species new to science, all awaiting description, the litter-dwelling ant fauna at the Nouragues Research Station might have a certain rate of endemism. Finally, among the 34 ubiquitous species, four were recorded for the first time in French Guiana: *Crematogaster wardi* Longino, *Pheidole scolioceps* Wilson, *Rogeria lirata* Kugler and *Strumigenys elongata* Roger (Bolton *et al*., 2006). Consequently, our results underscore the need to augment research efforts to better understand the uniqueness of this site in terms of its ant fauna and very probably other faunas.

Taxonomic structure of the litter-dwelling ant fauna

The taxonomic structure of the ant fauna at Nouragues is a perfect example of the characteristic Neotropical litter-dwelling ant fauna highlighted by Ward (2000): (1) the presence of some common litter-dwelling genera (like *Brachymyrmex*, *Octostruma*, *Pyramica*, *Rogeria* and *Wasmannia*), and all fungus-growing genera (particularly *Cyphomyrmex* in our study), (2) the virtual absence of the *Monomorium* and *Tetramorium* genera, and (3) a high diversity of *Pheidole* (higher species richness per sample in our study) and *Solenopsis*, mainly represented by small to minute, morphologically similar species (e.g. *Diplorhoptrum* subgenus). Also, the relative importance of the Ponerinae and Formicinae in our study corroborates data from the Brazilian Atlantic and Amazonian forests (Delabie *et al*., 2000a; Vasconcelos *et al*., 2000, 2003; Hites *et al*., 2005).

As expected the extremely diverse genus *Pheidole* was the most speciose genus in our study with 42 species (21% of all species collected; see Wilson, 2003). In comparison, the second most speciose genus, *Solenopsis*, represented by only 13 species, was probably undervalued (1.97 species per Winkler sample *versus* 3.14 noted by Ward, 2000). The same is true for the genera *Pheidole*, which although recently revised, needs still further revision (Wilson, 2003), and *Hypoponera* due to the need for a modern taxonomic revision (see Bolton *et al*., 2006). Moreover, it is likely that some species of collected genera belong to cryptic species complexes (leaf-cutting ants, *Hypoponera*, *Pachycondyla*, *Pheidole*, *Pyramica*, *Solenopsis* and *Strumigenys*), which increases the risk of underestimating the true species number.

To conclude, the high specific richness at the Nouragues Research Station confirms that this area can be used as a reference point for comparative studies. An exhaustive inventory of this diversity would imperatively require further surveys combining several extraction methods in other Guianese areas. Such an inventory would imply collecting ant species regardless of their ecology: subterranean, litter- and ground-dwelling; living in dead wood, semi-arboreal or canopy-dwelling, etc. Unfortunately, there is no standardised sampling protocol for collecting species that do not live in the ground, which greatly complicates their capture and represents a substantial time and monetary investment.

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Appendix 1. Species collected at each site, according to their classification: liana forest (LF), forested plateau (FP), transition forest (TF) and inselberg forest (IN). The first column indicates species new to science (NS) including among them, those being described (BD), and the species recorded for the first time in French Guiana (nsg).

	Species according to their classification	LF	FP	TF	IN
Subfamily AMBLYOPONINAE Bolton					
	Amblyoponini Forel				
nsg	*Amblyopone lurilabes* Lattke			3	
	Prionopelta sp.1		1		7
	Prionopelta sp.2			1	2
Subfamily DOLICHODERINAE Forel					
	Dolichoderini Forel				
	Azteca instabilis (Smith)			4	1
	Dolichoderus attelaboides (Fabricius)			3	
	Dolichoderus imitator Emery	2			2
Subfamily ECTATOMMINAE Lepeletier					
	Ectatommini Emery				
	Ectatomma lugens Emery	2	1	1	3
	Ectatomma edentatum Roger	4	3		
	Gnamptogenys acuminata (Emery)	1		2	
nsg	*Gnamptogenys enodis* Lattke, Fernandez & Palacio	4			
	Gnamptogenys haenschi Emery	1			
	Gnamptogenys horni (Santschi)	7	1	3	2
	Gnamptogenys mina (Brown)	1			
	Gnamptogenys minuta (Emery)	1			1
	Gnamptogenys mordax (Smith)		1		
	Gnamptogenys relicta (Mann)		2	2	1
	Gnamptogenys striatula Mayr	1	1		
	Gnamptogenys sulcata (Smith)			2	
	Typhlomyrmecini Emery				
BD	*Typhlomyrmex* sp. (sp. nov.4 *sensu* Lacau, 2005)	3	3	3	
Subfamily FORMICINAE Latreille					
	Brachymyrmecini Emery				
	Brachymyrmex sp.1		1	3	5
	Brachymyrmex sp.2			1	
	Camponotini Forel				
	Camponotus fastigatus Roger			1	
	Camponotus femoratus (Fabricius)	2	1		
	Camponotus rapax (Fabricius)			1	
	Lasiini Ashmead				
	Paratrechina fulva (Mayr)	10	12	8	14
	Paratrechina sp.1	1	4		16
	Paratrechina sp.2	4			
	Paratrechina sp.3	4	6		
	Paratrechina sp.4	1			
	Paratrechina sp.5	2			
	Plagiolepidini Forel				
	Acropyga fuhrmanni (Forel)				1
	Acropyga smithii Forel				2
Subfamily MYRMICINAE Lepeletier					
	Adelomyrmecini Fernández				
nsg	*Cryptomyrmex longinodus* (Fernández & Brandão)	2			
	Attini Smith				
	Acromyrmex octospinosus (Reich)	1			
	Apterostigma sp. group *pilosum*	16	15	1	1
	Cyphomyrmex bigibbosus Emery		1		
	Cyphomyrmex laevigatus Weber	2	2	1	
	Cyphomyrmex peltatus Kempf	15	9	1	6
	Cyphomyrmex salvini Forel	4			2
	Mycocepurus smithii Forel	1			

Appendix 1. *Continued*

	Species according to their classification	LF	FP	TF	IN
nsg	*Mycocepurus tardus* Weber		2		
	Myrmicocrypta sp.	5			1
	Sericomyrmex sp.1	1			
	Sericomyrmex sp.2		1		
	Trachymyrmex ixyodus Mayhé-Nunes & Brandão		1		
	Trachymyrmex sp.1		1		
	Trachymyrmex sp.2	3	1	2	1
	Basicerotini Brown				
	Octostruma balzani Emery	27	4		
	Octostruma betschi Perrault	16	8	7	
	Octostruma iheringi Emery				1
BD	*Octostruma* sp. near *iheringi*	1	1		
NS	*Rhopalothrix* sp.	3			
	Blepharidattini Wheeler & Wheeler				
	Wasmannia auropunctata (Roger)	3	6	5	3
nsg	*Wasmannia scrobifera* Kempf		4		
	Cephalotini Smith				
nsg	*Procryptocerus hylaeus* Kempf	1			
	Crematogastrini Forel				
nsg	*Crematogaster flavosensitiva* Longino	1			
	Crematogaster limata Smith	41	23	11	4
	Crematogaster longispina Emery	6		17	1
	Crematogaster nigropilosa Mayr	3		4	
nsg	*Crematogaster sotobosque* Longino	7	3		
	Crematogaster tenuicula Forel	3			
nsg	*Crematogaster wardi* Longino	13	3	22	1
	Dacetonini Forel				
nsg	*Pyramica appretiata* (Borgmeier)		1		
	Pyramica auctidens Bolton	23	1		
nsg	*Pyramica beebei* (Wheeler)	2		1	
nsg	*Pyramica deinomastax* Bolton	2		1	
	Pyramica denticulata (Mayr)	47	28	40	19
nsg	*Pyramica hadrodens* Bolton	1			
nsg	*Pyramica hyphata* (Brown)			2	
nsg	*Pyramica metopia* (Brown)				5
	Pyramica subedentata (Mayr)	4	2	2	
	Pyramica sp.1 near *longinoi*		1		
NS	*Pyramica* sp.2 group *thaxteri*		1		
	Pyramica sp.3 proche groupe *substricta*			1	
nsg	*Strumigenys cosmotela* Kempf	2			
nsg	*Strumigenys diabola* Bolton		5		
nsg	*Strumigenys dyseides* Bolton	16			4
nsg	*Strumigenys elongata* Roger	18	11	2	1
nsg	*Strumigenys lanuginosa* Wheeler		1		
nsg	*Strumigenys trudifera* Kempf & Brown	10			
	Formicoxenini Forel				
	Nesomyrmex tristani Emery				1
	Myrmicini Lepeletier				
	Hylomyrma balzani Emery	18	10	6	
	Hylomyrma immanis Kempf	2		1	
	Hylomyrma reginae Kutter	1			
	Hylomyrma sagax Kempf	1			
NS	*Hylomyrma* sp.		1		
	Ochetomyrmecini Emery				
	Ochetomyrmex neopolitus Fernández	1	2	2	
	Ochetomyrmex semipolitus Mayr	3	1	2	1
	Pheidolini Emery				
nsg	*Pheidole alienata* Borgmeier	7		3	
nsg	*Pheidole carinata* Wilson	4			

Appendix 1. *Continued*

	Species according to their classification	LF	FP	TF	IN
nsg	*Pheidole dolon* Wilson	2		1	
nsg	*Pheidole midas* Wilson	7			4
nsg	*Pheidole pedana* Wilson	32	13		3
nsg	*Pheidole scolioceps* Wilson	2	1	22	8
nsg	*Pheidole walacei* Mann		1		
	Pheidole sp.1 group *fallax*		1	3	
	Pheidole sp.2 group *fallax*		1		
	Pheidole sp.3 group *fallax* near *tijucana*	2			
	Pheidole sp.4 group *fallax*			1	1
	Pheidole sp.5 group *diligens* near *spilota*	2			1
	Pheidole sp.6 group *flavens*	8	3	9	
	Pheidole sp.7 group *diligens*	2		4	
	Pheidole sp.8 group *flavens*		4		
	Pheidole sp.9 group *diligens* near *medialis*	6	2		
	Pheidole sp.10 group *fallax*	3		14	1
	Pheidole sp.11 group *flavens*	11	5	4	1
	Pheidole sp.12 group *flavens*	1			3
	Pheidole sp.13		1		
	Pheidole sp.14 group *flavens*	1	1		4
	Pheidole sp.15 group *flavens*			1	1
	Pheidole sp.16 group *flavens*	4	10	2	
	Pheidole sp.17 group *flavens*		2		
	Pheidole sp.18	1			
	Pheidole sp.19 group *diligens*	5		5	
	Pheidole sp.20 group *fallax*	6	2		
	Pheidole sp.21 group *fallax*	1			
	Pheidole sp.22	1	2		
	Pheidole sp.23 group *fallax*	11	6		
	Pheidole sp.24	1			1
	Pheidole sp.25 group *fallax*			1	
	Pheidole sp.26 group *flavens*	8	1	1	1
	Pheidole sp.27 group *tristis* near *pepo*	1			
	Pheidole sp.28 group *fallax*	1			
	Pheidole sp.29 group *flavens*	3	1	1	
	Pheidole sp.30	2			
	Pheidole sp.31	2	1	1	
	Pheidole sp.32	4	3	3	8
	Pheidole sp.33	17	7		2
NS	*Pheidole* sp.34 group *tristis* near *securiger*	1	4		2
	Pheidole sp.35 group *flavens*	1			
	Pheidologetonini Emery				
nsg	*Carebara elongata* Fernández	2			
nsg	*Carebara urichi* Wheeler	5	6	2	
NS	*Carebara* sp.1			1	
NS	*Carebara* sp.2	1			
NS	*Carebara* sp.3	1			
	Solenopsidini Forel				
	Allomerus decemarticulatus Mayr	1			
	Carebarella sp.1	1			
	Carebarella sp.2	2			
	Megalomyrmex silvestrii Wheeler	1	2		
	Megalomyrmex sp.	2			
	Solenopsis (*Diplorhoptrum*) *pollux* Forel			5	
	Solenopsis virulens Smith	6	9		
	Solenopsis (*Diplorhoptrum*) sp.1	16			
	Solenopsis (*Diplorhoptrum*) sp.2	3			
	Solenopsis (*Diplorhoptrum*) sp.3	1			
	Solenopsis (*Diplorhoptrum*) sp.4	35	25	25	15
	Solenopsis (*Diplorhoptrum*) sp.5	32	20	12	10

Appendix 1. *Continued*

	Species according to their classification	LF	FP	TF	IN
NS	*Solenopsis* (*Diplorhoptrum*) sp.6	2		1	
	Solenopsis (*Diplorhoptrum*) sp.7	6	6		3
	Solenopsis (*Diplorhoptrum*) sp.8	13	7	22	9
	Solenopsis (*Diplorhoptrum*) sp.9	16	10	10	2
	Solenopsis (*Diplorhoptrum*) sp.10	10	3	1	
	Solenopsis (*Diplorhoptrum*) sp.11			1	
	Stegomyrmecini Wheeler				
nsg	*Stegomyrmex manni* Smith		1		
	Stenammini Ashmead				
nsg	*Lachnomyrmex pilosus* Weber	1			
BD	*Lachnomyrmex* sp.	1	1		
nsg	*Rogeria alzatei* Kugler	7		1	3
nsg	*Rogeria lirata* Kugler	1	1	1	1
	Rogeria micromma Kempf	4	2	1	6
nsg	*Rogeria scobinata* Kugler	11	6	4	11
nsg	*Rogeria subarmata* Kempf			1	
Subfamily PONERINAE Lepeletier					
	Ponerini Lepeletier				
	Anochetus diegensis Forel	6	2	2	1
	Anochetus horridus Kempf	3	2	1	2
	Anochetus inermis André	2	5		
	Anochetus mayri Emery			1	
	Anochetus simoni Emery		1		
	Hypoponera foreli Mayr	2	4	3	2
	Hypoponera sp.1	8	7	9	9
	Hypoponera sp.2	2	3	7	5
	Hypoponera sp.3		1		
	Hypoponera sp.4	1			
	Hypoponera sp.5	4	3	3	6
	Hypoponera sp.6	10	5	14	7
	Hypoponera sp.7	12	6	1	4
	Hypoponera sp.8	5	11	5	6
	Hypoponera sp.9	3		1	
	Hypoponera sp.10	1	1		2
	Leptogenys dasygyna Wheeler	1			3
	Odontomachus biumbonatus Brown	7	6		
	Odontomachus caelatus Brown		1		
	Odontomachus haematodus (Linnaeus)				1
	Odontomachus hastatus (Fabricius)		1		
	Odontomachus scalptus Brown	1	5	4	
	Pachycondyla arhuaca (Forel)	1			1
	Pachycondyla constricta (Mayr)	4	1	5	3
	Pachycondyla harpax (Fabricius)	5	2	2	5
	Pachycondyla stigma Fabricius	3	2	1	
	Pachycondyla striata Santschi	1			
	Pachycondyla sp.1 group *harpax*			1	1
	Pachycondyla sp.2 group *harpax*		1		
	Pachycondyla sp.3				1
	Thaumatomyrmecini Emery				
NS	*Thaumatomyrmex* sp.	2			
Subfamily PROCERATIINAE Bolton					
	Proceratiini Emery				
	Discothyrea denticulata Weber	5	1	1	
nsg	*Discothyrea sexarticulata* Borgmeier	7	1	1	
Subfamily PSEUDOMYRMECINAE Smith					
	Pseudomyrmecini Emery				3
	Pseudomyrmex tenuis Fabricius				
	Pseudomyrmex sp. group *pallidus*			1	

3.2. Article 2: The outstanding diversity and heterogeneous functional structure of leaf-litter ant assemblages in a pristine Guianese rainforest

En préparation pour une soumission à Insect Conservation and Diversity

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RUNNING TITLE: Amazing ant diversity in Guianese Amazonia

ABSTRACT

Aims Despite the very high level of ant diversity recorded in the Amazonian rainforest, the amount of diversity in French Guiana is still virtually unknown. Through this study, we compared ant assemblages from four very heterogeneous habitats, each characterized by a unique vegetal formation type, over a short elevational gradient of vegetation.

Location French Guiana

Methods Our survey focused on litter-dwelling ant faunas by combining the use of a litter extraction method with pitfall traps, and by using the Ants of the Leaf Litter Protocol, thus guaranteeing that a representative part of the ant community would be sampled.

Results Our substantial sampling effort (almost 80% of the estimated species richness) revealed exceptional leaf-litter ant diversity at the Nouragues Research Station. The extreme habitat heterogeneity resulted in a marked diversity gradient from the lowland rainforest to the top of the inselberg and obvious changes in species density and composition. The same was true for the functional structure. While the ant assemblages on the plateau and inselberg can be considered functionally common, that of the transition forest appeared relatively homogenous and characterized by open-area ant fauna. On the contrary, the assemblage in the liana forest appeared unexpectedly richer and more dense, surprisingly sheltering a very specialized litter-dwelling ant fauna dominated by numerous and abundant cryptic species.

Main results This outstanding diversity and functional richness show that this location should be listed as a reference point for the Amazonian rainforest. However, although pristine, this biodiversity hotspot may be threatened by the presence of introduced ant species, one of which – recorded for the first time anywhere in continental South and Central America – is known for its ability to be invasive. That is why the Nouragues Research Station is a conservation priority research site that should quickly be integrated into land monitoring and management programs.

Keywords: Litter-dwelling ant fauna, local scale, specific and functional structure, habitat heterogeneity, diversity gradient, pristine Amazonian rainforest, biodiversity hotspot, site of high conservation value.

INTRODUCTION

Although insects represent a large part of Amazonian biodiversity and the vast majority of forest animal biomass (Fittkau and Klinge, 1973), studies on diversity patterns in this region have focused on a restricted number of taxa (Kress *et al.*, 1998). In tropical rainforests worldwide, ants are highly diversified and represent the most dominant group of insects both in terms of biomass and number of individuals (Dunn *et al.*, 2009). So, they have gradually been more and more often included in studies on biodiversity.

Numerous recent surveys, namely in Guyana, Colombia, Ecuador, and Brazil (Jiménez *et al.*, 2007; Lapolla *et al.*, 2007; Vasconcelos and Vilhena, 2006; Ryder Wilkie *et al.*, 2009, 2010; Vasconcelos *et al.*, 2009), have enabled the understanding of the biodiversity of the Amazonian ant fauna to be greatly expanded; however, so far, only two studies have focused on Guianese ground-dwelling ant assemblages (Delabie *et al,.* 2009; Groc *et al.*, 2009). Nevertheless, despite this general infatuation with Neotropical ants, few surveys focusing on assemblages over long transects, comparing different biomes and dealing with the main components of diversity, have been conducted until now (Vasconcelos *et al.*, 2009).

It is fundamental to document how habitat heterogeneity (naturally or anthropogenically-induced) affects communities in the Amazonian forest, as changes in communities may ultimately result in the alteration of such ecosystem processes as productivity, the decomposition of organic matter and nutrient cycling (Laurance *et al.*, 2002), which may have a worldwide impact (Phillips *et al.*, 2009). Because of their major ecological role (Hölldobler and Wilson, 1990), their essential ecosystem functions (Folgarait, 1998), their relatively sedentary lifestyle, their ease of sampling (Bestelmeyer *et al.*, 2000), and their responsiveness to environmental changes, ants are currently being used as indicators of biodiversity and environmental disturbance based on the response of functional ant groups – a useful framework for understanding ant community dynamics (for a synthesis, see Hoffmann and Andersen, 2003), especially in Australia (for a synthesis see Underwood and Fisher, 2006). Indeed, to date, few studies have focused on the impact of environmental variation on such groups in South America (Bestelmeyer and Wiens, 1996; Silvestre *et al.*, 2003; Delabie *et al.*, 2006; Silva and Brandão, 2010), other than two recent studies on Amazonian ants (Ryder Wilkie *et al.*, 2009, 2010).

A preliminary study permitted us to record a high leaf-litter ant species richness at the Nouragues Research Station (Groc *et al.*, 2009); in French Guiana, this station is commonly used as a reference point for monitoring programs concerning plants (Bongers *et al.*, 2001). Here, using more complete sampling methods and substantially increasing the sampling

effort, we decided to go further into the examination of these assemblage patterns by focusing on their functional structure. So, the aim of this study was to understand why ant assemblages follow a gradient of diversity, and how these assemblages are structured in each habitat by using a functional group approach. The presence of the same functional groups in the different habitats should show that the same selective ecological pressures exist, thus reflecting a very similar evolutionary history in that area; whereas different functional ant structures between habitats should reveal that distinct ecological processes are maintaining biodiversity in these vegetal formations that have evolved in different ways.

METHODS

Study sites

The Nouragues Research Station is located in the Balenfois Mountains, southeast of Regina, French Guiana. Mainly dominated by hills, it is covered by an expanse of dense forest that has remained uninhabited for over two centuries. This site is particularly interesting because of its granitic inselberg, a tabular rocky outcropping rising abruptly from the surrounding rainforest to 430m above sea level (Bremer and Sander, 2000). The soil is acidic due to the two predominant geological substrates (i.e., Caribbean granite and metavolcanic rocks from the Paramaca series; Grimaldi and Riéra, 2001) and the vegetation is particularly heterogeneous.

Four distinct forested habitats were sampled along an elevation gradient of vegetation in March 2006 and October 2009 (liana forest: 120m; N4°04'58", W52°40'28"; N4°08'36", W52°64'47"; forested plateau: 140m; N4°05'20", W52°40'28"; N4°00'88", W52°67'72"; transition forest: 200m; N4°05'30", W52°40'38"; N4°09'32", W52°68'57"; inselberg forest: 430m; N4°05'47", W52°40'51"; N4°05'47", W52°40'51"). The liana forest is separated from the wide, forested plateau by a distance of 700m; the same is true for the distance between the transition forest and the summit of the inselberg, while only 400m separate the transition forest from the plateau.

The liana and the plateau forests, although different, have high tree species richness where Leguminosae and Lecythidaceae dominate (Larpin, 2001). The transition forest, composed of sparse patches of dense shrubs (no large trees) surrounded by sloping, rocky, bare ground, is much less diverse than the two previous sites. Finally, the top of the inselberg, characterized by a specific type of rock savannah vegetation adapted to drought, is dominated by evergreen shrubs belonging to the Clusiaceae, Myrtaceae and Bombacaceae families (Sarthou *et al.*, 2003). The layer of leaf litter, varying from one habitat to another depending on the altitude,

soil type and vegetation, is thick in the liana forest, on the plateau (typical primary rainforest) and at the top of the inselberg, whereas it is thin in the transition forest.

Experimental protocol

Because it is highly recommended for invertebrate inventories in forested habitats where litter abounds (Fisher, 1999; Delabie *et al.*, 2000), the Winkler method was used (see Bestelmeyer *et al.*, 2000). We collected ant workers from a series of 1m² leaf-litter samples that were weighed. As it is essential to combine several sampling methods to come as near as possible to an exhaustive inventory of the litter-dwelling ant fauna (Delabie *et al.*, 2000), pitfall traps were also used during the second field campaign (Bestelmeyer *et al.*, 2000).

The "Ants of the Leaf Litter" (ALL) Protocol (Agosti and Alonso, 2000), which suggests using a minimum of 20 sampling points separated by 10m intervals to collect at least 70% of the ant fauna at a given site, was applied. We selected 50 sampling points in all of the habitats, except for the inselberg forest (only 20) given its relatively small size. Thus, during the two field campaigns, two sets of 170 Winkler samples were collected and 170 pitfall traps were set, resulting in 510 leaf-litter samples.

All of the ant samples were preserved in 70% ethanol; for each sample at least one individual per morphospecies was kept in order to constitute a reference collection. We focused our analysis on the worker caste, since alates are difficult to identify. The ants were sorted to species or morphospecies was based on Bolton (1994). Voucher specimens were deposited in the *Laboratório de Mirmecologia*, Cocoa Research Centre CEPEC/CEPLAC (Ilhéus, Bahia, Brazil) and in the Royal Belgian Institute of Natural Sciences (RBINS; Brussels, Belgium).

Data analysis

Species × sample incidence (presence–absence) matrices

Four species × sample incidence matrices (one per habitat) were analyzed and compared between the four forests. Contrary to non-social insects whose individuals have an equal probability of being caught in the sampling universe, ants (like all social insects) are strongly aggregated in colonies so that, depending on the distance between the traps and the nests, colony size, and ant mobility, not all of the individuals have an equal chance of being caught; for this reason, presence/absence data are preferred over abundance data in the analyses (Longino, 2000). Thus, only species occurrences (i.e., the number of times that a given species was collected at a sampled site) were taken into account, and the percentages of species occurrences per sample (i.e., for a given species: total number of occurrences in a

given habitat/sample number × 100) were used as a proxy for ant abundance (Longino, 2000; Leponce *et al.*, 2004).

Sample-based rarefaction curves

The ESTIMATES 7.5 software (Colwell, 2005) was used to produce sample-based rarefaction curves with the Coleman method (*sensu* Gotelli and Colwell, 2001), representing the cumulated number of species according to species occurrences (Leponce *et al.*, 2004). These curves and their standard deviation (SD) were plotted (1) for all of the habitats combined (Sobs Mao Tau) with the Chao2 non-parametric estimator of species diversity, which provides a theoretical number of expected species, and (2) to estimate and standardize the comparison of ant sampling efficiency for each habitat. Because the order in which each sample is added influences the shape of these curves, the matrices of species occurrences were treated with 100 randomizations of the sampling order without replacement (Colwell *et al.*, 2004).

Alpha(α)-diversity of ant assemblages

Ant *α*-diversity in the four habitats was analyzed with Simpson's diversity (*1-D*) index and evenness ($E_{1/D}$) with a 95% confidence interval, and all possible inter-habitat comparisons were statistically tested using a bootstrapping procedure (with 1000 randomizations). The overdependence of the various published diversity indices on sampling effort is stated as one of the fundamental difficulties in all fields of biodiversity assessment (Warwick and Clarke, 2001). The Simpson's index is a notable exception making it one of the most meaningful and robust indices currently available (Magurran, 2004). Its evenness measurement is not sensitive to species richness, and is particularly useful when symmetry between rare and abundant species is required (Smith and Wilson, 1996).

Beta(β)-diversity and similarity of ant assemblages

The general turnover between the four ant assemblages was analyzed using two *β*-diversity indices based on presence/absence data: Whittaker's (β_W) and the second version of Harrison's (β_{H2}) indices. β_W is one of the simplest and best *β*-diversity indices; β_{H2} is an improvement over β_W, which was modified to be effective in analyzing pairwise differentiation between sites and is not sensitive to species richness trends (Magurran, 2004).

Moreover, one-way analyses of similarity comparisons (ANOSIM with 1000 permutations) were conducted to test the differences between the compositions of the ant assemblages

sampled. Then, their similarity was assessed using a cluster analysis based on Morisita's similarity index, which is not affected by sample number or species richness (Magurran, 1988), and recommended as a good means of measuring functional differences between ecosystems (Jost *et al.*, 2010). The resulting similarity matrix was analyzed through an Unweighted Pair-Group Method, Arithmetic average (UPGMA) cluster analysis.

Functional structure of ant assemblages

Information regarding diet and nesting habits were used to create two functional group matrices so as to reveal patterns of assemblage structure. Species were placed into functional groups based on recent classifications for Neotropical ants (Silvestre *et al.*, 2003; Brandão *et al.*, 2009; Silva and Brandão, 2010) and on personal observations of their foraging behavior, food choice, and nesting ecology. Species for which detailed dietary and nesting information are known were distributed widely within the functional group matrix; species belonging to rare, cryptic genera for which no information is available were placed into one functional group. The first matrix was based on four functional groups by only taking into account diet and foraging ecology (type A): 1) Obligate Coccidophile ants; 2) Fungus-growing ants; 3) Omnivorous ants; and 4) Predators. The second matrix, based on diet, foraging ecology and nesting strata, was composed of 10 groups (type B): 1) Obligate Coccidophile ants; 2) Leaf-cutter ants; 3) Cryptobiotic Attines; 4) Ground-dwelling Omnivorous ants; 5) Generalist Omnivorous ants; 6) Arboreal Omnivorous ants; 7) Ground-dwelling Generalist Predators; 8) Ground-dwelling Specialist Predators; 9) Raid-hunting Predators; and 10) Arboreal Predators (for details on the species in each functional group according to classification type, see Appendix S1 in Supporting Information). The B-type classification represented a further refinement to the functional ant organization than the A-type classification, and was thus more sensitive to revealing the influence of ecological variations in similar vegetal formations (*e.g.*, the liana and plateau forests) on ant assemblages. Two histograms based on the proportion of number of species and then species abundance (i.e., the number of occurrences per sample) per functional group were plotted for each habitat.

All of the rarefaction curves and histograms were plotted with SIGMAPLOT software (Brannan *et al.*, 2002) while PAST software (Hammer *et al.*, 2001) was used to compute the diversity indices, and conduct all of the statistical and cluster analyses.

RESULTS

Global specific richness, taxonomic structure and sampling efficiency

A total of 284 ant species belonging to 54 genera from nine subfamilies was collected. The most diversified subfamilies were the Myrmicinae, Ponerinae, Formicinae and Ectatomminae, and the most speciose genera were *Pheidole*, *Pachycondyla*, *Gnamptogenys*, *Camponotus*, *Solenopsis Strumigenys*, *Hypoponera* and *Pyramica* (Table 1). Thirteen monospecific genera and 125 "rare" species (84 uniques, 41 duplicates) were collected (see Appendix S2 in Supporting Information). The most abundant genera overall were *Pheidole*, *Crematogaster*, *Pyramica* and *Solenopsis*, and the most abundant species overall were *Pyramica denticulata* (occurring in 51% of all of the samples), followed by *Crematogaster carinata* and *Cre. limata* (28 and 25 %, respectively; see Appendix S2).

The global rarefaction curve and the curves corresponding to each habitat sampled steadily tended to decrease, coming near a horizontal asymptote corresponding to the total number of expected species. The Chao2 estimator thus confirmed that a representative part of the leaf-litter ant fauna was inventoried in the forests sampled at the Nouragues Research Station (Fig. 1; Table 1). The total number of occurrences was obviously lower in the inselberg forest than in the three other habitats (Table 1); the inferior sampling effort due to the limited size of this area might partly explain this result. Moreover, with an equal number of occurrences, the liana forest and the forested plateau ant diversities were comparable, while they were noticeably superior to that of the transition and inselberg forests (Fig. 1B).

α- / β-diversity and similarity of ant assemblages

The most species-/ genera-rich site was the liana forest (186 species; i.e., 66% of all of the species), and the poorest was the inselberg forest (88 species; 31%). The diversity of the two other habitats fell somewhere in between (plateau forest: 164 species; 58%; transition forest: 142 species; 50%; Table 1). We noted the ubiquitous presence of the Dolichoderinae, Ecitoninae, Ectatomminae, Formicinae, Myrmicinae, Ponerinae and Pseudomyrmecinae. The plateau forest was characterized by the highest number of Ponerine species compared to the other habitats, while the liana and transition forests sheltered the highest number of Myrmicinae and Formicinae, respectively. A total of approximately 90 generalist species (about 31% of the ubiquitous species plus those collected in three out of the four habitats) were recorded. Finally, we collected a notable proportion of habitat-specific species in the liana forest (47 species; 25%), the plateau forest (38 species; 23%), the transition forest (30 species; 21%) and the inselberg forest (12 species; 14%).

In all of the habitats, the value for Simpson's diversity index indicated a very high α-diversity: $1\text{-}D_{\text{(liana and plateau forests)}} = 0.98$ (0.97-0.984), $1\text{-}D_{\text{(transition and inselberg forests)}} = 0.97$ (0.97-0.98), that was quite equitably distributed: $E_{1\text{-}D\ \text{(liana forest)}} = 0.47$ (0.47-0.52), $E_{1\text{-}D\ \text{(plateau forest)}} = 0.50$ (0.50-0.56), $E_{1\text{-}D\ \text{(transition forest)}} = 0.51$ (0.51-0.58), $E_{1\text{-}D\ \text{(inselberg forest)}} = 0.61$ (0.59-0.68). Only the pairwise diversity comparisons between the inselberg forest and both the plateau and liana forests were significantly different (Table 2). The evenness values had an inverse order compared to species diversity: $E_{1\text{-}D\ \text{(inselberg forest)}} > E_{1\text{-}D\ \text{(transition forest)}} > E_{1\text{-}D\ \text{(plateau forest)}} > E_{1\text{-}D\ \text{(liana forest)}}$; Table 2). Indeed, the more the diversity increased, the less the species were equitably distributed; nevertheless, the differences were not significant.

The β-diversity values reflected a very poor species turnover between the four sampled ant faunas ($\beta_W = 0.96$; $\beta_{H2} = 0$). In addition, the UPGMA analysis showed that the ant faunas in the plateau and liana forests were the most similar (103 common species, 43% of the species shared; Fig. 2). This scanty species overlapping between all of the ant assemblages was then confirmed by the ANOSIM pairwise comparisons ($0.04 < R_{ANOSIM} < 0.17$; Table 3). Paradoxically, the average density of species by sample (8.5, 6.4, 5.2, 6.8 for the liana, plateau, transition and inselberg forests, respectively) was significantly different between habitats, except between that of the plateau and inselberg forests (Shapiro-Wilks: $0.83 < W < 0.98$, $9.67.10^{-7} < p < 0.01$; Kruskall-Wallis: $H = 47.85$, $p = 2.3.10^{-10}$; Table 4). In addition, the density peaked at 23 species per m² in the liana forest, appearing notably higher than in the other forests sampled (16 for the plateau and inselberg forests; 12 for the transition forest).

Functional structure of the ant assemblages

Type A-classification

Globally, the liana, plateau and inselberg forests had the same specific richness-based functional structure (about 40, 45 and 8-10 % for Predators, Omnivores, and Fungus-Growers, respectively), while that of the transition forest was notably characterized by the predominance of Omnivores over Predators, both in diversity (about 56 and 35%, respectively; Fig. 3) and abundance (about 66 and 31%, respectively; Fig. 4). However, when abundances were considered instead of proportion of species: (1) the equilibrium between Predators (P) and Omnivores (O) was disrupted in the liana, plateau and inselberg forests, with the Omnivores appearing proportionally more abundant, and (2) compared to that of the transition forest: $P_{\text{Liana, Plateau, Inselberg forests}}$ (40-44%) > $P_{\text{Transition forest}}$ (31%); $O_{\text{Transition forest}}$ (66%) > $O_{\text{Liana, Plateau, Inselberg forests}}$ (49-54%); Fig. 4). Fungus-Growing species were more abundant in the liana and inselberg forests than in the plateau and transition forests (about 6, 4

and 2.5%, respectively) although their proportion was similar everywhere; they were almost uniquely represented by Cryptobiotic Attine species (Fig. 4).

Type B-classification

Another general pattern appeared in all of the habitats: generalist species (i.e., Ground-dwelling Generalist Predators plus all of the omnivorous categories of species) were proportionally more diversified than specialist species, corresponding to about 50% of all of the species collected.

Moreover, the functional dissimilarity between the transition forest and the other habitats sampled was again highlighted, on the one hand, through the lower proportions of species richness and abundance of ground-dwelling species (the latter being compensated by the greater number of arboreal species predominantly occurring in the ground strata; Figs. 3 and 4). On the other hand, in all of the habitats except in the transition forest, Generalist Omnivores, the most abundant group, were as diversified as Generalist Predators, as well as Ground-dwelling Omnivores and Specialist Predators.

This classification also enabled us to point out functional dissimilarities between the liana forest and the other habitats sampled. First, in the plateau, transition and inselberg forests, Specialist and Generalist Predators were equally abundant, whereas, in the liana forest, Specialist Predators (as diversified as Ground-dwelling Omnivores) were as abundant as Generalist Omnivores, both representing 50% of the overall abundance, thus occupying a predominant, functional position in the community. Secondly, Ground-dwelling Omnivores in the liana forest were proportionally less abundant than in the other habitats sampled (Fig.4).

Among the most frequent species from each habitat, only a small fraction was responsible for the greater part of the overall abundance in each functional group; *e.g.*, four species were particularly abundant (number of occurrences > 50): *Bas. betschi* and *Pyr. denticulata* among the Specialist Predators, and *Cre. carinata* and *Cre. limata* among the Arboreal Omnivores (see Appendix S2).

DISCUSSION

Sampling efficiency

Our survey recorded a great diversity of litter-dwelling ants at the Nouragues Research Station where, based on the shape of the rarefaction curves, most of the species were actually collected. However, although it was demonstrated that a 50m² litter sample enables reliable estimations to be made with the Chao2 estimator (Leponce *et al.*, 2004), some surveys

conducted in Neotropical areas have shown that estimated richness using Chao2 seems to be affected by the number of uniques in communities with a high incidence of "rare" species (Silva *et al.*, 2007; Silvestre *et al.*, 2011). Nevertheless, there are two other pieces of evidence to demonstrate the quality of our sampling: (1) of the 13 monospecific genera collected, six concerned species that are very hard to sample (*e.g.*, army ants, cryptic and "rare" species such as *Cryptomyrmex* or very agile and mobile species like *Gigantiops*), three were cryptic hyperspecialized predators (*Amblyopone*, *Cerapachys* and *Thaumatomyrmex*), plus two arboreal (*Allomerus* and *Nesomyrmex*) and tramp species (*Technomyrmex* and *Tetramorium*); and (2) of the 125 "rare" species collected, 42 (i.e., 33% of all of the species) were characterized by a low probability of capture based on the extraction methods used due to their specific nesting habits; these included arboreal, raid-hunter, leaf-cutter, exclusive hypogaeous and subterranean, and tramp species. However, the actual diversity of leaf-litter ants is higher than the 284 species recorded, demonstrating that there is still much to learn about the Guianese ant communities.

It appears that the diversity of the litter-dwelling ants recorded in this study is one of the highest noted among the most comprehensive surveys conducted in Amazonia, including in Brazil (Oliveira *et al.*, 2009; Vasconcelos *et al.*, 2009), Ecuador (Ryder Wilkie *et al.*, 2010), Peru (Verhaagh, 1990), and the Guiana shield countries (Lapolla *et al.*, 2007). Note that this high ant diversity was recorded by sampling only leaf-litter ant fauna over a limited area (< 1 ha), while other studies were conducted over larger areas and dealt with the entire ant fauna (i.e., hypogaeic, epigaeic and arboreal species).

Overall specific richness and global taxonomic structure

As expected, the hyperdiverse genus *Pheidole* was the most speciose and abundant ground-dwelling genus in our study (Wilson, 2003; Lapolla *et al.*, 2007). Yet, the average density of the Neotropical *Pheidole* and *Solenopsis* species that we found (1 and 0.6 species/m², respectively) appeared far lower than previously recorded (5.45 and 3.14 species/m², respectively; Ward, 2000). The species number for these genera, plus *e.g.*, *Hypoponera* and *Nylanderia*, was probably underestimated because they are very difficult to identify despite the existence of a recent revision; *e.g.*, for *Pheidole* (Wilson, 2003; Longino, 2009). Also, some species certainly belong to cryptic species complexes, increasing the risk of underestimating the true species number (Ward, 2000).

Moreover, some species considered until now as endemic to one country or one region, sometimes very far from French Guiana, were unexpectedly recorded: *e.g.*, *Cyphomyrmex*

flavidus and *Pheidole tysoni* from North and Central America, respectively; *Pachycondyla pergandei* and *Rogeria tonduzi* from Central America; *Camponotus punctatus andigenus*, *Hylomyrma praepotens*, *Phe. rubiceps*, and *Trachymyrmex mandibularis* from northwestern Amazonia (Bolivia, Colombia, Peru and Venezuela), whereas the other species we collected were recorded as being endemic to adjacent countries: *e.g.*, *Acropyga romeo* in Guyana; and *Leptogenys vogeli*, *Phe. deima*, *Phe. gigas*, *Stegomyrmex olindae* and *Tra. farinosus* in Brazil (Bolton *et al.*, 2006).

We also detected three tramp species, namely *Tapinoma melanocephalum*, *Tetramorium bicarinatum* (for the first time in French Guiana) and *Technomyrmex vitiensis* (for the first time anywhere in Central and South America; Delabie *et al.*, 2011). The presence of *Tec. vitiensis* in this pristine forest is particularly worrying because this pest ant has a high invasive potential, and so could threaten the diversity and structure of the native ground-dwelling entomofauna, especially ants (Sanders *et al.*, 2003).

Diversity, taxonomic and functional structure of sampled ant faunas

Although the Nouragues ant sample is not exhaustive, the degree of representativeness of the ALL protocol transects enabled reliable inter-habitat comparisons to be made (Leponce *et al.*, 2004). Although undersampling might be partly responsible for the lower diversity and density in the inselberg forest, the average densities per habitat between the plateau and inselberg forests were the only sites that did not significantly differ. In addition, as their functional structure was also very similar, this might suggest that the litter layer in the inselberg forest may offer microclimatic conditions similar to that of the mature forest, enabling it to shelter a smaller but similar ant assemblage.

All of the sampled ant assemblages, composed of a few numerically dominant ants and of numerous "rare" species, were rather heterogeneously distributed. This might be explained by the slight clumping in the spatial distribution of uncommon, Neotropical species – indicative of their small colony size – associated with the generally clumped distribution of the most frequent species (Leponce *et al.*, 2004). In spite of this and the significant decrease in diversity from the liana to the inselberg forest, perhaps based on a microtopographic altitudinal gradient, species overlap was almost nonexistent, indicating the presence of a homogeneous, highly diversified pool of species at the Nouragues Research Station. Although little is known about the mechanisms that generate and maintain such high levels of diversity in ground-dwelling ant faunas in pristine rainforests (Silva and Brandão, 2010; Mezger and Pfeiffer, 2011), abiotic factors, including a microclimate, soil type, flooding and the structural

complexity of the vegetal formations, are known to influence ant community patterns in the Neotropics (Kaspari, 1993; Bihn *et al.*, 2008; Vasconcelos *et al.*, 2009). Furthermore, tropical leaf-litter ant communities seem to be structured by local resource availability (Theunis *et al.*, 2005), and greatly depend on the nature and quantity of the leaf-litter (McGlynn, 2006). Variations in assemblage composition might be explained by the features thought to shape ant communities; namely, litter biomass, soil moisture and stoichiometry or heterogeneous nutrient distribution (McGlynn *et al.*, 2009; Baccaro *et al.*, 2010).

If the inselberg forest is not taken into consideration, the ant fauna on the forested plateau represented the referential assemblage for a mature, preserved forest while that of the liana and transition forests were at the opposite extremes in terms of diversity, density and functional structure. The assemblage in the transition forest was poorer than in the others, thus corroborating numerous studies showing that less vegetal structure may lead to lower ant diversity (Bestelmeyer and Wiens, 1996). Its functional structure, conversely to the other ant faunas, surprisingly reflected a rather "typical" trophic pyramid for tropical ant communities (Tobin, 1994), where omnivores (mostly represented by formicine ants) clearly specifically and numerically dominated specialized predator species. In addition, due to the presence of small trees, the proportion of arboreal ant species was higher than in the three other assemblages, making this ant fauna perhaps close to that of open environments (*e.g.*, savannas). This naturally-disturbed habitat, where microclimatic conditions (i.e., a dry, thin and sparse litter layer, high temperatures and vast sun exposure during the daytime) are stressful for litter-dwelling arthropods, favors ecologically generalist species adapted to open areas whose foragers are active both day and night; they are often characterized by populous polygynous and/or polycalic colonies (Hölldobler and Wilson, 1990).

The case of the liana forest is particularly interesting due to its exceptional diversity (Groc *et al.*, 2009), but also to the unexpectedly high concentration of habitat-specific species and their density (*e.g.*, the dominance of specialized predators, as abundant as generalist omnivores, and the highest abundance of cryptobiotic attines noted in this study). This habitat, likely disturbed and altered a long time ago by both substantial paleofires and Amerindian tribes (Tardy, 1998), is still subject to continual, intermittent disturbances of varying intensities (Balée and Campbell, 1990). Lianas can cause treefall gaps and vegetal material to fall onto the ground (Phillips, 2005) thus maintaining a constant level of disturbance to the habitat, which is thought to produce high habitat heterogeneity (Levin and Paine, 1974), and, as a consequence, greater niche diversification (i.e., a thick layer of leaf litter) and specialization (i.e., the number of twigs and logs and quantity of dead and rotten wood lying

on ground). This thus favors more nest and foraging sites for ground-dwelling, specialized cryptic (*e.g.*, the lower attini) and strictly predaceous species (*e.g.*, *Pyramica* and *Strumigenys*) (Armbrecht *et al.*, 2004). Our results thus show that habitat specialization in the Neotropical rainforest is an important mechanism governing the organization and maintenance of the exceptional diversity in leaf-litter ant communities (Vasconcelos and Vilhena, 2006).

To conclude, the "reference point" status of the Nouragues Research Station seems justified for studies in French Guiana due to its isolation (access by helicopter or by boat on the Arrataye River, and then 5 hours on foot) (Bongers *et al.*, 2001) given the high ant species density and richness in addition to the uncommon functional structure of the habitat-specific ant assemblages. This functional dissimilarity may attest to different evolutionary histories resulting from particular colonization processes instead of a single, common one (Silvestre *et al.*, 2011). These peculiarities point out the great influence of environmental heterogeneity, which, through variable abiotic conditions, contributes to maintaining an exceptionally rich ant biodiversity in these Neotropical habitats. Finally, our survey represents a baseline study for future research on the comparative analysis of Neotropical ant diversity and abundance and possibly other terrestrial invertebrates. It also permits us to establish a foundation for continuing research in the Guianese Amazon, a region that has a high global conservation significance.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Functional group designation of ants at the Nouragues Research Station.

Appendix S2 Species collected from each habitat at the Nouragues Research Station according to their taxonomic classification. The first column indicates the species recorded for the first time in French Guiana in March 2006 (nsg; see Groc *et al.*, 2009) and in October 2009 (nsg).

FIGURE LEGENDS

Figure 1 Occurrence-based rarefaction curves representing the total cumulated number of observed (Sobs) and estimated (Chao2) species depending on the number of occurrences (± SD) for (A) all of the sampled environments pooled (N = 510 samples), and (B) for each habitat (N = 150 samples from the liana, plateau and transition forests; N = 60 samples from the inselberg forest).

Figure 2 Dendrogram of the similarities (Morisita's index, UPGMA cluster analysis) between the leaf-litter ant faunas in the four habitats sampled.

Figure 3 Proportion of ant species per functional group according to the A- and B-type classifications for each habitat sampled.

Figure 4 Abundance of ant species per functional group according to the A- and B-type classifications for each habitat sampled.

Figure 1

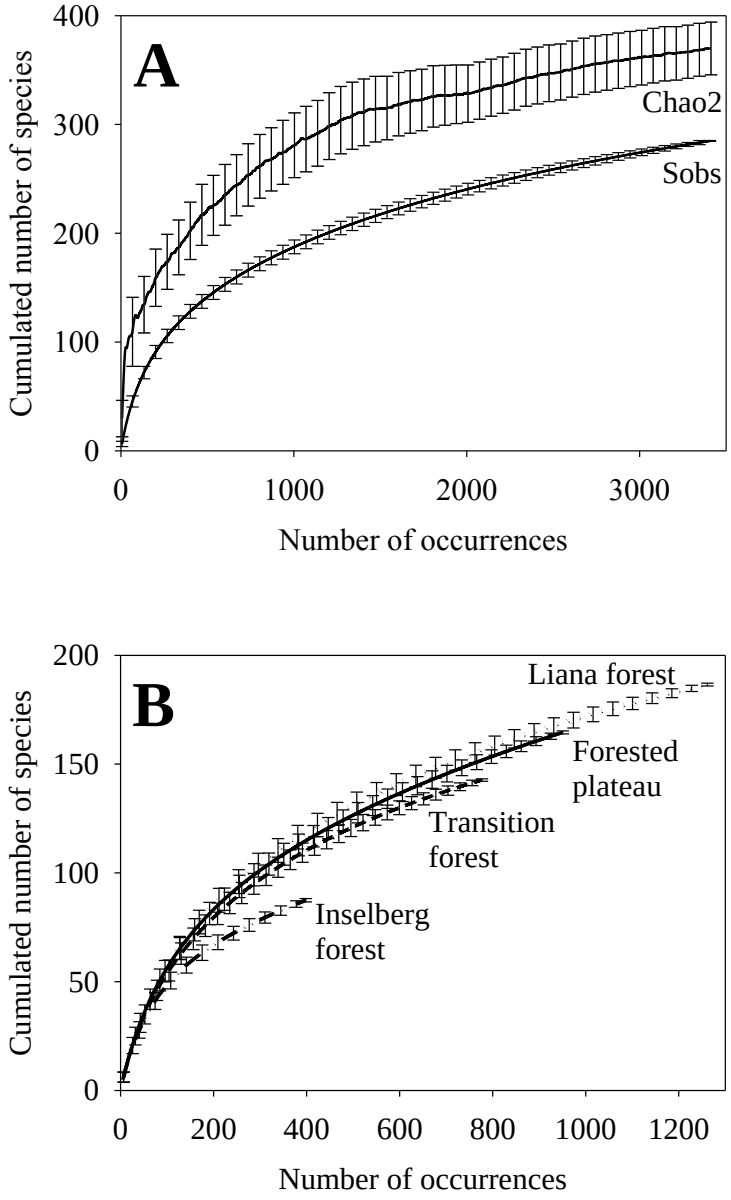
A
Chao2
Sobs
Cumulated number of species
Number of occurrences
0
100
200
300
400
0
1000
2000
3000
B
Liana forest
Forested plateau
Transition forest
Inselberg forest
Cumulated number of species
Number of occurrences
0
50
100
150
200
0
200
400
600
800
1000
1200

Figure 2

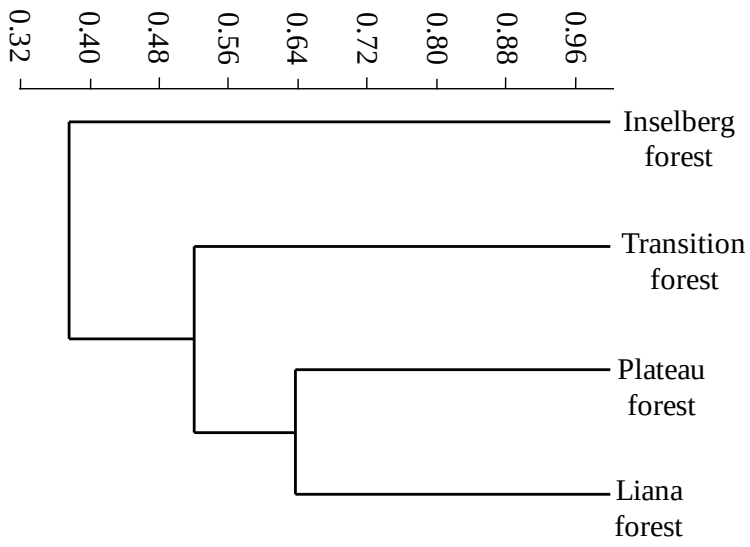
0.32
0.40
0.48
0.56
0.64
0.72
0.80
0.88
0.96
Inselberg forest
Transition forest
Plateau forest
Liana forest

Figure 3

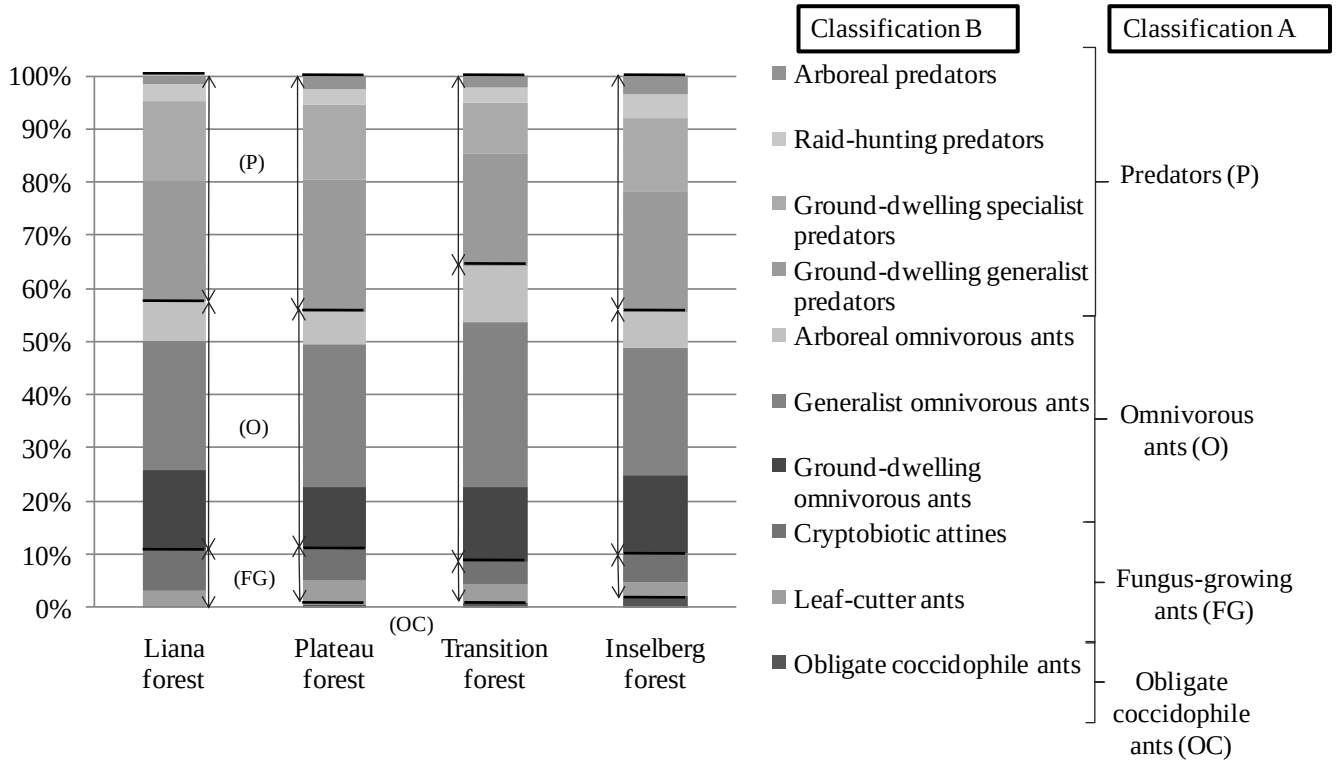
Classification B
Classification A
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
(P)
(O)
(FG)
(OC)
Liana forest
Plateau forest
Transition forest
Inselberg forest
Arboreal predators
Raid-hunting predators
Ground-dwelling specialist predators
Ground-dwelling generalist predators
Arboreal omnivorous ants
Generalist omnivorous ants
Ground-dwelling omnivorous ants
Cryptobiotic attines
Leaf-cutter ants
Obligate coccidophile ants
Predators (P)
Omnivorous ants (O)
Fungus-growing ants (FG)
Obligate coccidophile ants (OC)

Figure 4

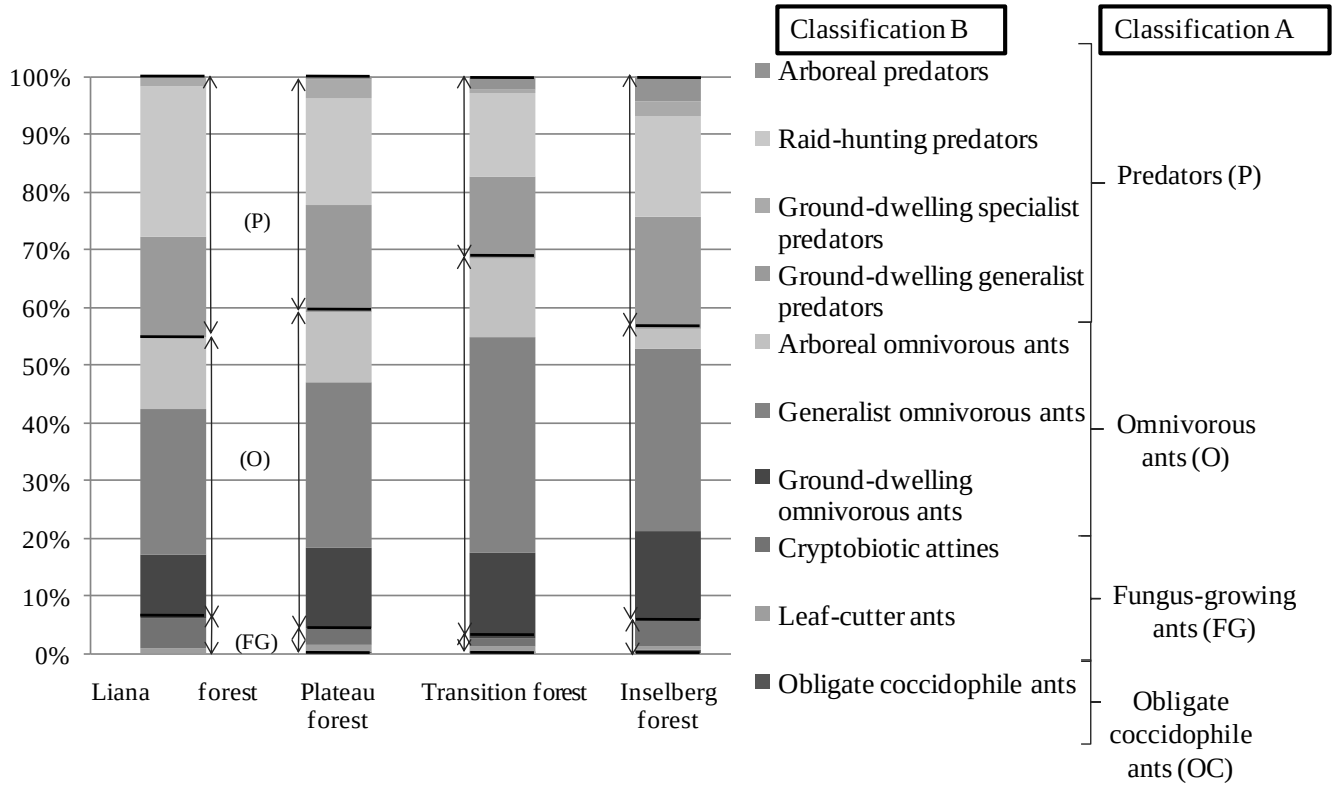
Classification B
Classification A
Arboreal predators
Raid-hunting predators
Ground-dwelling specialist predators
Ground-dwelling generalist predators
Arboreal omnivorous ants
Generalist omnivorous ants
Ground-dwelling omnivorous ants
Cryptobiotic attines
Leaf-cutter ants
Obligate coccidophile ants
Predators (P)
Omnivorous ants (O)
Fungus-growing ants (FG)
Obligate coccidophile ants (OC)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
(P)
(O)
(FG)
Liana forest
Plateau forest
Transition forest
Inselberg forest

Table 1 Number of samples, taxonomic characteristics and Chao2 estimations for the ant assemblages at the Nouragues Research Station and for each forest sampled.

	Liana forest	Forested plateau	Transition forest	Inselberg forest	Nouragues Research Station
Number of samples (Winklers-Pitfall traps)	150 (100-50)	150 (100-50)	150 (100-50)	60 (40-20)	510 (340-170)
Number of occurrences	1270	957	782	405	3413
Number of:					
1) observed species (Sobs)	186	164	142	88	284
2) genera	47	39	36	32	54
Chao2 estimations:					
1) number of species	255.87	241.52	186.27	143.17	369.83
2) % of species collected	73	68	76	62	77
Most speciose subfamilies (number of species/genera)					
Myrmicinae	113/25	92/22	78/15	49/16	164/29
Ponerinae	32/6	37/5	22/5	17/5	49/6
Formicinae	12/4	13/4	16/5	8/4	27/5
Ectatomminae	18/3	12/3	23/3	7/2	20/3
Most speciose genera (number of species)					
Camponotus	5	7	9	2	14
Gnamptogenys	15	8	6	5	16
Hypoponera	9	10	7	3	12
Pachycondyla	11	14	7	8	17
Pheidole	25	25	21	10	37
Pyramica	8	6	4	3	9
Solenopsis	11	7	10	3	14
Strumigenys	6	6	4	4	13

Table 2 *P*-values associated with the pairwise comparisons of Simpson's diversity index (*1-D*) and evenness (E_{1-D}) computed between ant assemblages for each habitat sampled (significant *P*-values are in bold).

Simpson's diversity and equitability (*1-D*) ; (E_{1-D})	Liana forest	Forested plateau	Transition forest	Inselberg forest
Liana forest	×			
Plateau forest	0.99 ; 0.34	×		
Transition forest	0.07 ; 0.56	0.09 ; 0.87	×	
Inselberg forest	0.01 ; 0.07	0.02 ; 0.17	0.24 ; 0.11	×

Table 3 Results of the one-wayANOSIM pairwise comparisons between the ant community composition for each habitat sampled (*R* values for which the *P*-value is significant – $0.001 < p < 0.005$ – are in bold).

	Liana forest	Forested Plateau	Transition forest	Inselberg Forest
Liana forest	×			
Plateau forest	0.04	×		
Transition forest	0.07	0.10	×	
Inselberg forest	0.09	0.17	0.07	×

Table 4 *P*-values associated with the pairwise comparisons of the average density of species between habitats using the Mann-Whitney test (*U* values for which the *P*-value is significant – $0.001 < p < 0.01$ – are in bold).

	Liana forest	Forested plateau	Transition forest	Inselberg Forest
Liana forest	×			
Plateau forest	8080	×		
Transition forest	6266	9457	×	
Inselberg forest	3499	3933	3146	×

SUPPORTING INFORMATION

Appendix S1

Classification A	Classification B			
Predators (P)	Arboreal predators	Raid-hunting predators	Ground-dwelling specialist predators	Ground-dwelling generalist predators
	Gnamptogenys[1]	*Eciton*	*Acanthognathus*	*Anochetus*
	Odontomachus[2]	*Labidus*	*Amblyopone*	*Gigantiops*
	Pachycondyla[3]	*Leptogenys*	*Basiceros*	*Gnamptogenys*[5]
	Pseudomyrmex	*Neivamyrmex*	*Cryptomyrmex*	*Hylomyrma*
		Pachycondyla[4]	*Discothyrea*	*Hypoponera*
			Prionopelta	*Megalomyrmex*[6]
			Pyramica	*Odontomachus*[7]
			Stegomyrmex	*Pachycondyla*[8]
			Strumigenys	
			Thaumatomyrmex	
			Typhlomyrmex	
Omnivores (O)	Arboreal omnivores	Generalist omnivores	Ground-dwelling omnivores	
	Allomerus	*Brachymyrmex*	*Carebara*	
	Azteca	*Camponotus*[12]	*Carebarella*	

	Camponotus[9]	*Crematogaster*[13]	*Gnamptogenys*[15]
	Cephalotes	*Dolichoderus*[14]	*Lachnomyrmex*
	Crematogaster[10]	*Ectatomma*	*Megalomyrmex*[16]
	Dolichoderus[11]	*Nylanderia*	*Ochetomyrmex*
	Nesomyrmex	*Pheidole*	*Rogeria*
	Procryptocerus	*Solenopsis*[18]	*Solenopsis*[21]
	Tapinoma[17]	*Tapinoma*[19]	*Wasmannia*[22]
		Technomyrmex	
		Tetramorium	
		Wasmannia[20]	
Fungus-growers (FG)	Cryptobiotic attines	Leaf-cutters	
	Apterostigma	*Acromyrmex*	
	Cyphomyrmex	*Atta*	
	Mycocepurus	*Trachymyrmex*	
	Myrmicocrypta		
	Sericomyrmex		
Obligate Coccidophiles (OC)	Obligate coccidophiles		
	Acropyga		

[1] *Gnamptogenys annulata, G. porcata* ; [2] *Odontomachus hastatus*; [3] *Pachycondyla crenata, Pac. unidentata*; [4] *Pacycondyla commutata, Pac. crassinoda, Pac. laevigata*; [5] *Gnamptogenys acuminata, Gna. continua, Gna. enodis, Gna. horni, Gna. mecotyle, Gna. minuta, Gna.mordax, Gna. relicta, Gna. striatula, Gna. tortuolosa* ; [6] *Megalomyrmex silvestrii* ; [7] *Odontomachus biumbonatus, Odo. caelatus, Odo. chelifer, Odo. haematodus, Odo. meinerti, Odo. scalptus* ; [8] *Pachycondyla arhuaca, Pac. constricta, Pac. cooki, Pac. harpax, Pac. holmgreni, Pac. pergandei, Pac. procidua, Pac. stigma, Pac. striata, Pac. verenae, Pac.* cf *apicalis* morphosp. II (sensu Delabie *et al.*, 2008[*]), *Pac.* cf *apicalis* morphosp. IV (sensu Delabie *et al.*, 2008) ; [9] *Camponotus atriceps, Cam. cacicus, Cam. femoratus, Cam. novogranadensis, Cam.* sp. cf *atriceps*; [10] *Crematogaster brasiliensis, Cre. limata, Cre. longispina, Cre. tenuicula*; [11] *Dolichoderus attelaboides, Dol. bidens, Dol. bispinosus, Dol. lutosus, Dol.* sp. cf *luederwaldti* ; [12] *Camponotus fastigatus, Cam. lespesii, Cam. melanoticus, Cam. punctulatus andigenus, Cam. rapax, Cam. renggeri, Cam.* (*Myrmaphaenus*) sp.4, *Cam.* sp.7 *paradoxus* complex, *Cam.* sp.23 *ager* complex; [13] *Crematogaster distans, Cre. flavosensitiva, Cre. nigropilosa, Cre. sotobosque, Cre. wardi*; [14] *Dolichoderus imitator*; [15] *Gnamptogenys haenschei, Gna. mina, Gna. pleurodon, Gna. sulcata* ;

[16] *Megalomyrmex incisus, Meg.* sp.8 *pusillus* group; [17] *Tapinoma melanocephalum*; [18] *Solenopsis virulens*; [19] *Tapinoma* sp.2; [20] *Wasmannia auropunctata*; [21] *Solenopsis pollux, Sol.* sp. *pygmaea* group, *Sol.* sp.5, 6, 7, 8, 10, 11, 12, 13, 15, 16 and 18 ; [22] *Wasmannia scrobifera*

[*] Delabie, J.H.C., Mariano, C.S.F., Mendes, L.F., Pompolo, S.G. and Fresneau, D. (2008) Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no Género *Pachycondyla* na região neotropical: o caso do complexo *apicalis*. *Insetos Sociais: da Biologiá a Aplicacão Vicosa, Minas Gerais* (ed. by E.F. Vilela, I.A. Santos, J.H. Schoereder, J.E. Serrão, L.A.O. Campos and J. Lino Neto), pp. 196-222. Editora da Universidade Federal de Viçosa, Viçosa.

Appendix S2

		Liana forest	Plateau forest	Transition forest	Inselberg forest
AMBLYOPONINAE Forel					
	Amblyoponini Forel				
nsg	*Amblyopone lurilabes* Lattke	1	0	3	0
	Prionopelta sp.1	1	0	0	0
	Prionopelta sp.2	0	0	0	1
	Prionopelta sp.3	0	0	0	1
DOLICHODERINAE Forel					
	Dolichoderini Forel				
	Dolichoderus attelaboides (Fabricius)	0	0	3	0
	Dolichoderus bidens (Linnaeus)	0	0	1	0
	Dolichoderus bispinosus (Olivier)	1	2	5	0
nsg	*Dolichoderus imitator* Emery	2	1	1	2
	Dolichoderus lutosus (Smith)	0	1	1	0
	Dolichoderus sp. cf *luederwaldti*	0	1	0	0
	Tapinoma melanocephalum (Fabricius)	1	0	0	0
	Leptomyrmecini Emery				
	Azteca instabilis (Smith)	0	0	4	1
	Azteca sp.1	0	4	0	0
	Azteca sp.2	0	0	2	0
	Azteca sp.3	1	0	2	0
	Tapinomini Emery				
	Tapinoma sp.2	0	0	1	0
nsg	*Technomyrmex vitiensis* Mann	1	0	1	0
ECITONINAE Forel					
	Ecitonini Forel				
	Eciton drepanophorum Smith	0	2	0	0
	Labidus coecus (Latreille)	6	5	2	5
	Neivamyrmex iridescens Borgmeier	0	0	0	1
ECTATOMMINAE Emery					
	Ectatommini Emery				

	Ectatomma edentatum Roger	14	14	11	1
	Ectatomma lugens Emery	24	30	12	19
	Ectatomma tuberculatum (Olivier)	0	1	3	0
	Gnamptogenys acuminata (Emery)	3	0	3	0
	Gnamptogenys annulata (Mayr)	1	0	0	0
nsg	*Gnamptogenys continua* (Mayr)	3	2	1	0
nsg	*Gnamptogenys enodis* Lattke	4	0	0	0
nsg	*Gnamptogenys haenschei* (Emery)	2	2	0	0
	Gnamptogenys horni (Santschi)	12	6	4	2
nsg	*Gnamptogenys mecotyle* Brown	1	0	0	0
nsg	*Gnamptogenys mina* (Brown)	1	0	0	0
	Gnamptogenys minuta (Emery)	3	0	0	1
	Gnamptogenys mordax Smith	1	1	0	0
nsg	*Gnamptogenys pleurodon* (Emery)	2	0	0	0
nsg	*Gnamptogenys porcata* (Emery)	1	1	2	1
nsg	*Gnamptogenys relicta* (Mann)	1	4	5	1
	Gnamptogenys striatula Mayr	1	1	0	0
	Gnamptogenys sulcata (Smith)	0	0	2	0
	Gnamptogenys tortuolosa (Smith)	1	4	0	3
	Typhlomyrmecini Emery				
	Typhlomyrmex sp. nov.4 (*sensu* Lacau, 2005**)	3	3	3	0
FORMICINAE Latreille					
	Camponotini Forel				
	Camponotus atriceps (Smith)	0	1	0	0
nsg	*Camponotus cacicus* Emery	1	0	0	0
	Camponotus fastigatus Roger	0	0	4	0
	Camponotus femoratus (Fabricius)	22	29	2	0
nsg	*Camponotus lespesii* Forel	0	1	0	0
nsg	*Camponotus melanoticus* Emery	0	1	1	0
	Camponotus novogranadensis Mayr	0	1	0	0
nsg	*Camponotus punctulatus andigenus* Emery	0	0	1	0

	Camponotus rapax (Fabricius)	10	1	5	5
	Camponotus renggeri Emery	1	3	3	0
	Camponotus sp. cf *atriceps*	0	0	1	1
	Camponotus (*Myrmaphaenus*) sp.4	0	0	1	0
	Camponotus sp.7 *paradoxus* comp.	0	0	1	0
	Camponotus sp.23 *ager* comp.	1	0	0	0
	Gigantiopini Ashmead				
	Gigantiops destructor (Fabricius)	2	0	9	0
	Lasiini Ashmead				
nsg	*Acropyga decedens* (Mayr)	0	3	0	0
nsg	*Acropyga fuhrmanni* (Forel)	0	0	0	1
nsg	*Acropyga romeo* LaPolla	0	0	1	0
nsg	*Acropyga smithii* Forel	0	0	0	2
	Plagiolepidini Forel				
	Brachymyrmex heeri Forel	0	0	7	6
	Brachymyrmex sp.2 cf *heeri*	2	2	8	7
	Nylanderia fulva (Mayr)	10	12	8	14
nsg	*Nylanderia guatemalensis*(Forel)	2	1	0	0
	Nylanderia sp.2 cf *guatemalensis*	2	1	0	0
	Nylanderia sp.3	0	0	2	0
	Nylanderia sp.4	3	0	0	0
	Nylanderia sp.5	10	13	23	10
MYRMICINAE Lepeletier					
	Adelomyrmecini Fernández				
nsg	*Cryptomyrmex longinodus* (Fernández and Brandão)	4	1	0	0
	Attini Smith				
	Acromyrmex octospinosus (Reich)	1	0	0	0
nsg	*Acromyrmex subterraneus* (Forel)	3	0	0	0
	Apterostigma urichii Forel	0	0	0	1
	Apterostigma sp.2 *pilosum* comp.	4	4	0	0
	Apterostigma sp.3 *pilosum* comp.	1	0	0	0
	Apterostigma sp.6	1	0	0	0

	Atta cephalotes (Linnaeus)	0	1	0	0
	Cyphomyrmex bigibbosus Emery	0	1	0	0
	Cyphomyrmex faunulus Wheeler	4	0	1	0
nsg	*Cyphomyrmex flavidus* Pergande	10	0	3	1
	Cyphomyrmex laevigatus Weber	8	5	2	0
nsg	*Cyphomyrmex peltatus* Kempf	18	10	1	7
nsg	*Cyphomyrmex salvini* Forel	4	0	0	2
	Cyphomyrmex transversus Emery	6	1	2	0
	Mycocepurus smithii (Forel)	3	0	0	0
nsg	*Mycocepurus tardus* Weber	0	2	0	0
	Myrmicocrypta sp.6	1	0	0	0
	Myrmicocrypta sp.7	2	1	0	0
	Myrmicocrypta sp.8	2	0	0	0
	Sericomyrmex sp.1	0	1	1	0
	Sericomyrmex sp.2	2	0	0	9
	Sericomyrmex sp.3	0	2	0	0
nsg	*Trachymyrmex compactus*	0	1	2	0
	Mayhé-Nunes and Brandão				
	Trachymyrmex cornetzi (Forel)	3	0	4	1
nsg	*Trachymyrmex farinosus* (Emery)	3	2	0	0
	Trachymyrmex ixyodus	0	1	0	0
	Mayhé-Nunes and Brandão				
nsg	*Trachymyrmex mandibularis* Weber	2	4	2	1
nsg	*Trachymyrmex opulentus* (Mann)	0	1	0	0
	Trachymyrmex relictus Borgmeier	0	0	1	0
	Trachymyrmex sp.7	0	1	0	0
	Trachymyrmex sp.8	0	1	0	0
	Trachymyrmex sp.9	1	0	1	0
	Basicerotini Brown				
	Basiceros balzani (Emery)	55	7	6	8
	Basiceros betschi (Perrault)	31	13	14	2
	Basiceros emeryi (Forel)	1	0	0	0
	Basiceros iheringi (Emery)	0	0	0	1

	Basiceros sp. near *iheringi*	1	1	0	0
	Basiceros sp.1	1	3	0	0
	Basiceros sp.2	1	0	0	0
	Blepharidattini Wheeler and Wheeler				
	Wasmannia auropunctata (Roger)	10	15	25	4
nsg	*Wasmannia scrobifera* Kempf	0	6	0	5
	Cephalotini Smith				
	Cephalotes atratus (Linnaeus)	0	0	2	0
nsg	*Cephalotes maculatus* (Smith)	1	0	0	0
	Cephalotes sp.10 *angustus* clade	0	0	1	0
nsg	*Procryptocerus hylaeus* Kempf	1	0	0	0
	Procryptocerus sp.1	1	0	0	0
	Crematogastrini Forel				
nsg	*Crematogaster brasiliensis* Mayr	2	0	0	0
	Crematogaster carinata Mayr	62	51	24	5
nsg	*Crematogaster distans* Mayr	1	0	0	0
	Crematogaster flavosensitiva Longino	2	6	6	4
	Crematogaster limata Smith	56	26	41	4
	Crematogaster longispina Emery	6	0	17	1
nsg	*Crematogaster nigropilosa* Mayr	3	0	4	0
nsg	*Crematogaster sotobosque* Longino	8	10	2	0
	Crematogaster tenuicula Forel	3	1	1	0
nsg	*Crematogaster wardi* Longino	13	3	22	1
	Dacetini Forel				
nsg	*Acanthognathus brevicornis* Smith	1	0	0	0
nsg	*Acanthognathus ocellatus* Mayr	0	0	1	0
nsg	*Pyramica alberti* (Forel)	3	0	0	0
nsg	*Pyramica appretiata* (Borgmeier)	0	1	0	0

	Pyramica auctidens Bolton	41	20	0	1
nsg	*Pyramica beebei* (Wheeler)	3	2	1	0
nsg	*Pyramica crassicornis* Mayr	4	0	0	0
nsg	*Pyramica deinomastax* Bolton	2	0	1	0
	Pyramica denticulata Mayr	86	69	67	37
nsg	*Pyramica hadrodens* Bolton	1	1	0	0
	Pyramica subedentata (Mayr)	6	7	2	1
nsg	*Strumigenys cosmostela* Kempf	2	0	0	0
nsg	*Strumigenys diabola* Bolton	5	0	0	0
nsg	*Strumigenys dyseides* Bolton	16	0	0	4
nsg	*Strumigenys elongata* Roger	31	19	8	5
nsg	*Strumigneys hyphata* (Brown)	0	0	2	0
nsg	*Strumigenys lanuginosa* Wheeler	0	1	0	0
nsg	*Strumigenys metopia* (Brown)	0	0	0	5
nsg	*Strumigenys perparva* Brown	3	9	3	6
nsg	*Strumigenys saliens* Mayr	1	0	0	0
nsg	*Strumigenys trudifera* Kempf and Brown	13	0	0	0
	Strumigenys sp.1 near *longinoi*	0	1	0	0
	Strumigenys sp.2 *thaxteri* group	0	1	0	0
	Strumigenys sp.3 near *substricta* group	0	0	1	0
	Formicoxenini Forel				
nsg	*Nesomyrmex tristani* (Emery)	0	0	0	2
	Ochetomyrmex neopolitus Fernández	3	5	5	2
	Ochetomyrmex semipolitus Mayr	7	32	19	1
	Myrmicini Lepeletier				
nsg	*Hylomyrma balzani* (Emery)	23	13	6	0
nsg	*Hylomyrma immanis* Kempf	2	0	4	1
nsg	*Hylomyrma praepotens* Kempf	0	0	1	0
nsg	*Hylomyrma reginae* Kutter	1	0	3	6
nsg	*Hylomyrma sagax* Kempf	1	2	0	0
	Hylomyrma sp.6	0	1	1	0
	Pheidolini Emery				
nsg	*Pheidole alienata* Borgmeier	7	0	3	0

nsg	*Pheidole allarmata* Wilson	1	9	1	1
	Pheidole astur Wilson	2	10	0	0
nsg	*Pheidole bruesi* Wheeler	0	1	2	0
nsg	*Pheidole carinata* Wilson	4	0	0	0
nsg	*Pheidole deima* Wilson	0	1	0	0
	Pheidole dolon Wilson	2	0	1	0
nsg	*Pheidole gigas* Wilson	0	0	1	0
	Pheidole midas Wilson	22	4	7	4
nsg	*Pheidole pedana* Wilson	32	13	0	3
	Pheidole radoszkowskii Mayr	0	1	0	0
nsg	*Pheidole rubiceps* Wilson	0	0	1	0
nsg	*Pheidole scolioceps* Wilson	2	1	22	8
nsg	*Pheidole synarmata* Wilson	6	2	2	2
nsg	*Pheidole terribilis* Wilson	0	2	11	0
nsg	*Pheidole transversostriata* Mayr	20	8	7	0
nsg	*Pheidole tysoni* Forel	14	15	4	9
nsg	*Pheidole wallacei* Mann	0	1	0	0
	Pheidole sp. cf *brandaoi*	7	9	1	1
	Pheidole sp.4 *fallax* group	1	1	0	0
	Pheidole sp.6 *flavens* group	1	0	0	0
	Pheidole sp.7 *fallax* group	2	0	0	0
	Pheidole sp.8 *fallax* group	0	2	0	0
	Pheidole sp.10	1	0	0	0
	Pheidole sp.11 *flavens* group	13	14	23	0
	Pheidole sp.12 *diligensis* group	9	2	13	0
	Pheidole sp.13 *tristis* group	10	12	4	1
	Pheidole sp.15 *flavens* group	7	5	17	14
	Pheidole sp.16 *tristis* group	0	1	0	0
	Pheidole sp.18 *flavens* group	0	1	0	0
	Pheidole sp.19 *flavens* group	0	0	1	0
	Pheidole sp.25 *flavens* group	10	11	4	16
	Pheidole sp.30 near *transversostriata*	1	1	0	0
	Pheidole sp.40 *flavens* comp.	15	22	12	0

	Pheidole sp.41 *flavens* comp.	1	0	0	0
	Pheidole sp.51	0	0	2	0
	Pheidole sp.55 *flavens* comp.	1	0	0	0
	Solenopsidini Forel				
	Allomerus decemarticulatus Mayr	1	0	0	0
nsg	*Carebara elongata* Fernández	2	0	0	0
nsg	*Carebara urichi* (Wheeler)	10	7	2	0
	Carebara sp.4 *lignata* group	0	2	4	4
	Carebarella sp.1	1	0	0	0
	Carebarella sp.2	2	0	0	0
nsg	*Megalomyrmex incisus* Smith	0	0	0	1
	Megalomyrmex silvestrii Wheeler	1	2	0	0
	Megalomyrmex sp.8 *pusillus* group	2	1	0	0
nsg	*Solenopsis pollux* Forel	0	0	5	0
nsg	*Solenopsis virulens* (Smith)	11	9	0	0
	Solenopsis sp. *pygmaea* group	0	0	1	0
	Solenopsis sp.5	2	0	0	0
	Solenopsis sp.6	1	0	2	0
	Solenopsis sp.7	1	0	0	0
	Solenopsis sp.8	3	1	0	0
	Solenopsis sp.10	0	1	1	0
	Solenopsis sp.11	0	0	4	0
	Solenopsis sp.12	7	11	7	0
	Solenopsis sp.13	6	11	6	1
	Solenopsis sp.15	31	30	34	10
	Solenopsis sp.16	18	5	14	17
	Solenopsis sp.18	1	0	1	0
	Stegomyrmecini Wheeler				
nsg	*Stegomyrmex manni* Smith	0	1	0	0
nsg	*Stegomyrmex olindae* Feitosa, Brandão and Diniz	0	1	0	0
	Stenammini Ashmead				
nsg	*Lachnomyrmex pilosus* Weber	4	0	0	0

	Lachnomyrmex sp.	1	1	0	0
nsg	*Rogeria alzatei* Kugler	7	0	1	3
nsg	*Rogeria germaini* Emery	1	0	0	0
nsg	*Rogeria lirata* Kugler	2	1	1	1
	Rogeria micromma Kempf	4	2	1	6
nsg	*Rogeria scobinata* Kugler	11	6	4	11
nsg	*Rogeria subarmata* (Kempf)	0	0	1	0
nsg	*Rogeria tonduzi* Forel	7	10	0	0
	Rogeria sp.5	1	0	0	0
	Rogeria sp.10 cf *besucheti*	0	1	0	1
	Tetramoriini Emery				
nsg	*Tetramorium bicarinatum* (Nylander)	0	1	0	0
PONERINAE Lepeletier					
	Ponerini Lepeletier				
	Anochetus bispinosus (Smith)	0	1	0	0
nsg	*Anochetus diegensis* Forel	8	2	2	1
nsg	*Anochetus horridus* Kempf	6	7	2	7
nsg	*Anochetus inermis* André	2	8	0	0
	Anochetus mayri Emery	0	0	1	0
nsg	*Anochetus neglectus* Emery	5	1	0	3
	Anochetus simoni Emery	0	1	0	0
nsg	*Hypoponera foreli* (Mayr)	2	4	3	2
nsg	*Hypoponera opacior* (Forel)	1	2	0	0
	Hypoponera sp.1	7	6	0	0
	Hypoponera sp.2	27	14	0	0
	Hypoponera sp.3	0	3	1	0
	Hypoponera sp.4	1	0	1	0
	Hypoponera sp.5	0	2	0	3
	Hypoponera sp.6 *foreli* group	0	0	4	0
	Hypoponera sp.10	5	4	0	0
	Hypoponera sp.11	7	20	10	0
	Hypoponera sp.12	3	1	2	7
	Hypoponera sp.13	5	7	11	0

	Leptogenys dasygyna Wheeler	1	0	0	3
	Leptogenys langi Wheeler	1	0	0	0
nsg	*Leptogenys vogeli* Borgmeier	0	0	1	0
	Leptogenys sp.3	1	0	0	0
	Leptogenys sp.5	0	0	1	0
	Odontomachus biumbonatus Brown	7	6	0	0
	Odontomachus caelatus Brown	0	5	0	0
	Odontomachus chelifer (Latreille)	0	0	0	15
	Odontomachus haematodus (Linnaeus)	5	1	2	1
	Odontomachus hastatus (Fabricius)	0	1	0	0
	Odontomachus meinerti Forel	3	3	2	0
	Odontomachus scalptus Brown	11	7	4	0
	Pachycondyla arhuaca (Forel)	1	0	0	1
	Pachycondyla commutata (Roger)	1	2	0	0
	Pachycondyla constricta (Mayr)	15	4	9	7
nsg	*Pachycondyla cooki* Mackay and Mackay	0	1	0	0
	Pachycondyla crassinoda (Latreille)	7	20	1	1
	Pachycondyla crenata (Roger)	0	0	0	1
	Pachycondyla harpax (Fabricius)	27	16	11	10
	Pachycondyla holmgreni (Wheeler)	0	1	0	0
	Pachycondyla laevigata (Smith)	0	1	0	0
nsg	*Pachycondyla pergandei* (Forel)	1	0	2	1
	Pachycondyla procidua Emery	0	2	0	0
	Pachycondyla stigma (Fabricius)	5	4	1	0
nsg	*Pachycondyla striata* Smith	1	1	1	0
	Pachycondyla unidentata Mayr	0	2	0	0
	Pachycondyla verenae Forel	3	1	0	4
	Pachycondyla cf *apicalis* morphosp. II (*sensu* Delabie *et al.*, 2008*)	1	6	0	5
	Pachycondyla cf *apicalis* morphosp. IV (*sensu* Delabie *et al.*, 2008*)	1	1	3	0
	Thaumatomyrmecini Emery				
nsg	*Thaumatomyrmex soesilae Makhan*	2	2	0	0

PROCERATIINAE Emery					
	Proceratiini Emery				
	Discothyrea denticulata Weber	9	2	4	0
nsg	*Discothyrea sexarticulata* Borgmeier	8	6	1	0
PSEUDOMYRMECINAE Smith					
	Pseudomyrmecini Smith				
	Pseudomyrmex tenuis (Fabricius)	1	0	13	6
	Pseudomyrmex sp. *pallidus* group	0	1	1	0

[*] Delabie, J.H.C., Mariano, C.S.F., Mendes, L.F., Pompolo, S.G. and Fresneau, D. (2008) Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no Género *Pachycondyla* na região neotropical: o caso do complexo *apicalis*. *Insetos Sociais: da Biologiá a Aplicacão Vicosa, Minas Gerais* (ed. by E.F. Vilela, I.A. Santos, J.H. Schoereder, J.E. Serrão, L.A.O. Campos and J. Lino Neto), pp. 196-222. Editora da Universidade Federal de Viçosa, Viçosa.

[**] Lacau, S. (2005) *Morphologie et systématique du genre* Typhlomyrmex *Mayr, 1862 (Formicidae: Ectatomminae)*. PhD thesis, Muséum National d'Histoire Naturelle, Paris.

<u>CHAPITRE 2 :</u> ÉVOLUTION DES COMMUNAUTÉS DE FOURMIS DE LA LITIÈRE SUITE À LA CONVERSION DE LA FORÊT MATURE EN PLANTATIONS ET DANS UN CONTEXTE DE RÉGÉNÉRATION

Ce chapitre concerne, d'une part, les effets de l'utilisation traditionnelle des sols (ou de la terre) sur les communautés de fourmis de la litière selon un gradient de régénération forestière (Article 3), et d'autre part, les effets de la perturbation de ces communautés engendrée par la formation d'un chablis complexe comparés à ceux causés par la transformation forestière en différentes monocultures. (Article 4). Ces deux articles se focalisent sur deux aspects : un premier où prédomine l'aspect biologique (concernant à la fois la diversité et la structure des myrmécofaunes), et un second d'ordre méthodologique (l'application d'un protocole d'échantillonnage simplifié et/ou l'utilisation d'une méthode statistique – relativement récente en écologie terrestre ; Groc et al., 2007 – permettant des interprétations écologiques fiables).

1. Aspect biologique - conclusion

Dans les forêts tropicales humides amazoniennes, comme ailleurs, les communautés natives des fourmis de la litière sont plus ou moins altérées par la fragmentation (MacKay et al., 1991 ; Vasconcelos, 1999 ; Vasconcelos et al., 2000 ; Kalif et al., 2001) et la conversion des forêts en plantations (Roth et Perfecto, 1994 ; Bestelmeyer et Wiens, 1996 ; DeSouza et al., 2001 ; Graham et al., 2008). Les résultats des deux études présentées dans ce chapitre montrent que la diversité spécifique est dans la majorité des cas négativement affectée. Alors que, dans la littérature, l'influence sur la diversité varie parfois positivement, et négativement dans la plupart des cas (Armbrecht et al., 2005 ; Sarty et al., 2006 ; Vasconcelos and Vilhena, 2006 ; Lassau and Hochuli, 2004 ; Lassau et al., 2005 ; Hill et al., 2008), l'abondance et la densité en espèces sont toujours affectées négativement. Cependant, il existe un gradient d'intensité d'altération des communautés allant de la formation d'un chablis et de la fragmentation forestière aux monocultures de certaines essences (parfois natives d'Amazonie, comme l'hévéa ou plus ou moins exotiques comme l'acacia ou le pin caraïbes), les effets de l'utilisation traditionnelle des terres par les amérindiens et la monoculture de cacaoyers étant

intermédiaires. Les parcelles forestières perturbées naturellement ou fragmentées, tout comme certaines plantations (*e.g.* cacaoyères, plantations de manioc abandonnées) abritent des myrmécofaunes relativement proches de celle de la forêt mature environnante. Par contre, la composition des communautés dans les plantations d'acacias, de manioc (entretenues), d'hévéas et de pins caraïbes est très différente, caractérisée par la dominance de certaines espèces natives hyperabondantes, le remplacement d'espèces forestières typiques par des espèces généralistes et opportunistes, ainsi que l'installation d'espèces exotiques. Plus l'altération est profonde, plus la régénération forestière sera longue (Turner, 1996 ; Roth et al., 1994 ; Vasconcelos, 1999 ; Floren et Linsenmair, 2001 ; Kalif et al., 2001 ; Watt et al., 2002 ; Floren et Linsenmair, 2005).

2. Aspect méthodologique - conclusion

Dans un contexte où les études de biodiversité sont très coûteuses en temps et en argent, particulièrement en milieu tropical (Lawton et al., 1998 ; Balmford and Whitten, 2003 ; Gardner et al., 2007), l'argent investi doit être dépensé de façon optimale. Une des grandes préoccupations actuelles est donc d'avoir en main des outils fiables permettant d'évaluer rapidement la diversité des taxons cibles, et de repérer facilement les modifications locales des écosystèmes causées par l'activité humaine. Hormis quelques exceptions (*e.g.* le cas des fourmis en Australie, Andersen et Majer, 2004), les invertébrés terrestres, reconnus pour leur potentiel en bioindication, sont systématiquement ignorés dans les programmes de contrôle et de suivi environnementaux. Ceci est essentiellement dû à leur nombre démesuré, aux défis taxonomiques et au coût d'échantillonnage qu'ils représentent (Cranston, 1990 ; Vane-Wright et al., 1994 ; Oliver et Beattie, 1996), et à une méconnaissance générale les concernant, ce qui les rend intimidants pour la plupart des gestionnaires du territoire (New, 1996). Démontrer la fiabilité d'un groupe indicateur n'est donc pas suffisant car il est primordial de développer et posséder des raccourcis robustes impliquant soit une réduction d'effort d'échantillonnage (Article 3), soit une perte de résolution taxonomique pour révéler les réponses des communautés d'arthropodes terrestres à l'anthropisation (Groc et al. 2010 : Annexe 2). Ceci engendrerait le développement de protocoles pouvant facilement être intégrés dans le processus de gestion environnementale et accessibles à tous les non spécialistes (Andersen, 1999). Bien qu'il existe des protocoles bien développés pour les études complètes sur les fourmis de la litière (protocole « ALL » ; Agosti et Alonso, 2000), il devient urgent que des approches simplifiées pour l'échantillonnage et le traitement des données puissent fournir rapidement des résultats accessibles, précis et fiables.

Un des moyens disponibles pour faciliter l'inclusion des invertébrés terrestres dans les études environnementales est l'utilisation d'outils statistiques performants, peu sensibles au sous-échantillonnage, permettant de maximiser la robustesse des résultats en réduisant l'effort d'échantillonnage. C'est par exemple le cas de la méthode des réseaux de neurones ou « SOM » (« Self-Organizing Maps » ; Kohonen, 2001). Cette approche, communément utilisée dans les études de bioindication en écologie aquatique, n'a été appliquée en écologie des communautés d'arthropodes terrestres qu'une seule fois. Il s'agit d'une étude portant sur la structure des communautés de fourmis en zone naturelle tempérée (Groc et al., 2007).

Cette approche, utilisée dans le cadre d'études d'impact de l'anthropisation sur les communautés terrestres tropicales pour la première fois dans la présente étude se montre

robuste et fiable. En effet, les patrons de distribution des espèces de fourmis en réponse à une perturbation ont bien été mis en évidence (1) dans un contexte de sous-échantillonnage couplé l'utilisation d'une méthode de piégeage très sélective (les pièges à fosse), appliquée au sein de parcelles de superficie réduite, ce qui s'inscrit dans la philosophie des RAP – Rapid Assessment Programs ; Alonso et al., Conservation International – (Article 3) et (2) lors d'absence de réplicats pour chaque type d'habitat (Article 4). Ces patrons généraux sont apparus clairs, pertinents et facilement interprétables en dépit des biais induits par le protocole (méthode d'échantillonnage, type d'essence, âge de la plantation, taille de la parcelle, distance par rapport à la matrice, « effet de lisière »). Cette méthode apparaît donc comme particulièrement bien adaptée pour analyser les patrons des communautés de fourmis de litière dans des parcelles fragmentées ou converties en agrosystèmes, que ce soit dans un contexte de gradient d'anthropisation ou de régénération forestière. Ainsi, cette approche, qui permet de détecter, analyser et comprendre les réponses des communautés de fourmis de la litière de façon optimale, contribuera certainement à faciliter l'inclusion des fourmis dans les programmes d'évaluation et gestion de la santé des écosystèmes.

3. Articles

3.1. Article 3 : Ants as biological indicators of Wayana Amerindian land use in French Guiana

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COMPTES RENDUS BIOLOGIES

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Ants as biological indicators of Wayana Amerindian land use in French Guiana

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Abstract

We examined the ecological impact of traditional land use by Wayana Amerindians in French Guiana using ants as bio-indicators. Ants were sampled through a rapid assessment method and the core results analyzed using Kohonen's self-organizing maps (SOM). Our sample sites included: (1) a Wayana village; (2) a cassava plantation; (3) an abandoned cassava plantation; (4) a forest fragment near the village; (5) a riparian forest; and (6) a primary *terra firma* forest. The ant diversity decreases according to the degree to which the habitat is disturbed. The SOM allowed us to compare the ecological succession between the six habitats. The protocol used is robust since the same conclusions were drawn using partial data. ***To cite this article: J.H.C. Delabie et al., C. R. Biologies 332 (2009).***

Résumé

Les fourmis comme indicateurs biologiques de l'utilisation de la terre par les Amérindiens Wayana en Guyane Française. Nous avons examiné l'impact de l'utilisation traditionnelle de la terre par les Amérindiens Wayanas de Guyane Française en utilisant les fourmis comme bio-indicateurs. Ces fourmis ont été capturées grâce à une méthode d'échantillonnage rapide et les résultats analysés au moyen de cartes auto-organisatrices de Kohonen (SOM). Nous avons échantillonné : (1) le village Wayana ; (2) une plantation de manioc ; (3) une plantation abandonnée depuis 6 ans ; (4) un fragment de forêt près du village ; (5) une ripisylve ; et (6) une forêt primaire. La diversité des fourmis décroît en fonction du degré de perturbation de l'habitat. Le SOM permet de suivre la succession écologique entre les six habitats. Le protocole utilisé est robuste car les mêmes conclusions sont atteintes après contrôle utilisant une information fragmentaire. ***Pour citer cet article : J.H.C. Delabie et al., C. R. Biologies 332 (2009).***

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Keywords: Landscape ecology; Traditional land use; Formicidae; Rapid assessment; Pit-fall traps; Self-Organizing Maps

Mots-clés : Écologie du paysage ; Utilisation traditionnelle de la terre ; Formicidae ; Échantillonnage rapide ; Pièges *pifall* ; Self-Organizing Maps

1. Introduction

Any alteration in or perturbation to an ecosystem – such as agriculture, road construction, logging, or other forms of human use of a habitat otherwise in equilibrium – provokes an unbalanced situation which has, even when discrete, strong repercussions on the plant and animal communities. As a result, their specific compositions change, whether momentarily or over the long term. A great concern for modern ecologists is to have the tools at hand that allow them to quickly evaluate the diversity of focal taxa and to easily pinpoint local changes in ecosystems caused by human activity. In this context, ants are among the most utilized biological indicators (e.g., species or communities whose function, population, or status can be used to determine ecosystem or environmental integrity) due to their functional importance in ecosystems and sensitivity to environmental changes; the ease of sampling, sorting and identifying them; and their local richness and abundance (i.e., Conservation International's Rapid Assessment Program; see [1–5]). Also, the anthropogenic alteration of ecosystems allows the introduction and/or dissemination of exotic species or, more generally, favors the spread of certain endemic ones. Concerning ants, any exogenous species will interact with native communities and sometimes be responsible for the localized extinction of endemic organisms [6]. Given these settings, there is a need to develop analytical approaches that can maximize the information extracted from available data, such as "simple" presence–absence data.

In this study conducted in French Guiana, we examined the impact of traditional land use by Wayana Amerindians through a comparison of the ant communities in habitats presenting a gradient of anthropization: from pristine forests to a village itself. This is the first study where ants are used to examine traditional land use and forest regeneration. We also hope to show that a simplified assessment method is particularly useful and perfectly reliable for such a study where the resources (especially time and space) for sampling are greatly limited. For that reason, we schematically represented traditional land use by Amerindian using Kohonen's Self-Organizing Maps (SOM, neural network) [7] based on data obtained from our study on ants in and around the village. The SOM yields a clear bi-dimensional projection of a relatively large volume of site-specific data on species occurrences. In addition the "weight" (or connection intensity) of each species in each cell of the SOM can be interpreted as its probability of occurrence in a given area (with reference to land use in this study), even in areas in which they did not occur during sampling.

2. Material and methods

2.1. Some characteristics of Wayana Amerindians in French Guiana

The Wayana live along several rivers in Brazil, French Guiana and Suriname. Irregularly distributed in small villages of 20 to 200 inhabitants, their total population is around 1400 individuals [8], only 750 of whom reside in French Guiana, according to the French Demographic Census of 1996. Their main traditional source of food results from "slash-and-burn" agriculture augmented by fishing and hunting. This sort of agriculture, adapted to the infertile soils prevalent in the Amazon region, has been practiced for centuries by many Amerindian nations and their mixed-race descendants living along rivers. Despite a recent tendency to settle in one place, the Wayana were not traditionally limited by space, and they moved their villages more or less every 7 years [8]. Like other Amerindian peoples, the Wayana practice shifting cultivation where plots are farmed for short periods of 2–3 years, followed by long periods of fallow of 2 or more decades [9–12].

2.2. Study site and methods

This study was carried out during three field outings (2000–2002) to the Wayana village of Tidamali, 3 km south of Maripasoula (3.6°N, 54.0°W), French Guiana, on the banks of the Maroni River that separates French Guiana from Suriname.

Six areas were sampled using the pit-fall trap technique: (1) the village; (2) a recent cassava plantation with most plant individuals more than 3 m tall; (3) a cassava plantation abandoned for 6 years dominated by 10–15 m tall *Apeiba tibourbou* (Tiliaceae); (4) a *terra firma* forest fragment preserved by villagers in the middle of their cultivated lands; (5) a riparian forest (e.g., a forested area of land adjacent to a body of water such as a river, stream, lake etc. in this case, the Maroni River);

and (6) a primary *terra firma* forest. Both of the latter are located 4 kilometers from the village. The village and all of the plots were set up at the edge of the *terra firma* forest. In each area, 20 pit-fall traps were placed at 25 m intervals and left for 24 hours (the sampled area in each parcel is thus estimated to be 1.25 ha; 120 samples in total: 6 sites × 20 pit-fall traps). Each trap consisted of a plastic cup, with a volume of 25 cm^3, buried to its lip and containing around 2 cm of water with a few drops of liquid soap [13]. The ants were sorted in the field, then preserved in alcohol and identified later at the *Laboratório de Mirmecologia* in Itabuna, Bahia, Brazil. Voucher specimens were deposited in the laboratory's collection (CPDC), catalogue number #5295. The nomenclature of the identified material comes from Bolton [14,15].

Although they cannot be considered as a blanket solution for sampling ants because the results they provide may be biased [13,16,17], pit-fall traps permit ground-dwelling ants to be rapidly inventoried, especially in highly anthropized areas, where the ground is trampled and laid bare [18,19]. The other most common method, Winkler extraction, is only useful for leaf-litter fauna [13]. Because in this study we used the minimum number of samples recommended for a rapid inventory allowing comparable data [20] to be gathered (i.e., 20 samples at ca. 20 m intervals; 25 m in this case), we verified the validity of this protocol through the SOM (see below).

2.3. Ant diversity

The results are expressed as the number of samples where the species studied was found (presence/absence). Several ecological indices were used: Alpha, Shannon's and Simpson's Diversity Indices, and Berger–Parker Dominance Index [21].

2.4. Modeling procedure

In this study we analyzed data with the Self-Organizing Map algorithm [7] already used to pattern species assemblages using site-specific data on species occurrences [5,22,23]. Combining clustering and ordering abilities, the SOM is an unsupervised learning procedure, which transforms multi-dimensional input data into a two-dimensional map subject to a topological (neighborhood preserving) constraint [7].

The structure of the SOM consists of two layers of neurons connected by weights (or connection intensities): the input layer is composed of 75 neurons (one per ant species) connected to the 120 samples (pit-fall traps); the output layer is composed of 55 neurons (represented as hexagonal cells) organized in a grid containing 11 rows and 5 columns (see Fig. 1A). At the end of the learning process, pit-fall traps that are next to each other on the grid are expected to have similar ant assemblages, while pit-fall traps located very far from each other on the grid represent different ant assemblages (similar procedure was used as in [23]). The K-means algorithm was applied to the weights of the biological variables in the output neurons in order to identify the cluster boundaries on the SOM [24]. Fig. 1B provides a gradient analysis of the species' distribution for each ant. Using a qualitative presence/absence dataset, the model calculated continuous, quantitative values between 0 and 1. More specifically, the connection intensity between input and output layers calculated during the learning process can be considered as the probability of occurrence for each species in the area concerned. The probability of occurrence for each species in a given area corresponding to the connection intensity is shown on the SOM map in shades of grey, which therefore allowed us to analyze the effect of each variable (species) on the patterning input dataset (sites), and even to predict the probability of occurrence for each species in the sites (or clusters) where they were not consistently collected during the sampling (see [23]).

To test the robustness of our interpretation of the dataset and the protocol used, we divided it into two new datasets arbitrarily chosen by sample number (odd- or even-numbered samples; $n = 60$ samples in each case). The SOM procedure was repeated for each set, making the best use of each of the two maps containing 40 units organized into five clusters. Data were interpreted in the same way, allowing us to test if similar conclusions drawn from original data could be drawn using fewer data.

Fig. 1. (A) Distribution of the 120 pit-fall trap samples on the Self-Organizing Map (SOM; 55 hexagons) according to the presence or absence of 75 ant species. Numbers correspond to the pit-fall traps. The different clusters (delineated with bold lines) were derived from the K-means algorithm. (B) Gradient analysis of the probability of occurrence for each of the 75 ant species on the trained SOM (presented in "A"), shown in a shaded scale (dark = high probability of occurrence, light = low probability of occurrence). Each smaller map, corresponding to one ant species, can be superimposed on map "A", thus showing the probabilities of presence of each ant species within each pit-fall trap cluster.

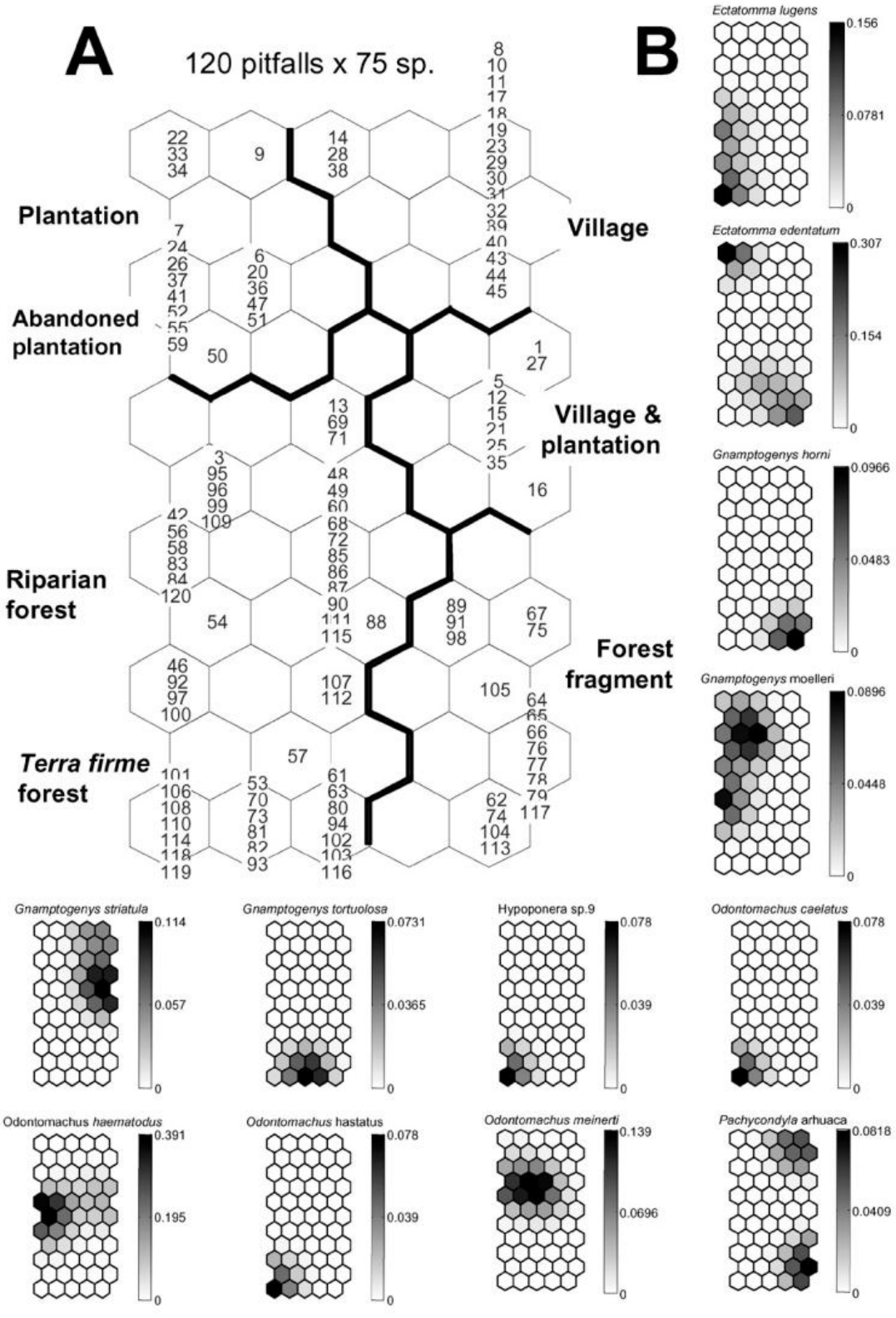

Fig. 1.

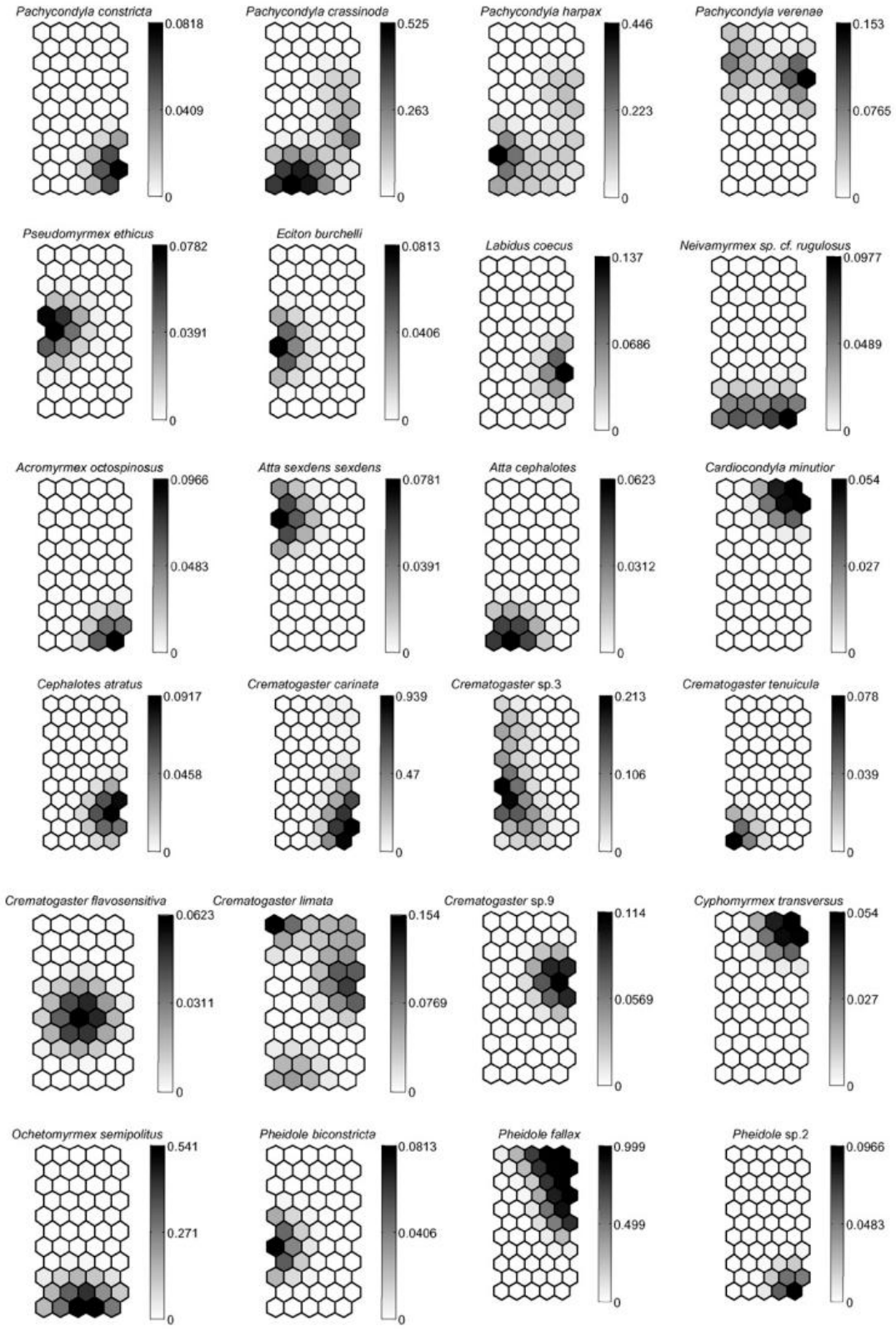

Fig. 1. Continued.

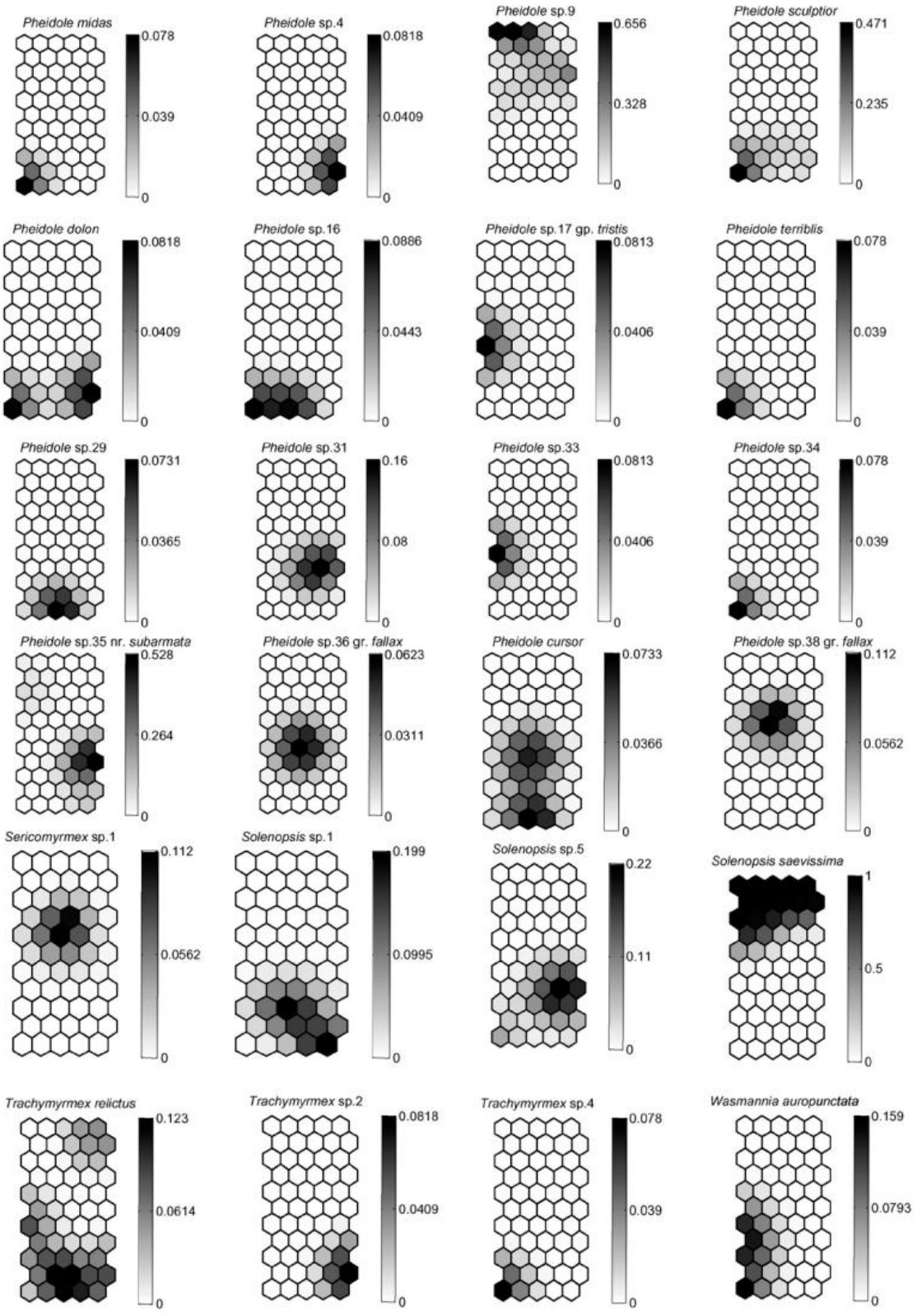

Fig. 1. Continued.

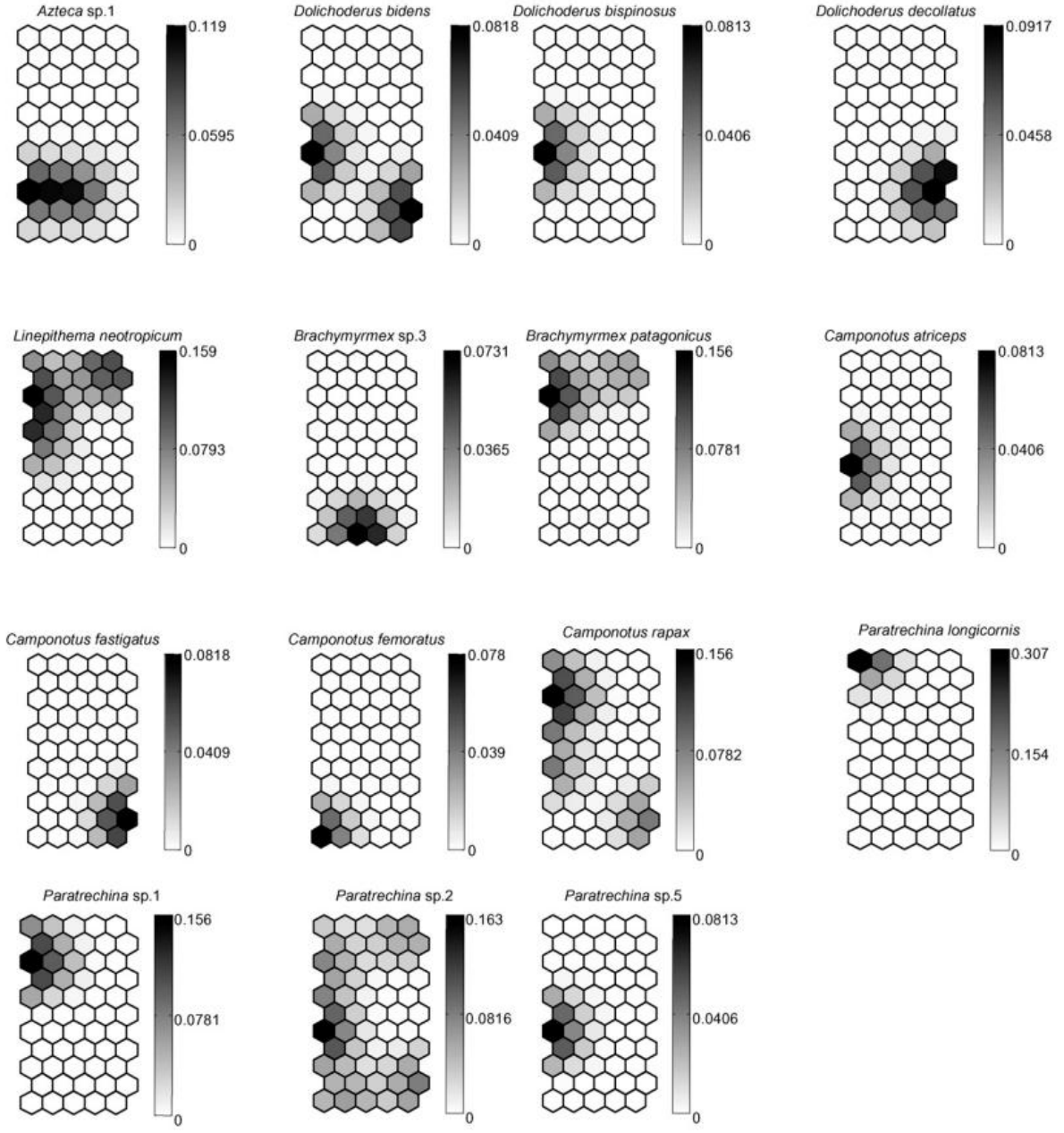

Fig. 1. Continued.

3. Results and discussion

3.1. Ant diversity and habitat disturbance

Among the different biological indicators considered as useful for studying landscape disturbance in terrestrial ecosystems, ants present numerous advantages over other arthropods and vertebrates. Indeed, occurring worldwide and taxonomically well known, they generally constitute the largest fraction of the animal biomass, occupy different places in the food web (e.g., they can be direct or indirect herbivores, scavengers, generalists or predators), and respond to stress on a finer scale than other animals; moreover, the sampling protocols for ground-dwelling species have been fine-tuned and standardized [2,4,13–20,25]. Consequently, ants have been used as indicators of environmental change in landscapes disturbed by activities such as mining, agri-

culture and military training [4,26–29], but never as indicators related to traditional land use as in the present study.

Ant diversity is known to decrease with the level of disturbance [26–29], something globally noted in this study (Table 1). Yet, slight disturbance, permitting species already present to remain (although their density decreases) while new species begin to appear, can result in a slight increase in diversity [29]. This was again the case in this study where the forest fragment near the villagers' dwellings and situated along a river was more species-rich than the natural riparian forest (Tables 1 and 2). Consequently, as discussed below, ant assemblages, each represented by emblematic species, characterize the degree of disturbance more than ant diversity does.

In the present study, the village and recent plantations are characterized by the presence of *Gnamptogenys striatula*, *Ph. fallax*, *S. saevissima* and *Linepithema neotropicum* (Fig. 1B). These species, that commonly nest in well-trampled places such as the paths used by the villagers, are among the best indicators of anthropization. *Solenopsis saevissima*, also present in both types of plantations (Table 1), characterizes all anthropized areas of the Amazonian Basin [30]. Moreover, its aggressiveness and numerical dominance make its presence one of the strongest impediments to the regeneration – from the ground up – of abandoned plantations into secondary forests [30]. It is certainly the cause of the major differences we noted between the anthropogenetic and forested communities (Fig. 1A, B).

Because the ground was well shaded in the recent plantation, the ant assemblage was intermediary between that of the village with bare soil (cluster "Village & Plantation" characterized by *Gnamptogenys striatula*, a Neotropical species frequent in urban parks and secondary vegetation [31]; Fig. 1A) and the abandoned plantation well shaded by shrubs (cluster "Plantation" and "Abandoned plantation"; Fig. 1A).

While it retains characteristics of the most anthropized habitats due both to its proximity to the village and history of human activity, the abandoned cassava plantation resembled a forest in that forest ants were beginning to re-colonize it (Fig. 1A, B). The similarities in the relative frequencies in the pit-fall traps of *P. crassinoda* and other large Ponerinae suggest that they are good indicators of the start of the forest's regeneration in the abandoned plantation. The final phases are the longest; Meggers [10] estimated it to take about 20 years, but several hundred years are necessary for the vegetation in the Brazilian Atlantic forest to recover [32].

Although close to the village and both logged and burned accidentally, the forest fragment, left intact in the middle of cultivated fields, maintained an ant fauna very similar to that found in the unspoiled forests (Fig. 1A, B). Arboreal species such as *Cephalotes atratus* and *Crematogaster carinata* are present (the workers of arboreal species also forage on the ground; see [33]).

The transition between the forest fragment and riparian and *terra firma* forests appears as a gradient of occurrence for several ant species, particularly *Odontomachus* spp., *Pachycondyla* spp., *Camponotus rapax* and *Ochetomyrmex semipolitus*. Finally, the habitat quality of the pristine, *terra firma* forest was mostly marked by the diversity of the genus *Pheidole* and the occurrence of other species such as *Ochetomyrmex semipolitus* (Fig. 1B).

3.2. Biological insights

The Berger–Parker index clearly shows that species dominance may be a good parameter of anthropogenic disturbance [34] (Table 2). Indeed, we noted five "dominant" species or species observed more than 10 times in the six sampling sites: *Crematogaster carinata*, *Pachycondyla crassinoda*, *Pheidole* sp.9, *Ph. fallax* and *Solenopsis saevissima*. This kind of dominance needs to be distinguished from the notion of "numerical dominance" [36] that rather pertains to species with large colonies.

Among the Myrmicinae, the distribution of leaf-cutting, fungus-growing ants reflects their known distribution [35], although these ants are reported to avoid pit-fall traps. *Atta sexdens* is adapted to living in semi-open habitats, while *A. cephalotes* is typically found in pristine forest, and the more generalist *Acromyrmex octospinosus* is here limited to the forest fragment (Fig. 1B).

Only three ant species (i.e., *O. haematodus*, *P. crassinoda* and *P. harpax*), all Ponerinae, were noted in four to five habitats. Although no statistical analyses could be conducted due to our limited sampling, the frequency of the two *Pachycondyla* species seems to be linked to undisturbed habitats. The genus *Pheidole*, which is the most species-rich ant genus in the Neotropics [37], was, as expected, very diverse with 19 total species, and its species number increased according to the state of habitat preservation. Its diversity is therefore a good indicator of local ant species richness and accounts for approximately 1/7 (poor conservation) to 1/3 (good conservation) of the diversity of the ant community in the habitats [37]. Among the Formicinae, *Camponotus rapax* characterizes primary or secondary forests in the

Table 1
Ants collected with pit-fall traps in different cultivated and natural areas near Tidamali village, Maripasoula, French Guiana. The numbers presented in the table correspond to the numbers of occurrences for each ant species among the 20 pit-fall traps placed at 25 m intervals and left for 24 hours.

Ant species	Village	Recent plantation	Abandoned plantation	Forest fragment	Riparian forest	Primary forest	Total
Ectatomminae							
Ectatomma edentatum Roger		2		1		2	5
Ectatomma lugens Emery					1	2	3
Gnamptogenys horni (Santschi)						1	1
Gnamptogenys moelleri (Forel)			1			1	2
Gnamptogenys striatula Mayr	2						2
Gnamptogenys tortuolosa (Smith)				1			1
Ponerinae							
Hypoponera sp.9						1	1
Odontomachus caelatus Brown						1	1
Odonto. haematodus (Linnaeus)	1	1			3	1	6
Odontomachus hastatus (Fabricius)						1	1
Odontomachus meinerti Forel			1	1			2
Pachycondyla arhuaca (Forel)	1			1			2
Pachycondyla constricta (Mayr)				1			1
Pachycondyla crassinoda (Latreille)		1	2	4	3	3	13
Pachycondyla harpax (Fabricius)		1	1		3	3	8
Pachycondyla verenae (Forel)		2					2
Pseudomyrmecinae							
Pseudomyrmex ethicus (Forel)	1						1
Ecitoninae							
Eciton burchelli (Westwood)					1		1
Labidus coecus (Latreille)				1			1
Neivamyrmex sp. cf. *rugulosus*				2			2
Myrmicinae							
Acromyrmex octospinosus (Reich)						1	1
Atta sexdens sexdens (Linnaeus)		1					1
Atta cephalotes (Linnaeus)				1			1
Cardiocondyla minutior Forel	1						1
Cephalotes atratus (Linnaeus)						1	1
Crematogaster carinata Mayr	2			11		4	17
Cremato. flavosensitiva Longino				1			1
Crematogaster limata Fr. Smith		2	2				4
Crematogaster sp.3			5				5
Crematogaster sp.9		1					1
Crematogaster tenuicula Forel						1	1
Cyphomyrmex transversus Emery			1				1
Ochetomyrmex semipolitus Mayr				4	1	4	9
Pheidole biconstricta Mayr			1				1
Pheidole cursor Wilson				2			2
Pheidole dolon Wilson						2	2
Pheidole fallax Mayr	14	13	3				30
Pheidole midas Wilson						1	1
Pheidole sculptior Forel						8	8
Pheidole sp.2 gp. *diligens*						1	1
Pheidole sp.4				1			1
Pheidole sp.9	4	6				1	11
Pheidole sp.16						2	2
Pheidole sp.17 gp. *tristis*						1	1
Pheidole sp.29						1	1
Pheidole sp.31					2		2
Pheidole sp.33						1	1
Pheidole sp.34						1	1
Pheidole sp.35 nr. *subarmata*			1	3	3		7
Pheidole sp.36 gp. *fallax*					1		1

(*continued on next page*)

Table 1 (*Continued*)

Ant species	Village	Recent plantation	Abandoned plantation	Forest fragment	Riparian forest	Primary forest	Total
Pheidole sp.38 gp. *fallax*				1			1
Pheidole terribilis Wilson						1	1
Sericomyrmex sp.1				1			1
Solenopsis sp.1						4	4
Solenopsis sp.5					2	2	4
Solenopsis saevissima (Smith)	13	16	10				39
Trachymyrmex relictus Borgmeier			3	2			5
Trachymyrmex sp.2						1	1
Trachymyrmex sp.4						1	1
Wasmannia auropunctata (Roger)			1			3	4
Dolichoderinae							
Azteca sp.1					1	1	2
Dolichoderus bidens (Linnaeus)				1	1		2
Dolichoderus bispinosus (Olivier)					1		1
Dolichoderus decollatus Smith						1	1
Linepithema neotropicum Wild	3		2				5
Formicinae							
Brachymyrmex sp.3						1	1
Brachymyrmex patagonicus Mayr	1	2					3
Camponotus atriceps (Smith)			1				1
Camponotus fastigatus Roger				1			1
Camponotus femoratus (Fabricius)						1	1
Camponotus rapax (Fabricius)			2	1	1		4
Paratrechina longicornis (Latreille)		2					2
Paratrechina sp.1			2				2
Paratrechina sp.2			5	1			6
Paratrechina sp.5					1		1
Number of species	**11**	**13**	**18**	**22**	**15**	**35**	**75**
Number of samples	20	20	20	20	20	20	120

Table 2
Diversity indices applied to the different habitats sampled around Maripasoula (Tidamali village grounds), French Guiana.

Habitat	Alpha	Shannon	Simpson	Berger–Parker
Village	3.76	1.62	3.38	0.325
Recent plantation	5.70	2.00	5.66	0.320
Abandoned plantation	11.49	2.57	12.53	0.250
Forest fragment	17.96	2.68	12.74	0.255
Riparian forest	15.91	2.55	21.42	0.120
Primary forest	35.14	3.34	34.76	0.129

Amazonian Basin, while the genus *Paratrechina* occurs mostly in anthropized areas [36].

We noted three "tramp species" likely to be invasive. "Tramp species" are ant pests transported worldwide through human activity that have a propensity to displace local ant species when introduced; move out when disturbed; show an absence of intraspecific, but a high rate of interspecific aggressiveness; are polygynous; and reproduce by colony fission [6]. Two of them, *Cardiocondyla minutior* and *Paratrechina longicornis*, were supposedly introduced from Africa [38]. Even though they were found in and around human habitats, their occurrence was relatively low (Fig. 1B). *Wasmannia auropunctata*, a Neotropical species, is present everywhere in the leaf-litter in South American forests. Its populations sometimes explode in cultivated areas, so that its presence usually indicates human-related perturbation [39]. This species occurred only a few times in our study and did not seem influenced by human activity in these particular conditions.

The presence of the forest fragment can play a role in favoring the colonization of abandoned plantations due to its proximity and thanks to the conservation of both riparian fauna and flora (see Fig. 1B). We do not know

if leaving a forest fragment in the middle of cultivated lands is truly a traditional practice, but, while traveling on the river, we noted that large areas of native riparian vegetation were interspersed between Wayana villages and their cultivated plots, sometimes even among the plots, favoring forest regeneration. This must have also been true in the recent past as zones corresponding to abandoned villages were easily recognizable due to the presence of *Cecropia* spp., mango and coconut trees.

3.3. Verification of the quality of the results obtained using the Self-Organizing Maps

When testing the robustness of our interpretation of the dataset and the protocol used, we obtained very similar results using our original data and only even-numbered samples. However, some differences occurred for the odd-numbered samples that, nevertheless, separated the forest (riparian, *terra firma* forest and forest fragment) from the anthropized areas (village, recent and abandoned plantations) (figures not shown). Consequently, the experimental protocol used in this study is appropriate for comparing the ant assemblages; even a relatively weak data set (20 pit-fall traps for each area compared) can produce valuable and robust information for the study of such a succession cycle.

Our conclusion is three-fold: (1) The use of the pit-fall trap technique, well adapted to this study, can be recommended for other studies at geographically remote sites because it involves only a minimum amount of equipment and time; (2) The SOM is a powerful tool for studying and comparing ant communities, allowing the interactions between faunal components and vegetal structure to be solidly interpreted, even when the data seem relatively weak; (3) The combination of using pit-fall traps to sample ants and the SOM algorithm to interpret the data appears to be very well adapted to analyzing a succession cycle where the plots to be sampled are of different sizes and distances from each other as is the case in this landscape influenced by traditional Amerindian agricultural practices.

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3.2. Article 4 : Plantations make a contribution to leaf-litter ant diversity in Neotropical agrosystems

En préparation pour une soumission à Biological Conservation

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Abstract

One the greatest threat for biodiversity and sustainable functioning of ecosystems is forest destruction for agriculture. In the Neotropics, two of the most common agrosystems are agroforests and monocultural plantations. In this study, we (1) analyzed the impact of forest conversion into four monoculture types over native leaf-litter ant communities, through changes in species richness, diversity, abundance and taxonomic composition, and (2) compared the alteration of communities with the effects caused by a treefall gap formation, both by using the Self-Organizing Map approach. This approach enabled us to highlight obvious patterns despite the weak global species turnover. Although effects caused by disturbance are shallower than those of alteration, global richness, diversity and equitability decreased. In plantations, communities were characterized by a noticeable loss of native species, an increase of generalist and dry biomes-dwelling species, and the dominance of one or few native species. Surprisingly, the most deeply altered ant communities were that of acacia and rubber tree plantations, while that of pines appeared more similar than that of forest. As expected, the ant fauna of cocoa tree plantation was the most resembling to the forest one. Furthermore, cocoa tree plantations are suitable for maintaining most forest-dwelling native ant species. The usefulness of Self-Organizing Maps for analyzing the impact of natural and anthropogenic disturbances over ant communities was also highlighted; it seems promising for rapid and accurate impact assessment of disturbances over ground-dwelling tropical entomofauna in the near future.

***Keywords**:* Forest native ant fauna; Disturbance; Ant community alteration; Agrosystem diversity; Neotropical tree monocultures; Self-Organizing Map.

Introduction

Global-scale conversion of natural ecosystems to agriculture is recognized as one of the major threat to biodiversity and ecosystem functioning and sustainability (Hoekstra et al., 2005). Agricultural intensification through the clearing of native vegetation, fragmentation and destruction of natural habitats causes native species elimination and may favor exotic species introduction (Schmidt and Diehl, 2008). Preserving high quality agricultural habitats is thus a priority in the biodiversity conservation agenda because they represent the matrix within which forest fragments are embedded (Schroth et al., 2004).

In the Neotropics, multistrata agroforestry systems, e.g. shaded cocoa plantations, are particularly valuable for biodiversity conservation because of their ability to provide biodiversity refuges in areas with little remaining native forest, and thus preserving an associated ant biodiversity very similar to the native one. They can also play the role of template for sustainable agricultural production systems (Schroth and Harvey, 2007). Monocultural systems frequently involve *Hevea brasiliensis* Müll. Arg., a common Amazonian native species of high economic value due to latex yields for rubber production (Silva et al., 1998), and fast-growing exotic tree species. Among them *Acacia mangium* Willd.), *Pinus caribaea* Mordelet and *Eucalyptus* spp. are widely planted for timber production and protection against erosion. *Acacia mangium* is also used to rehabilitate degraded soils due to its association with nitrogen fixing bacteria and its high ability to build soil organic matter (Bernhard-Reversat et al., 1993). Monospecific plantations generally have a number of drawbacks in terms of ecological function such as deeply altered entomofauna, especially ant assemblages (Bickel and Watanasit, 2005; Pacheco et al., 2009). Indeed age, nature, size, or maintenance of plantation, edge permeability to propagules during (re)colonization process, as well as the quality of and distance from forest matrix are fundamental factors influencing ground-dwelling ant communities (Feener, 2000; Kaspari and Weiser, 2000; Brühl et al., 2003; Dauber and Wolters, 2004; Armbrecht et al., 2004; Philpott et al., 2004, 2010).

Ants are commonly used as focal taxon in terrestrial biodiversity studies and environmental management and monitoring, especially in an agroecological context (Underwood and Fisher, 2006; Philpott and Armbrecht, 2006). Indeed, they are ubiquitous, diverse abundant, and ecologically dominant, sensitive to habitat changes, easy to be studied, and have a straightforward taxonomy for genera level and most of species, especially in Neotropics (Bolton, 1994; Agosti et al., 2000; Fernández, 2003; Underwood and Fisher, 2006; Pacheco et al., 2009). Ants may have considerable implications in agroecosystem functioning.

In addition to be considered as ecosystem engineers, ants are among the major predators in tropical agroforestry systems and may be key biological agents controlling a range of pests (insects, bacterial and fungal pathogens) (Folgarait, 1998; Schmitz et al., 2000; Philpott and Armbrecht, 2006).

To our knowledge, comprehensive surveys comparing the alterations imposed on ground-dwelling ant communities through both natural disturbance (treefall) and monospecific plantations with native or exotic fast-growing tree species have never been documented yet. This is partly owing to the fact that, for many non-mutually exclusive reasons (time- and cost-efforts, detection difficulties, non-standardized sampling, etc.), quantitative data such as population densities cannot be consistently obtained over a large number of sampling sites (Agosti et al., 2000), thus preventing conservationists from optimizing large and heterogeneous datasets built on field and/or literature data. Therefore, there is a need to develop alternative analytical approaches which can maximize the information extracted from "simple" presence-absence data (Céréghino et al., 2005). Inspired by the structure and the mechanism of the human brain, Artificial Neural Networks (ANNs) provide convenient tools to extract information from large ecological datasets. The Self-Organizing Map (SOM, Kohonen, 2001) is one of the most well-known unsupervised neural networks. The SOM performs a topology-preserving projection of the input data onto a regular two-dimensional space. In the output layer of the network, the neurons act as virtual samples and approximate the probability density function of the input data. Therefore, using a binary dataset of species occurrences, the SOM calculates quantitative continuous values which vary between 0 and 1, so that the occurrence probability of any species in a given area, in the form of the connection intensity, can be visualized onto a virtual map.

In addition, to date, only two studies have previously used the Self-Organizing Map (SOM) method to analyze the diversity patterns and the composition of ground-dwelling ant assemblages in relation to temperate habitats (Groc et al., 2007) or according to a gradient of anthropization in a Neotropical forest area (Delabie et al., 2009). This powerful tool allows the interactions between faunal components and vegetal structure to be solidly interpreted, even when the data seem relatively weak (Groc et al., 2007; Delabie et al., 2009). Thus, our objective was to analyze (1) the global impact of disturbance on the diversity, composition and structure of native forest leaf-litter ant assemblages, and (2) compare their response after a treefall gap formation or in monocultures with native and exotic tree species, by using an advanced modeling technique.

Material and Methods

Study sites

Ant sampling was conducted at the Paracou experimental site, a pristine lowland *terra firme* rainforest (5°18'N 52°55'W), near Sinnamary, French Guiana (Gourlet-Fleury et al., 2004), during the 2009 and 2010 dry seasons. The site receives nearly two-thirds of the annual 2875 mm (mean from 1986 to 2005) of precipitation between mid-March and mid-June, and <50 mm per month in September and October (Bonal et al., 2000). Topographic contours within the site range between 0 m and 35 m above sea level (Epron et al., 2006). This site lies on the Precambrian bedrock of Guiana shield and consists mainly of schists (Choubert, 1974).

Given the dominant plant subfamilies (Appendix A), the rainforest of Paracou belongs to the Caesalpiniaceae stage of the vegetal succession (Sabatier and Prevost, 1990). We collected samples in six different habitats, all located in the surroundings of the Paracou Research Station, so that our study deals with local scale: two in the classic *terra firme* rainforest (an undisturbed area and one disturbed by a recent huge expending treefall gap) and four monospecific non shaded plantations of exotic or Neotropical essences (plantations of acacia, cocoa, rubber and pine trees), all having a worldwide economic importance (for physical characteristics of sampled habitats, see Table 1; Appendix A).

Experimental protocol

Because it is highly recommended for ant inventories in forest-like habitats where leaf litter abounds (Delabie et al., 2000), the Winkler method was used (Bestelmeyer et al., 2000). We collected ant workers from a series of 1m² leaf-litter samples that were weighted. As it is essential to combine several sampling methods to come as near as possible to an exhaustive inventory of the litter-dwelling ant fauna (Delabie *et al.* 2000), pitfall traps were also used during the second field campaign (Bestelmeyer *et al.* 2000), but not performed at the same time than Winkler extraction. Winkler and pitfall traps sampled ants during 48 hours.

The "Ants of Leaf Litter" (ALL) Protocol (Agosti et al., 2000), which suggests using a minimum of 20 sampling points separated by 10m intervals to collect between 45 and 70% of the ant fauna at a given site (Leponce et al., 2004), was applied. We selected 50 sampling points in all of the habitats, whenever possible (Appendix A). Thus, during the field campaigns, 291 Winkler samples and pitfall traps were collected, resulting in 582 leaf-litter samples.

All of the ant samples were preserved in 70% ethanol; for each sample at least one individual per morphospecies was kept in order to constitute a reference collection. We

focused our analysis on the worker caste, since alates are difficult to identify. The ants were sorted to species or morphospecies was based on Bolton (1994). Voucher specimens were deposited in the *Laboratório de Mirmecologia*, Cocoa Research Centre CEPEC/CEPLAC (Ilhéus, Bahia, Brazil) and in the Royal Belgian Institute of Natural Sciences (RBINS; Brussels, Belgium).

Data analysis

Species × sample incidence (presence–absence) matrices

Six species × sample incidence matrices (one per habitat) were analyzed and compared between the two forests and the four plantations. Contrary to non-social insects whose individuals have an equal probability of being caught in the sampling universe, ants (like all social insects) are strongly aggregated in colonies so that, depending on the distance between the traps and the nests, colony size, and ant mobility, not all of the individuals have an equal chance of being caught; for this reason, presence/absence data are preferred over abundance data in the analyses (Longino 2000). Thus, only species occurrences (i.e., the number of times that a given species was collected at a sampled site) were taken into account, and the percentages of species occurrences per sample (i.e., for a given species: total number of occurrences in a given habitat/sample number × 100) were used as a proxy for ant abundance (Longino 2000; Leponce *et al.* 2004).

Occurrence-based rarefaction curves

The EstimateS 7.5 software (Colwell, 2005) was used to calculate occurrence-based species rarefaction curves with the Coleman method (100 randomizations of the sampling order without replacement). In order to standardize the comparisons between habitats and to estimate the sampling completeness, these curves and the Chao 2 non-parametric estimator of total species richness were plotted (Colwell et al., 2004).

Diversity and similarity of ant assemblages

Ant local (α) diversity in the four habitats was analyzed with two "traditional" non-parametric measures of diversity: Simpson's diversity index (Simpson, 1949), which is one of the most meaningful and robust index currently available (Magurran, 2004), and Shannon's equitability (Krebs, 1989). Then, all possible inter-habitats comparisons were statistically tested using a bootstrapping procedure (1000 randomizations). The global turnover between the four ant assemblages was analyzed using two β-diversity indices based on

presence/absence data (described in Koleff et al., 2003): Whittaker's (β_W=(S/α)-1; Whittaker, 1960) and the second version of Harrison's (β_{H2}=[(S/α_{max})-1]/(N-1); Harrison et al., 1992) indices. β_W is one of the simplest and the best β-diversity index (Wilson and Schmida, 1984); β_{H2} is an improvement of β_W , which was modified to become effective in analyzing pairwise differentiation between sites and insensitive to species richness trends (Magurran, 2004). All diversity indices and their pairwise comparisons were performed by using by PAST software (Hammer et al., 2001) whereas similarity pairwise comparisons between habitats by the Chao-Sorensen index (abbreviated as "CS" in the text) and its standard deviation ("SD") were calculated with the EstimateS 7.5 software (Colwell, 2005).

Modeling procedure

The Self-Organizing Map algorithm (SOM; Kohonen, 2001) is relevant to extract patterns in species assemblages using site-specific data on species occurrences (Ruggiero et al., 2008). Combining clustering and ordering abilities, the SOM is an unsupervised neural network, which transforms multi-dimensional input data into a two-dimensional map subject to a topological (neighborhood preserving) constraint (Kohonen, 2001). In order to reduce the initial number of sample units (582), we pooled Winkler and pitfall samples for each sampling point, thus creating a composite matrix of species occurrences at 291 sampling points.

The structure of the SOM consists of two layers of neurons connected by weights (or connection intensities): the input layer was composed of 245 neurons (one per ant species) connected to the 291 samples; the output layer was composed of 91 neurons (represented as hexagonal cells) organized in a grid containing 13 rows and 7 columns (Figure 2A). At the end of the learning process, samples that are next to each other on the grid are expected to have similar ant assemblages, while those located very far from each other on the grid represent different ant assemblages (see Jabiol et al., 2009 for mathematical details). The Ward algorithm was applied to the weights of the biological variables in the output neurons in order to identify the cluster boundaries on the SOM (Céréghino and Park, 2009), these clusters thus reflecting the sample classification into subsets according to the specific distribution pattern of each ant species. Figure 2B provides a gradient analysis of the distribution for each ant species. Using a qualitative, presence/absence dataset, the model calculated continuous, quantitative values between 0 and 1. More specifically, the connection intensity between input and output layers calculated during the learning process can be considered as the probability of occurrence for each species in the area concerned. The probability of occurrence for each species in a given area corresponding to the connection

intensity is shown on the SOM map in shades of grey, which therefore allowed us to analyze the effect of each variable (species) on the patterning input dataset (sites), and even to predict the probability of occurrence for each species in the sites (or clusters) where they were not consistently collected during the sampling (see Céréghino et al., 2005 for details). The optimal map size and quality of the training were assessed as per Céréghino and Park (2009).

Finally, boxplots were used to illustrate the species density by clusters, and the leaf-litter weight by m² and ant species density in cocoa plantation and other samples in clusters D and E. The mean differences were then tested using Kruskall-Wallis (H) test and Mann-Whitney pairwise comparisons.

Results

A total of 245 ant species belonging to 48 genera in 10 subfamilies, representing 4,336 occurrences, was collected (Appendix B). The most species rich subfamilies were Myrmicinae (137 species in 23 genera), Ponerinae (36 species in 5 genera), and Formicinae (32 species in 6 genera), and the most speciose genera were *Pheidole* (35 species), *Camponotus* (19), and *Pachycondyla* (13), *Solenopsis* (13) and *Strumigenys* (13). At least 26 species were recorded for the first time in French Guiana, some of them being until now recorded in only one country (e.g. *Apterostigma pariense*, *Megalomyrmex gnomus*, *Rogeria besucheti*, *Pachycondyla guianensis* or *Pac. Lunaris*; Bolton *et al.* 2006) (Appendix B).

Occurrence-based rarefaction curves and local (α) diversity of ant assemblages

The rarefaction curves for each habitat sampled steadily tended to slow down, approaching a horizontal asymptote corresponding to the total number of species in the community. The Chao 2 estimator thus confirmed that a representative part of the leaf-litter ant fauna was inventoried at the Paracou research station (Chao2 = 303.93 species; Sobs = 245 species *i.e* ≤ 80.6% of total expected richness), and in each habitat sampled (non-disturbed forest: 124 species, 70.4%; treefall gap: 101, 83.1%; acacias: 98, 78.5%; cocoa trees: 97, 85.5%; rubbers: 90, 71.5%; pines: 96, 63.4%; Figure 1). Globally, the ant fauna at Paracou was very rich (0.961 < Simpson index < 0.976). The species richness and evenness were significantly higher in the natural forest and in the cocoa plantation than in the other plantations, namely that of acacia, rubber and pine trees, while, conversely, the global occurrences of species – cocoa trees, treefall gap and non-disturbed forest: 666, 472 and 744, respectively – appeared less important than in these plantations, particularly that of acacia and rubber trees 814 and 875, respectively (Figure 1; Table 2). The species richness of treefall gap was intermediate

between that of non-disturbed forest and cocoa plantation, while the species evenness did not differ significantly. Moreover, the ant richness and evenness in acacia and pine plantations were significantly higher than that of rubber plantation, suggesting that the rubber plantation ant fauna was the more simplified compared to that of the surroundings (Table 2).

Ant assemblages of sampled habitats

After training the SOM with the species occurrence data, Ward's algorithm applied to the weight of the output neurons allowed us to identify five clusters of sites (except for cocoa trees, one per habitat; A-E: rubber trees, acacia trees, pine trees, treefall gap and preserved forest, respectively; Figure 2A). This shows that each habitat shelters a unique and homogeneous assemblage in spite of the poor global species overlap between them (β_W = 1.44; β_{H2} = 0.19). Although samples from cocoa plantation were divided into clusters D and E (38% and 60% of cocoa tree samples, respectively), they were not muddled up with other samples, but instead clearly segregated, also demonstrating the specificity of this assemblage (Figure 2A). Some frequent species belonging to common genera (e.g. *Odontomachus haematodus* or *Strumigenys denticulata*) were more or less generalist while others appeared characteristic to similar habitats, for example species noted only in plantations (e.g. *Pac. harpax*, or *Cardiocondyla obscurior*, a cosmopolitan tramp species, and *Solenopsis geminata*), or only in the natural forest (disturbed or not) (e.g. *Cam. rapax*, *Ochetomyrmex semipolitus*, *Odo. meinerti*; Figure 2B; Appendix B). Furthermore, the species diversity of some genera was "indicator" of disturbance intensity; this is the case for the most speciose genera from natural forest (*Crematogaster*, *Gnamptogenys*, *Pheidole* and *Ochetomyrmex*), or from acacia and rubber plantations (*Brachymyrmex, Camponotus*, *Nylanderia* and *Tapinoma*).

The most robust cluster boundary of the SOM map separated samples of acacia and rubber plantations (clusters A and B; Figure 2) from the other habitats. Indeed, these two very similar ant faunas, whose average species density only significantly differed from that of cluster D, showed clear dissimilarities in the global composition of ant fauna with other habitats (Figure 3; Table 3). Thus, 59 more or less frequent species (24% of all species collected at Paracou) were characteristic to either cluster A or B or both of them. Among them we noted in the acacia plantation several arboreal species (*Cephalotes*, *Crematogaster*, *Dolichoderus* and *Pseudomyrmex* genera). Otherwise, we noted species adapted to open areas (some *Camponotus* species, *Ectatomma brunneum* and *Ect. tuberculatum*), or to disturbed ecosystems (i.e. opportunists; *Linepithema neotropicum*, *Nylanderia* and *Brachymyrmex* species). We even noted tramp species (e.g. *Cardiocondyla obscurior*) or potentially invasive

ants, such as *Atta cephalotes* (only in rubber plantation) or *Wasmannia auropunctata* (Figure 2B; Appendix B). Although very similar and characterized by an equivalent species density, acacia and rubber plantations sheltered their own "poor" specific ant assemblage, apparently the most altered comparing to natural ant faunas.

The second group of clusters gathered samples from natural (disturbed and undisturbed) forest and plantations of cocoa and pine trees. Indeed, despite the lowest average species density of cluster D, the similarity between the treefall gap and non-disturbed forest ant faunas as well as that of pines with both of them was among the highest (Figure 3; Table 3), and some more or less frequent species were characteristic of these habitats, including forest generalists and predators. The pine tree ant fauna differed from the others by noticeably more cryptic species (43% of species; 38% for natural forest habitats and less for the others), less attines and generalists (including opportunists) and particularly numerous specific species of more or less specialized predators (50% of all species collected and 61% of pine specific species) (e.g. *Carebara*, *Hypoponera* and *Pachycondyla* species, *Acanthognathus brevicornis*, *Basiceros bolaui*, *Discothyrea denticulata* and *Ect. Lugens*). Moreover, clusters D and E gathered three different ant assemblages: that of non-disturbed forest and treefall gap with numerous specific species and that of cocoa plantation (25 characteristic species, i.e. 26% of all species collected in cocoa plantation; e.g. several *Rogeria* and *Typhlomyrmex* species, *Sol. Globularia*). Although the cocoa plantation shared several species with non-disturbed forest, it also sheltered a frequent potentially invasive fire ant, *Sol. saevissima* (Figure 2B, Appendix B).

The clustering of the samples collected in the cocoa plantation coherently reflected their spatial distribution during sampling: all samples in cluster D (with treefall gap samples) were collected near the plantation edge while that in cluster E (with non-disturbed forest samples) were collected in the depths of the plantation (Appendix C). It was corroborated by the significant difference of litter weight between cocoa plantation samples and those from other plantations (clusters D and E; Figure 4A). We noted (1) significant differences in species richness of the cocoa tree plantation from Cluster D (62 species) and Cluster E (83 species) compared to other samples (Cluster D and E: 108 and 127 species, respectively) (Figure 4B), and also (2) variations in species composition between the cocoa tree plantation and other samples from cluster D and E (one rare species shared; seven species shared, respectively). Yet, the global composition of both cocoa tree and other samples from clusters D and E were much more similar than with the other samples of the same cluster (inter-cocoas CS = 0.84; inter-"other samples" = 0.83; cluster D: CS = 0.65; cluster E: CS = 0.69).

Discussion

To date, our study is the first using SOM as a powerful tool to study both the impact of natural forest disturbance (treefall gap) and forest transformation into plantations over terrestrial entomofauna, and particularly leaf-litter ant communities. Moreover, although our survey lacks replicates for each habitat type, our fairly complete and so representative ant sampling led to the emergence of obvious, well statistically-supported patterns, which might not be detected by other statistic methods, due to the low global species overlap between habitats. The SOM analysis thus enabled us to detect and distinguish the ant species subset affected by edge effect to that dwelling in the center of the cocoa plantation, as previously pointed out in other agroecosystems (Golden and Crist, 2000).

Our results illustrate the global impact of habitat disturbance caused either by treefall gap or forest replacement by monospecific plantations, namely a decline of species richness and evenness, an increase of species abundance from forest to plantations, that of treefall gap being intermediate. We also noted a noticeable change in species composition, especially in acacia, rubber and pine tree plantations. We thus corroborated the fact that human disturbance results in greater changes in ant species composition than natural disturbances (e.g. treefall gaps, fire, short floods; Philpott et al., 2010). As previously showed (Delabie et al., 2009), the reduced diversity of *Pheidole* appeared as a good "indicator" of disturbance in Amazon forests. Moreover, in the treefall gap and the plantations, we classically noted the loss of native forest ant species (e.g. *Och. semipolitus*) corresponding to the elimination of ecologically specialized ants (Philpott et al., 2010). This consequently favored generalist species (e.g. belonging to the genera *Brachymyrmex*, *Camponotus*, *Nylanderia*, *Pheidole*, *Solenopsis*) that are sufficiently tolerant to persist in altered habitat conditions (Feener and Schupp, 1998; Sinclair and New, 2004). They presumably take advantage of changing resource bases, especially when disturbance puts them very competitive (Hoffmann and Andersen, 2003). This also favored non-forest species (e.g. *Ect. Brunneum*; Vasconcelos et al., 2000), some of them belonging to drier Neotropical biomes (e.g. savannas or sea-shore habitats; species belonging to the *Myrmaphaenus* subgenus of *Camponotus*: *Cam. fastigatus*, *Cam. leydigi* and *Cam.* spp.; Delabie, unpublished data).

As recurrently showed, in all sampled plantations, the similar factors causing the loss of native species facilitated the proliferation of disturbance-tolerant native species(e.g. *Atta cephalotes* in the rubber tree plantation; *Ect. Brunneum* and *Was. Auropunctata* both in the acacia and rubber tree plantations; *Pac. harpax*, *Och. Neopolitus* in the pine tree plantation; *Sol. geminata* in all plantations; *Sol. saevissima* which characterizes all anthropized areas of

the Amazonian Basin; Delabie et al., 2009). They also facilitated the invasion by tramp ants (e.g. *Cardiocondyla oscurior*; Philpott et al., 2010) that were never found in natural treefall gaps (Feener and Schupp, 1998; this study). Despite these widely recognized general trends, our results also showed that alteration of native leaf-litter ant community may strongly depend on the monospecific plantation type leading to habitat-specific leaf-litter ant assemblages.

While the deep alteration of ant assemblages in acacia and rubber plantations highlighted once again the harmful impact of monocultures over ground-dwelling fauna (Corley et al., 2006; Brühl and Eltz, 2009), the pine ant fauna was surprising by its strong similarity to that of natural forest. Indeed, pine trees generally shelters dramatically reduced ground-dwelling ant communities compared to native forest (Sinclair and New, 2004; Corley et al., 2006). This is due to the extremely simplified understorey and the hard microhabitat conditions for bacterial, fungal and faunal diversity to develop due to allelopathic effects caused by the pine needles (Rice, 1984; Nissanka et al., 2005). Our pine tree ant assemblage distinguished from the other plantations by its unexpected high diversity of predator and a particularly high proportion of cryptic specialized taxa, including species of Basicerotini, Dacetini (Myrmicinae) and Proceratiinae (Pacheco et al., 2009). Also, the low level of Attini is due to the chemical properties of pine resin that hinder the cultivation of the symbiotic fungus (Hernández et al., 1999).

Our survey confirms that the cacao plantation is one of the best compromise between agriculture and conservation of native leaf-litter ant fauna in tropical forests (Philpott and Armbrecht, 2006; Delabie et al., 2007). Indeed, some frequent recorded species belonging to emblematic cryptic genera (e.g. *Typhlomyrmex*) highlighted that cocoa trees actually provide valuable habitat to maintaining the diversity of specialist hypogaeous ants and their trophic interactions (Delabie et al., 2007). This conservation potential would be greatly improved by using shaded trees (Philpott and Armbrecht, 2006; Delabie et al., 2007). However, in spite of their conservation value, cocoa plantations also commonly shelter generalist, opportunistic species, numerically and behaviorally dominant that play a structuring role in organism communities (Schoereder et al., 2004). This is the case for *Was. auropunctata* and *Sol. Geminata*, both having the ability to be invasive even in their native range (Orivel et al. 2009).

Conclusions

In this study, we advocate, that some agroforests (e.g. cocoa plantations) can provide a high-quality matrix within which biodiversity is conserved (Philpott and Armbrecht, 2006;

Schroth et al., 2011). Additionally, shaded cocoa plantations can play a role of ecological corridors in case of tropical forest fragmentation (Delabie et al., 2007; Cassano et al., 2008), facilitating fragment interconnectivity and consequently biodiversity maintenance, especially in Neotropical areas (Perfecto and Vandermeer, 1996). However, the contribution of cocoa agroecosystems to the conservation of biodiversity is dependent on their structure, composition and management, as well as on the quantity, quality and location of remnants of native forest habitat in the landscape (Schroth and Harvey, 2007). Finally, through this study we also highlighted the usefulness of a powerful statistical tool for analyzing the impact of natural and anthropogenic disturbances over native leaf-litter ant communities of Amazon forest.

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Appendices A., B., C. Supplementary materials

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Figure captions

Fig. 1. Occurence-based rarefaction curves representing the number of species collected in each habitat (N = 100 samples for all sampled environments except for the treefall gap and the cocoa plantation, N = 98 and 84 samples, respectively).

Fig. 2. (A) Distribution of samples (e.g. Aech1, Hech3; CHAech20, etc.) on the self-organizing map (SOM) according to the ant species, and clustering of the trained SOM; samples from cocoa plantation are encircled with a black line. (B) Synthetic gradient analysis of density for each species on the trained SOM, represented by a shaded scale (dark = high values, light = low values). Each small map (corresponding to one species) is to compared to (or to superimposed onto) the map representing the distribution of samples presented in Figure 2A, thus showing the occurrence probabilities for each species (in shades of grey) within each cluster. [1-13] refer to characteristic species of cluster(s) which are listed in Appendix B.

Fig. 3. Boxplots (box: median, 25th and 75th percentiles; whiskers: 90th and 10th percentiles; points: outliers) representing the species density by cluster of the trained SOM ($H=47.8$; $p<0.0001$, different letters indicate significant differences).

Fig. 4. Boxplots (box: median, 25th and 75th percentiles; whiskers: 90th and 10th percentiles; points: outliers) representing the sifted leaf-litter weight in 1m² quadrates (A) and species density (B) for cocoa tree and other samples in clusters D and E (Kruskall-Wallis test: $H_{\text{litter weight}}=14.34$, $H_{\text{species density}}=47.95$; $p<0.0001$, different letters indicate significant difference).

Fig. 1.

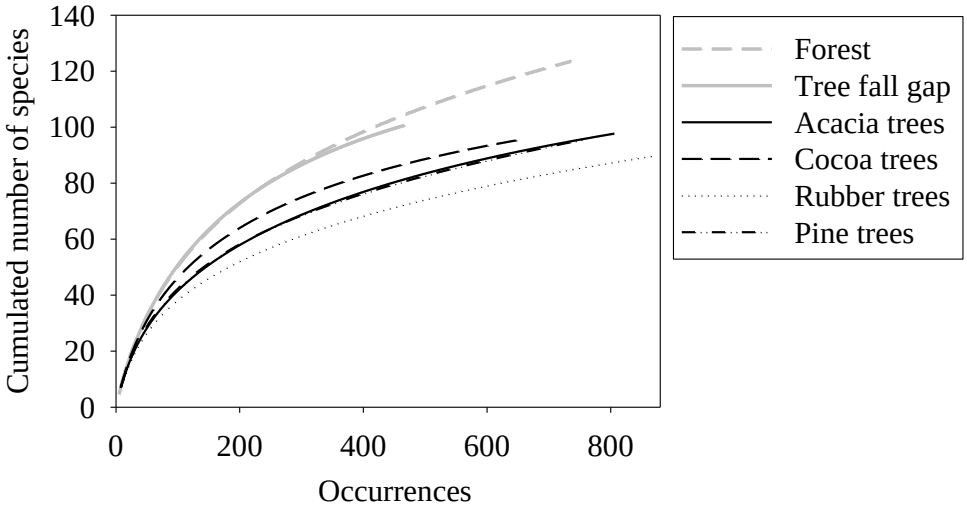

Cumulated number of species
140
120
100
80
60
40
20
0
0
200
400
600
800
Occurrences
Forest
Tree fall gap
Acacia trees
Cocoa trees
Rubber trees
Pine trees

Fig. 2.

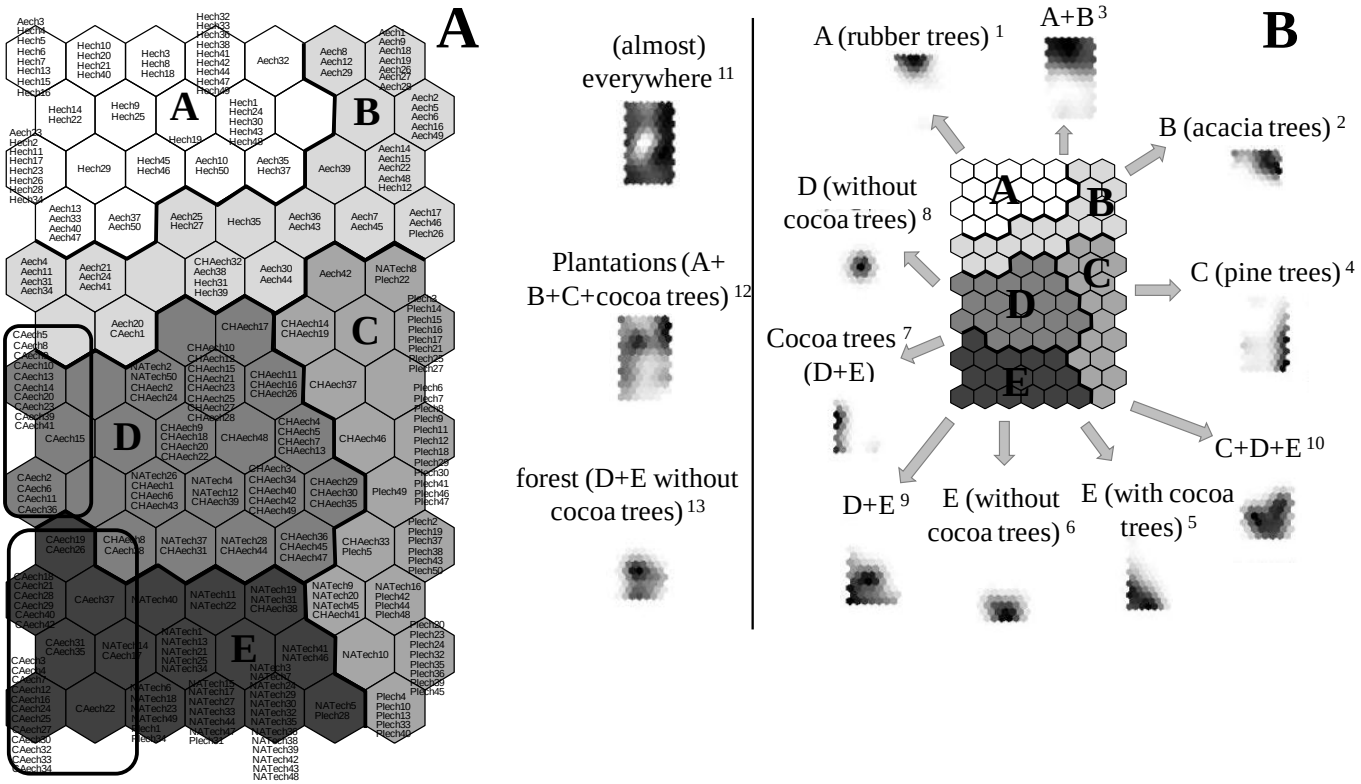

A
B
(almost) everywhere 11
Plantations (A+ B+C+cocoa trees) 12
forest (D+E without cocoa trees) 13
A (rubber trees) 1
A+B 3
B (acacia trees) 2
D (without cocoa trees) 8
C (pine trees) 4
Cocoa trees (D+E) 7
C+D+E 10
D+E 9
E (without cocoa trees) 6
E (with cocoa trees) 5

Fig. 3.

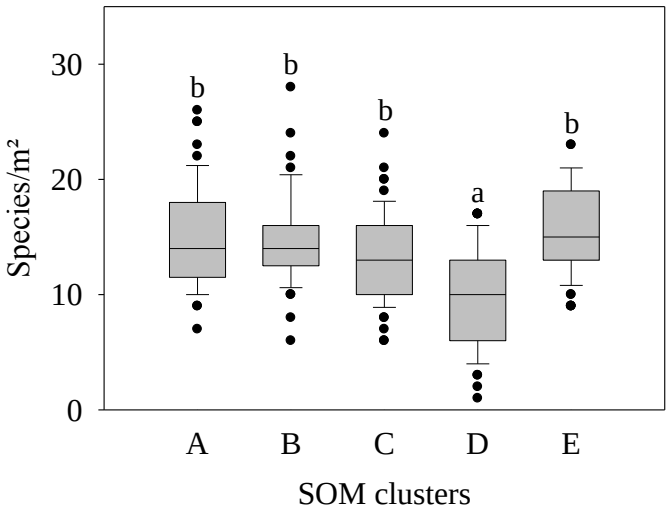


Fig. 4.

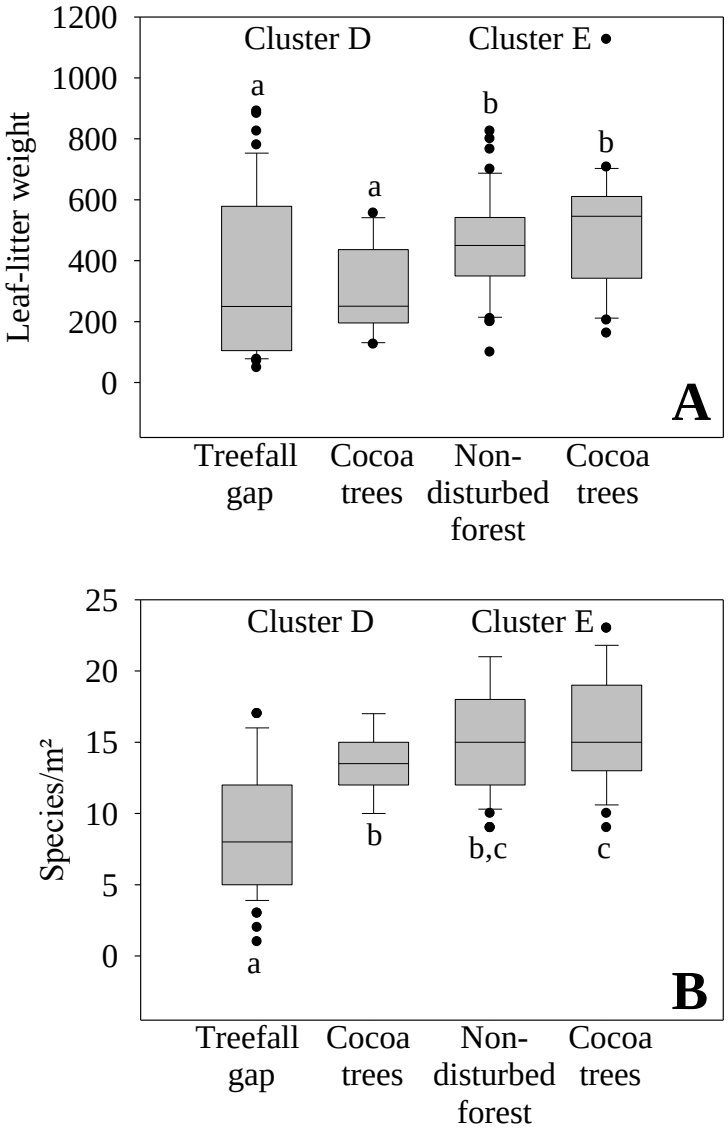

Cluster D
Cluster E
Leaf-litter weight
1200
1000
800
600
400
200
0
a
a
b
b
A
Treefall gap
Cocoa trees
Non-disturbed forest
Cocoa trees
Cluster D
Cluster E
Species/m²
25
20
15
10
5
0
a
b
b,c
c
B
Treefall gap
Cocoa trees
Non-disturbed forest
Cocoa trees

Table 1

Physical characteristics of the habitats sampled.

	Natural rainforest		Monospecific plantations			
	Undisturbed forest	Treefall gap	Cocoa trees	Pine trees	Acacia trees	Rubber trees
Area	surrounding matrix	< 1 Ha	< 1 Ha	1-2 Ha	1-2 Ha	1-2 Ha
Vegetation structure						
* big tall trees	abundant	Absent	/	/	/	/
* canopy	closed	Open	not continuous	closed	not continuous	open
* ground incident light	+	++	++	+	++	+++
* rainfall water on ground	+	++	++	+	++	+++
* dead wood on ground	++	+++	+	+	++	+
* understorey	very complex	Pioneer vegetation	absent	Heliconiaceae flowers	virtually absent	absent
Leaf-litter						
* humidity	+++	+	+++	+++	++	+
* thickness	++	+++	+++	+++	++	+
* decomposition/ fragmentation	+++	++	++	+	++	+
Plantations						
* age	/	/	rather old	rather old	very old	very old

* spatial structuration of trees	/	/	rows	rather randomly	rather randomly	rows
* shade trees	/	/	absent	absent	absent	absent
* epiphytes	/	/	absent	absent	absent	absent

Table 2

P-values associated with the pairwise comparisons of the α-diversity indices computed between ant assemblages of each sampled habitat (significant *P*-values are in bold).

Diversity index	Habitat	Forest	Treefall gap	Acacia trees	Cocoa trees	Rubber trees
Equitability H	Forest	×	×	×	×	×
	Treefall gap	0.152	×	×	×	×
	Acacias	0.006	0.002	×	×	×
	Cocoa trees	0.407	0.312	0.001	×	×
	Rubbers	0	0	0.158	0	×
	Pines	0.045	0.003	0.282	0.011	0.019
Simpson index	Forest	×	×	×	×	×
	Treefall gap	0.445	×	×	×	×
	Acacias	0	0.002	×	×	×
	Cocoa trees	0.108	0.587	0.004	×	×
	Rubbers	0	0	0.036	0	×
	Pines	0.001	0.027	0.342	0.023	0.002

Table 3

Similarity matrix based on Chao-Sorensen index (± SD) for inter-habitat pairwise comparisons.

	Preserved forest	Treefall gap	Acacia trees	Cacao trees	Rubber trees	Pine trees
Preserved forest	×	0.84 ± 0.04	0.69 ± 0.07	0.67 ± 0.06	0.63 ± 0.01	0.85 ± 0.07
Treefall gap		×	0.70 ± 0.07	0.69 ± 0.06	0.68 ± 0.08	0.89 ± 0.05
Acacia trees			×	0.76 ± 0.08	0.94 ± 0.02	0.82 ± 0.06
Cacao trees				×	0.84 ± 0.08	0.9 ± 0.06
Rubber trees						0.76 ± 0.08

Appendix A. Characteristics of protocol applied and sampled habitats.

Habitat type	Dominant vegetation	Samples		
		Number[(b)]	Sampling period	
			Winkler	Pitfall traps
Lowland rainforest				
Natural rainforest	Lecythydaceae (15.7%), Caesalpiniaceae (13.7%), Chrysobalanaceae (11.3%), Clusiaceae (5.9%), Euphorbiaceae (5.5%), Sapotaceae (5.5%)[(a)]	100	April 2009	November 2009
Treefall gap		98	March 2009	September 2009
Plantations				
Acacia trees	*Acacia crassicarpa*, *A. mangium*	100	April 2009	February 2010
Cocoa trees	*Theobroma cacao*	84	March 2010	October 2009
Rubber trees	*Hevea brasiliensis*	100	April 2009	February 2010
Pine trees	*Pinus caribaea*	100	March 2010	March 2010

[(a)] Morneau, F., 2007. Effets d'un gradient d'engorgement sur la structure et la dynamique d'une forêt tropicale humide (Paracou, Guyane française). PhD., EcoFoG, Kourou.

[(b)] 50% Winkler samples, 50% pitfall traps

Appendix B. Species collected in each habitat of the Paracou Research Station, according to their taxonomic classification, and the SOM clusters they characterize in Figure 2B (the most frequent are written in bold). The first column indicates the species firstly recorded at the Nouragues Research Station, another French Guianese rainforest (NRS; see Groc et al., 2009[(a)], in prep.[(b)]) and those collected for the first time in French Guiana (nsg).

Appendix B. Species collected in each habitat of the Paracou Research Station, according to their taxonomic classification, and the SOM clusters they characterize in Figure 2B (the most frequent are written in bold). The first column indicates the species firstly recorded at the Nouragues Research Station, another French Guianese rainforest (NRS; see Groc et al., 2009[(a)], in prep.[(b)]) and those collected for the first time in French Guiana (nsg).

		SOM (Fig. 2B)	Habitats					
			Preserved forest		Plantations			
			Preserved forest	Treefall gap	Acacias	Cocoa trees	Rubbers	Pines
AMBLYOPONINAE Forel								
	Amblyoponini Forel							
	Prionopelta sp.1	6	1	0	0	0	0	0
CERAPACHYINAE Forel								
	Acanthostichini Emery							
	Acanthostichus sp.1 cf *brevicornis*	6	1	0	0	0	0	0
	Cerapachyini Forel							
nsg	*Cerapachys neotropicus* Weber	6	1	0	0	0	0	0
DOLICHODERINAE Forel								
	Dolichoderini Forel							

	Azteca sp.1	4	1	0	0	0	0	1
	Azteca sp.2	4	2	0	0	0	0	4
	Azteca sp.3	5	1	0	0	0	0	0
	Dolichoderus bidens (Linnaeus)	2	0	0	1	0	0	0
	Dolichoderus bispinosus (Olivier)	2	0	1	4	1	0	1
	Dolichoderus debilis Emery	7	0	0	0	1	0	0
	Dolichoderus decollatus Smith		1	0	0	0	0	1
NRS	*Dolichoderus imitator* Emery	12	2	0	18	5	3	3
	Dolichoderus lutosus (Smith)	8	1	0	0	0	0	0
	Linepithema neotropicum Wild (Fabricius)	1	0	0	0	6	8	0
ECITONINAE Forel								
	Ecitonini Forel							
	Labidus coecus (Latreille)	3	0	0	8	0	2	0
nsg	*Neivamyrmex diana* (Forel)	3	0	0	0	0	1	0
	Neivamyrmex iridescens Borgmeier	7	0	0	0	4	1	1
	Neivamyrmex sp. nov.	2	0	0	1	0	0	0
ECTATOMMINAE Emery								
	Ectatommini Emery							
	Ectatomma brunneum Smith	3	0	0	58	11	55	2

	Ectatomma edentatum Roger	[6]	22	3	0	0	0	1
	Ectatomma lugens Emery	[4]	2	2	0	0	0	11
	Ectatomma tuberculatum (Olivier)	[3]	1	0	6	2	16	5
	Gnamptogenys acuminata (Emery)	[2]	1	0	4	0	0	1
NRS	*Gnamptogenys continua* (Mayr)	[4]	0	1	0	0	0	0
NRS	*Gnamptogenys haenschei* (Emery)		1	0	0	0	0	0
	Gnamptogenys horni (Santschi)		8	11	10	0	1	0
NRS	*Gnamptogenys mecotyle* Brown		0	0	1	0	0	1
	Gnamptogenys minuta (Emery)	[7]	1	0	0	2	1	0
NRS	*Gnamptogenys pleurodon* (Emery)	[8]	0	2	0	0	0	0
NRS	*Gnamptogenys porcata* (Emery)	[13]	2	0	0	0	0	0
NRS	*Gnamptogenys relicta* (Mann)		22	2	0	0	0	13
	Gnamptogenys tortuolosa (Smith)	[9]	6	3	0	7	0	2
	Gnamptogenys sp.10		2	0	0	0	0	0
	Gnamptogenys sp.13	[5]	0	0	0	0	0	1
	Typhlomyrmecini Emery							
	Typhlomyrmex schmidti Menozzi	[7]	0	0	0	2	0	0
	Typhlomyrmex sp. nov1 (*sensu* Lacau S., unpublished)	[7]	0	0	0	3	0	0
	Typhlomyrmex sp. nov.		0	0	0	1	0	1

FORMICINAE Latreille								
	Camponotini Forel							
	Camponotus atriceps (Smith)	2	3	0	2	0	0	0
nsg	*Camponotus crassus* Mayr	2	0	0	4	0	2	0
	Camponotus fastigatus Roger	1	0	0	3	0	8	0
	Camponotus femoratus (Fabricius)	6	1	0	0	0	0	0
	Camponotus latangulus Roger	6	1	0	0	0	0	0
	Camponotus leydigi Forel	1	0	0	2	1	5	0
NRS	*Camponotus lespesii* Forel		0	1	0	0	0	0
NRS	*Camponotus melanoticus* Emery		0	0	0	5	3	1
	Camponotus nidulans (Smith)	13	2	1	0	0	0	0
	Camponotus rapax (Fabricius)	13	10	2	0	0	0	0
	Camponotus renggeri Emery	11	4	1	3	0	1	0
	Camponotus rectangularis Emery	3	0	0	1	0	4	0
	Camponotus (Myrmaphaenus) sp.4	7	0	0	3	4	2	0
	Camponotus (*Myrmaphaenus*) sp.5	1	0	0	0	0	1	0
	Camponotus sp.7 comp. *paradoxus*	2	1	0	2	0	0	0
	Camponotus sp. cf *atriceps*	11	2	4	2	1	0	0
	Camponotus (*Tanaemyrmex*) sp.17	4	0	0	0	0	0	1
	Camponotus sp.18	2	0	0	0	0	1	0

	Camponotus (*Myrmobrachys*) sp.20	[6]	0	0	0	1	0	0
	Gigantiopini Ashmead							
	Gigantiops destructor (Fabricius)	[12]	0	0	16	1	6	7
	Lasiini Ashmead							
NRS	*Acropyga decedens* (Mayr)		0	2	0	0	0	0
NRS	*Acropyga fuhrmanni* (Forel)		0	2	0	0	0	0
	Plagiolepidini Forel							
	Brachymyrmex heeri Forel	[3]	0	0	1	0	6	3
	Brachymyrmex patagonicus Mayr	[3]	0	0	6	1	23	0
	Brachymyrmex sp.2 cf *heeri*	[1]	3	2	4	2	19	4
	Brachymyrmex sp.4	[3]	0	0	1	0	1	0
	Myrmelachista sp.	[8]	0	1	0	0	0	0
NRS	*Nylanderia guatemalensis* (Forel)	[2]	0	0	1	0	0	0
	Nylanderia sp.2 cf *guatemalensis*	[2]	0	0	0	0	1	0
	Nylanderia sp.3	[11]	0	4	6	0	2	1
	Nylanderia sp.5	[11]	36	8	45	15	61	34
	Nylanderia sp.6	[3]	0	1	1	0	2	0
MYRMICINAE Lepeletier								
	Attini Smith							
nsg	*Acromyrmex rugosus* (Smith)		0	1	0	0	0	0

nsg	*Apterostigma pariense* Lattke		2	0	1	0	1	0
	Apterostigma urichii Forel	5	1	0	0	1	0	0
	Apterostigma sp.1 comp. *pilosum*	2	0	0	6	0	0	0
	Apterostigma sp.2 comp. *pilosum*	7	2	2	4	13	5	2
	Apterostigma sp.3 comp. *pilosum*	3	3	0	2	0	2	0
	Atta cephalotes (Linnaeus)	1	1	0	6	0	32	0
nsg	*Cyphomyrmex costatus* Mann	6	4	0	0	0	0	0
NRS	*Cyphomyrmex flavidus* Pergande	3	9	6	23	4	39	12
NRS	*Cyphomyrmex peltatus* Kempf		3	0	0	0	1	1
NRS	*Cyphomyrmex transversus* Emery	3	3	6	37	11	45	17
	Mycocepurus smithii (Forel)	8	0	2	0	0	0	0
	Myrmicocrypta sp.1		0	1	0	7	8	0
	Myrmicocrypta sp.2	6	6	3	0	0	0	0
	Myrmicocrypta sp.3	7	0	1	0	3	0	0
	Myrmicocrypta sp.5	8	0	4	0	0	0	0
	Myrmicocrypta sp.9	1	0	0	0	0	1	0
	Myrmicocrypta sp.10	1	1	0	0	0	1	0
	Sericomyrmex sp.1	4	1	4	0	0	0	1
	Sericomyrmex sp.2	10	5	3	2	5	0	11
	Sericomyrmex sp.3		3	3	0	0	0	2

	Sericomyrmex sp.5	[13]	0	1	0	0	0	0
NRS	*Trachymyrmex compactus* Mayhé-Nunes and Brandão	[6]	1	0	0	0	0	0
	Trachymyrmex cornetzi (Forel)	[11]	9	2	3	1	1	5
NRS	*Trachymyrmex farinosus* (Emery)	[11]	2	4	2	1	3	1
NRS	*Trachymyrmex mandibularis* Weber	[11]	5	4	1	6	2	1
	Trachymyrmex relictus Borgmeier		0	2	0	6	21	0
	Trachymyrmex sp.6	[7]	0	0	0	2	0	0
	Basicerotini Brown							
	Basiceros balzani (Emery)	[7]	3	0	0	5	0	0
	Basiceros betschi (Perrault)		10	5	1	1	0	6
	Basiceros bolaui (Mayr)	[4]	0	0	0	0	0	1
	Basiceros emeryi (Forel)		0	0	0	6	0	6
	Basiceros sp.1	[13]	2	2	0	0	0	0
	Blepharidattini Wheeler and Wheeler							
	Wasmannia auropunctata (Roger)	[3]	6	8	58	2	93	21
NRS	*Wasmannia scrobifera* Kempf	[7]	1	0	0	1	0	0
	Cephalotini Smith							
	Cephalotes atratus (Linnaeus)	[2]	0	0	1	0	0	0
NRS	*Cephalotes maculatus* (Smith)	[2]	0	0	1	0	0	0

nsg	*Cephalotes minutus* (Fabricius)		1	0	1	1	0	0
nsg	*Cephalotes pallidoides* De Andrade	8	0	1	0	0	0	0
nsg	*Cephalotes pallidus* De Andrade	6	0	0	0	1	0	0
	Cephalotes spinosus (Mayr)	2	0	0	1	0	0	0
	Crematogastrini Forel							
	Crematogaster abstinens Forel	7	0	0	0	3	1	0
NRS	*Crematogaster brasiliensis* Mayr	7	0	0	0	2	0	0
NRS	*Crematogaster carinata* Mayr	13	34	8	1	0	0	0
NRS	*Crematogaster flavosensitiva* Longino		12	9	15	11	2	14
NRS	*Crematogaster limata* Smith	12	3	4	18	10	11	10
NRS	*Crematogaster sotobosque* Longino	10	10	15	0	0	0	2
nsg	*Crematogaster stolli* Forel	6	1	0	0	0	0	0
NRS	*Crematogaster tenuicula* Forel	4	1	0	0	0	0	3
	Crematogaster sp. gp. *bryophilia*	2	1	1	2	0	0	1
	Crematogaster sp. gp. *limata*	6	1	0	0	0	0	0
	Crematogaster sp.8	8	0	2	0	0	0	0
	Dacetini Forel							
NRS	*Acanthognathus brevicornis* Smith	4	0	0	0	0	0	5
	Pyramica auctidens Bolton	13	2	3	0	0	0	1
NRS	*Pyramica beebei* (Wheeler)	6	1	0	0	0	0	0

NRS	*Pyramica crassicornis* Mayr	[3]	0	0	0	0	1	0
	Pyramica denticulata Mayr	[11]	34	29	49	38	32	48
NRS	*Pyramica hadrodens* Bolton		1	3	0	0	0	0
	Pyramica subedentata (Mayr)	[1]	1	3	4	0	6	0
	Pyramica villiersi (Perrault)	[6]	1	0	0	0	0	0
nsg	*Strumigenys cordovensis* Mayr		0	0	3	2	3	0
NRS	*Strumigenys elongata* Roger	[2]	4	5	19	0	0	3
NRS	*Strumigenys perparva* Brown	[10]	7	5	0	26	0	12
NRS	*Strumigenys saliens* Mayr	[1]	0	0	0	0	1	0
nsg	*Strumigenys trinidadensis* Wheeler	[3]	0	0	2	0	1	0
	Strumigenys sp.1 cf *microthrix*	[3]	0	0	2	0	18	0
	Formicoxenini Forel							
nsg	*Cardiocondyla obscurior* Wheeler	[7]	0	0	0	5	2	0
nsg	*Nesomyrmex wilda* (Smith)	[3]	0	0	0	0	2	0
	Ochetomyrmex neopolitus	[4]	3	2	2	3	1	49
	Fernández							
	Ochetomyrmex semipolitus Mayr	[13]	9	5	0	0	0	0
	Myrmicini Lepeletier							
NRS	*Hylomyrma balzani* (Emery)	[3]	0	0	25	4	5	0
NRS	*Hylomyrma immanis* Kempf	[4]	0	0	0	0	0	3

NRS	*Hylomyrma reginae* Kutter	6	5	0	0	0	0	0
	Pheidolini Emery							
NRS	*Pheidole allarmata* Wilson	6	11	1	0	1	0	4
NRS	*Pheidole bruesi* Wheeler		6	2	8	1	1	37
nsg	*Pheidole cramptoni* Wheeler	11	9	9	3	5	8	7
NRS	*Pheidole gigas* Wilson	7	5	12	0	44	1	1
nsg	*Pheidole impressa* Mayr	5	7	0	0	9	0	0
NRS	*Pheidole midas* Wilson	10	13	7	1	0	2	22
NRS	*Pheidole rubiceps* Wilson	5	8	0	0	6	0	0
NRS	*Pheidole scolioceps* Wilson	6	8	0	0	0	0	0
NRS	*Pheidole synarmata* Wilson	10	2	2	0	1	0	0
NRS	*Pheidole terribilis* Wilson	4	1	3	0	0	0	0
NRS	*Pheidole transversostriata* Mayr	11	10	15	6	2	3	1
	Pheidole sp. cf *brandao*	5	1	0	0	2	0	0
	Pheidole sp.4 gp. *fallax*	8	1	1	0	0	0	0
	Pheidole sp.5 gp. *diligens*	3	0	0	2	0	0	0
	Pheidole sp.10	8	0	1	0	0	0	0
	Pheidole sp.11 gp. *flavens*	5	35	0	1	27	0	0
	Pheidole sp.13 gp. *tristis*	8	0	1	0	0	0	0
	Pheidole sp.19 gp. *flavens*	8	1	2	0	0	0	0

	Pheidole sp.25 gp. *flavens*		0	0	1	0	0	1
	Pheidole sp.26 gp. *tristis*	7	0	0	0	1	0	0
	Pheidole sp.27 gp. *tristis*	6	0	2	0	0	0	0
	Pheidole sp.29	6	1	0	0	0	0	0
	Pheidole sp.30 cf *transversostriata*	3	2	3	31	14	44	0
	Pheidole sp.32 comp. *subarmata*	8	1	5	0	0	0	0
	Pheidole sp.33 gp. *flavens*	6	2	0	0	0	0	0
	Pheidole sp.34 gp. *flavens*	6	1	0	0	0	0	0
	Pheidole sp.35 gp. *tristis*	8	0	1	0	0	0	0
	Pheidole sp.37 gp. *diligens*	6	10	0	0	0	0	1
	Pheidole sp.40 comp. *flavens*	11	35	32	22	12	10	40
	Pheidole sp.41 comp. *flavens*	10	9	22	0	6	0	21
	Pheidole sp.51		1	0	3	0	0	2
	Pheidole sp.52		0	0	0	1	1	0
	Pheidole sp.53	1	0	0	0	0	1	0
	Pheidole sp.54	6	1	0	0	0	0	0
	Pheidole sp.57 gp. *fallax*	4	0	0	0	0	0	1
	Solenopsidini Forel							
NRS	*Carebara urichi* (Wheeler)	4	0	0	0	0	0	4
	Carebara sp.2 gp. e*scherichi*	7	0	0	1	11	1	0

	Carebara sp.3 cf *peruviana*	[6]	1	0	0	0	0	1
	Carebara sp.4 gp. *lignata*	[4]	0	0	0	0	0	13
nsg	*Megalomyrmex cuatiara* Brandão		3	0	2	0	0	0
	Megalomyrmex drifti Kempf	[4]	1	3	2	0	0	4
nsg	*Megalomyrmex gnomus* Kempf		0	0	0	1	0	3
	Megalomyrmex silvestrii Wheeler		0	0	0	3	3	0
	Megalomyrmex sp. gp. *modestus*	[2]	0	0	3	0	0	0
	Solenopsis geminata (Fabricius)	[1]	0	1	8	11	24	0
nsg	*Solenopsis globularia* (Smith)	[7]	0	0	0	1	0	0
	Solenopsis saevissima (Smith)	[7]	0	0	0	4	0	0
NRS	*Solenopsis virulens* (Smith)	[7]	0	0	0	2	0	0
	Solenopsis sp. gp. *pygmaea*	[12]	0	1	9	13	4	6
	Solenopsis sp.6		3	0	0	0	0	0
	Solenopsis sp.9	[6]	0	0	0	0	1	0
	Solenopsis sp.12	[10]	7	2	4	1	0	15
	Solenopsis sp.13	[6]	0	1	0	0	0	0
	Solenopsis sp.15	[11]	38	26	46	36	39	43
	Solenopsis sp.16	[11]	14	8	0	8	3	4
	Solenopsis sp.18	[1]	5	0	1	3	15	7
	Solenopsis sp.28		36	29	44	30	24	47

	Stenammini Ashmead							
nsg	*Rogeria besucheti* Kugler	[7]	0	0	1	7	0	1
	Rogeria blanda (Smith)	[2]	0	0	1	0	0	0
nsg	*Rogeria foreli* (Mayr)	[2]	0	0	4	0	1	0
NRS	*Rogeria lirata* Kugler		5	1	0	0	0	4
NRS	*Rogeria tonduzi* Forel	[7]	0	2	0	9	0	1
	Rogeria sp.7		0	0	1	0	0	0
	Rogeria sp.10 cf *besucheti*	[7]	1	0	0	2	0	1
PONERINAE Lepeletier								
	Ponerini Lepeletier							
	Anochetus bispinosus (Smith)	[11]	0	8	9	25	18	4
NRS	*Anochetus horridus* Kempf	[10]	2	3	0	2	0	1
NRS	*Anochetus inermis* André		4	1	0	0	0	0
	Anochetus mayri Emery	[7]	0	0	0	1	0	0
NRS	*Anochetus neglectus* Emery		6	6	1	3	0	3
NRS	*Hypoponera opacior* (Forel)		0	0	0	0	0	2
	Hypoponera sp.1		0	0	15	24	13	8
	Hypoponera sp.2		2	8	3	4	0	0
	Hypoponera sp.3	[2]	0	0	11	0	1	0
	Hypoponera sp.4	[7]	0	0	0	3	0	0

	Hypoponera sp.5	8	1	3	0	0	0	0
	Hypoponera sp.6 gp. *foreli*	11	10	5	8	0	1	2
	Hypoponera sp.8	5	31	0	0	20	0	10
	Hypoponera sp.9	4	1	6	0	0	0	13
	Hypoponera sp.10	3	0	1	12	0	3	0
	Leptogenys langi Wheeler		0	1	0	2	0	1
nsg	*Leptogenys pusilla* Emery	7	0	0	0	1	0	0
	Leptogenys sp. - CPDC #1706	2	0	0	1	0	0	0
	Leptogenys sp.3		0	0	1	0	0	1
nsg	*Odontomachus brunneus* (Patton)	2	0	0	1	0	0	0
	Odontomachus haematodus (Linnaeus)	11	7	7	2	23	11	0
NRS	*Odontomachus meinerti* Forel	13	4	1	0	0	0	0
	Pachycondyla constricta (Mayr)		0	5	16	2	6	1
	Pachycondyla crassinoda (Latreille)	11	10	1	10	0	8	12
nsg	*Pachycondyla ferruginea* (Smith)	8	0	1	0	0	0	0
nsg	*Pachycondyla guianensis* (Weber)	8	0	1	0	0	0	0
	Pachycondyla harpax (Fabricius)		4	6	8	2	24	37
nsg	*Pachycondyla lunaris* (Emery)	4	0	0	0	0	0	2
NRS	*Pachycondyla pergandei* (Forel)	4	0	0	0	0	0	3

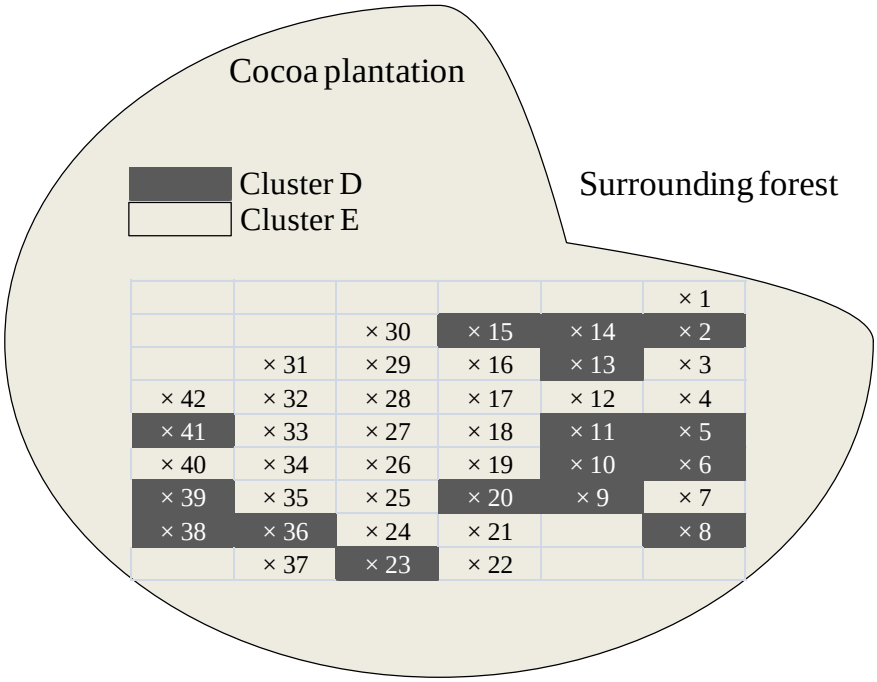
	Pachycondyla stigma (Fabricius)	4	0	0	0	0	1	5
NRS	*Pachycondyla striata* Smith	10	3	3	0	0	0	0
NRS	*Pachycondyla verenae* Forel	4	0	0	0	0	0	15
	Pachycondyla villosa (Fabricius)	1	0	0	0	0	1	0
	Pachycondyla cf *apicalis* morphosp. IV (*sensu* Delabie et al., 2008)[(c)]	6	1	0	0	0	0	0
	Pachycondyla sp. cf *harpax*	7	0	0	0	19	0	1
PROCERATIINAE Emery								
	Proceratiini Emery							
	Discothyrea denticulata Weber	4	2	1	0	0	0	14
PSEUDOMYRMECINAE Smith								
	Pseudomyrmecini Smith							
	Pseudomyrmex gracilis (Fabricius)	2	0	0	1	0	0	0
	Pseudomyrmex tenuis (Fabricius)	11	6	0	1	1	3	0
	Pseudomyrmex termitarius (Smith)	1	0	0	0	0	6	0

[(a)] Groc, S., Delabie, J.H.C., Fernández, F., Leponce, M., Silvestre, R., Dejean, A. The outstanding diversity and heterogeneous functional structure of leaf-litter ant assemblages in a Guianese pristine rainforest, submitted to Journal of Animal Ecology.

[(b)] Groc, S., Orivel, J., Dejean, A., Martin, J.M., Etienne, M.P., Corbara, B., Delabie, J.H.C., 2009. Baseline study of the leaf-litter ant fauna in a French Guianese forest. Insect Conservation and Diversity 2, 183–193.

[(c)] Delabie, J.H.C., Mariano, C.S.F., Mendes, L.F., Pompolo, S.G., Fresneau, D., 2008. Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no Género Pachycondyla na região neotropical: o caso do complexo apicalis. In: Vilela, E.F., Santos, I.A., Schoereder, J.H., Serrão, J.E., Campos, L.A.O., Lino Neto, J. (Eds.), Insetos Sociais: da Biologiá a Aplicacão Vicosa, Minas Gerais, Editora da Universidade Federal de Viçosa, Viçosa, pp. 196–222.

Appendix C. Sampling diagram of the 42 collected samples in the cocoa plantation, with distinction of samples gathered in clusters D and E of the SOM.



CONCLUSION GÉNÉRALE

1. Synthèse

1.1. Contribution à la connaissance de la distribution et la systématique des fourmis néotropicales

Au total, les échantillonnages ont permis de récolter, au cours de ma thèse et lors de la campagne à Maripasoula, 443 espèces correspondant à un total de 12.276 occurrences (Annexe 3). Ces 443 espèces appartiennent à 64 genres correspondant à 11 sous-familles (Annexe 4). Ainsi, cette première étude constitue un travail de base solide pour les futurs inventaires de biodiversité, études d'écologie, de distribution et de conservation des espèces de fourmis guyanaises, et même néotropicales. En effet, en plus du dépôt de collections de référence dans différents laboratoires et muséums, les données produites seront valorisées et accessibles sur internet via, notamment, le site de la Station de Recherche des Nouragues (http://www.nouragues.cnrs.fr/) ou des sites répertoriant les listes et la distribution des espèces néotropicales (http://projects.biodiversity.be/ants) ou des genres et espèces du monde entier (http://www.antmacroecology.org/ant_genera/index.html; www.antweb.org), ou encore, à plus long terme, la mise en ligne de photographies destinées à faciliter l'identification des espèces néotropicales les plus communes (http://projects.biodiversity.be/ants).

1.2. Collecte du matériel biologique, traitement et analyse des données

1.2.1. Difficultés d'échantillonnage et biais des méthodes utilisées

Malgré leur abondance et la facilité à les collecter dans la plupart des écosystèmes, plusieurs caractéristiques de la biologie des Formicidae compliquent leur échantillonnage. En effet, au sein d'une communauté, chaque espèce est distribuée de façon variable à différentes échelles spatiales. A petite échelle (*e.g.* quadrat de 1m²), l'agrégation des individus dans les colonies est un paramètre déterminant, alors qu'aux échelles supérieures, ce sont principalement les facteurs abiotiques, biotiques, liés à la biologie des espèces et/ou à la

stochasticité qui sont responsables de la répartition irrégulière des colonies (Crist and Wiens, 1996).

La complémentarité des deux méthodes d'échantillonnage utilisées dans cette étude a permis d'échantillonner de façon efficace les communautés de fourmis du sol (Bestelmeyer et al., 2000 ; Delabie et al., 2000b): alors que les extracteurs de litière, comme la méthode Winkler, ont plutôt tendance à récolter les espèces vivant dans la litière et parfois le sol, souvent de petite taille, cryptiques (au sens écologique du terme, cf Andersen, 2000) et peu mobiles, à l'inverse, les pièges à fosses favorisent la capture d'espèces mobiles à la surface du sol, souvent de plus grande taille, qui prospectent leur milieu efficacement (Olson, 1991 ; Groc, 2006). Les espèces caractérisées par un niveau d'activité faible et qui utilisent des ressources spécialisées au sein de l'habitat sont ainsi moins susceptibles d'être capturées par les pièges à fosse (Marsh, 1984 ; Olson, 1991). Cependant, chaque méthode d'échantillonnage possède des biais dus aux limitations pratiques et aux différences biologiques entre les espèces qui influencent la performance de leur capture. Les facteurs impliqués dans ces biais sont : la densité des populations, la distribution des nids, la taille du corps des ouvrières, leur niveau d'activité, leur comportement d'évitement des pièges ou leur capacité d'évasion, et enfin la structure de l'habitat (Luff, 1975 ; Southwood, 1978 ; Honék, 1988 ; Topping, 1993 ; Melbourne, 1999 ; Yanoviak and Kaspari, 2000).

1.2.2. Courbes de raréfaction - impossibilité de saturation

Cependant, maximiser l'effort d'échantillonnage permet de réduire l'effet de ces biais méthodologiques sur la représentativité de la part de la communauté piégée. En effet, notre échantillonnage nous a permis de récolter la majorité (mais pas la totalité) des espèces composant les communautés des fourmis de la litière dans chacune des localités échantillonnées (Nouragues : Articles 1-2 ; Paracou : Articles 3-4 ; Kaw et Chutes Voltaire) ; ce qui a pu être vérifié par l'utilisation des courbes de raréfaction (*sensu* Gotelli and Colwell, 2001). Plusieurs raisons peuvent expliquer pourquoi il est quasiment impossible, surtout en milieu tropical, que les courbes de raréfaction se saturent (atteignent leur asymptote horizontale correspondant au nombre total d'espèces observées pour un milieu donné). Même un effort d'échantillonnage très important ne conduira jamais (excepté au sein d'habitats très simplifiés ou éventuellement en milieu tempéré) à la récolte de la communauté de fourmis

dans son intégralité du fait de l'inclusion des espèces rares et « touristes » – *sensu* Belshaw and Bolton, 1993 – (Longino et al., 2002).

1.3. Dynamique des communautés des fourmis de la litière de forêt mature en Guyane française

La dynamique spatiotemporelle des communautés d'organismes vivants est le résultat d'une perpétuelle adaptation et évolution des espèces en réponse aux changements environnementaux. Issues de processus agissant aux échelles locales et du paysage (Holt, 1993 ; Brotons et al., 2003 ; Leibold et al., 2004), les forces (biotiques ou abiotiques) structurant les communautés dépendent des conditions environnementales naturelles, de la saisonnalité, mais aussi du degré d'altération ou de régénération des écosystèmes perturbés et anthropisés.

1.3.1. Importance des facteurs abiotiques dans la structuration des communautés des fourmis de la litière

Les communautés de fourmis sont généralement affectées par les changements de température, d'humidité, de structure du microhabitat, de disponibilité de sites de nidification, de quantité et de qualité de nourriture (Byrne, 1994 ; Kaspari, 1996b ; Brühl et al., 1999 ; Bestelmeyer et al., 2000 ; Kaspari and Majer, 2000 ; Kaspari and Weiser, 2000 ; Kaspari et al. 2000a ; Delsinne et al., 2007 ; Ribas and Schoereder, 2007 ; Vineesh et al., 2007 ; Sabu et al., 2008).

En forêt tropicale particulièrement, la litière est une ressource essentielle pour la myrmécofaune car une grande partie des espèces du sol en dépendent pour leur nidification et leur alimentation (Vasconcelos, 1990 ; Kaspari, 1993 ; Byrne, 1994 ; Belshaw and Bolton, 1994 ; Delabie et al., 2000a ; Yanoviak and Kaspari, 2000a ; Armbrecht et al., 2006). Dans la litière, certains facteurs importants, qui régissent la distribution, l'abondance et la densité des nids des espèces de fourmis, sont la nature et l'étendue de la canopée forestière, en particulier l'exposition aux radiations solaires – via les variations de température et d'humidité –, mais aussi la topographie du milieu (Wilson, 1958b ; Levings, 1983 ; Levings and Windsor, 1984 ; Brühl et al., 1999 ; Kaspari et al., 2000b ; Fisher and Robertson, 2002 ; Vineesh et al., 2007 ; Sabu et al., 2008 ; Vasconcelos et al., 2003 ; Armbrecht et al., 2006).

Dans notre étude, le cas de la forêt de transition (Nouragues) illustre parfaitement l'importance de ces conditions abiotiques sur la composition taxonomique et fonctionnelle des communautés de fourmis de la litière (Articles 1-2). La structure de l'habitat sur les flancs d'inselberg (avec poches arbustives clairsemées sur du rocher apparent) induit (1) une faible accumulation de litière répartie de façon très hétérogène (à la base des arbustes ou dans certaines anfractuosités de la roche), et (2) une forte exposition du sol aux radiations solaires (stress de dessiccation) et aux précipitations. Ces dernières constituent une source de perturbation naturelle par lessivage et inondation avec parfois destruction de la litière lors de la chute de branches ou d'arbres (Phillips et al., 1994 ; Vasconcelos et al., 2003). Nos résultats sont conformes aux prédictions du modèle des groupes fonctionnels développé par Andersen (1995, 1997) qui prédit une augmentation des opportunistes et des spécialistes de climat chaud dans les habitats à la structure simplifiée par les effets de la perturbation (Greenslade, 1978 ; Bestelmeyer and Wiens, 1996 ; Hoffmann and Andersen, 2003), phénomène déjà documenté dans la littérature (Andersen, 1990 ; King et al., 1998 ; Lassau et Hochuli, 2004 ; Calcaterra et al., 2010). Ainsi, dans notre cas, les espèces forestières natives ont été substituées par des espèces opportunistes, généralistes ou spécialistes de climat chaud dont la préférence pour les environnements ouverts avec une couverture végétale clairsemée a déjà été observée (Calcaterra et al., 2010).

En forêt tropicale mature, deux facteurs abiotiques fondamentaux structurent les communautés de fourmis de la litière tropicales. Il s'agit de la nature (i.e. l'épaisseur, la composition, la densité, la qualité, la quantité, l'humidité et la température) et de la variabilité spatiotemporelle de la couche de litière (Jansen, 1973 ; Vasconcelos, 1990 ; Olson, 1994 ; Höfer et al., 1996 ; Kaspari, 1996a,b ; Brühl et al., 1998 ; Carvalho and Vasconcelos, 1999 ; Theunis et al., 2005; voir aussi Articles 1 et 4 pour l'influence du poids de litière sur la richesse spécifique). Également, la composition et la structure de la végétation prédéterminant les caractéristiques de la litière interviennent. Nos résultats, en accord avec la grande majorité des études, ont clairement montré que le type de formation végétale (naturelle ou d'origine anthropique) influence fortement la richesse et la diversité spécifique, mais également la composition taxonomique et fonctionnelle des communautés de fourmis de la litière. Nous avons ainsi pu identifier, parfois même sur de faibles distances, des assemblages d'espèces de la litière hautement spécifiques au type d'habitat (Articles 1 à 4).

1.3.1.1. Impact sur la richesse spécifique

Dans la plupart des habitats, les communautés de plantes font partie des principaux déterminants de la structure physique de l'environnement, donc des conditions microclimatiques. Elles ont, par conséquent, une influence sur la disponibilité en nourriture et sites de nidification. Plus indirectement, elles jouent sur les interactions interspécifiques au sein des myrmécofaunes du sol (Wilson, 1958b; Feener and Schupp, 1998 ; Bestelmeyer and Wiens, 2001 ; Sanders et al., 2003 ; Lassau et Hochuli, 2004). Bien que la diversité des fourmis du sol soit, en général, positivement associée à la complexité de la forêt dans la plupart des habitats (Lassau et al., 2005 ; Sarty et al., 2006 ; Vasconcelos and Vilhena, 2006 ; Hill et al., 2008), il existe quelques cas où elle est négativement affectée (Lassau and Hochuli, 2004). Contrairement à la littérature abondante concernant les variations de diversité spécifique an fonction de la complexité de structurale de l'environnement, peu d'études se sont attachées à examiner les changements dans les compositions spécifique et fonctionnelle, à l'échelle locale, entre différents types d'habitats naturels. Notre travail apporte donc des éléments nouveaux répondant à cette problématique (Article 2).

1.3.1.2. Impact sur la composition spécifique

Comme la végétation détermine la composition de l'assemblage d'espèces et les interactions interspécifiques (Carroll and Janzen, 1973 ; Ribas and Schoereder, 2002), les changements dans la structure de la communauté de plantes entrainent des modifications dans la composition des assemblages d'organismes y vivant. Ainsi, la composition spécifique des communautés de fourmis répond à la succession de formations végétales (Lassau et Hochuli, 2004 ; Lassau et al., 2005 ; Barrow and Parr, 2008 ; Cardoso et al., 2010). Par conséquent, il y a souvent un haut degré de renouvellement des espèces entre les habitats (Bestelmeyer and Wiens, 2001 ; Vasconcelos and Vilhena, 2006 ; Ribas and Schoereder, 2007 ; Vasconcelos et al., 2008). Cependant, au sein de notre étude, les indices de β-diversité calculés ne nous ont pas permis de mettre ceci en évidence (Articles 1, 2 et 4).

1.3.2. Coexistence d'un grand nombre d'espèces au sein des communautés de fourmis de la litière

Notre travail a permis un premier inventaire – convenable mais non exhaustif – de biodiversité des fourmis de la litière de Guyane, lequel a révélé une diversité globale très élevée, parfois même exceptionnelle dans certains habitats (forêt de lianes aux Nouragues ; Articles 1-2) ou certains sites (Montagne de Kaw), notamment via la présence d'espèces cryptiques emblématiques (comme *Tatuidris kapasi* Lacau and Groc, la deuxième espèce de *Tatuidris* (Agroecomyrmecinae) décrite à ce jour ; Lacau et al. soumis : Annexe 5). Cette diversité implique la coexistence localement d'un très grand nombre d'espèces. Pour se maintenir au sein d'une communauté, chaque espèce doit être spécialiste d'un rôle ou d'une niche en particulier, c'est-à-dire dépendre de ressources (alimentaires ou site de nidification) et/ou être limitée par des groupes d'ennemis – prédateurs, parasites, parasitoïdes ou pathogènes – (Gotelli, 1993 ; Amarasekare, 2003 ; Adler et al., 2007 ; Lebrun et Feener, 2007). Dans le cas des communautés des fourmis de la litière, l'hypothèse du partitionnement des niches n'est pas suffisante pour expliquer en totalité la coexistence d'un si grand nombre d'espèces (densité) à petite échelle. Les interactions biotiques jouent aussi un rôle notamment via la compétition ou l'exclusion du fait de la dominance numérique (Hölldobler and Wilson, 1990 ; Lach et al., 2010), la prédation sélective par les fourmis chassant en raids (fourmis légionnaires ou certaines espèces de *Gnamptogenys*, *Cerapachys* ou *Leptogenys*) (Wilson, 1958a ; Sudd and Franks, 1987 ; Otis et al., 1986 ; Perfecto, 1992 ; Kaspari, 1996a), ou encore les comportements d'évitement permettant un chevauchement spatiotemporel dans l'utilisation des ressources alimentaires (Byrne, 1994 ; Amarasekare, 2003).

D'autres mécanismes contribuent également à l'absence de territorialité au sein des communautés des fourmis de la litière (Yanoviak and Kaspari, 2000 ; Ward, 2000), contrairement à celles vivant dans la canopée (Majer et al., 1994 ; Dejean et al., soumis). (1) La complexité structurale de la litière réduit directement la fréquence et l'intensité des interactions interspécifiques en influant sur la mobilité des organismes et augmente la complexité structurale du microhabitat. Elle maximise donc le partitionnement de l'habitat et limitant la compétition (Vasconcelos, 1990 ; Yanoviak and Kaspari, 2000). (2) Le fait que les fourmis de la litière déménagent leur nid régulièrement à cause des conditions microclimatiques instables (Byrne, 1994) empêche les nids de croître jusqu'à saturation (Kaspari, 1996a,b). (3) La dégradation continue de la litière et la chute constante de feuilles maintiennent une abondance élevée de ressources nutritives et de sites de nidification au sol.

En forêt tropicale, l'absence de territorialité au niveau des communautés de fourmis du sol et de la litière suggère que les relations interspécifiques (compétition et dominance) jouent un rôle structurant moins important que ne le font les ressources disponibles et les facteurs abiotiques (Kaspari, 1993; Byrne, 1994 ; Kaspari, 1996a,b ; Andersen, 2000 ; Soares and Shoereder, 2001 ; Amarasekare, 2003 ; Theunis et al., 2005).

1.3.3. Mécanismes régissant la diversité et la structure des communautés natives

1.3.3.1. Hétérogénéité naturelle de l'habitat

En règle générale, la diversité spécifique est typiquement distribuée de façon hétérogène, que ce soit à l'échelle des habitats, du paysage ou régionale (Rahbek, 2005 ; Fahr and Kalko, 2011). Sous les tropiques, les communautés de fourmis de la litière sont caractérisées par une hétérogénéité très marquée de densité de nids, les nombreuses espèces de fourmis se distribuant sous forme de « patches » (Wilson, 1958b ; Levings, 1983 ; Levings and Windsor 1984 ; Kaspari, 1993 ; Byrne, 1994 ; Olson, 1994 ; Kaspari, 1996a,b ; Vasconcelos and Delabie, 2000 ; Leponce et al., 2004). Les résultats issus de notre échantillonnage aux Nouragues illustrent bien ce phénomène globalement, mais aussi l'effet d'une hétérogénéité plus ou moins importante par rapport à un référentiel (la forêt de grand plateau) selon un gradient de successions végétales : diversité et densité d'espèces maximales dans la forêt de lianes, minimales dans la forêt de transition (Articles n°1-2). Par exemple, Kaspari (2000) a noté de 1 à 17 espèces de fourmis nichant dans 1m² de litière. Plusieurs facteurs peuvent expliquer cette distribution en patch : (1) les colonies des fourmis de la litière sont généralement de taille petite ou moyenne (Yanoviak and Kaspari, 2000), (2) les fourmis chassant en raids qui sont responsables de perturbations entrainant de petits « vides myrmécologiques » à l'échelle du m² au niveau de la litière (Kaspari, 1996a), et (3) la capacité de dispersion et le mode de reproduction propre à chaque espèce.

Notre étude (Articles 1, 2 et 4) corrobore ce qui est déjà reporté pour les forêts tropicales. Cette diversité spécifique hétérogène est créée, maintenue et accentuée par des processus issus de perturbations (*e.g.* les formations de chablis, installation de forêts de lianes pérennes) et de successions environnementales (e.g les gradients de végétation). Ces facteurs influencent la dynamique des espèces, et par conséquent les communautés écologiques (Kolasa et Pickett, 1991 ; Tilman, 1994 ; Tews et al., 2004). « L'hypothèse de l'hétérogénéité de l'habitat »,

fondamentale en écologie (*e.g.* Simpson, 1949 ; MacArthur and Wilson, 1967, 2001), est proposée pour expliquer les variations de diversité spécifique à l'échelle locale et du paysage (Tews et al., 2004). Elle stipule que les habitats structurellement complexes fournissent potentiellement plus de niches et de moyens d'exploiter les ressources environnementales disponibles, donc plus d'options pour la colonisation, la reproduction et la survie des organismes, et ainsi augmentent la diversité spécifique (Loucks, 1970 ; Hall et al., 1997 ; Wettstein and Schmid, 1999 ; Romero-Alcaraz and Avila, 2000 ; Tews et al., 2004). En d'autres termes, cela facilite la spécialisation et l'évitement de la compétition grâce à la ségrégation spatiale. Les habitats les plus complexes offrent donc un panel plus diversifié de niches, lesquelles abriteront potentiellement des richesses spécifiques parmi les plus élevées (Finke and Snyder, 2008), comme cela a été vérifié dans la forêt de lianes aux Nouragues (Articles n°1-2). Enfin, cette hypothèse suggère que l'hétérogénéité de l'habitat module les processus écologiques, influence la façon dont les espèces coexistent dans l'espace et dans le temps, et par conséquent, affecte le fonctionnement de l'écosystème dans son ensemble (Cardinale et al., 2000).

Bien que l'hypothèse de l'hétérogénéité de l'habitat ait été testée dans des contextes variés (Levey, 1988 ; Willig, 2000 ; Willig et al., 2003 ; Cardoso et al., 2010), la littérature scientifique, jusqu'à présent, montre une préférence nette pour les études concernant les habitats anthropisés plutôt que pour l'hétérogénéité naturelle des habitats (Tews et al., 2004). D'où l'intérêt supplémentaire de notre étude qui intègre cette hypothèse à la fois dans un contexte de succession de formations végétales dont la matrice forestière est soumise à une perturbation permanente (Articles 1-2), mais également dans un contexte de conversion forestière en terres agricoles (Article 4) ou au sein d'un gradient d'anthropisation incluant la régénération forestière (Article 3). Notre travail apporte donc des éléments supplémentaires quant à la compréhension des patrons de distribution et de la structure des communautés de fourmis natives des forêts amazoniennes et de la façon dont le changement d'utilisation traditionnelle ou moderne (i.e. intensive) des terres les affecte.

1.3.3.2. Perturbation naturelle ou anthropique

Les perturbations qui affectent les communautés de fourmis (*e.g.* les formations de chablis ou les formations végétales spatio-temporellement stables issues d'une perturbation passée) sont en partie responsables des patrons de distribution des espèces au sein des forêts naturelles. Bien que ce soit le cas lors de formation de chablis (Lach et al., 2010 ; Article 4), une perturbation n'induit pas forcément une diminution de la richesse spécifique totale, laquelle correspond à une extinction des spécialistes de l'habitat. Il est possible que l'environnement local varie de telle manière que des ressources alternatives deviennent disponibles et permettent une coexistence des espèces généralistes et spécialistes au sein du même habitat. Cela entraine une augmentation de la richesse spécifique totale comme nos résultats le montrent dans le cas de la forêt de lianes aux Nouragues (Articles 1-2) et du fragment de forêt mature laissé par les Amérindiens près du Maroni (Article 3). Ce fragment est plus riche en espèces que la zone de forêt naturelle ripicole avoisinante (voir aussi Huston 1994 ; Lawton et al., 1998, Speight et al., 2003 ; Basset et al., 2008a ; Graham et al., 2009). Le cas de la forêt de lianes (Articles 1-2) en est aussi un parfait exemple (diversité et densité largement supérieures à celle de la matrice forestière environnante). Ce phénomène est probablement exacerbé par l'âge de cette formation végétale ainsi que l'effet de l'épaisseur de la litière.

1.4. Impact de la fragmentation forestière et de la conversion en monocultures sur les communautés forestières natives de fourmis de la litière

Le contexte classique des études d'impact de l'homme sur les écosystèmes concerne habituellement un paysage fragmenté, en général par le changement d'utilisation des sols. Il est formé de plusieurs fragments de végétation native ou fragments, de taille variable, plus ou moins isolés au sein d'une matrice environnementale perturbée. Cette matrice peut se composer de différents habitats caractérisés par un degré d'anthropisation plus ou moins élevé, allant d'habitats artificiels (e.g. routes ou milieux urbains) aux agrosystèmes (agroforêts, cultures, monocultures, pâturages) (Gascon et al., 2000). Elle représente une source d'espèces approvisionnant les communautés au sein des fragments d'habitats naturels,

mais la diversité, la composition la structure et même la dynamique des communautés dépendent fortement du type de matrice (Vasconcelos, 1999 ; Ambrecht et Ulloa-Chacón ; 1999 ; DeSouza et al., 2001). Une des particularités de notre étude est que la situation est inversée dans le sens où nous nous sommes essentiellement focalisés sur les communautés de fourmis du sol au sein d'un paysage constitué de parcelles de terres cultivées (traditionnellement ou intensivement) entourées d'une matrice forestière tropicale native (Articles 3-4).

1.4.1. Facteurs structurant les communautés de fourmis dans les fragments forestiers et les agrosystèmes

La perte et la fragmentation des habitats naturels, souvent concomitantes de la conversion des forêts en agrosystèmes, ont généralement un impact considérable sur les communautés de fourmis via la modification de la structure de la végétation (Greenslade and Greenslade, 1977), de la richesse spécifique végétale et surtout des variations dans la couverture de canopée (Wilson, 1958b ; Levings, 1983 ; Perfecto and Vandermeer, 1996). Ces modifications ont une influence sur la disponibilité de nourriture et de sites de nidification, et l'abondance de mutualistes et de compétiteurs.

Il existe une grande variabilité des effets de l'anthropisation sur les communautés en fonction des espèces et du type d'habitat, mais la taille de la parcelle ou du fragment de forêt, l'isolement, et l'effet de lisière affectent lourdement les communautés de fourmis (Lovejoy et al., 1986 ; Murcia, 1995 ; Boudjemadi et al., 1999 ; Bruhl et al., 2003 ; Dauber and Wolters, 2004 ; Sobrinho and Shoereder, 2007), particulièrement en forêt amazonienne (Didham, 1997a ; Carvalho et Vasconcelos, 1999 ; Vasconcelos and Delabie, 2000 ; Laurance and Vasconcelos, 2004 ; Laurance et al., 2002 ; Vasconcelos et al., 2001).

Certaines études suggèrent que les effets de lisière dans les forêts tropicales humides peuvent affecter les communautés de fourmis jusqu'à 200 m à l'intérieur de la forêt (Carvalho and Vasconcelos, 1999 ; Laurance and Vasconcelos, 2004 ; Laurance et al., 2002 ; Dauber and Wolters, 2004). La création de lisières permet également la pénétration du vent et de la lumière dans les fragments forestiers, altérant ainsi le climat et la structure de la végétation forestière (*e.g.* Kapos et al., 1997 ; Ferreira and Laurance, 1997 ; Laurance et al., 1997). De tels changements sont nuisibles à un grand nombre d'organismes forestiers natifs, favorisant l'invasion par des espèces non forestières, essentiellement généralistes (Terayama and

Murata, 1990 ; Vasconcelos et al., 2001). Ce phénomène est accentué dans les fragments ou parcelles cultivées de taille réduite (Shoereder et al., 2004). Enfin, l'isolement et le type de transition entre la végétation du fragment et de la matrice (nette ou graduelle) est fondamental puisqu'il détermine les taux d'immigration des espèces, pouvant ainsi directement influencer l'opportunité de (re)colonisation des espèces (Schoener, 1991 ; Turner, 1996 ; Huxel and Hastings, 1998; Boudjemadi et al., 1999 ; Gascon et al., 1999 ; Vasconcelos, 1999 ; Kotze et Samways, 2001). De plus, lors de la conversion de la forêt en plantations, l'âge, la nature (notamment l'essence cultivée comme nos résultats le suggèrent ; Article 4), et l'entretien de la plantation (Brühl et al., 2003) ainsi que la perméabilité aux propagules durant le processus de (re)colonisation, jouent également un rôle très important dans la structuration des communautés de fourmis du sol. (Kaspari and Weiser, 2000 ; Holway et al., 2002 ; Armbrecht et al., 2004).

1.4.2. Perte des espèces natives

En général, la diversité des fourmis diminue avec le niveau de perturbation anthropique, particulièrement lors du changement d'utilisation des sols (Lawton et al., 1998 ; Graham et al., 2009 ; Articles 3-4). Nos résultats vont également dans le sens d'une augmentation nette de l'abondance totale des fourmis dans le cas de la conversion de la forêt en monocultures (Article 4), ce qui corrobore le résultat de nombreuses études sur différentes essences dans le monde entier (Vasconcelos, 1999 ; Graham et al., 2009 ; Philpott et al., 2010), et celles considérant des gradients de régénération forestière, au moins dans les stades de régénération les plus jeunes (Vasconcelos et al., 2001). Par exemple, l'effet de lisière, que nous avons pu mettre en évidence dans la plantation de cacaoyers à Paracou (Article 4), a deux conséquences. (1) Une plus grande abondance de dolichoderines dominantes et de spécialistes de climat chaud (*sensu* Andersen, 1995, 1997) dans la matrice environnante et les habitats de bordure. (2) Des abondances supérieures de myrmicines généralisées, d'espèces cryptiques et de spécialistes de climat froid (*sensu* Andersen, 1995, 1997) au sein des habitats de fragments naturels (Debuse et al., 2007). Pour les forêts amazoniennes, par exemple, la richesse spécifique de fourmis diminuerait de moitié ou du tiers par rapport à sa valeur initiale le long de gradients de succession d'habitats issus d'une perturbation anthropique (Carvalho et Vasconcelos, 1999 ; Vasconcelos, 1999 ; Vasconcelos et al., 2000b ; Silva et al., 2007). De plus, la perte d'espèces natives ne se traduit pas qu'en termes de diversité spécifique, mais

aussi au niveau des associations écologiques et de leur complexité, ayant probablement un impact sur le fonctionnement des écosystèmes (Armbrecht et al., 2004 ; Crist, 2009).

1.4.3. Coexistence des espèces généralistes et spécialistes au sein des communautés de fourmis de la litière altérées

En accord avec la littérature (Silva et al., 2007), nos résultats (Articles 3-4) ont confirmé qu'un grand pourcentage d'espèces natives de fourmis manque à l'appel dans les fragments forestiers isolés ou les monocultures. En effet, il existe de plus en plus de preuves que la conversion de la forêt en terres agricoles a un effet majeur à long terme sur les populations d'espèces forestières natives spécialistes au sein des assemblages d'insectes (Holloway et al., 1992 ; Fermon et al., 2000 ; Davis et al., 2001 ; Jones et al., 2003 ; Silva et al., 2007 ; Armbrecht et al., 2004). Ainsi, les communautés de fourmis du sol sont majoritairement composées d'espèces généralistes et opportunistes adaptées aux perturbations et/ou à des surfaces disponibles de taille réduite (Schoereder et al., 2004). Ces espèces, dont l'étendue du régime alimentaire empiète sur celui des spécialistes, proviennent de la matrice environnante, et appartiennent généralement à des genres très diversifiés, *e.g. Brachymyrmex, Camponotus, Crematogaster, Nylanderia* (Delabie et al., 2000a ; Silvestre et al., 2003 ; Schoereder et al., 2004 ; Silva et al., 2007 ; Cardoso et al., 2010). Deux mécanismes généraux peuvent expliquer ce phénomène (Spiesman and Cumming, 2008). (1) Les espèces généralistes ont supplanté les spécialistes par des processus de compétition liés à la dynamique spatiale (Holt, 2004). (2) L'extinction stochastique ou indépendante des espèces spécialistes (Gascon and Lovejoy, 1998; Suarez et al., 1998 ; Ricklefs and Lovette, 1999). Cette extinction, couplée à une dispersion des espèces limitée, empêche la recolonisation par les spécialistes, permettant l'installation et le maintien des généralistes. Cependant, la perte de l'habitat natif peut engendrer l'invasion par des espèces généralistes bien qu'elles soient initialement moins compétitives que les spécialistes de cet habitat (Marvier et al., 2004). Cette dynamique n'implique pas forcément l'extinction des spécialistes de l'habitat, et si l'environnement local varie de telle sorte que des ressources alternatives deviennent disponibles, cela permettrait aux généralistes de coexister avec les spécialistes (Spiesman and Cumming, 2008). Ce mécanisme permet d'expliquer la similarité des myrmécofaunes du sol des plantations de cacaoyers et de pins caraïbes par rapport à la forêt mature mais surtout la coexistence d'un grand nombre d'espèces cryptiques spécialistes de la litière (souvent des prédateurs) avec les quelques

espèces numériquement dominantes au sein de la communauté (Article 4). Cette dynamique pourrait aussi conduire à une augmentation de la richesse spécifique totale, comme nous l'avons montré dans le cas du fragment forestier près du village amérindien Wayanas, à proximité du Maroni (Article 3).

1.4.4. Hyper-abondance de quelques espèces natives

A des faibles niveaux de perturbation, comme à des niveaux très élevés de productivité, peu d'espèces peuvent atteindre une dominance compétitive telle qu'elles excluent les autres espèces, induisant ainsi une réduction de la diversité totale. A l'inverse, à des niveaux élevés de perturbation ou de faible productivité, seules quelques espèces tolérantes au stress ou généralistes peuvent survivre (Bestelmeyer and Wiens, 1996). Au sein des paysages anthropiques, certaines espèces natives déclinent alors que d'autres deviennent hyperabondantes, donc numériquement dominantes (Laurance et al., 2002 ; Martin et al., 2011). Nous l'avons montré pour *Atta cephalotes*, *Ochetomyrmex neopolitus*, *Solenopsis geminata* et *Wasmannia auropunctata* dans les plantations d'acacias, de cacaoyers, d'hévéas et de pins caraïbes. Ces espèces, dont l'abondance est corrélée à l'intensité de l'utilisation des terres et la perturbation dans la matrice environnante (Armbrecht et Ulloa-Chacon, 2003), pourraient donc être utilisées comme des indicateurs de perturbations anthropiques en Amazonie (Delabie et al., 2007 ; Article 3).

De nombreuses études ont documenté l'augmentation des populations de fourmis coupeuses de feuille avec l'augmentation de la déforestation, de la perturbation et le changement d'utilisation des terres (Fowler et al., 1986 ; Jaffé and Vilela, 1989 ; Vasconcelos and Cherret, 1995). Ainsi, des densités de colonies largement supérieures à celle trouvées dans la forêt mature (jusqu'à plus de 20 fois; Vasconcelos and Cherrett, 1995) ont été relevées dans les terres converties en pâturages et en plantations (Fowler, 1983), mais également dans les stages précoces de régénération forestière (Vasconcelos and Cherrett, 1995) et des fragments forestiers isolés (Terborgh et al., 2001). Certaines de ces espèces semblent avoir un rôle crucial dans les processus de régénération forestière amazonienne (Nepstad et al., 1990). Par exemple, *Solenopsis geminata*, une espèce dont l'abondance augmente proportionnellement à la perturbation forestière (Vasconcelos, 1999), est considérée comme une espèce clé de voûte du fait de son effet structurant à la fois sur les communautés de plantes et d'arthropodes (Rish and Caroll, 1982 ; Carroll and Risch, 1984). De plus, les

changements locaux des conditions environnementales suite à une perturbation tendent à modifier l'équilibre des compétitions interspécifiques, permettant une redistribution des relations de dominance parmi les espèces (Begon et al., 1999). Ainsi, *W. auropunctata* montre des patrons d'interférence et d'exploitation et parfois même de déplacement d'autres espèces de fourmis similaires à *Linepithema humile* (une espèce de fourmi envahissante) à travers l'agression physique par les ouvrières ou par l'exploitation plus performante des ressources alimentaires (Human and Gordon, 1996 ; Holway, 1999 ; Holway et al., 2002).

1.4.5. Espèces exotiques et envahissantes

La déforestation favorise l'installation et le maintien d'espèces exotiques, envahissantes et de pathogènes, qui, en retour, fragmentent davantage les populations d'espèces natives, ce qui diminue leur possibilité de migration à travers le paysage pour survivre à la perturbation (Samways, 2007). Les invasions d'espèces dépendent du type de matrice, de la taille du fragment, du ratio taille/lisière, et de son isolement (Kapos et al, 1997 ; Gascon and Lovejoy, 1998 ; Carvalho and Vasconcelos, 1999 ; Gascon et al., 1999 ; Crist, 2009). Lors de notre étude, nous avons noté la présence de trois espèces exotiques potentiellement envahissantes (*Cardiocondyla minutior*, *Paratrechina longicornis* et *Technomyrmex vitiensis* ; Article 3 ; Delabie et al., 2011 : Annexe 1). Les fourmis envahissantes sont extrêmement compétitives et peuvent bouleverser les entomofaunes locales (Cook, 2003), particulièrement les communautés de fourmis natives et ainsi modifier certains processus écosystémiques (Holway et al., 2002 ; Dejean et al., 2010), lesquels peuvent intervenir dans la régénération forestière après l'abandon des terres cultivées.

1.4.6. Régénération forestière

Notre étude a montré que la fragmentation (suite à la formation d'un chablis complexe ou au changement de l'utilisation des terres) de la forêt mature semble avoir des effets moins importants sur les communautés de fourmis du sol que la conversion en plantation (Articles 3-4). En effet, la communauté de fourmis du chablis ou celle du fragment de forêt proche du village Amérindien situé sur le Maroni (partiellement déforesté, accidentellement brûlé par le passé, mais laissé intact aux milieux des zones cultivées) sont apparues très semblables à celles des forêts intactes environnantes. De plus, nos résultats corroborent des études antérieures, à savoir que la richesse spécifique et la composition des communautés de fourmis de la litière montrent de grandes différences le long du gradient de régénération forestière comparé à la matrice forestière (Roth et Perfecto, 1994 ; Moutinho, 1998 ; Vasconcelos, 1999 ; Floren and Linsenmair, 2001 ; Watt et al., 2002 ; Coelho and Ribeiro, 2006 ; Silva et al., 2007).

Les effets de la déforestation induisent des changements plus ou moins importants au sein des communautés de fourmis du sol qui auront des implications sur la réinstallation progressive de la faune native lors de la régénération forestière future si ces terres sont abandonnées. Par exemple, dans notre étude, les résultats issus de l'échantillonnage aux alentours du village amérindien Wayanas ont révélé que la myrmécofaune de la plantation de manioc abandonnée ressemble à celle de la matrice forestière environnante du fait de la présence d'espèces forestières (*e.g.* des grandes ponérines) qui l'ont colonisée récemment (Article 3). Les phases finales de régénération sont les plus longues mais la durée nécessaire estimée pour retrouver une communauté de fourmis semblable à celle de la forêt mature varie selon les types de forêts, ou selon que l'on considère la richesse spécifique totale ou la composition en espèces (Meggers, 1985 ; Dunn, 2004b). De plus, même après 25 ans de régénération forestière, le nombre d'espèces et surtout la composition taxonomique n'ont pas retrouvé le niveau des communautés de fourmis de la forêt primaire. En effet, le retour à une composition taxonomique d'origine semble être beaucoup plus long que celui de la richesse spécifique (Dunn, 2004b ; Liebsch et al., 2008).

Cependant, la recolonisation par la faune native dépend fortement de l'historique, du type et de l'intensité de l'utilisation des terres (Moutinho, 1998 ; Vasconcelos et al., 2001). En Amazonie, si le terrain est abandonné rapidement après la déforestation, la recolonisation des espèces natives et le retour à une richesse et une composition similaire à la forêt mature semble rapide (environ 13 ans). Au contraire, si la forêt est détruite, brûlée et convertie en

champ ou en plantation, le nombre d'espèces collectées 10 ans après l'abandon du champ sera 30% inférieur à celui de la forêt mature et la similarité de la composition sera faible (Vasconcelos et al., 2001). Ainsi, plus les pratiques de gestion des terres induisent un haut niveau de perturbation, plus les myrmécofaunes ont tendance à se régénérer lentement. Ainsi, certains systèmes agricoles traditionnels, comme les plantations de cacaoyers (Delabie et al., 2007) ou de caféiers (Perfecto and Snelling, 1995), sont moins destructeurs que les systèmes de monoculture modernes, comme le suggèrent nos résultats (Article 4).

1.5. Préservation de la biodiversité dans les agrosystèmes et protocoles adaptés pour les études de conservation et d'impact

Plusieurs études soutiennent que seules les forêts primaires et secondaires âgées sont capables de préserver la plus grande part de biodiversité native (Majer, 1992, 1996 ; Dunn, 2004b ; Schulze et al., 2004 ; Silva et al., 2007 ; Gibson et al., 2011). Nous corroborons le fait que conserver des zones des forêts matures intactes de taille maximale est fondamental pour conserver des assemblages natifs d'espèces de fourmis de la litière suffisamment diversifiés et complexes pour alimenter les zones alentours fragmentées et converties en agrosystèmes. Toutefois, notre étude, conformément à celles d'autres travaux menés en zone néotropicale (Philpott and Armbrecht, 2006 ; Delabie et al., 2007 ; Schroth et al., 2011), montre que les plantations de cacaoyers ou de caféiers, ont un potentiel de conservation réel qu'il serait dommage de minimiser. De plus, les plantations sous ombrage semblent fournir une matrice encore plus adaptée pour la préservation des espèces de fourmis natives, et pourraient être utilisées pour augmenter la connectivité des communautés de fourmis entre les habitats forestiers (Perfecto and Vandermeer, 2002). En outre, la présence de fragments forestiers pourrait jouer un rôle dans la facilitation de la colonisation des plantations abandonnées (Article 3).

Enfin, beaucoup d'espèces sont toujours inconnues de la science. De plus les écologues et les biologistes de la conservation se heurtent à une difficulté d'ordre taxonomique réelle (peu d'experts), et à une rareté de protocoles adaptés pour un échantillonnage exhaustif des organismes cibles. C'est pourquoi nous sommes actuellement confrontés à la nécessité de développer des protocoles adaptés pour simplifier et intégrer les fourmis de façon fiable dans les études de conservation, de contrôle et de suivi de la santé des écosystèmes pour pouvoir faciliter la gestion environnementale future (Article 3 ; Groc et al., 2010 : Annexe 2).

2. Perspectives

Plusieurs perspectives à court terme se dégagent de cette étude. Premièrement, l'aspect fonctionnel des myrmécofaunes devra être approfondi pour pouvoir comprendre le rôle des communautés de fourmis du sol dans le fonctionnement des écosystèmes forestiers naturels et ainsi pouvoir déterminer de quelle façon la conversion des forêts en agrosystèmes affecte les processus écosystémiques assurés par les fourmis. Pour cela, il sera d'abord nécessaire de s'intéresser aux groupes fonctionnels pour avoir une idée globale de la structure fonctionnelle des myrmécofaunes, avant de pouvoir affiner l'analyse en se focalisant sur les stratégies d'adaptation de chaque espèce selon le filtrage environnemental, par l'intermédiaire d'études de traits. Deuxièmement, il sera nécessaire d'échantillonner des réplicats des habitats étudiés, soit à un temps t donné (e.g. pour les plantations à Paracou), soit à différentes saisons (e.g. pour les Nouragues et Kaw) pour pouvoir fournir des conclusions solides et généralisables quant aux effets de l'hétérogénéité et des perturbations naturelles ou de la conversion de la forêt en plantations sur les myrmécofaunes forestières natives. Enfin, la prochaine étape sera d'identifier quels sont les facteurs abiotiques essentiels dans la structuration des communautés de fourmis du sol.

A plus long terme, c'est dans un contexte de conservation et de gestion du territoire que nos perspectives s'insèrent. Tout d'abord, préserver et maintenir une hétérogénéité au sein d'habitats menacés par les activités humaines contribuerait au maintien du plus large éventail possible de conditions et de processus écologiques. De plus, préserver les entomofaunes natives via le maintien des interactions trophiques, des espèces endémiques mais aussi d'espèces ou de paysages typiques garantirait la pérennité des services écosystémiques qu'elles assurent. Enfin, il est primordial de se concentrer sur le potentiel de conservation des agrosystèmes et des fragments de végétation naturelle au sein du paysage anthropique. Alors que certaines monocultures intensives ne constituent clairement pas une matrice de qualité, préserver certains systèmes de culture traditionnels (e.g. plantations de cacaoyers ou caféiers sous ombrage d'arbres natifs) serait un très bon moyen de conserver à long terme les espèces forestières natives (Delabie et al., 2007 ; Philpott et al., 2008) et ainsi contribuer au bon fonctionnement futur des écosystèmes terrestres.

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ANNEXES

ANNEXE 1 : The tramp ant *technomyrmex vitiensis* (Hymenoptera: formicidae: dolichoderinae) on South America

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THE TRAMP ANT *TECHNOMYRMEX VITIENSIS* (HYMENOPTERA: FORMICIDAE: DOLICHODERINAE) ON SOUTH AMERICA

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Invasive ants are among the most harmful and problematic bioinvaders, with about 150 species having been introduced into new environments by humans (Holway et al. 2002). The biology of the species belonging to the genus *Technomyrmex* remains poorly known; yet ants in the *Albipes* group of *Technomyrmex* are especially feared because their populations can occupy very wide areas in different terrestrial ecosystems and can extend from the ground to the tree crowns. They perturb vertebrate pollination and seed dispersion of endangered flora, and outnumber native ant species, etc. (Deyrup 1991, Warner, cited in Bolton 2007; Wetterer 2008; Hansen & Müller 2009; Dejean et al. 2010).

With 91 extant species (Bolton 2007; Fernández & Guerrero 2008), *Technomyrmex* is an ant genus whose species are essentially distributed in the Old World. In the New World, only 2 native species are currently known, i.e., *Technomyrmex fulvus* W. Wheeler (Colombia, Costa Rica, Panama) and *Technomyrmex gorgona* Fernández & Guerrero (Colombia) (Fernández & Guerrero 2008).

Two exotic species also occur in the New World. Possibly native to Madagascar and distributed in southern Asia and Oceania (Bolton 2007), *Technomyrmex difficilis* Forel was first discovered in 1986 in Florida (Deyrup 1991), and was misidentified as *Technomyrmex albipes* (F. Smith). Subsequently it spread rapidly, mostly in Florida, Georgia, Louisiana, and South Carolina, but also to the tropical house of the Seattle Zoo, Washington, and some West Indies islands, e.g., Puerto Rico, St. Thomas, St. Croix, Nevis, and Antigua (Wetterer 2008).

On the other hand, *Technomyrmex vitiensis* Mann, which is widespread in continental and insular southeast Asia, on islands from the Indian Ocean to Polynesia, and in some European greenhouses (Bolton 2007; Fernández & Guerrero 2008; Wetterer 2008), has been found in the New World only at the Golden Gate Park Conservatory, San Francisco, California (Bolton 2007).

All of the published occurrences of *Technomyrmex albipes* (F. Smith) in the USA until 2007 belong to 1 of these 2 species (Bolton 2007; Wetterer 2008). Indeed, these ants were generally wrongly classified as *T. albipes*; whereas they form a complex group of tramp species that includes *Technomyrmex pallipes* (F. Smith), i.e., the *Albipes* group, distributed in tropical and subtropical regions. Moreover, both the real *T. albipes* as well as *T. pallipes* are expected in the New World in the future (Fernández & Guerrero 2008).

We consulted specimens of the following *Technomyrmex* species [CPDC]: *T. vitiensis*: India: Bangalore, #5114, 1995, R. Gadagkar col.; Western Ghats, #5114b, 1995, R. Gadagkar col.; Réunion: Béthléem, #5310, K11, xii.2000, F. Blard leg.; St Pierre, "on pineapples brought to France", xi.2000, H. Bolzinger leg.; *T. difficilis*: Malaysia: #4464, 1991, K.C. Khoo leg.; *T. fulvus*: Colombia: Chocó, La Balsa, Estación Silvicultura Bajo Atrato, 70°2'26"N 77°20'16"W, L. Mendoza leg., iii.1994, pitfall trap, ICN-HYM057, id. R. J. Guerrero & F. Fernández.

Here we report the first occurrence of *T. vitiensis* on continental South America. This ant was recorded in 2 samples from 2 sites in the forest surrounding the Nouragues Research Station, French Guiana, operated by the French *Centre National de la Recherche Scientifique* (CNRS). Voucher specimens were deposited in the *Laboratório de Mirmecologia collection do Centro de Pesquisas do Cacau*, Ilheus, Bahia, Brazil [CPDC], under the references: French Guiana, Nouragues Station, #5635, FT2Tr5W30, Transition Forest, 04°09'N 52°68'W, ix.2009, Winkler trap, Sarah Groc et al. leg.; same locality, #5637, FL2Tr2PF46, Liana Forest, 04°08'N 52°64'W, ix.2009, pitfall trap, Sarah Groc et al. leg. This station is located in a scarcely accessible region in the flourishing pristine forest of the Guiana Shield (Bongers et al. 2001), about 100 km distant from the Atlantic coast where most of the Guianese population is concentrated.

The mechanism by which *T. vitiensis* arrived in French Guiana remains unclear, because this ant was previously unknown in any region bordering the Atlantic Ocean. Thus it seems there might be a "French connection" to explain the introduction of this species through the continuous trade and population flows between various French over-

seas territories (Rauzduel 1995). *T. vitiensis* has been recorded on New Caledonia, in French Polynesia, and Reunion island in the Indian Ocean, where Blard et al. (2003) misidentified it as *T. albipes* (Bolton 2007). It is therefore thought, but not confirmed, that its occurrence in inhabited areas near the coast of French Guiana is an intermediate step in its introduction into the rest of the country. Like *T. difficilis* in southeast USA and the West Indies, *T. vitiensis* likely will rapidly disperse to neighboring regions through trade and travel, particularly with Surinam and the Brazilian State of Amapá.

Summary

Technomyrmex vitiensis is a tramp ant that has spread through many parts of the Old World tropics via human commerce. This species has been previously reported only once in the New World, from San Francisco, California. Here, we report the first records of *T. vitiensis* in South America, from two sites deep in the forest of French Guiana. It is not clear how these ants were transported to such remote sites, 100 km inland.

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ANNEXE 2 : A new method based on taxonomic sufficiency to simplify studies on neotropical ant assemblages

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A new method based on taxonomic sufficiency to simplify studies on Neotropical ant assemblages

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ABSTRACT

Insects, particularly ants, are good bioindicators of the state of ecosystems. Nevertheless, incorporating them into conservation surveys is expensive due to problems associated with their identification, which is exacerbated by the fact that there are fewer and fewer taxonomists working today. "Taxonomic sufficiency" (TS), which identifies organisms to a level of taxonomic resolution sufficient enough to satisfy the objectives of a study, has never been applied to Neotropical ant communities. We analysed five Neotropical datasets representing ant assemblages collected with different sampling methods in various habitats. We first treated them using two complementary and cumulative TS methods, higher-taxon and "indicator taxa" surrogacies, before testing a new approach called "mixed-level method" that combines the two previous approaches. For the higher-taxon surrogacy, we showed that, above species, genus is the most informative taxonomic level. Then, mixed-level method provided more information on ant assemblages than did the two others, even though the "indicator taxa" surrogacy was based on relevant indicator genera. Although habitat type has no effect on its efficiency, this new method is influenced by the dataset structure and the type of sampling method used to collect data. We have thus developed a new method for analyzing Neotropical ant faunas that enables the taxonomic work linked to the identification of problematic species to be significantly reduced, while conserving most of the information on the ant assemblage. This method should enhance the work of Neotropical entomologists not specialised in taxonomy, particularly those concerned with biological conservation and indication.

1. Introduction

Human-induced (influence on biogeochemical cycles, land use change, biological invasions by non-native species) and global climate changes are having a tremendous impact upon terrestrial ecosystems worldwide (Vitousek, 1994; Thomas et al., 2004), particularly in South America (Rull and Vegas-Vilarrúbia, 2006). Although most previous bioindication and conservation surveys rather concerned vertebrates and vascular plants (Fazey et al., 2005), detecting and monitoring the consequences of environmental change on terrestrial invertebrates is especially important, given that they constitute the bulk of animal biodiversity (Groombridge and Jenkins, 2000) and have a major role in ecosystem functioning (Ponder and Lunney, 1999). That is why they have increasingly been represented in surveys dealing with diversity or the assessment and monitoring of the state of the environment (McGeoch, 1998; Basset et al., 2008).

Unfortunately, we have been witnessing a gradual tendency for scientists to specialise in areas other than taxonomy, with, as a result, the taxonomic groups that are widely used in environmental impact studies being taxonomically poorly known or insufficiently studied by practicing taxonomists (Basset et al., 2004). As a consequence of the difficulties encountered in having terrestrial invertebrates identified, their inclusion in conservation and bioindication surveys is often considered to be impractical or prohibitively expensive (Krell, 2004). They are thus routinely ignored in environmental monitoring and assessment programs (New, 1996); the only remarkable exception is the wide and common use of ants as bioindicators in Australia (for a synthesis see Andersen and Majer, 2004). But the situation is progressively changing since it is becoming apparent that detecting changes in the structure of

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assemblages does not necessarily require identification to species (Pik et al., 2002; Grimbacher et al., 2008).

Identifying organisms to a level of taxonomic resolution that still provides significant information in an economical way is known as "taxonomic sufficiency" (TS; Ellis, 1985). TS provides a means of measuring and analyzing ecological diversity while reducing the costs associated with precise taxonomic analyses. It frees investigators from a dependence on taxonomists (Williams and Gaston, 1994), reduces the burden for taxonomists of routine identifications that do not contribute to systematics research, and allows more resources to be allocated to the spatial and temporal replication of surveys (Grimbacher et al., 2008). Although its usefulness may be dependent on scale, location and biotic group (Vanderklift et al., 1998), it is recognized that the changes or differences in assemblages observed at the species level may also be manifest at higher taxonomic levels such as genus or sometimes even phylum (Pik et al., 2002; Schnell et al., 2003). This approach has proven to be very efficient in measuring the responses of benthic communities to water pollution (Vanderklift et al., 1998). Yet, despite more than 30 years of research on the effectiveness of TS for aquatic systems, little effort has been made to investigate its potential for terrestrial studies, although the concept is starting to be applied to terrestrial invertebrate assemblages (Oliver and Beattie, 1996; Pik et al., 2002), particularly ants (Schnell et al., 2003).

Several TS methods exist. Two do not require species identification: the use of Recognizable Taxonomic Units (RTU's: groups that are easily distinguishable by external, unambiguous morphological features that are obvious to those who are not professional taxonomists; Oliver and Beattie, 1993, 1996), and higher-taxon surrogacy (William and Gaston, 1994; Báldi, 2003). We do not investigate the use of RTU's in this study. A third approach that relies on species-level identifications but is still considered a form of TS is to focus on certain "indicator taxa" instead of all taxa, also called bioindicators (*sensu* McGeoch, 1998). These surrogates are expected to respond in a predictable way to environmental parameters or disturbances, and/or represent a value of some functional attribute (McGeoch, 1998). Several studies conducted in tropical regions demonstrated that taxonomically distant "indicator taxa" tend not to be good indicators of changes in the richness of other taxa (Lawton et al., 1998; Pineda et al., 2005). Moreover, although "indicator taxa" have sometimes been used as surrogates for assemblages of taxonomically close invertebrates (Pik et al., 1999; Lindenmayer et al., 2000), species belonging to selected "indicator genera" rather than to an entire family have never been used in ant surveys. We develop here a new TS method: a mixed-level approach, in which higher-taxon surrogacy is combined with species or morphospecies of "indicator taxa".

Among terrestrial invertebrates, ants are frequently used in surveys dealing with conservation or environmental monitoring and assessment (Andersen and Majer, 2004) due to their ecological dominance in most terrestrial ecosystems – especially in the Tropics – (Hölldobler and Wilson, 1990), the relative ease of sampling them (Agosti et al., 2000), and their sensitivity to environmental changes (Kaspari and Majer, 2000). They are important (1) bioindicators of the diversity of other taxa (Alonso, 2000) and (2) ecological bioindicators of environmental disturbance caused by anthropization such as agriculture, fires, habitat fragmentation, logging, military and mining activities. (Andersen and Majer, 2004; Delabie et al., 2009). Furthermore, the Neotropics represent an area with one of the richest ant faunas in the world (Fernández and Sandoya, 2004), and ant identification to species level is not always easy or feasible, even for specialists. Fortunately, ant genera are generally clearly defined and robust, permitting them to be easily identified through widely available keys (Bolton, 1994; Fernández, 2003). Consequently, using genus-level diversity instead of species diversity could potentially simplify ant biodiversity surveys (Andersen, 1995; Andersen et al., 2002).

Here, we use five datasets for Neotropical ants from different regions to evaluate the efficacy of three TS approaches: higher-taxon surrogacy, "indicator taxa" and mixed-level method. By having thorough species-level identifications to start with, we were able to investigate the effects of different levels of taxonomic resolution; our aim was to conserve the maximum amount of information on ant assemblages while reducing the amount of identification work required.

2. Materials and methods

2.1. Datasets

Five datasets from Central and South American countries (three datasets from Brazil, one from Costa Rica, and one from French Guiana) were analysed (Table 1). The datasets contained one or more species × sample matrices for different sites within the dataset's study region. A total of 34 data matrices were available for analysis. The ants in the different datasets were collected with a range of sampling methods. A variety of habitats were sampled across the studies: several types of forest, pastures, and cocoa plantations (Table 1).

We confined our analysis to results gathered from the worker caste, since alates are difficult to identify and the presence of a worker is clear evidence of the presence of a colony. For the datasets used in our survey, the ants were sorted by experienced taxonomists to species. Contrary to non-social insects whose individuals have an equal probability of being sampled in the sampling universe, ants (like all social insects) are strongly aggregated when sampling methods capture colonies; for this reason presence–absence data may be preferred over abundance data in the analyses (Longino, 2000). Thus only species occurrences were taken into account in the species × sample incidence (presence–absence) matrices (*i.e.* datasets) on which this study is based.

2.2. Higher-taxon surrogacy

For each site in each dataset, the fully-resolved taxonomic matrix, based on species and morphospecies, was aggregated to produce less-resolved taxonomic matrices at three levels: genus, tribe and subfamily. Thus, four sample × taxon matrices were constructed for each site, based on the four levels of taxonomic resolution.

Sample by taxon matrices are most often used to compare measures of *alpha* or *beta* diversity among groups of samples. In this study, we focus on *beta* diversity. *Beta* diversity is often measured using indices of species overlapping between pairs of samples. We used the Jaccard index (Rohlf, 1989), one of the oldest and most widely used similarity indices to assess the compositional similarity of assemblages (Manthey and Fridley, 2009). It is simple to compute (Magurran, 2004) and is based solely on the presence–absence of species in paired assemblages. For each site, we calculated four Jaccard distance matrices based on the four previous sample × taxon matrices.

To assess the amount of information lost by a decrease in taxonomic resolution, the Mantel correlation test (Mantel, 1967) was conducted to compare the sample distance matrices of each site based on the different levels of taxonomic resolution. The Mantel test determines the similarity between two given distance matrices based on distances. Within each site, the fully-resolved, species-level matrix was compared to the three higher taxon matrices: genus, tribe, and subfamily. The Mantel correlation coefficients were calculated with *R* statistical software (R Development

Table 1
Information concerning the datasets analysed in this study.

Origin of data set	Sampled sites	Number of samples	Habitat	Sampling method
Delabie et al. (2000, 2007)	Site 2	500	Cocoa plantation	Winkler extraction
Delabie et al. (2007)	Site 9	50		
Campiolo and Delabie (2000), Delabie et al. (2007)	Sites 3–6, 8	50	Forest	Winkler extraction
Campiolo and Delabie (2000), Delabie et al. (2007)	Sites 1, 7, 10	50	Pasture	Winkler extraction
Brazil, Bahia				
Majer and Delabie (1994)	Site 1	7	"Planalto" forest	Baiting, beating, hand-collecting, sweeping, Winkler extraction
Brazil, Pará, Amazon	Site 2	7	"Flanco" forest	Baiting, beating, hand-collecting, sweeping, Winkler extraction
	Site 3	7	"Varzea" forest	Baiting, beating, hand-collecting, sweeping, Winkler extraction
Vasconcelos et al. (2006)	Site 1	32	Pooled data of 32 forests	Baits, hand-collecting, Winkler extraction
Brazil, Pará, Amazon				
Longino et al. (2002)	Sites 1, 4, 5, 7,	14	Forest	Berlèse extraction
Costa Rica, La Selva	8, 10, 12, 13			
	Site 2	13	Forest	Berlèse extraction
	Sites 3, 11	12	Forest	Berlèse extraction
	Site 9	15	Forest	Berlèse extraction
	Sites 17, 20	10	Forest	Berlèse extraction
	Sites 18	9	Forest	Berlèse extraction
Groc et al. (2009)	Site 1	50	Liana forest	Winkler extraction
French Guiana, Les Nouragues	Site 2	50	Forested plateau	Winkler extraction
	Site 3	50	Transition forest	Winkler extraction
	Site 4	20	Inselberg forest	Winkler extraction

Core Team, 2008). For all comparisons, the correlation significance was determined for 1000 random permutations per matrix (Mantel, 1967).

2.3. "Indicator taxa" surrogacy

In addition to investigating the level of taxonomic resolution in general, we also analysed the effect of focusing on a subset of "indicator taxa." Our comparison of 17 surveys (including the five datasets analysed here) on Neotropical ants from 13 countries (Argentina, Bolivia, Brazil, Colombia, Costa Rica, the Dominican Republic, Ecuador, French Guiana, Guyana, Mexico, Panama, Peru, Venezuela; Appendix A) helped us to draw up a list of genera represented by three species or more. Then the following speciose genera were removed because a taxonomic revision is needed or the identification to species level was deemed to be too difficult: *Acropyga*, *Azteca*, *Brachymyrmex*, *Hypoponera*, *Paratrechina*, *Pheidole*, *Solenopsis* and *Trachymyrmex*. Consequently, the "indicator taxa" retained were genera that (1) contained more than three species across all five datasets, (2) were taxonomically well known, and (3) contained species that could be identified using conspicuous external morphological characters; those that satisfied these criteria were *Anochetus*, *Apterostigma*, *Camponotus*, *Crematogaster*, *Cyphomyrmex*, *Dolichoderus*, *Gnamptogenys*, *Hylomyrma*, *Octostruma*, *Odontomachus*, *Pachycondyla*, *Pseudomyrmex*, *Pyramica*, *Rogeria* and *Strumigenys*. The distance matrix based on the "indicator taxa" was compared to the fully-resolved, species-level matrix by the Mantel correlation test using the methodology previously described.

2.4. Mixed-level method

In a final comparison, matrices were constructed in which the indicator taxa described above were left fully resolved to species, while all non-indicator taxa were also included but only to genus. For each site, the mixed-level matrix was compared with the fully-resolved, species-level matrix.

2.5. Other statistical analyses

The Mantel correlation coefficient (mean ± SD) was then plotted for the three TS methods and for each dataset, habitat type and sampling method (SIGMAPLOT 8.0 software; Systat, 2005; Fig. 1). Then, the higher-taxon surrogacy approach was only represented by the most informative level, namely the genus level. The means of each Mantel correlation coefficients were statistically compared (normality and homoscedasticity: Shapiro–Wilks and Bartlett tests; analysis of variance: ANOVA with Tukey's *post hoc* tests; non parametric tests: Kruskall–Wallis and Mann–Whitney pairwise comparisons) with the PAST program (Hammer et al., 2001).

3. Results

The Mantel correlation coefficient values relative to the higher-taxon surrogacy oscillated between 0.32–0.84, 0.34–0.84 and 0.12–0.71 for the comparisons of species–genus, tribe and subfamily matrices respectively. In 82% of the cases (28 out of 34), the coefficient value was highest for the comparison of the species and genus matrices, and lower for comparisons with tribe and subfamily matrices. In five of the cases, the coefficient was similarly high for genus-level and tribe-level comparisons. In one case, the tribe-level correlation was slightly higher than the genus-level correlation. Subfamily-level correlations were always the lowest, although they were significant in 39% of the cases (Table 2). Thus, among the levels higher than species, genus is the most informative for all of the datasets analysed. Concerning the "indicator taxa" surrogacy, the tests were significant and the Mantel coefficient values were between 0.32 and 0.84, except for the data gathered by Longino et al. (2002) for which the test was non-significant in

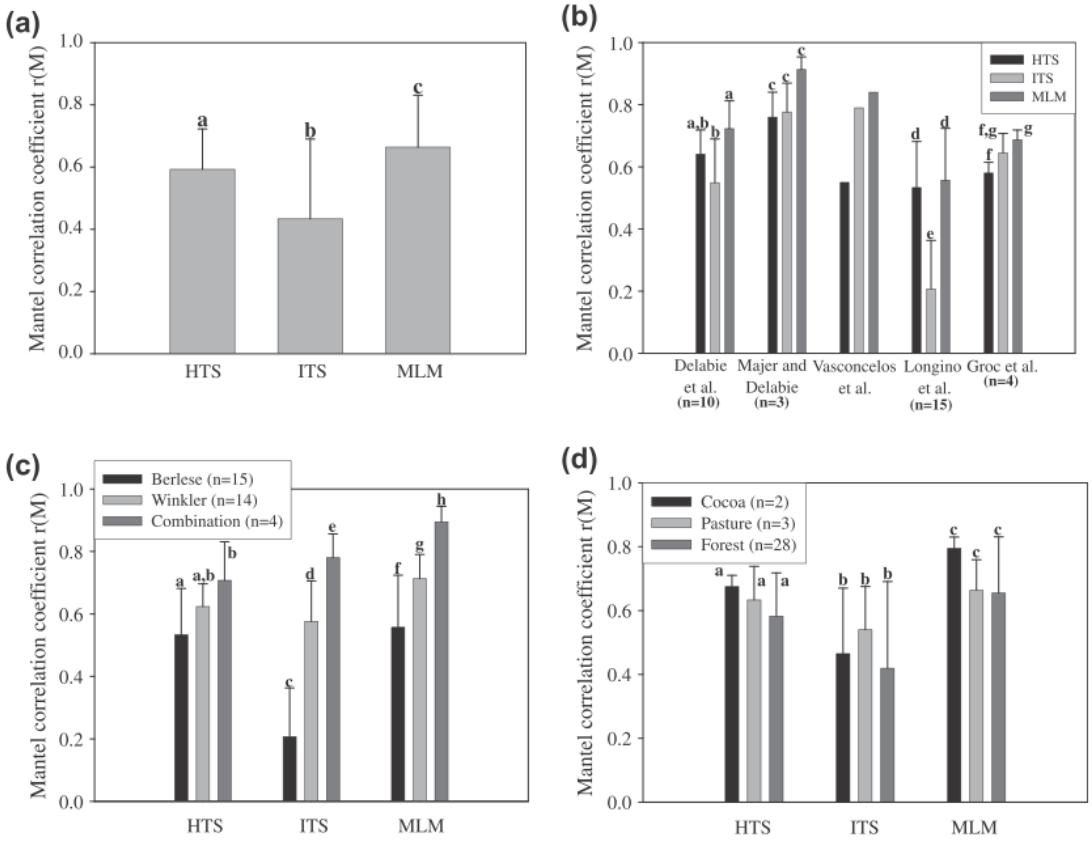

Fig. 1. Means (±SD) for the Mantel correlation coefficients (a) using the three TS methods compared ($n = 33$) depending on the dataset analysed (b), the habitat type (c) and the sampling method (d) (HTS = higher-taxon surrogacy, ITS = "indicator taxa" surrogacy, MLM = mixed-level method). The different letters above the SD bars represent the significant differences whose values are given in Table 3.

53% of the cases. The coefficient value exceeded 0.5 in 83% of the cases, showing that the species in the 15 selected genera are good "indicator taxa" (Table 2). For all of the comparisons in the mixed-level method, the test was significant; the Mantel coefficient value was between 0.30 and 0.87 for the data gathered by Longino et al. (2002), and 0.56 and 0.96 for the other datasets (Table 2). This means that this new TS method – made up of the combination of indicator taxa and genus-level identifications – captures more of the *beta* diversity patterns than either method used alone.

Moreover, although the "indicator taxa" surrogacy is based on good "indicator taxa" (Table 2), the mean for the Mantel correlation coefficient, significantly lower than those of the two other methods, make this approach the less efficient (Fig. 1a, Table 3). In addition to having the highest coefficient value with a highly significant test in nearly 79% of the cases (Table 2), the mean for the mixed-level method coefficient was significantly higher than that of higher-taxon and "indicator taxa" surrogacies (Fig. 1a, Table 3: $U = 371.5$, $p = 0.027$; $U = 357.5$, $p = 0.017$; $n = 33$).

Whatever the dataset structure, the sampling method or the habitat type, there is always the same pattern between the means for the Mantel correlation coefficient for the three TS methods (Fig 1b–d; Table 3: r(M) MLM > r(M) HTS > r(M) ITS). For all datasets analysed – for which $n > 3$ –, the mean for the mixed-level-method coefficients is always significantly higher than at least one of the two other methods (Fig. 1b; Table 3). Thus, the mixed-level method is the best compromise between reducing the amount of taxonomic work and conserving an enough amount of information sufficient to characterize the ant assemblage.

However, although habitat type has no effect (Fig. 1d; Table 3) and the dataset structure only some influence (Fig. 1b; Table 4) on the efficiency of the three TS methods, the value for the Mantel coefficient is strongly biased by the sampling method (Fig. 1c; Table 3). While Berlese extraction results in the lowest values for the three TS methods, the combination of techniques leads to the highest coefficient value (Fig. 1c; Table 3); this is also shown in Fig. 1b for the datasets collected with several complementary sampling methods.

4. Discussion

In ecology, many of the characteristics of communities have often been measured using species × sample data coupled with diversity indices to answer various questions about biodiversity. We innovated in using the Mantel test based on the Jaccard distance to reflect similarity in both the number and identity of ant species. Although similarity indices seem to be biased by pairwise comparisons (Manthey and Fridley, 2009), the utility of spatial scale (Koleff et al., 2003) and particularly the taxonomic level of identification (generally leading to their underestimation) is becoming increasingly recognized in studies incorporating higher-taxon richness and evenness (Izsák and Price, 2001).

Substituting species richness patterns by those of higher taxa has received growing attention in studies on terrestrial biodiversity – e.g., Acari, Aranae, Coleoptera, Diptera, Formicidae – (Báldi, 2003; Cardoso et al., 2004); it provides obvious benefits in the con-

Table 2
Results of the Mantel correlation test (Mantel correlation coefficient value (rM) and significance) for each comparison of matrices for the three methods of taxonomic sufficiency used.

Origin of the dataset	Sampled sites	Higher-taxon surrogacy[a,b]			"Indicator taxa" surrogacy	Mixed-level method[b]
		Species *vs.* genus (rM)	Species *vs.* tribes (rM)	Species *vs.* subfamily (rM)	Species *vs* species of "indicator taxa" (rM)	Species *vs* multi-taxonomic (rM)
Campiolo and Delabie (2000)	Site 1	**0.53*****	0.47***	0.24***	0.67***	0.68***
Delabie et al. (2000, 2007)	Site 2	**0.65*****	0.57***	0.12**	0.61***	0.82***
	Site 3	**0.65*****	0.57***	0.23**	0.35***	0.69***
	Site 4	**0.56*****	0.37***	0.15 NS	0.59***	0.75***
	Site 5	**0.53*****	0.37***	0.16***	0.67***	0.73***
	Site 6	**0.72*****	0.58***	0.25***	0.70***	0.86***
	Site 7	**0.74*****	0.65***	0.25***	0.40***	0.56***
	Site 8	**0.70*****	0.53***	0.08 NS	0.63***	0.62***
	Site 9	**0.70*****	0.54***	0.14***	0.32***	0.77***
	Site 10	**0.63*****	0.52***	0.26***	0.55***	0.75***
Majer and Delabie (1994)	Site 1	**0.84*****	**0.84*****	0.71*	0.82***	0.89***
	Site 2	**0.68*****	0.38 NS	0.47*	0.67*	0.89***
	Site 3	**0.76*****	0.68**	0.10 NS	0.84***	0.96***
Vasconcelos et al. (2006)	Site 1	**0.55*****	0.35***	0.10 NS	0.79***	0.84***
Longino et al. (2002)	Site 1	**0.69*****	0.45***	0.30*	0.33*	0.70***
	Site 2	**0.35****	**0.35****	0.21 NS	0.18 NS	0.35**
	Site 3	**0.66*****	0.61***	0.03 NS	0.04 NS	0.67***
	Site 4	0.32***	**0.34*****	0.04 NS	0.18*	0.30**
	Site 5	**0.63*****	0.58***	0.42***	0.11 NS	0.65***
	Site 7	**0.57*****	0.55***	0.45***	0.28**	0.61***
	Site 8	**0.68*****	**0.68*****	0.42***	0.02 NS	0.69***
	Site 9	**0.53*****	0.49***	0.45***	0.35**	0.62***
	Site 10	**0.61*****	0.55***	0.33*	0.47**	0.71***
	Site 11	**0.82*****	0.61***	0.07 NS	0.23*	0.87***
	Site 12	**0.41*****	**0.41*****	0.12 NS	0.02 NS	0.40***
	Site 13	**0.51*****	0.43***	0.04 NS	0.47**	0.55***
	Site 17	**0.39****	**0.39****	0.08 NS	0 NS	0.39**
	Site 18	**0.38****	0.26 NS	0.12 NS	0.28 NS	0.38**
	Site 20	**0.45****	0.43***	0.43 NS	0.15 NS	0.47**
Groc et al. (2009)	Site 1	**0.59*****	0.42***	0.26***	0.72***	0.73***
	Site 2	**0.61*****	0.51***	0.18***	0.66***	0.67***
	Site 3	**0.53*****	0.47***	0.14***	0.57***	0.66***
	Site 4	**0.59*****	0.56***	0.43***	0.63***	0.69***

Significance levels:
NS = not significant.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
[a] In the higher-taxon surrogacy approach, the comparison having the highest Mantel correlation coefficient value (*i.e.* showing the most informative taxonomic level) highlighted in bold.
[b] The comparison(s) having the highest Mantel correlation coefficient value (*i.e.* showing the best method among the higher-taxon and "indicator taxa" surrogacies and the mixed-level method) are underlined.

text of limited financial and human resources, which is extremely useful when rapid biodiversity surveys are required in biological conservation and indication. While a number of studies on aquatic communities have shown that most information is retained after data aggregation (Khan, 2006), literature on terrestrial faunas is scarce (Caruso and Migliorini, 2006). Our study has also corroborated this in showing that changing from fully-resolved species-level data to some subset or aggregated version of the data revealed the same patterns.

Although the efficacy of TS may vary with the taxonomic group considered (Vanderklift et al., 1998), higher-taxon surrogacy may potentially be the most beneficial when higher taxa contain numerous species that are difficult to identify (Andersen, 1995). Andersen et al. (2002) stated that the genus level is the best taxonomic sufficiency tool for ant surveys. Several authors have shown that using higher taxonomic levels, and especially genus-level identification in surveys on ant faunas (Andersen et al., 2002; Schnell et al., 2003) to compare assemblages, is as relevant for large areas (Gaston and Blackburn, 1995) as for local and regional applications (Pik et al., 2002; Grimbacher et al., 2008). However its efficacy varies widely between biogeographical regions (Andersen, 1995), and data at higher taxonomic levels may not discriminate as well as species-level data for places with different histories of disturbance (Nahmani et al., 2006). This suggests that resolution to higher taxa may not always be sufficient enough to detect subtle changes in the specific richness and composition of the assemblages of terrestrial invertebrates. It may be necessary to identify organisms to the species level to detect a subtle environmental change affecting only species.

The potential "indicator genera" (widespread, diverse and identifiable) used in this study act as good surrogates for the diversity of Neotropical ant species, so that they can be considered as good

Table 3
Results of the variance analysis and nonparametric tests on the mean for the Mantel coefficient correlation for the three TS methods for each dataset analyzed, and depending on habitat type and sampling methods (HTS = higher-taxon surrogacy, ITS = "indicator taxa" surrogacy, MLM = mixed-level method). Significant *p*-values are in bold.

Data	ANOVA (*F*)/Kruskal–Wallis test (*H*)	Pairwise comparisons	Tukey *post hoc* test/Mann–Whitney test (*U*)
Fig. 1a			
	$H = 16.67$, $\mathbf{p = 24.10^{-5}}$	HTS–ITS	$U = 357.5$, $\mathbf{p = 0.017}$
		MLM–HTS	$U = 371.5$, $\mathbf{p = 0.027}$
		MLM–ITS	$U = 248.5$, $\mathbf{p = 15.10^{-5}}$
Fig. 1b			
Majer and Delabie	$H = 5.49$, $p = 0.067$	–	–
Delabie et al.	$F = 6.71$, $\mathbf{p = 43.10^{-4}}$	HTS–ITS	$p = 0.148$
		MLM–HTS	$p = 0.214$
		MLM–ITS	$\mathbf{p = 31.10^{-4}}$
Longino et al.	$F = 23.27$, $\mathbf{p = 16.10^{-8}}$	HTS–ITS	$\mathbf{p = 12.10^{-5}}$
		MLM–HTS	$p = 0.908$
		MLM–ITS	$\mathbf{p = 12.10^{-5}}$
Groc et al.	$F = 5.81$, $\mathbf{p = 0.024}$	HTS–ITS	$p = 0.157$
		MLM–HTS	$\mathbf{p = 0.02}$
		MLM–ITS	$p = 0.411$
Fig. 1c			
HTS	$F = 4.23$, $\mathbf{p = 0.024}$	Berlese–Winkler	$p = 0.307$
		Berlese–Combination	$\mathbf{p = 0.019}$
		Winkler–Combination	$p = 0.358$
ITS	$H = 23.44$, $\mathbf{p = 83.10^{-7}}$	Berlese–Winkler	$U = 8.5$, $\mathbf{p = 27.10^{-6}}$
		Berlese–Combination	$U = 0$, $\mathbf{p = 0.003}$
		Winkler–Combination	$U = 3$, $\mathbf{p = 0.009}$
MLM	$H = 15.43$, $\mathbf{p = 45.10^{-5}}$	Berlese–Winkler	$U = 42$, $\mathbf{p = 63.10^{-4}}$
		Berlese–Combination	$U = 1$, $\mathbf{p = 44.10^{-4}}$
		Winkler–Combination	$U = 1$, $\mathbf{p = 48.10^{-4}}$
Fig. 1d			
HTS	$H = 1.638$, $p = 0.44$	–	–
ITS	$H = 0.48$, $p = 0.79$	–	–
MLM	$H = 2.06$, $p = 0.36$	–	–

Table 4
Results of the variance analysis and nonparametric tests on the mean for the Mantel coefficient correlation for the three TS methods depending on the dataset (HTS = higher-taxon surrogacy, ITS = "indicator taxa" surrogacy, MLM = mixed-level method). Significant *p*-values are in bold.

TS methods	ANOVA (*F*)/Kruskal–Wallis test (*H*)	Pairwise comparisons	ANOVA/Mann–Whitney test (*U*)
HTS	$H = 9.486$, $\mathbf{p = 0.024}$	Delabie-Majer	$U = 4$, $p = 0.074$
		Delabie-Longino	$U = 38.5$, $\mathbf{p = 0.045}$
		Delabie-Groc	$U = 10$, $p = 0.176$
		Majer-Longino	$U = 3.5$, $\mathbf{p = 0.028}$
		Majer-Groc	$U = 0$, $\mathbf{p = 0.05}$
		Longino-Groc	$U = 25$, $p = 0.652$
ITS	$F = 24.37$, $\mathbf{p = 58.10^{-9}}$	Delabie-Majer	$p = 0.058$
		Delabie-Longino	$\mathbf{p = 0.002}$
		Delabie-Groc	$p = 0.679$
		Majer-Longino	$\mathbf{p = 16.10^{-5}}$
		Majer-Groc	$p = 0.429$
		Longino-Groc	$\mathbf{p = 26.10^{-5}}$
MLM	$H = 14.56$, $\mathbf{p = 0.002}$	Delabie-Majer	$U = 0$, $\mathbf{p = 0.014}$
		Delabie-Longino	$U = 28$, $\mathbf{p = 99.10^{-4}}$
		Delabie-Groc	$U = 12$, $p = 0.287$
		Majer-Longino	$U = 0$, $\mathbf{p = 0.009}$
		Majer-Groc	$U = 0$, $\mathbf{p = 0.05}$
		Longino-Groc	$U = 14$, $p = 0.121$

biodiversity indicators (*sensu* McGeoch, 1998) for Neotropical ant assemblages. According to Andersen (1995), species richness within particularly speciose and widespread genera might be more useful than genus richness as a surrogate for total ant species richness. Nevertheless, we must be mindful of the low taxonomic resolution resulting from the use of higher-taxon richness as a surrogate for biodiversity in megadiverse groups of organisms because there is the risk of considering both taxonomic groups poor in species and very speciose ones in the same way (Balmford et al., 2000).

Our results demonstrate that, for all of the ant faunas considered, coupling the species from the selected "indicator genera" to the remaining individuals identified to the genus level (mixed-level method) leads to information very close to that gained from data encompassing all species. Thus, using these multi-taxonomic assemblages appears to be the best compromise between obtaining the maximum amount of information on the ant assemblage and considerably reducing the amount of taxonomic work, particularly that related to the identification of the species from problematic genera which are often hyper-diversified in Neotropical surveys (e.g., *Hypoponera*, *Pheidole* or *Solenopsis*). Although the formal identification of species requires the attention of professional taxonomists, morphospecies can be assigned by a non-specialist using characters sufficient enough to classify specimens into RTU's resembling distinct species (Oliver and Beattie, 1993, 1996).

In conclusion, we have developed an accurate, robust and cost-effective method based on taxonomic sufficiency, including biodiversity indicators, that is applicable to Neotropical ant assemblages and perhaps other faunas, and which can be very helpful in assessing ant biodiversity in conservation and bioindication surveys. This mixed-level method consists of identifying to the species level only the species belonging to the previously-listed "indicator genera" and in identifying the remaining ants to the genus level. Like in other studies on terrestrial faunas dealing with higher-taxon surrogacy, this methodological efficiency is not influenced by habitat type (Cardoso et al., 2004), but greatly depends on dataset structure, sampling intensity (Cardoso et al., 2004), and a strong correlation between higher-taxon richness and species richness (Williams and Gaston, 1994). Contrary to the study by Cardoso et al. (2004), its efficacy is also influenced by the type of sampling method and can be greatly improved when a combination of complementary techniques is used to collect data, since it maximises the information collected on the ant community (Groc et al., 2007). Finally, the mixed-level method significantly reduces the amount of taxonomic work linked to the identification of problematic species while at the same time conserving most of the information on the ant assemblage (all of the individuals collected are considered). It should enhance the work of entomologists and biological survey staff, most of whom are not specialists in ant taxonomy.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.07.034.

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ANNEXE 3°: Position taxonomique et occurrences des espèces par habitat pour chacune des localités échantillonnées

443 espèces - 12276 occurrences	Maripasoula[5]						Nouragues[6]				Kaw[7]					Chutes[8] Voltaire	Paracou[9]					
	V	MR	MA	FF	ZFR	FM	GP	FL	FT	IN	V1	V2	V3	V4	V5		FM	CH	AC	CA	HE	PI
AGROECOMYRMECINAE Carpenter																						
Agroecomyrmicini Carpenter																						
Tatuidris kapasi[10]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
AMBLYOPONINAE Forel																						
Amblyoponini Forel																						
*Amblyoponelurilabes*Lattke	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Prionopelta sp.1	0	0	0	0	0	0	0	1	0	0	2	0	1	1	0	0	1	0	0	0	0	0
Prionopelta sp.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Prionopelta sp.3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Prionopelta sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
CERAPACHYINAE Forel																						
Acanthostichini Emery																						
Acanthostichus sp.1 cf *brevicornis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cerapachyini Forel																						

[5] V : village ; MR : plantation de manioc récente ; MA : plantation de manioc abandonnée ; FF : fragment forestier ; ZRF : zone forestière ripicole ; FM : forêt mature
[6] GP : forêt de grand plateau ; FL : forêt de lianes ; FT : forêt de transition ; IN : forêt sommitale d'inselberg
[7] V1 : versant 1 ; V2 : versant 2 ; V3 : versant 3 ; V4 : versant 4
[8] CV : Chutes Voltaire
[9] FM : forêt mature ; CH : chablis ; AC : plantation d'acacias ; CA : plantation de cacaoyers ; HE : plantation d'hévéas ; PI : plantation de pins caraïbes
[10] voir annexe 5 pour la description de *Tatuidris kapasi* Lacau & Groc, 2011

Cerapachys neotropicus Weber	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
DOLICHODERINAE Forel																						
Dolichoderini Forel																						
Azteca instabilis (Smith)	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0
Azteca sp.1	0	0	0	0	0	0	4	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Azteca sp.2	0	0	0	0	0	0	0	0	2	0	3	0	1	0	0	0	2	0	0	0	0	4
Azteca sp.3	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0
Azteca sp.4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Dolichoderus attelaboides (Fabricius)	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Dolichoderus bidens (Linnaeus)	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Dolichoderus bispinosus (Olivier)	0	0	0	0	1	0	2	1	5	0	5	0	3	5	0	1	0	1	4	1	0	1
Dolichoderus decollatus Smith	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Dolichoderus debilis Emery	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dolichoderus imitator Emery	0	0	0	0	0	0	1	2	1	2	3	5	6	0	5	3	2	0	18	5	3	3
Dolichoderus laminatus (Mayr)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dolichoderus lutosus (Smith)	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Dolichoderus sp. cf *luederwaldti*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linepithema neotropicum Wild	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	8	0
Tapinoma melanocephalum (Fabricius)	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	3	0	13	0
Tapinoma sp.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Technomyrmex vitiensis Mann	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
ECITONINAE Forel																						
Ecitonini Forel																						
Eciton burchelli (Westwood)	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Eciton drepanophorum Smith	0	0	0	0	0	0	2	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
Labidus coecus (Latreille)	0	0	0	1	0	0	5	6	2	5	0	0	0	1	0	0	0	0	8	0	2	0

Neivamyrmex diana (Forel)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Neivamyrmex iridescens Borgmeier	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	1	1
Neivamyrmex sp. nov	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Neivamyrmex sp. cf *rugulosus*	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neivamyrmex sp.4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
ECTATOMMINAE Emery																						
Ectatommini Emery																						
Ectatomma brunneum Smith	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	11	55	2
Ectatomma edentatum Roger	0	2	0	1	0	2	14	14	11	1	1	6	12	7	2	9	22	3	0	0	0	1
Ectatomma lugens Emery	0	0	0	0	1	2	30	24	12	19	0	0	3	1	6	6	2	2	0	0	0	11
Ectatomma tuberculatum (Olivier)	0	0	0	0	0	0	1	0	3	0	0	0	1	0	1	0	1	0	6	2	16	5
Gnamptogenys acuminata (Emery)	0	0	0	0	0	0	0	3	3	0	1	0	0	2	0	0	1	0	4	0	0	1
Gnamptogenys annulata (Mayr)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnamptogenys continua (Mayr)	0	0	0	0	0	0	2	3	1	0	0	0	0	1	1	0	0	1	0	0	0	0
Gnamptogenys enodis Lattke	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnamptogenys haenschei (Emery)	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gnamptogenys horni (Santschi)	0	0	0	0	0	1	6	12	4	2	3	4	2	4	8	3	8	11	10	0	1	0
Gnamptogenys mecotyle Brown	0	0	0	0	0	0	0	1	0	0	4	0	2	0	0	0	0	0	1	0	0	1
Gnamptogenys mina Brown	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnamptogenys minuta (Emery)	0	0	0	0	0	0	0	3	0	1	1	1	0	0	0	0	1	0	0	2	1	0
Gnamptogenys moelleri (Forel)	0	0	1	0	0	1	0	0	0	0	1	2	1	3	0	0	0	0	0	0	0	0
Gnamptogenys mordax Smith	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Gnamptogenys pleurodon (Emery)	0	0	0	0	0	0	0	2	0	0	1	2	1	3	4	0	0	2	0	0	0	0
Gnamptogenys porcata (Emery)	0	0	0	0	0	0	1	1	2	1	0	0	0	0	0	1	2	0	0	0	0	0
Gnamptogenys regularis Mayr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Gnamptogenys relicta (Mann)	0	0	0	0	0	0	4	1	5	1	1	0	10	2	1	0	22	2	0	0	0	13

Gnamptogenys striatula Mayr	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnamptogenys sulcata (Smith)	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	0	0
Gnamptogenys tortuolosa (Smith)	0	0	0	1	0	0	4	1	0	3	0	0	0	1	0	1	6	3	0	7	0	2
Gnamptogenys sp. cf *horni*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Gnamptogenys sp.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Gnamptogenys sp.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Typhlomyrmecini Emery																						
Typhlomyrmex rogenhoferi Mayr	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Typhlomyrmex schmidti Menozzi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Typhlomyrmex sp nov1 (*sensu* Lacau, unpublished)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Typhlomyrmex sp nov (*sensu* Lacau, unpublished)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Typhlomyrmex sp. nov4 (*sensu* Lacau, 2005[11])	0	0	0	0	0	0	3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0
FORMICINAE Latreille																						
Camponotini Forel																						
Camponotus atriceps (Smith)	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	2	0	0	0
Camponotus cacicus Emery	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camponotus crassus Mayr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	0
Camponotus fastigatus Roger	0	0	0	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	3	0	8	0
Camponotus femoratus (Fabricius)	0	0	0	0	0	1	29	22	2	0	1	1	2	10	3	4	1	0	0	0	0	0
Camponotus latangulus Roger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Camponotus leydigi Forel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	5	0

[11] Lacau, S. (2005) Morphologie et systématique du genre *Typhlomyrmex* Mayr, 1862 (Formicidae: Ectatomminae). PhD thesis, Muséum National d'Histoire Naturelle, Paris.

Camponotus lespesii Forel	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Camponotus melanoticus Emery	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	5	3	1
Camponotus nidulans (Smith)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0
Camponotus novogranadensis Mayr	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0
Camponotus punctulatus andigenus Emery	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Camponotus rapax (Fabricius)	0	0	2	1	1	0	1	10	5	5	1	1	1	1	0	0	10	2	0	0	0	0
Camponotus rectangularis Emery	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	4	0
Camponotus renggeri Emery	0	0	0	0	0	0	3	1	3	0	0	0	0	1	0	0	4	1	3	0	1	0
Camponotus (Myrmaphaenus) sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Camponotus (Myrmobrachys) sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp. cf *atriceps*	0	0	0	0	0	0	0	0	1	1	5	0	0	0	1	0	2	4	2	1	0	0
Camponotus (*Myrmaphaenus*) sp.4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	4	2	0
Camponotus (*Myrmaphaenus*) sp.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Camponotus sp.7 comp. *paradoxus*	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	2	0	0	0
Camponotus (*Tanaemyrmex*) sp.17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Camponotus sp.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Camponotus (*Myrmobrachys*) sp.20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Camponotus sp.23 comp. *ager*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camponotus sp.26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp.30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp.31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp.32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Gigantiopini Ashmead																						
Gigantiops destructor (Fabricius)	0	0	0	0	0	0	0	2	9	0	0	1	0	0	1	0	0	0	16	1	6	7
Lasiini Ashmead																						

Acropyga decedens (Mayr)	0	0	0	0	0	0	3	0	0	0	2	8	1	4	0	0	0	2	0	0	0	0
Acropyga fuhrmanni (Forel)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0	0	0	0
Acropyga romeo Lapolla	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Acropyga smithii Forel	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Acropyga sp.3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0
Plagiolepidini Forel																						
Brachymyrmex heeri Forel	0	0	0	0	0	0	0	0	7	6	0	3	6	3	7	1	0	0	1	0	6	3
Brachymyrmex patagonicus Mayr	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	23	0
Brachymyrmex sp.2 cf *heeri*	0	0	0	0	0	0	2	2	8	7	10	18	6	11	8	2	3	2	4	2	19	4
Brachymyrmex sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Brachymyrmex sp.8	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Myrmelachista sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nylanderia fulva (Mayr)	0	0	0	0	0	0	12	10	8	14	0	0	0	0	0	0	0	0	0	0	0	0
Nylanderia guatemalensis (Forel)	0	0	0	0	0	0	1	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Nylanderia sp.2 cf *guatemalensis*	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nylanderia sp.3	0	0	0	0	0	0	0	0	2	0	5	2	1	2	1	0	0	4	6	0	2	1
Nylanderia sp.4	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Nylanderia sp.5	0	0	0	0	0	0	13	10	23	10	7	17	16	8	32	5	36	8	45	15	61	34
Nylanderia sp.6	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	2	0	1	1	0	2	0
Paratrechina longicornis (Latreille)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MYRMICINAE Lepeletier																						
Adelomyrmecini Fernández																						
Cryptomyrmex longinodus (Fernandez and Brandão)	0	0	0	0	0	0	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Attini Smith																						
Acromyrmex octospinosus (Reich)	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Acromyrmex rugosus (Smith)	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0
Acromyrmex subterraneus (Forel)	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Apterostigma jubatum Wheeler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Apterostigma pariense Lattke	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	2	0	1	0	1	0
Apterostigma tachirense Lattke	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Apterostigma urichii Forel	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0
Apterostigma sp.1 comp. *pilosum*	0	0	0	0	0	0	0	0	0	0	1	3	0	0	2	4	0	0	6	0	0	0
Apterostigma sp.2 comp. *pilosum*	0	0	0	0	0	0	4	4	0	0	4	5	8	4	4	0	2	2	4	13	5	2
Apterostigma sp.3 comp. *pilosum*	0	0	0	0	0	0	0	1	0	0	3	13	0	7	6	0	3	0	2	0	2	0
Apterostigma sp.6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atta cephalotes (Linnaeus)	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	6	0	32	0
Atta sexdens sexdens (Linnaeus)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyphomyrmex bigibbosus Emery	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyphomyrmex costatus Mann	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Cyphomyrmex faunulus Wheeler	0	0	0	0	0	0	0	4	1	0	2	2	1	0	0	0	0	0	0	0	0	0
Cyphomyrmex flavidus Pergande	0	0	0	0	0	0	0	10	3	1	5	3	3	1	5	11	9	6	23	4	39	12
Cyphomyrmex laevigatus Weber	0	0	0	0	0	0	5	8	2	0	2	1	7	0	0	0	0	0	0	0	0	0
Cyphomyrmex peltatus Kempf	0	0	0	0	0	0	10	18	1	7	15	18	25	9	22	22	3	0	0	0	1	1
Cyphomyrmex salvini Forel	0	0	0	0	0	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Cyphomyrmex transversus Emery	0	0	1	0	0	0	1	6	2	0	0	0	1	0	1	0	3	6	37	11	45	17
Mycocepurus smithi (Forel)	0	0	0	0	0	0	0	3	0	0	1	0	0	0	1	0	0	2	0	0	0	0
Mycocepurus tardus Weber	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrmicocrypta sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	7	8	0
Myrmicocrypta sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	3	0	0	0	0
Myrmicocrypta sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	3	0	0
Myrmicocrypta sp.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0

Myrmicocrypta sp.6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrmicocrypta sp.7	0	0	0	0	0	0	1	2	0	0	0	0	4	0	2	0	0	0	0	0	0	0
Myrmicocrypta sp.8	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrmicocrypta sp.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myrmicocrypta sp.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Sericomyrmex sp.1	0	0	0	0	0	0	1	0	2	0	0	0	0	1	0	0	1	4	0	0	0	1
Sericomyrmex sp.2	0	0	0	0	0	0	0	2	0	9	0	2	1	0	3	0	5	3	2	5	0	11
Sericomyrmex sp.3	0	0	0	0	0	0	2	0	0	0	1	1	1	0	0	1	3	3	0	0	0	2
Sericomyrmex sp.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Trachymyrmex compactus	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
Mayhé-Nunes and Brandão																						
Trachymyrmex cornetzi (Forel)	0	0	0	0	0	0	0	3	4	1	0	3	6	3	2	7	9	2	3	1	1	5
Trachymyrmex farinosus (Emery)	0	0	0	0	0	0	2	3	0	0	0	2	0	0	0	3	2	4	2	1	3	1
Trachymyrmex ixyodus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mayhé-Nunes & Brandão																						
Trachymyrmex mandibularis Weber	0	0	0	0	0	0	4	2	2	1	0	0	2	0	1	7	5	4	1	6	2	1
Trachymyrmex opulentus (Mann)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachymyrmex relictus Borgmeier	0	0	3	2	0	0	0	0	1	0	0	2	0	0	0	2	0	2	0	6	21	0
Trachymyrmex sp.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Trachymyrmex sp.7	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachymyrmex sp.8	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Basicerotini Brown																						
Basiceros balzani (Emery)	0	0	0	0	0	0	7	55	6	8	6	15	21	5	11	4	3	0	0	5	0	0
Basiceros betschi (Perrault)	0	0	0	0	0	0	13	31	14	2	3	11	1	1	6	12	10	5	1	1	0	6
Basiceros bolaui (Mayr)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Basiceros emeryi (Forel)	0	0	0	0	0	0	0	1	0	0	3	6	4	2	7	3	0	0	0	6	0	6

Basiceros iheringi (Emery)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Basiceros sp. proche *iheringi*	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Basiceros (Octostruma) sp.1	0	0	0	0	0	0	3	1	0	0	0	1	0	0	0	0	2	2	0	0	0	0
Basiceros (Rhopalothrix) sp.2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Blepharidattini Wheeler & Wheeler																						
Wasmannia auropunctata (Roger)	0	0	1	0	0	3	15	10	25	4	1	5	8	0	3	18	6	8	58	2	93	21
Wasmannia scrobifera Kempf	0	0	0	0	0	0	6	0	0	5	1	8	1	0	0	2	1	0	0	1	0	0
Cephalotini Smith																						
Cephalotes atratus (Linnaeus)	0	0	0	0	0	1	0	0	2	0	1	0	0	1	0	1	0	0	1	0	0	0
Cephalotes maculatus (Smith)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cephalotes minutus (Fabricius)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Cephalotes pallidoides De Andrade	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cephalotes pallidus De Andrade	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cephalotes spinosus (Mayr)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cephalotes sp.6	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cephalotes sp.10 clade *angustus*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Procryptocerus hylaeus Kempf	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Procryptocerus sp.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crematogastrini Forel																						
Crematogaster abstinens Forel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0
Crematogaster brasiliensis Mayr	0	0	0	0	0	0	0	2	0	0	7	5	2	1	8	0	0	0	0	2	0	0
Crematogaster carinata Mayr	2	0	0	11	0	4	51	62	24	5	10	9	8	8	1	6	34	8	1	0	0	0
Crematogaster distans Mayr	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster flavosensitiva Longino	0	0	0	1	0	0	6	2	6	4	15	17	10	19	0	10	12	9	15	11	2	14
Crematogaster limata Smith	0	2	2	0	0	0	26	56	41	4	32	17	21	35	44	22	3	4	18	10	11	10
Crematogaster longispina Emery	0	0	0	0	0	0	0	6	17	1	0	0	0	0	0	0	0	0	0	0	0	0

Crematogaster nigropilosa Mayr	0	0	0	0	0	0	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sotobosque Longino	0	0	0	0	0	0	10	8	2	0	0	0	0	0	0	0	10	15	0	0	0	2
Crematogaster stolli Forel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Crematogaster tenuicula Forel	0	0	0	0	0	1	1	3	1	0	2	2	0	2	0	2	1	0	0	0	0	3
Crematogaster wardi Longino	0	0	0	0	0	0	3	13	22	1	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sp. gp. *bryophilia*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	1
Crematogaster sp. gp. *limata*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Crematogaster sp.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Crematogaster sp.9	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Crematogaster sp.20	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0
Dacetini Forel			-																			
Acanthognathus brevicornis Smith	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Acanthognathus ocellatus Mayr	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyramica alberti (Forel)	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyramica appretiata (Borgmeier)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyramica auctidens Bolton	0	0	0	0	0	0	20	41	0	1	3	14	23	11	6	7	2	3	0	0	0	1
Pyramica beebei (Wheeler)	0	0	0	0	0	0	2	3	1	0	0	1	0	0	1	0	1	0	0	0	0	0
Pyramica crassicornis Mayr	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Pyramica deinomastax Bolton	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyramica denticulata Mayr	0	0	0	0	0	0	69	86	67	37	38	45	28	35	41	35	34	29	49	38	32	48
Pyramica hadrodens Bolton	0	0	0	0	0	0	1	1	0	0	0	3	2	1	0	0	1	3	0	0	0	0
Pyramica inusitata (Lattke)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pyramica subedentata (Mayr)	0	0	0	0	0	0	7	6	2	1	0	13	11	7	10	6	1	3	4	0	6	0
Pyramica villiersi (Perrault)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0
Pyramica zeteki (Brown)	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Pyramica sp.1 cf *microthrix*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	18	0

Strumigenys borgmeieri Brown	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Strumigenys cordovensis Mayr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	3	0
Strumigenys cosmostela Kempf	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strumigenys diabola Bolton	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strumigenys dyseides Bolton	0	0	0	0	0	0	0	16	0	4	0	0	0	1	0	0	0	0	0	0	0	0
Strumigenys elongata Roger	0	0	0	0	0	0	19	31	8	5	10	18	9	6	14	1	4	5	19	0	0	3
Strumigneys hyphata (Brown)	0	0	0	0	0	0	0	0	2	0	1	1	0	1	0	0	0	0	0	0	0	0
Strumigenys lanuginosa Wheeler	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strumigenys metopia (Brown)	0	0	0	0	0	0	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0
Strumigenys perparva Brown	0	0	0	0	0	0	9	3	3	6	9	26	16	15	18	7	7	5	0	26	0	12
Strumigenys precava Brown	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Strumigenys saliens Mayr	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Strumigenys trinidadensis Wheeler	0	0	0	0	0	0	0	0	0	0	0	1	3	2	0	0	0	0	2	0	1	0
Strumigenys trudifera Kempf & Brown	0	0	0	0	0	0	0	13	0	0	4	7	1	3	0	5	0	0	0	0	0	0
Strumigenys sp.1 proche *longinoi*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strumigenys sp.2 gp. *thaxteri*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strumigneys sp.3 proche gp. *substricta*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Formicoxenini Forel																						
Cardiocondyla minutior Forel	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiocondyla obscurior Wheeler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	0
Nesomyrmex wilda (Smith)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Nesomyrmex tristani (Emery)	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0
Ochetomyrmex neopolitus Fernández	0	0	0	0	0	0	5	3	5	2	2	7	15	4	0	9	3	2	2	3	1	49
Ochetomyrmex semipolitus Mayr	0	0	0	4	1	4	32	7	19	1	0	2	3	1	1	4	9	5	0	0	0	0
Myrmicini Lepeletier																						

Hylomyrma balzani (Emery)	0	0	0	0	0	0	13	23	6	0	9	10	6	6	5	0	0	0	25	4	5	0
Hylomyrma immanis Kempf	0	0	0	0	0	0	0	2	4	1	1	0	0	0	0	0	0	0	0	0	0	3
Hylomyrma praepotens Kempf	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylomyrma reginae Kutter	0	0	0	0	0	0	0	1	3	6	0	0	0	0	0	0	5	0	0	0	0	0
Hylomyrma sagax Kempf	0	0	0	0	0	0	2	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Hylomyrma sp. cf *immanis*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hylomyrma sp.6	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylomyrma sp.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Hylomyrma sp.11	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pheidolini Emery			-																			
Pheidole alexeter Wilson	0	0	0	0	0	0	0	0	0	0	5	3	4	6	2	4	0	0	0	0	0	0
Pheidole alienata Borgmeier	0	0	0	0	0	0	0	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole allarmata Wilson	0	0	0	0	0	0	9	1	1	1	13	8	5	15	6	2	11	1	0	1	0	4
Pheidole astur Wilson	0	0	0	0	0	0	10	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole biconstricta Mayr	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole bruesi Wheeler	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	6	2	8	1	1	37
Pheidole carinata Wilson	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole cramptoni Wheeler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	9	3	5	8	7
Pheidole cursor Wilson	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole deima Wilson	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole dolon Wilson	0	0	0	0	0	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole fallax Mayr	14	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole gigas Wilson	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	5	12	0	44	1	1
Pheidole impressa Mayr	0	0	0	0	0	0	0	0	0	0	7	2	0	4	4	0	7	0	0	9	0	0
Pheidole jeannei Wilson	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Pheidole midas Wilson	0	0	0	0	0	1	4	22	7	4	11	8	4	2	3	14	13	7	1	0	2	22

Pheidole pedana Wilson	0	0	0	0	0	0	13	32	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole radoszkowskii Mayr	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole rubiceps Wilson	0	0	0	0	0	0	0	0	1	0	1	0	2	0	4	0	8	0	0	6	0	0
Pheidole scolioceps Wilson	0	0	0	0	0	0	1	2	22	8	1	0	3	8	0	4	8	0	0	0	0	0
Pheidole sculptior Forel	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole synarmata Wilson	0	0	0	0	0	0	2	6	2	2	3	0	9	0	2	21	2	2	0	1	0	0
Pheidole terribilis Wilson	0	0	0	0	0	1	2	0	11	0	0	0	0	2	2	2	1	3	0	0	0	0
Pheidole transversostriata Mayr	0	0	0	0	0	0	8	20	7	0	6	6	3	6	1	3	10	15	6	2	3	1
Pheidole tysoni Forel	0	0	0	0	0	0	15	14	4	9	10	4	6	14	9	4	0	0	0	0	0	0
Pheidole wallacei Mann	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp. cf *brandaoi*	0	0	0	0	0	0	9	7	1	1	10	11	16	12	7	15	1	0	0	2	0	0
Pheidole sp. gp. *fallax*	0	0	0	0	0	0	0	0	0	0	0	2	3	0	3	1	0	0	0	0	0	0
Pheidole sp. gp. *diligens*	0	0	0	0	0	0	0	0	0	0	5	6	8	7	0	8	0	0	0	0	0	0
Pheidole sp.4 gp. *fallax*	0	0	0	0	0	0	1	1	0	0	3	4	3	7	11	2	1	1	0	0	0	0
Pheidole sp.5 gp. *diligens*	0	0	0	0	0	0	0	0	0	0	0	3	5	2	3	0	0	0	2	0	0	0
Pheidole sp.6 gp. *flavens*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp.7 gp. *fallax*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp.8 gp. *fallax*	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp.10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pheidole sp.11 gp. *flavens*	0	0	0	0	0	0	14	13	23	0	5	0	13	2	16	11	35	0	1	27	0	0
Pheidole sp.12 gp. *diligensis*	0	0	0	0	0	0	2	9	13	0	4	4	0	3	0	1	0	0	0	0	0	0
Pheidole sp.13 gp. *tristis*	0	0	0	0	0	0	12	10	4	1	2	0	4	3	9	18	0	1	0	0	0	0
Pheidole sp.15 gp. *flavens*	0	0	0	0	0	0	5	7	17	14	0	0	1	0	0	5	0	0	0	0	0	0
Pheidole sp.16 gp. *tristis*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp.19 gp. *flavens*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0
Pheidole sp.25 gp. *flavens*	0	0	0	0	0	0	11	10	4	16	1	0	2	1	0	0	0	0	1	0	0	1

Pheidole sp.26 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pheidole sp.27 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Pheidole sp.29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pheidole sp.30 proche *transversostriata*	0	0	0	0	0	0	1	1	0	0	1	1	1	4	1	5	2	3	31	14	44	0
Pheidole sp.32 comp. *subarmata*	0	0	0	0	0	0	0	0	0	0	0	2	1	2	1	0	1	5	0	0	0	0
Pheidole sp.33 gp. *flavens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Pheidole sp.34 gp. *flavens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pheidole sp.35 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pheidole sp. 37 gp. *diligens*	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	10	0	0	0	0	1
Pheidole sp.40 comp. *flavens*	0	0	0	0	0	0	22	15	12	0	25	15	33	30	28	36	35	32	22	12	10	40
Pheidole sp.41 comp. *flavens*	0	0	0	0	0	0	0	1	0	0	1	0	7	0	1	2	9	22	0	6	0	21
Pheidole sp.50 cf *scolioceps*	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0
Pheidole sp.51	0	0	0	0	0	0	0	0	2	0	6	3	24	6	9	10	1	0	3	0	0	2
Pheidole sp.52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Pheidole sp.53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pheidole sp.54 gp. *diligens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Pheidole sp.55 comp. *flavens*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pheidole sp.56 gp. *diligens*	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0
Pheidole sp.57 gp. *fallax*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pheidole sp.58 comp. *flavens*	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0
Pheidole sp.59 gp. *diligens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pheidole sp.60 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Pheidole sp.61 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Pheidole sp.62 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Pheidole sp.63 gp. *tristis*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Solenopsidini Forel																						
Allomerus decemarticulatus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mayr																						
Carebara elongata Fernández	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carebara urichi (Wheeler)	0	0	0	0	0	0	7	10	2	0	0	5	4	4	5	2	0	0	0	0	0	4
Carebara sp.2 gp. e*scherichi*	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	1	0	0	1	11	1	0
Carebara sp.3 cf *peruviana*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Carebara sp.4 gp. *lignata*	0	0	0	0	0	0	2	0	4	4	0	2	1	1	7	3	0	0	0	0	0	13
Carebarella sp.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carebarella sp.2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalomyrmex cuatiara Brandão	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	4	3	0	2	0	0	0
Megalomyrmex drifti Kempf	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	1	3	2	0	0	4
Megalomyrmex gnomus Kempf	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	3	0	0	0	1	0	3
Megalomyrmex incisus Smith	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Megalomyrmex leoninus Forel	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0
Megalomyrmex silvestrii Wheeler	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	3	3	0
Megalomyrmex sp. gp. *modestus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Megalomyrmex sp.8 gp. *pusillus*	0	0	0	0	0	0	1	2	0	0	1	2	2	0	2	4	0	0	0	0	0	0
Megalomyrmex sp.9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Megalomyrmex sp.10 gp. *pusillus*	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
Monomorium floricola (Jerdon)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Solenopsis geminata (Fabricius)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	11	24	0
Solenopsis globularia (Smith)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Solenopsis (*Diplorhoptrum)*	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
pollux Forel																						

Solenopsis saevissima (Smith)	13	16	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Solenopsis virulens (Smith)	0	0	0	0	0	0	9	11	0	0	3	24	4	10	24	0	0	0	0	2	0	0
Solenopsis sp. gp. *pygmaea*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	9	13	4	6
Solenopsis sp.5	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp.6	0	0	0	0	0	0	0	1	2	0	1	0	0	1	0	3	3	0	0	0	0	0
Solenopsis sp.7	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp.8	0	0	0	0	0	0	1	3	0	0	8	0	2	9	11	5	0	0	0	0	0	0
Solenopsis sp.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Solenopsis sp.10	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp.11	0	0	0	0	0	0	0	0	4	0	0	0	2	3	1	5	0	0	0	0	0	0
Solenopsis sp.12	0	0	0	0	0	0	11	7	7	0	3	5	0	8	7	2	7	2	4	1	0	15
Solenopsis sp.13	0	0	0	0	0	0	11	6	6	1	2	2	0	2	8	4	0	1	0	0	0	0
Solenopsis sp.15	0	0	0	0	0	0	30	31	34	10	34	6	4	7	19	24	38	26	46	36	39	43
Solenopsis sp.16	0	0	0	0	0	0	5	18	14	17	7	29	30	33	25	43	14	8	0	8	3	4
Solenopsis sp.18	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	5	0	1	3	15	7
Solenopsis sp.28	0	0	0	0	0	0	0	0	0	0	13	39	39	38	29	48	36	29	44	30	24	47
Solenopsis sp.30	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Tranopelta gilva Mayr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Stegomyrmecini Wheeler																						
Stegomyrmex manni Smith	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stegomyrmex olindae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feitosa, Brandão and Diniz																						
Stenammini Ashmead																						
Lachnomyrmex pilosus Weber	0	0	0	0	0	0	0	4	0	0	1	0	3	1	1	0	0	0	0	0	0	0
Lachnomyrmex sp.	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rogeria alzatei Kugler	0	0	0	0	0	0	0	7	1	3	0	0	0	0	0	0	0	0	0	0	0	0

Rogeria besucheti Kugler	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	1	7	0	1
Rogeria blanda (Smith)	0	0	0	0	0	0	0	0	0	0	3	3	4	3	1	6	0	0	1	0	0	0
Rogeria ciliosa Kugler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Rogeria foreli (Mayr)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0
Rogeria germaini Emery	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Rogeria lirata Kugler	0	0	0	0	0	0	1	2	1	1	0	0	0	0	5	0	5	1	0	0	0	4
Rogeria micromma Kempf	0	0	0	0	0	0	2	4	1	6	0	0	0	0	0	0	0	0	0	0	0	0
Rogeria scobinata Kugler	0	0	0	0	0	0	6	11	4	11	0	0	0	0	0	0	0	0	0	0	0	0
Rogeria subarmata (Kempf)	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0
Rogeria tonduzi Forel	0	0	0	0	0	0	10	7	0	0	0	3	0	5	1	5	0	2	0	9	0	1
Rogeria sp.5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rogeria sp.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rogeria sp.10 cf *besucheti*	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	2	0	1
Tetramoriini Emery																						
Tetramorium bicarinatum (Nylander)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PONERINAE Lepeletier																						
Ponerini Lepeletier																						
Anochetus bispinosus (Smith)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	8	9	25	18	4
Anochetus diegensis Forel	0	0	0	0	0	0	2	8	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Anochetus emarginatus (Fabricius)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0
Anochetus horridus Kempf	0	0	0	0	0	0	7	6	2	7	14	22	10	12	16	4	2	3	0	2	0	1
Anochetus inermis André	0	0	0	0	0	0	8	2	0	0	2	15	22	15	9	16	4	1	0	0	0	0
Anochetus mayri Emery	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Anochetus neglectus Emery	0	0	0	0	0	0	1	5	0	3	3	3	3	8	16	1	6	6	1	3	0	3
Anochetus simoni Emery	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anochetus targionii Emery	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0

Hypoponera foreli (Mayr)	0	0	0	0	0	0	4	2	3	2	0	0	0	0	0	0	0	0	0	0	0	0
Hypoponera opacior (Forel)	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Hypoponera sp.1	0	0	0	0	0	0	6	7	0	0	9	13	11	14	17	33	0	0	15	24	13	8
Hypoponera sp.2	0	0	0	0	0	0	14	27	0	0	4	16	6	8	22	22	2	8	3	4	0	0
Hypoponera sp.3	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	11	0	1	0
Hypoponera sp.4	0	0	0	0	0	0	0	1	1	0	4	8	0	3	2	4	0	0	0	3	0	0
Hypoponera sp.5	0	0	0	0	0	0	2	0	0	3	1	1	1	2	2	5	1	3	0	0	0	0
Hypoponera sp.6 gp. *foreli*	0	0	0	0	0	0	0	0	4	0	5	6	5	2	1	1	10	5	8	0	1	2
Hypoponera sp.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	0	0	20	0	10
Hypoponera sp.9	0	0	0	0	0	0	0	0	0	0	8	13	5	4	0	15	1	6	0	0	0	13
Hypoponera sp.10	0	0	0	0	0	0	4	5	0	0	22	22	13	16	0	18	0	1	12	0	3	0
Hypoponera sp.11	0	0	0	0	0	0	20	7	10	0	0	0	0	0	0	12	0	0	0	0	0	0
Hypoponera sp.12	0	0	0	0	0	0	1	3	2	7	0	0	0	0	0	0	0	0	0	0	0	0
Hypoponera sp.13	0	0	0	0	0	0	7	5	11	0	2	7	8	10	18	11	0	0	0	0	0	0
Leptogenys dasygyna Wheeler	0	0	0	0	0	0	0	1	0	3	0	0	0	0	1	0	0	0	0	0	0	0
Leptogenys langi Wheeler	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	1
Leptogenys pusilla Emery	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Leptogenys vogeli Borgmeier	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptogenys sp.CPDC #1706	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Leptogenys sp.3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1
Leptogenys sp.5	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0
Leptogenys sp.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Odontomachus biumbonatus Brown	0	0	0	0	0	0	6	7	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Odontomachus brunneus (Patton)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Odontomachus caelatus Brown	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontomachus chelifer (Latreille)	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0

Odontomachus haematodus (Linnaeus)	1	1	0	0	3	1	1	5	2	1	5	1	0	4	4	0	7	7	2	23	11	0
Odontomachus hastatus (Fabricius)	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontomachus meinerti Forel	0	0	1	1	0	0	3	3	2	0	6	6	5	13	12	0	4	1	0	0	0	0
Odontomachus scalptus Brown	0	0	0	0	0	0	7	11	4	0	2	15	7	1	6	0	0	0	0	0	0	0
Pachycondyla arhuaca (Forel)	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla commutata (Roger)	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pachycondyla constricta (Mayr)	0	0	0	1	0	0	4	15	9	7	11	7	1	4	5	0	0	5	16	2	6	1
Pachycondyla cooki Mackay and Mackay	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla crassinoda (Latreille)	0	1	2	4	3	3	20	7	1	1	0	0	0	0	0	4	10	1	10	0	8	12
Pachycondyla crenata (Roger)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla ferruginea (Smith)	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0
Pachycondyla guianensis (Weber)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pachycondyla harpax (Fabricius)	0	1	1	0	3	3	16	27	11	10	1	0	0	0	1	2	4	6	8	2	24	37
Pachycondyla holmgreni (Wheeler)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla laevigata (Smith)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla lunaris (Emery)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Pachycondyla oberthueri Emery	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla pergandei (Forel)	0	0	0	0	0	0	0	1	2	1	0	3	5	4	10	4	0	0	0	0	0	3
Pachycondyla procidua Emery	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pachycondyla stigma (Fabricius)	0	0	0	0	0	0	4	5	1	0	4	5	11	4	5	0	0	0	0	0	1	5
Pachycondyla striata Smith	0	0	0	0	0	0	1	1	1	0	0	2	0	1	1	0	3	3	0	0	0	0
Pachycondyla unidentata Mayr	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla verenae Forel	0	2	0	0	0	0	1	3	0	4	0	0	0	0	0	1	0	0	0	0	0	15
Pachycondyla villosa (Fabricius)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Pachycondyla sp. cf *apicalis* morphosp. II (*sensu* Delabie et al. 2008)[12]	0	0	0	0	0	0	6	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla sp. cf *apicalis* morphosp. IV (*sensu* Delabie et al. 2008)	0	0	0	0	0	0	1	1	3	0	0	0	0	0	2	0	1	0	0	0	0	0
Pachycondyla sp. cf *harpax*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	1
Simopelta sp. nov	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Thaumatomyrmecini Emery																						
Thaumatomyrmex soesilae Makhan	0	0	0	0	0	0	2	2	0	0	1	0	1	0	0	1	0	0	0	0	0	0
PROCERATIINAE Emery																						
Proceratiini Emery																						
Discothyrea denticulata Weber	0	0	0	0	0	0	2	9	4	0	3	7	1	2	8	0	2	1	0	0	0	14
Discothyrea sexarticulata Borgmeier	0	0	0	0	0	0	6	8	1	0	4	2	3	0	1	1	0	0	0	0	0	0
PSEUDOMYRMECINAE Smith																						
Pseudomyrmecini Smith																						
Pseudomyrmex ethicus (Forel)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudomyrmex gracilis (Fabricius)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pseudomyrmex tenuis (Fabricius)	0	0	0	0	0	0	0	1	13	6	2	0	0	3	0	6	6	0	1	1	3	0
Pseudomyrmex termitarius (Smith)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
Pseudomyrmex sp. gp. *pallidus*	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0

[12] Delabie, J.H.C., Mariano, C.S.F., Mendes, L.F., Pompolo, S.G. & Fresneau, D. (2008) Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no Género *Pachycondyla* na região neotropical: o caso do complexo *apicalis*. Insetos Sociais: da Biologiá a Aplicacão Vicosa, Minas Gerais (ed. by E.F. Vilela, I.A. Santos, J.H. Schoereder, J.E. Serrão, L.A.O. Campos and J. Lino Neto), pp. 196-222. Editora da Universidade Federal de Viçosa, Viçosa.

ANNEXE 4°: Rangs taxonomiques supérieurs des espèces collectées dans toutes les localités échantillonnées

GENRES	TRIBUS	SOUS-FAMILLES
Tatuidris Brown and Kempf	**Agroecomyrmecini** Carpenter	**Agroecomyrmecinae** Carpenter
Amblyopone Erichson ***Prionopelta*** Mayr	**Amblyoponini** Forel	**Amblyoponinae** Forel
Acanthostichus Mayr	**Acanthostichini** Emery	**Cerapachyinae** Forel
Cerapachys Smith	**Cerapachyini** Forel	
Dolichoderus Lund ***Linepithema*** Mayr	**Dolichoderini** Forel	**Dolichoderinae** Forel
Azteca Forel	**Leptomyrmecini** Emery	
Tapinoma Foerster ***Technomyrmex*** Mayr	**Tapinomini** Emery	
Eciton Latreille ***Labidus*** Jurine ***Neivamyrmex*** Borgmeier	**Ecitonini** Forel	**Ecitoninae** Forel
Ectatomma Smith ***Gnamptogenys*** Roger	**Ectatommini** Emery	**Ectatomminae** Emery
Typhlomyrmex Mayr	**Typhlomyrmecini** Emery	
Camponotus Mayr	**Camponotini** Forel	**Formicinae** Latreille
Gigantiops Roger	**Gigantiopini** Ashmead	
Acropyga Roger	**Lasiini** Ashmead	
Brachymyrmex Mayr ***Myrmelachista*** Roger ***Nylanderia*** Emery	**Plagiolepidini** Forel	
Cryptomyrmex Fernández	**Adelomyrmicini** Fernández	**Myrmicinae** Lepeletier
Acromyrmex Mayr ***Apterostigma*** Mayr ***Atta*** Fabricius ***Cyphomyrmex*** Mayr ***Mycocepurus*** Forel ***Myrmicocrypta*** Smith ***Sericomyrmex*** Mayr ***Trachymyrmex*** Forel	**Attini** Smith	

Basiceros Schulz	**Basicerotini** Brown	
Wasmannia Forel	**Blepharidattini** Wheeler and Wheeler	
Cephalotes Latreille ***Procryptocerus*** Emery	**Cephalotini** Smith	
Crematogaster Lund	**Crematogastrini** Forel	
Acanthognathus Mayr ***Pyramica*** Roger ***Strumigenys*** Smith	**Dacetini** Forel	
Cardiocondyla Emery ***Nesomyrmex*** Wheeler	**Formicoxenini** Forel	
Hylomyrma Forel	**Myrmicini** Lepeletier	
Ochetomyrmex Mayr	**Ochetomyrmecini** Emery	
Pheidole Westwood	**Pheidolini** Emery	
Allomerus Mayr ***Carebara*** Westwood ***Carebarella*** Emery ***Megalomyrmex*** Forel ***Monomorium*** Mayr ***Solenopsis*** Weswood ***Tranopelta*** Mayr	**Solenopsidini** Forel	
Lachnomyrmex Wheeler ***Rogeria*** Emery	**Stenammini** Ashmead	
Stegomyrmex Emery	**Stegomyrmecini** Wheeler	
Tetramorium Mayr	**Tetramoriini** Emery	
Anochetus Mayr ***Hypoponera*** Santschi ***Leptogenys*** Roger ***Odontomachus*** Latreille ***Pachycondyla*** Smith ***Simopelta*** Mann	**Ponerini** Lepeletier	**Ponerinae** Lepeletier
Thaumatomyrmex Mayr	**Thaumatomyrmecini** Emery	
Discothyrea Roger	**Proceratiini** Emery	**Proceratiinae** Emery
Pseudomyrmex Lund	**Pseudomyrmecini** Smith	**Pseudomyrmecinae** Smith

ANNEXE 5 : *Tatuidris kapasi* sp. nov., a new armadillo ant from French Guiana (Formicidae: Agroecomyrmecinae)

Soumis à Psyche (révision majeure)

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Tatuidris kapasi sp. nov., a new armadillo ant from French Guiana (Formicidae: Agroecomyrmecinae).

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Abstract. *Tatuidruis kapasi* sp. nov. (Formicidae: Agroecomyrmecinae), the second known species of "armadillo ant", is described after a remarkable specimen collected in French Guiana. This species can be easily distinguished from *Tatuidris tatusia* by characters related to the shape of the mesosoma and petiole, as well as to the pilosity, the sculpture and the color.

Key-words. Agroecomyrmecinae, *Tatuidris kapasi* sp. nov., French Guiana.

Introduction. As a result of the constant acquisition of new morphological and molecular data, combined with a big increase in the collection of biological material, the last decades have seen a true revolution in ants systematics and phylogeny [1,2]. In spite of this, some rare genera of ants still remain unusually mysterious. A long time after their original description, they continue to reveal a low taxonomical diversity and are rarely collected in the field. Frequently, their phylogenetic relationships also remain poorly understood. The Neotropical genus *Tatuidris* (Formicidae: Agroecomyrmecinae) was described by Brown and Kempf in the 1967 issue of Psyche [3] after a peculiar new species collected from El Salvador. Until now, this genus has remained monotypic and very isolated in the Family Formicidae: the type

species, *Tatuidris tatusia*, is known only from the very distinctive morphology of the worker that combines some primitive and derived characters, while its biology is completely unknown [4]. In addition, morphological and molecular studies have caused some authors to hold differing points of view regarding the phylogenetic position of *Tatuidris* in the family Formicidae. Thus, based on its morphology, the genus was initially placed in the subfamily Myrmicinae [3], within the tribe Agroecomyrmecini. The genus was then transferred to the Agroecomyrmecinae [5], a new subfamily proposed by Bolton, who has suggested that this taxon might be the sister group to all Myrmicinae. More recently, the genus was again combined in the Myrmicinae [6], and then returned to the Agroecomyrmecinae as a Poneroid [7], and more latterly as a Poneromorph [8]. However, based on morphological characters, in a very recent paper, Keller [9] followed the Bolton's former proposal [5] in suggesting that *Tatuidris* is the sister group to the Myrmicinae. Recently, some new molecular data have led other authors to argument that *Tatuidris* may be the sister group to the subfamily Paraponerinae in some rooted trees, but placed it next to Amblyoponinae in some other analyses [10-12].

In such a context, the search for new species of *Tatuidris* and the study of their morphology represents an important challenge for better understanding the phylogenetic relationships of this genus with the whole Formicidae. Here we report the recent finding in French Guiana of a remarkable single specimen of *Tatuidris* that differs from *T. tatusia* in several distinctive morphological characters, and this paper aims to describe it.

Material and methods. Morphological examination of specimens was completed at various magnifications using a light stereomicroscope Olympus SZX7. Morphometric measures were made with a Carl Zeiss measuring microscope and recorded to the nearest 0.01mm. All measurements are given in millimeters, using the definitions and abbreviations:

CI - Cephalic Index: HW*100/HL.

EL - Eye Length: the maximum diameter of the eye.

GL - Gaster length: the length of the gaster in lateral view from the anteriormost point of first gastral segment (third abdominal segment) to the posterior most point.

HFL - Hind Femur Length: maximum length of hind femur in anterior view.

HL - Head Length: the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior margin from its highest points.

HW - Head Width: the maximum width of the head in full face view.

LA7 - Length of Antennal segment 7: maximum length of the seventh antennal segment.

ML - Mandible Length: straight-line length of a mandible measured in ventro-lateral view, from the base at the insertion into the head capsule, to the apex.

PeI - Petiole Index: (PeW*100/PeL).

PeL - Petiole Length: the maximum length of the petiole node in dorsal view.

PeNL - Petiolar Node Length: the maximum length of the petiole node in dorsal view.

PeNW - Petiolar Node Width: the maximum width of the petiole node in dorsal view.

PpL - Postpetiole Length: the maximum postpetiole length in lateral view.

PpNL - Postpetiolar Node Length: the maximum length of the postpetiole node in dorsal view.

PpNW - Postpetiolar Node Width: the maximum width of the postpetiole node in dorsal view.

PrW - Pronotum Width: the maximum width of the pronotum in dorsal view.

SL - Scape Length: the maximum straight line of the antennal scape, excluding the condylar bulbo.

TL - Total Length (HL+ML+WL+PL+PPL+GL).

WL - Weber's Length: diagonal length, measured in lateral view, from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe.

The microphotographs were made using the following sequential process: the specimen was first filmed using a video camera (Sony Full HD 1080 AVCHD, 10.2 Mp) mounted on a light microscope (Zeiss Jena), while the resolution was continuously scanned from the top to the bottom of the holotype specimen; the videos (in format .mts) were processed using the free software ImagGrab 5.0 (available at: http://paul.glagla.free.fr/imagegrab.htm) in order to extract the sharpest images referable to differing focal points, and composite pictures were then assembled using the free software Combine ZM (available at: http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm). Finally, each optimum microphotograph was improved using Adobe Element Photoshop software (version 6.0).

The terminology for the external morphology and the surface sculpturing follows [13-15]. In the description and the diagnosis of this new species, our terminology referring to the pilosity describes the variation in size of the setae observed in *T. tatusia* and *Tatuidris kapasi* sp. nov. Thus, we recognize four setal types depending on their length: i.e., very short (about 0.016 mm), short (about 0.05 mm), intermediate (about 0.11 mm) and long (about 0.3 mm).

Also, the characters of the tribe and the genus are not mentioned (for a complete summary of the taxonomic characters, see [3] and [5]).

Depository of the Holotype. The unique known specimen of the taxon is deposited in the Myrmecological Collection of the Cocoa Research Center at CEPLAC (Itabuna-BA, Brazil), referred to by the CPDC acronym [16].

Results.

Tatuidris kapasi Lacau and Groc, new species

(Figs. 1-6)

Type material. Holotype worker. Specimen deposited at [CPDC] and labeled: "Guyane Française, Montagne de Kaw, N04°38.21'/W052°17.36', Alt. 260 m., ix.2008, Winkler trap, Col. S. Groc, A. Dejean and B. Corbara".

Etymology. "kapasi" is the Wayanas' Amerindian (French Guiana, Surinam and Brazil) word for 'armadillo', a mammal belonging to the Order Cingulata. The generic and specific names of the first described species [6] referred to the same animal group.

Diagnosis. The worker of *Tatuidris kapasi* exhibits all the diagnostic characters of the tribe Agroecomyrmecini and the genus *Tatuidris*. It differs from the worker of *T. tatusia* in the following characters (states for *T. tatusia* indicated in brackets): occipital border a little more concave [nearly straight]; about 5-6 facets in each eye [about 10 facets]; clypeus with the free margin medially straight and laterally concave [free margin concave overall]; pronotum with the ventral sector of lateral faces smooth and shining [with longitudinal rugulae]; dorsum of mesosoma mostly sculptured with concentric rugulae and carinulae [mostly smooth and shining]; posterior margin of mesosoma as seen from above wider [narrower]; mesopleuron with anterior crest wider and ventrally truncated [crest narrower and not truncated]; mesopleuron smooth and shining, except for punctations and areolae on its ventral margin [with longitudinal rugulae and areolations]; metapleuron punctate and areolate, and with longitudinal rugulae around the metapleural gland orifice [metapleuron with areolations]; the bulla of the metapleural gland (visible through the integument when observed in profile), forming a ring whose posterodorsal margin is fused with the postero-lateral margin of the propodeum [the bulla of the metapleural gland forming a the ring that is distinctly separated from the posterolateral margin of propodeum]; propodeal declivity less concave in lateral

view [more concave]; propodeal spiracle separated from declivitous margin of propodeum by two diameters [separated by no more than one diameter]; viewed dorsally, petiolar node twice as wide as long [viewed dorsally, shape of petiolar node subrectangular, the node no more than about 1.5 times as wide as long]; viewed dorsally, shape of postpetiolar node rectangular, and not wider behind than in front [viewed dorsally, shape of postpetiolar node subrectangular, and a little wider behind than in front]; dorsum of the petiolar and postpetiolar nodes with superficial concentric rugulae and carinulae [smooth and shining]. Moreover, the pilosity is markedly more dense all over the body [morescattered] and does not include any long suberect setae [long suberect setae present].

Furthermore, despite the fact that *T. kapasi* is only known by a single specimen and *T. tatusia* by two specimens formally described, the following comparative measurements suggest an overall size differential between the two species: the head shape is a little wider in *T. kapasi* (CI: 125,78) than in *T. tatusia* (CI: 118,2±1.56, min-max: 117.07-119.28 (n=2)), the scape is slightly shorter in *T. kapasi* (SL 0,32) than in *T. tatusia* (SL 0,4 (n=1)), the pronotum narrowers in *T. kapasi* (PrW 0,64) than in *T. tatusia* (PrW 0,79 (n=1)), and the shape of the petiole node in dorsal view is more noticeably rectangular in *T. kapasi* (PeNI 200) than in *T. tatusia* (PeNI 153.64 (n=1)).

Description.

Worker. Measurements (Holotype): TL 3.42, CI 125.80, EL 0.05, GL 1.00, HFL 0.50, HL 0.70, HW 0.93, LA7 0.27, ML 0.39, PeL 0.21, PeNI 200, PeNL 0.18, PeNW 0.36, PpL 0.28, PpNL 0.25, PpNW 0.45, PrW 0.64, SL 0.32, WL 0.80.

Except for the diagnostic characters, the external morphology of *Tatusia kapasi* sp. nov. is very similar to that of *T. tatusia*. In our discussion, the shared characters are regarded by ourselves as sufficient for the two species to be placed within the same genus. The spatial distribution and patterns of the sculpture and pilosity, as well as the body color of this new species are described hereafter.

Sculpture. Head dorsum wholly smooth and shining, except that the occipital sector is covered with transverse carinulae; outer face of mandibles smooth and shining except for longitudinal superficial striae on the ventral (external) margin; ventrolateral sector of the head longitudinally carinulate; antennal scape shagreened and superficially areolate; pronotum with the ventral sector of lateral faces smooth and shining; dorsum of mesosoma with concentric rugulae and carinulae; mesopleuron smooth and shining except for punctations and areolae on its ventral margin; metapleuron with punctations and areolae and longitudinal rugulae around

the metapleural gland orifice; propodeal declivity almost completely smooth and shining but also finely striate and reticulate; lateral faces of the petiolar and postpetiolar nodes finely longitudinally carinulate.

Pilosity. Dorsum of the head, the mesosoma, the petiole and the postpetiole with abundant setae, all fine, flexuous and decumbent and varying in size and distribution as follows: some setae very short and relatively dense (i.e., those on the clypeus and the outer surface of mandibles); others short and dense (those on the dorsum of the head, the clypeus, o the mesosoma, the petiolar and postpetiolar nodes, and the gaster); others intermediate and dense (namely, the setae on the dorsum of the head, the mesosoma, the petiolar and postpetiolar nodes, the dorsum of the gaster d, and the tibiae). No long setae present.

Color. Body brownish-ferruginous, thick margins often appearing more blackish; legs brownish-yellowish.

Gyne and male: unknown.

Geographic range. This new species is known only from the type locality in French Guiana, situated at 260m altitude in the Kaw Mountains, on a side exposed to the trade winds, near a great cave sheltering a big bat community. The local vegetation is typical of Amazonian lowland rainforest that never gets flooded. New records of this species will probably occur in other localities of the Guyana shield in the near future. However, the fact that no other specimen of *Tatuidris* has been recorded yet in the recent studies on ants biodiversity, in the Guiana Shield, even using Winkler traps or other methods at a large scale [17, 18,], suggests that this genus is genuinely rare in the field, its members possibly spatially separated in small, isolated populations.

Biology. The biology of this species remains unknown, but the fact that the type specimen was found in a leaf-litter sample, using a Winkler trap, suggests that it nests in some micro-habitats of the leaf-litter or more or less deeply in the soil. It is also noteworthy that the leaf-litter sample (surface of 1 m^2) in which *T. kapasi* was caught was characterized by a very high specific richness: a total of 20 other ant species belonging to 12 genera was recorded (Groc et al., unpublished information):. Such richness in a unique leaf-litter sample is uncommon in Neotropical forests [18].

Comments and discussion.

The description of this new species of *Tatuidris* is an important event for Myrmecology, since the genus has remained monotypic for over 40 years. However, as noted by Longino [4], the advent of litter sifting and Winkler extraction as a popular method of ant collecting in the

last decade led to the discovery of new species belonging to genera previously considered as rare and poorly diversified. This is the case for the new species here described. This genus has been revealed to be not as rare as it was believed to be since several new specimens were recently collected in various Neotropical countries : Brazil, Colombia, Costa Rica, El Salvador, Ecuador, French Guyana, Mexico, Nicaragua, Panama and Peru. In this context, D. Donoso is currently performing a first revision of this genus based on the new material deposited in myrmecological collections in the world, some of them being imaged on the Internet Sites of AntWeb (http://www.antweb.org/description.do?subfamily=agroecomyrmecinaeandgenus=tatuidrisandname=tatusiaandrank=speciesandproject=worldants) and Longino http://academic.evergreen.edu/projects/ants/genera/tatuidris/home.html).

While *T. kapasi* exibits a distinct morphology from that of *T. tatusia*, it possesses all the diagnostic characters of Agroecomyrmecinae and Agroecomyrmecini. The following characters shared with *T. tatusia* are here considered as being of generic level (some originally offered by Brown and Kempf [3] as being of specific level in the description of *T. tatusia*): head dorsum wholly smooth and shining, except for the occipital sector, which is covered with transversal carinulae; clypeal suture obsolete, marked only by a shallow median sulcus; clypeus with the free margin concave overall, but with an almost invisible, low, thin, transparent median lobe that forms a median convexity in front of a darker, evenly concave internal line that is visible through the integument (this dark line is very prominent, and at first sight looks like the free margin proper); toruli visible through the integument, which is transparent directly above them; outer surface of mandibles smooth and shining, except for longitudinal superficial striae on the ventral margin; dorsum of mesosoma with the lateral margins bearing longitudinally oriented, superficial rugae and carinulae; dorsal sector of the lateral faces of pronotum with longitudinal rugulae; lateral faces of propodeum with longitudinal rugulae and areolations; postpetiolar node with an anterior rim and a large and deep sternum; legs predominantly smooth and shining.

The next step will consist in studying the whole biology of these ants for which literature is particularly scarce. *Tatuidris kapasi* has peculiar mandibular brushes and a powerful elongated sting similar to that of *T. tatusia*. Brown and Kempf suggested that such adaptations indicates that armadillo ants might be specialist predators of active or slippery arthropod prey [3]. Also, we note that the flat pencil of stiff, curved yellow setae borne at the extensor angle on the forelegs, a strong apomorphy of this genus, may be used by these ants in order to clean the mandibular brush through a movement directed anteriorly. Thus, these characters could potentially represent an adaptation to predating on prey bearing a defensive pilosity.

Moreover, the morphology of the gyne and the male of *Tatuidris* have never been described yet. However, microphotographs of a gyne and a male, together winged, are offered in the site ANTWEB, suggesting that a normal sexual reproduction by swarming occurs in this genus.

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Caption to figures.

Figures 1-2: *Tatuidris kapasi*, holotype worker. 1: Habitus, left lateral view; 2: Head, full-face view.

Figures 3-6: *Tatuidris kapasi*, holotype worker. 3: Detail of head, left side view; 4: Mesosoma in dorsal view; 5: Detail of petiole and postpetiole, left lateral view; 6: Detail of petiole and postpetiole, dorsal view.


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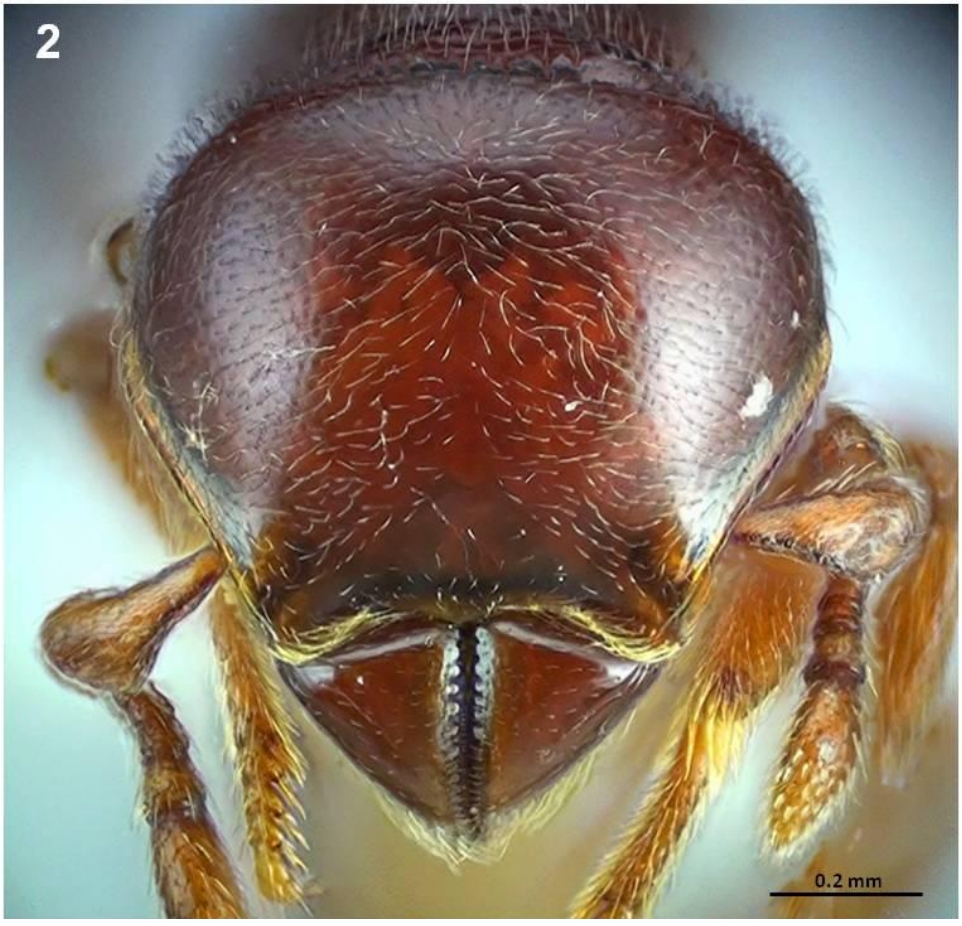
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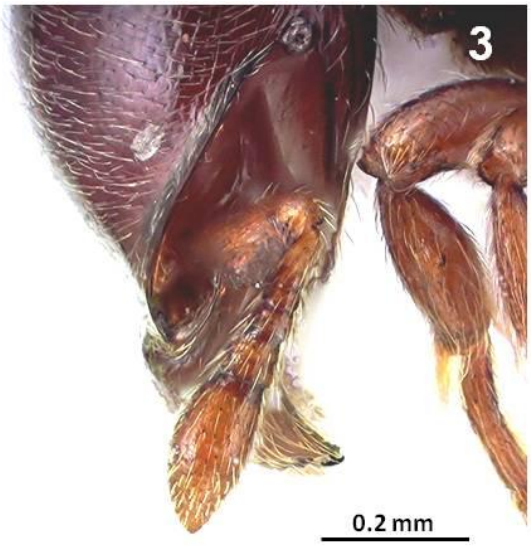
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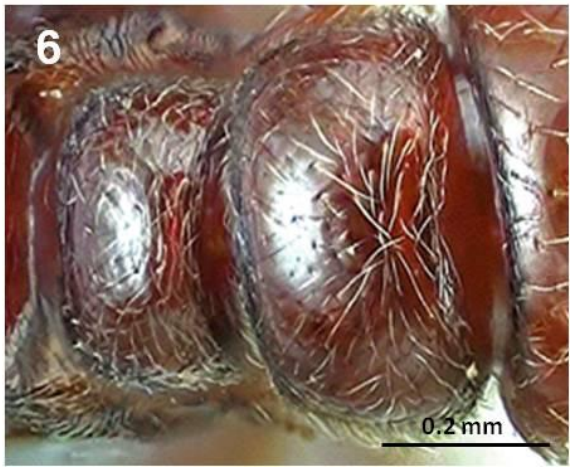
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RÉSUMÉ

Les fourmis sont des organismes cibles appropriés pour les études environnementales. Au cours de notre étude, nous nous sommes focalisés sur les fourmis de la litière via l'application de deux méthodes de récolte complémentaires selon le protocole ALL (*Ants of Leaf Litter*). Dans les forêts naturelles de Guyane française, l'hétérogénéité environnementale et les perturbations structurent les communautés de fourmis de la litère en influençant la richesse, la diversité, l'abondance et la densité en espèces ainsi que les compositions taxonomique et fonctionnelle. Chaque type de formation végétale possède une communauté spécifique. La fragmentation et la conversion des forêts en plantations ont entrainé une altération plus ou moins profonde des communautés; cette variabilité est fonction du type d'agriculture et des espèces d'essences cultivées. Bien que l'altération des communautés se soit révélée maximale dans la plupart des monocultures, les plantations de cacaoyers ont un potentiel de conservation réel. Enfin, dans un contexte où il est urgent de simplifier l'intégration des arthropodes dans les études de conservation, de contrôle et de suivi de la santé des écosystèmes terrestres, la méthode des réseaux de neurones est apparue comme un outil puissant pour mettre en évidence et analyser les patrons des communautés de fourmis.

Mots-clefs : fourmis de la litière ; communautés forestières natives ; altération des myrmécofaunes ; hétérogénéité environnementale ; perturbations naturelles et anthropiques ; fragmentation ; agriculture traditionnelle ; conversion en monocultures.

ABSTRACT

Ants are reliable and relevant target organisms for environmental surveys. In our study, we focused on litter-dwelling ants through the use of two complementary sampling methods that were implemented according to the Ants of Leaf Litter (ALL) protocol. In pristine forests of French Guiana, leaf-litter ant communities are structured by environmental heterogeneity and natural perturbations - which influence species richness, diversity, abundance and density, as well as taxonomic and functional composition. This results in habitat-specific communities for each vegetal formation. Forest fragmentation and conversion into monocultures have led to a more or less deep alteration of the ant communities; this variability depends on the type of agricultural system and cultivated tree species. Although the intensity of community alteration peaked in tree monocultures, cocoa plantation exhibited a real potential for native species conservation. Finally, in the current context where simplifying the integration of arthropods into conservation programs as well as into surveys designed to monitor and manage the environment is critical, the use of neural networks appears to be a powerful tool for reliably highlighting and analyzing ant communities patterns.

Keywords: litter-dwelling ants; communities of forest native species; ant fauna alteration; environmental heterogeneity; natural and human-induced perturbations; fragmentation; traditional agriculture; forest conversion in plantations**.**