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Sous la direction de Jérôme ORIVEL

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RESUME

Les perturbations d’origine anthropique sont à l’origine de l’érosion de la biodiversité avec des conséquences sur la structure des communautés et pour le fonctionnement des écosystèmes. La vitesse de ces changements a stimulé de nombreuses recherches portant sur les effets de ces modifications sur la biodiversité des organismes et leurs propriétés fonctionnelles. En effet il a été montré que les traits des espèces sont plus importants que leur identité elle-même pour tenir compte de leurs rôles écologiques. Même si la majorité de ces travaux ont étudié la réponse des producteurs primaires sur les écosystèmes terrestres, la contribution d’autres organismes est toutefois essentielle pour maintenir un fonctionnement et une résilience des écosystèmes corrects.

Les fourmis sont des organismes cibles intéressants pour étudier de telles modifications du fait de leur abondance et de leur dominance écologique. En effet elles ont une distribution cosmopolite et participent à de nombreuses fonctions dans l’écosystème terrestre. Elles sont également faciles à étudier et des méthodes d’échantillonnage standard existent. Bien que de nombreuses recherches aient démontré des modifications dans la composition spécifique des fourmis dans des gradients environnementaux, un nombre réduit d’entre elles ont étudié la contribution de ces organismes sur le fonctionnement des écosystèmes. De plus, les traits responsables de la stabilité des communautés de fourmis en réponse à ces modifications sont encore peu connus. Il est donc nécessaire de développer une méthodologie capable d‘identifier la participation des fourmis dans des processus écosystémiques permettant également de quantifier leur activité afin de comprendre comment ces organismes agissent sur les capacités de résistance et résilience des écosystèmes.

Ainsi, cette thèse vise mettre en lumière i) en quoi la simplification des habitats liée aux activités humaines a des répercussions sur les communautés de fourmis, ii) quels sont les traits responsables du succès écologique d’une espèce ou de son déclin au sein d’un environnement donné, et iii) comment ces variations en composition spécifique impactent l’intensité de participation des fourmis aux processus écosystémiques.

SUMMARY

Land-use changes have deep consequences on species diversity, community structure and ecosystem functioning. Consequently, many works have tried to understand the effects of such changes on the diversity and functional properties of organisms. It has been demonstrated that species traits are oftenly more important than the identity of species *per se* in order to account understand the ecological roles of species. Besides, while the majority of assessments about land-use change effects on ecosystem functioning have focused on primary producers, the contribution of other organisms is essential to maintain the functioning and resilience of ecosystems.

Ants are interesting organisms to track land-use changes due to their abundance, ubiquity and ecological dominance. Ants are present in most of terrestrial biomes and participate in several ecosystem processes through their consumption of food resources. They are also easy to sample and standard methods exist to provide accurate comparisons between studies. While a number of studies have demonstrated abrupt changes in ant species composition along environmental gradients, only a reduced number of such studies have tried to understand how ant community changes affect ecosystem processes. Moreover, the traits responsible for the stability of ant communities in response to land-use changes are little known. It is therefore necessary to develop a methodology that enables a proper identification of ant participation to different ecosystem processes and their contribution to ecosystems' resistance and resilience.

In this thesis I aim to bring some light about i) how land-use changes affect ant community structure? ii) what traits are responsible of the ecological success of a species or it's extinction from a given environment? iii) how changes in the species or trait composition affect the participation intensity of ants in different ecosystem processes?

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I. INTRODUCTION GENERALE

Le succès écologique de notre espèce a des conséquences dramatiques sur la biodiversité et le fonctionnement des écosystèmes du monde entier (Vitousek et al. 1997, Díaz et al. 2006b, Hooper et al. 2012). Les changements globaux tels que la pollution, le réchauffement climatique ainsi que les changements d'usage des terres ont des répercussions sur la diversité et l'identité des organismes (Vitousek et al. 1997). En effet la perte d'habitat, les perturbations des réseaux trophiques et les variations dans les conditions environnementales macro et microclimatiques provoquent le plus souvent une diminution du nombre d'espèces présentes localement ainsi que le remplacement de certaines espèces par d'autres ayant des caractéristiques écologiques différentes (Duffy 2003, Mantyka-pringle et al. 2011). Or, ces organismes agissent à leur tour sur les processus écosystémiques et sur le fonctionnement des écosystèmes (Chapin et al. 1997, 2000, Loreau et al. 2001). Le défi est donc de résoudre un puzzle de règles déterminant la persistance des espèces dans les communautés et de déterminer comment ces dernières agissent ensemble pour maintenir les processus écologiques (Hooper et al. 2005, Schmitz et al. 2015).

Avant de continuer, il semble nécessaire d'établir une série de définitions à propos des écosystèmes et de leur fonctionnement, notamment en raison de l'ambiguïté de certaines notions qui leurs sont associées dans la littérature (Pickett and Cadenasso 2002, Jax 2005). Une définition possible de la notion d' « écosystème » est celle d'une condition émergente, née des interactions entre les organismes et leur environnement abiotique. Ces interactions sont issues de mécanismes autorégulateurs et rétroactifs qui mènent à un équilibre dynamique parmi plusieurs autres possibles (Folke et al. 2004). Ces équilibres vont fournir une structure prédictible et stable aux différents types d'habitat. Ces derniers vont alors agir comme un moule, donnant forme aux stratégies écologiques des espèces qui vont s'y trouver (Southwood 1977). Par ailleurs, ce que l'on entend par « processus écosystémique » est l'utilisation, le déplacement, la transformation de matière et d'énergie (Chapin et al. 1997, MEA 2005). Le fonctionnement des écosystèmes reflète les activités collectives des organismes (e.g. leur nutrition, leur croissance, leur mouvement, leur excrétion…) ainsi que les effets de ces activités sur l'environnement. Ainsi, en accord avec la notion d'« équilibre », il est attendu d'un écosystème qu'il soit identifiable grâce aux taux de processus caractéristiques de tous les écosystèmes du même type (Folke et al. 2004, Jax 2005). Par exemple on prévoit que les taux de processus écosystémiques de deux forêts différentes soient plus proches que ceux d'une forêt comparée à un écosystème anthropisé.

I.1 EFFETS DU CHANGEMENT D’USAGE DES TERRES ET DES PERTURBATIONS SUR LA BIODIVERSITE ET LE FONCTIONNEMENT DES ECOSYSTEMES

La transformation d’écosystèmes naturels en terrains agricoles et zones urbaines est l’une des causes majeures de la dégradation et de la fragmentation des habitats (United Nations 1992, Foley et al. 2005). Il s’agit également de la plus grande menace pour la diversité des espèces et le maintien des processus écologiques qui régissaient jusqu’ alors les écosystèmes (Sala et al. 2000, Newbold et al. 2015). Ce processus d’anthropisation a lieu depuis les temps préhistoriques, et on peut aujourd’hui supposer que toute la surface de la terre a été modifiée par l’Homme ou a au moins été en contact avec lui (Goudie 2013). Cependant, au cours des dernières décennies, l’intensification des activités humaines a pris des proportions jamais atteintes auparavant (Vitousek et al. 1997, Foley et al. 2005). Aujourd’hui, les transformations du paysage ont lieu de manière plus intense notamment sous les tropiques; bien qu’il s’agisse des régions possédant la plus grande biodiversité (Myers 1988). En effet la moitié des forêts tropicales a été défrichée en à peine un siècle, ce qui rend urgente la tâche d’identifier les conséquences de ces modifications (Morris 2010).

Les changements d’usage des terres sont à l’origine de modifications des flux de matière et d’énergie, provoquant également la disparition de nombreuses espèces et entrainant leur substitution par d’autres espèces ayant des traits différents. L’ensemble de ces modifications provoque en général de fortes variations dans les propriétés des écosystèmes et leur fonctionnement (Sala et al. 2000, MEA 2005, Lindemayer et al. 2012). Les effets provoqués sur la biodiversité et le fonctionnement des écosystèmes, peuvent alors être directs ou indirects, et les conséquences varient en fonction de l’intensité, de la régularité et de l’étendue de ces changements (Fischer and Lindenmayer 2007, Newbold et al. 2015). D’une part, l’intensification de ces perturbations ainsi que la simplification des écosystèmes qui leur est liée, sont souvent accompagnées d’une réduction importante de la richesse spécifique locale et régionale (Fischer and Lindenmayer 2007, Lindemayer et al. 2012, Newbold et al. 2015). D’autre part, l’extraction de biomasse végétale appauvrit les écosystèmes (notamment en nutriments) et affecte directement des processus tels que l’érosion et le cycle de l’eau, déstabilisant ainsi les cycles biogéochimiques (Vitousek et al. 1997, Tilman et al. 2001). Ces modifications dans les conditions environnementales, ou dans la teneur en ressources peuvent modifier indirectement l’équilibre compétitif entre les espèces d’un environnement donné, ce qui amène, le plus souvent à des modifications de leur identité et de leur abondance relative

(Loreau et al. 2001, Hooper et al. 2005). Par exemple, de nombreuses études suggèrent une croissante homogénéisation des stratégies écologiques parmi les espèces capables de survivre dans les milieux anthropisés du monde entier (McKinney and Lockwood 1999, Olden et al. 2004, Flynn et al. 2009). Ces modifications peuvent entraîner une diminution de la résistance de l'écosystème face à des perturbations ou des épisodes de stress, tels que la sécheresse, ou les invasions biologiques. En effet, une plus grande diversité (d'espèces et de stratégies écologiques) a été associée à une majeure stabilité des écosystèmes face à des évènements climatiques ou biologiques extrêmes (Symstad and Tilman 2001). Finalement, la configuration du paysage joue un rôle fondamental dans la représentativité et la connectivité des différents types d'habitat. La surface et la distribution de différents types d'habitat, par exemple, conditionnent l'abondance d'espèces présentes dans la région et leur capacité à recoloniser les fragments d'habitat qui leurs sont favorables (Franklin 1993, Tscharntke et al. 2005, Fischer and Lindenmayer 2007). Ainsi, après une perturbation, la capacité des écosystèmes à retrouver leur état précédent est fortement dépendante de la présence d'espèces capables de recoloniser les habitats modifiés dans la même région (Bengtsson et al. 2003, Symstad et al. 2003). C'est pourquoi la résilience des écosystèmes dépend entièrement de la simplification généralisée des paysages (Tscharntke et al. 2005).

I.2 CARACTERISATION ECOLOGIQUE DES ESPECES

Depuis l'Antiquité, les humains ont essayé de caractériser les espèces en fonction de leur morphologie, de leur alimentation ou leur(s) habitat(s) (Magner 2002). Au cours du 18ème siècle, l'observation et la description d'espèces se sont popularisées donnant lieu à d'innombrables travaux portant sur l'histoire naturelle des espèces et sur la description de la « fonction de leur forme » (Russell 1916, Farber 2000a). Ces nombreux naturalistes se sont intéressé aux liens entre la morphologie des espèces et leur écologie. En effet, de nombreux auteurs de l'époque avaient remarqué des similarités de formes chez les plantes ou chez les animaux qui partageaient une même « fonction » : c'est-à-dire, des organismes associés à des milieux ou des régimes alimentaires similaires (Farber 2000b). Cette période atteint son apogée lors de la formulation de « la théorie de l'Evolution » par Charles Darwin (1859). En effet, cette théorie exemplifiée par les désormais célèbres pinsons, présente la diversité des formes sur terre comme étant la conséquence des interactions entre les espèces et leur milieu, et de la sélection des formes les plus adaptées.

Le concept de « fonction » sera ultérieurement remplacé par celui de « niche », terme qui a ensuite adopté différentes significations selon le contexte (Hutchinson 1957, Pocheville 2015). Les bases de la théorie de la niche sont notamment énoncés dans les travaux de Grinnell (1924) et de Elton (1927), qui classifient les espèces respectivement, par rapport aux habitats qu'elles occupent et aux ressources dont elles ont besoin. La définition la plus moderne et inclusive de la notion de niche considère qu'il s'agit des besoins et des effets d'un organisme sur son environnement (Chase and Leibold 2003). L'identification de la niche des espèces nécessite une compréhension de leur dynamiques populationnelles en rapport, notamment, avec leur habitat, leurs ressources et les interactions interspécifiques qu'elles entretiennent (Tilman 1982, Chesson 2000, Levine and Hille Ris Lambers 2009). Mais caractériser la niche des espèces devient plus difficile et en même temps moins informatif dès que l'on se penche sur des communautés riches en espèces (McGill et al. 2006, Ricklefs 2012a). En effet, à un même moment et dans un même habitat, quelques populations semblent augmenter tandis que d'autres disparaissent. Une manière d'aborder ces changements est d'établir des classifications fonctionnelles afin de grouper des espèces présentant des caractéristiques communes (Wilson 1999, Blondel 2003), ou encore d'identifier les traits des espèces liés à leur capacité de survie dans différentes conditions (Violle et al. 2007). En écologie fonctionnelle, un « trait » est défini comme « toute caractéristique comportementale, morphologique ou physiologique mesurable à l'échelle de l'individu qui est liée à la performance écologique des espèces » (Calow 1987, Keddy 1992a, McGill et al. 2006).

Parallèlement l'utilisation de classifications *a priori* a influencé le progrès de la recherche sur les relations entre biodiversité et fonctionnement des écosystèmes (Lavorel and Garnier 2002). A titre d'exemple, un modèle marquant concernant les producteurs primaires a été proposé par Grime afin d'expliquer le succès écologique des plantes selon leur position au sein de trois axes de variation écologique (1998) : en fonction de leur capacité à résister aux perturbations (i.e. mécanismes limitant la croissance en causant la destruction), de leur résistance au stress environnemental (i.e. la croissance est limitée par des contraintes inhérentes à l'habitat telles qu'un déficit de ressources), ou de leur aptitude à dominer les autres espèces dans des conditions favorables. Des exemples de classifications existent également chez les animaux, qui sont plus typiquement groupés en guildes trophiques (Blondel 2003). Cependant, la caractérisation d'espèces en plusieurs catégories montre de nombreuses limites. Par exemple, l'emploi d'une seule catégorie pour délimiter des espèces masque d'autres informations potentiellement importantes pour comprendre les réponses de ces dernières aux conditions environnementales ou à la compétition interspécifique (Lavorel and Garnier 2002, Wright et al. 2006).

Par ailleurs, l'utilisation de traits offre l'opportunité de comparer les organismes et les communautés en traitant le *biota* comme une distribution continue de traits fonctionnels (Vandewalle et al. 2010, Violle et al. 2014). Dans une perspective d'écologie des communautés, les traits fonctionnels devraient nous permettre d'identifier le rôle de l'habitat dans le filtrage des espèces ayant des caractéristiques spécifiques, ainsi que les interactions biotiques entre les espèces qui co-occurrent (McGill et al. 2006, Violle and Jiang 2009, Garnier and Navas 2012). Dans une perspective d'écologie des écosystèmes, les traits doivent également permettre d'identifier les caractéristiques des éléments de la biodiversité responsables du maintien de différents processus écosystémiques (Enquist et al. 2015, Schmitz et al. 2015).

Mais de nombreuses questions restent ouvertes ou sans réponse sur la manière dont la caractérisation d'espèces permet d' expliquer leur richesse, leur distribution ainsi que leur contribution et complémentarité dans leur participation aux processus écosystémiques grâce à leur traits fonctionnels ou d'autres caractéristiques (Hillebrand and Matthiessen 2009, Loreau 2010). Par exemple, distinguer les traits responsables de la survie et du succès reproductif ainsi que les traits responsables de la performance des espèces dans l'obtention de différents ressources est encore un défi à relever (Lavorel and Garnier 2002, Naeem and Wright 2003, Hillebrand and Matthiessen 2009). Mais l'ambiguïté avec laquelle les mesures de traits sont parfois appliquées est un problème récurrent. Par exemple, en mesurant une liste de traits sur de nombreux organismes présents dans différents endroits, beaucoup d'études omettent d'identifier les implications biologiques à l'origine de ces différences de traits (Keddy 1992a, Götzenberger et al. 2012). Dans le but de mieux comprendre les mécanismes de substitution et de complémentarité d'espèces qui sous-tendent les processus écologiques, il semble plus pertinent d'identifier comment co-varient les éléments constituant ces traits et les niches écologiques (Violle and Jiang 2009, Kearney et al. 2010, Götzenberger et al. 2012). Or, ceci nécessite un examen dans des conditions environnementales variables afin de confirmer que les relations entre valeurs de trait et de niche sont généralisables (Hawlena et al. 2011, Schmitz et al. 2015).

I.3 REGLES D’ASSEMBLAGE: ROLE DANS LA MAINTENANCE DES COMMUNAUTES ECOLOGIQUES

Une communauté écologique est un groupe d’espèces partageant un environnement et ayant une influence réciproque de manière directe ou indirecte à travers leurs activités. La première description d’une communauté est sûrement celle décrite par Karl August Möbius en (1877) dans son livre: *Die Auster und de Austernwirschaft* (Nyhart 1998). Mobius fournit une description d’une communauté animale qu’il va nommer “biocenose” maintenue dans un état d’équilibre grâce à des limitations de ressources. Les bases de l’écologie des communautés moderne sont forgées sur les paradigmes de la capacité de survie différente des espèces en fonction du milieu (Grinnell 1924, Watt 1947, Hutchinson 1959) ainsi que leurs différences compétitives pour l’obtention de ressources limitantes (Elton 1927, Gause 1934a, Hutchinson 1959, MacArthur and Levins 1967). En plus, les aspects historiques et spatiaux semblent des éléments primordiaux pour expliquer la biodiversité présente au sein de différentes régions (Ricklefs 1987).

En groupant ces trois considérations, l’écologie des communautés essaie d’expliquer la configuration d’espèces locales en considérant l’abondance relative de différentes espèces dans une région et les différences écologiques responsables de leur distribution (Ricklefs 2004, Hille Ris Lambers et al. 2012). L’hypothèse est alors que ces différences écologiques expliquent l’affinité de différentes espèces avec des conditions environnementales hétérogènes ainsi que leurs interactions déterminant les combinaisons d’espèces possibles localement (Diamond 1975, Keddy 1992b, Weiher and Keddy 1999). Ce processus de sélection a été conceptuellement décrit comme une succession hiérarchique de « filtres » qui vont agir a des échelles spatiales de plus en plus fines, imposant des règles dans les assemblages d’espèces. Ainsi dans une région donnée les espèces présentes sont issues de son histoire, notamment lors des évènements de spéciation, colonisation et extinction, comme établi par la théorie neutre (Hubbell 2001). Au sein de la région la diversité et la distribution d’espèces dans différents environnements seront expliquées par leurs affinités avec différents habitats (Weiher and Keddy 1999). Au sein de chacun de ces habitats, certaines combinaisons d’espèces semblent « interdites », et il est souvent attendu que les espèces soient complémentaires localement dans leur utilisation de ressources (Diamond 1975). Les aspects biogéographiques et évolutifs ne font pas partie de cette étude. Ainsi, par la suite, je me consacrerai uniquement à l’explication des facteurs responsables de la distribution et organisation d’espèces dans différents patches d’habitat locaux à travers des filtres environnementaux et biotiques.

La première barrière à franchir pour une installation réussie d’une espèce dans un environnement donné est son adaptation aux conditions environnementales caractéristiques de ce type d’habitat. Cette barrière est que l’on appelle souvent « filtre environnemental ». Cette notion peut être symbolisée par une passoire ou par un filtre qui permettraient uniquement le passage des particules ayant la taille ou la forme adéquates (Fig.1). Ceci illustre le fait que seulement les espèces possédant certaines caractéristiques arrivent à survivre dans un milieu donné en fonction des conditions environnementales qui agissent donc comme un filtre. On attend ainsi une convergence, au moins pour certaines caractéristiques écologiques, au sein des espèces partageant un même habitat. Ces variations environnementales peuvent alors agir sur la diversité et la composition d’espèces et sur leurs traits écologiques associés. D’abord, si la substitution d’espèces d’un habitat à l’autre est reliée à leur phénotype, la moyenne de valeurs de traits peut varier en réponse à des variations de conditions environnementales entre habitats (Keddy 1992b, Garnier et al. 2004). En outre, la capacité d’un écosystème à entretenir/contenir une certaine biodiversité peut être comprise, *sensu* Hutchinson (1957), comme un volume, ou un espace écologique qui s’étend le long d’un nombre de dimensions égale au nombre de facteurs écologiques considérés. Ainsi, le nombre d’espèces présentes dans une communauté peut être directement liée au volume total occupé par cette communauté ; il représente la richesse de stratégies écologiques viables (Cornwell et al. 2006, Ricklefs 2012b).

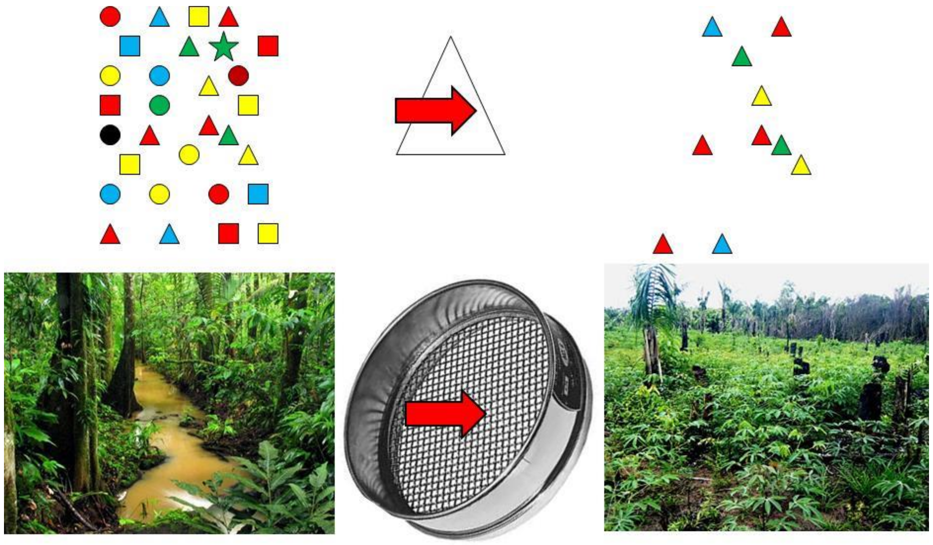


Figure 1. Concept de « filtre écologique » : lors de la transformation d'un habitat, uniquement les espèces possédant certaines caractéristiques sont capables de coloniser et survivre. Par exemple ici, parmi toutes les espèces présentes dans la forêt, uniquement les triangles sont capables de survivre dans un abattis.

De plus, l'installation d'une espèce dans un habitat ne suffit pas à sa survie. En effet les interactions biotiques conditionnent la survie des espèces comme expliqué par le principe de l'exclusion compétitive (Hardin 1960). Ainsi, les espèces possédant les caractéristiques les plus adaptées vont subir un succès reproducteur plus important que d'autres (Keddy 1992b, Grime 1998). En conséquence, la question la plus souvent relevée par les écologues est la suivante : qu'est ce qui empêche ces espèces dominantes de monopoliser tout l'habitat disponible et exclure d'autres espèces ? Une série de mécanismes ont été décrits comme capables de réguler les dynamiques populationnelles de différents espèces de telle manière que la coexistence soit possible. Par exemple, la performance compétitive des espèces peut varier selon les environnements, les saisons ou même être affectée par la présence d'ennemis naturels (Pianka 1966, Connell 1971, Menge and Sutherland 1976, Ricklefs 1977, Wiens 1977). Ces mécanismes se basent sur le fait que la croissance populationnelle de chaque espèce garde une relation négative avec la taille de la population (Chesson 2000). Ceci implique que plus la densité populationnelle d'une espèce est grande plus les individus de cette espèce sont limités par des conspécifiques plutôt que par des individus d'autres espèces (Chesson 2000, Hille Ris Lambers et al. 2012). Certains des mécanismes mentionnés (fluctuations environnementales, ennemis naturels) vont maintenir le nombre d'individus et d'espèces en dessous d'un seuil qui représente la saturation de l'habitat, et ainsi empêcher l'exclusion compétitive (Lawton 1999, Weiher and Keddy 1999, Cavender-Bares et al. 2009). Cependant, l'aspect qui a retenu la plus grande attention parmi les écologues est la compétition

Deux grands modèles ont essayé d'expliquer la coexistence d'espèces en présence de compétition. Le premier modèle considère que si chaque espèce est limitée par des ressources différentes, la croissance populationnelle de chacune d'entre elle est plus fortement limitée par la compétition intraspécifique que par la compétition interspécifique (Gause 1934a). Ainsi, la partition de la niche a longuement été considérée comme étant l'une des causes majeures de la coexistence d'espèces (MacArthur and Levins 1967, Tilman 1982, Abrams 1983). Le deuxième modèle propose un mécanisme de coexistence sans partition de niche, mais avec une partition de l'espace (Levins and Culver 1971). Ce modèle essaye d'expliquer la coexistence d'espèces à travers d'un compromis entre la dominance écologique (ou capacité à exclure des compétiteurs inférieurs des ressources limitantes ou des patches d'habitat) et une habilité plus grande à coloniser ces ressources avant que l' espèce dominante n'arrive (Levins and Culver 1971, Calcagno et al. 2006).

Malgré une longue tradition d'études ayant pour objectif d'expliquer la stabilité des communautés par rapport à la compétition (Schoener 1982, Fargione and Tilman 2002, Amarasekare 2002), cette voie n'est pas restée sans critiques (Wiens 1977, Lawton 1999, Hubbell 2001). Par exemple, le fait de trouver des différences écologiques entre espèces ne constitue pas une preuve de compétition présente ou passé (Connor and Simberloff 1979, Connell 1983). En effet, ces différences peuvent apparaître par des mécanismes d'évolution neutre, par spéciation allopatrique etc… Néanmoins, il est possible de tester si la distribution d'espèces est liée à un processus déterministe. Par exemple, l'organisation d'espèces, et notamment de leurs caractéristiques écologiques à différents niveaux spatiaux peuvent nous permettre de déduire différents mécanismes à l'aide de modèles nuls (Weiher and Keddy 1995, Gotelli and Graves 1996). Les effets d'un filtre environnemental sont censés opérer dans toute l'extension de l'habitat. Cependant, les interactions biotiques et les effets du microhabitat sont des facteurs locaux (Weiher and Keddy 1999, Webb 2000). Quand une agrégation d'espèces ou des espèces possédant des traits similaires apparaissent ensemble plus souvent qu'au hasard; ce résultat est souvent lié à un processus de filtrage environnemental. Au contraire, si les interactions entre espèces sont plus importantes, certaines paires d'espèces ne seront pas trouvées ensemble, même si à *priori* ces espèces privilégient le même type d'habitat. Egalement, les espèces possédant des traits similaires seront moins souvent ensemble que celles ayant des caractéristiques complémentaires : principe de la similarité limitante (MacArthur and Levins 1967). Cette conception a néanmoins été critiquée du fait de la simplicité d'une considération dichotomique. En effet, rien n'empêche les forces environnementales et biotiques d'agir de manière simultanée, ou d'agir sur des traits différents (Mayfield and Levine 2010, de Bello 2012, Adler et al. 2013). L'analyse de patterns de distribution d'espèces ou de traits en fonction des échelles spatiales reste cependant un outil puissant et efficace pour identifier l'effet de différents facteurs écologiques, mais uniquement quand les liens entre ces mécanismes et ces traits ou interactions sont identifiés (Enquist et al. 2015).

I.4 LES RELATIONS COMPLEXES ENTRE BIODIVERSITE ET LES PROCESSUS ECOSYSTEMIQUES ET LE FONCTIONNEMENT DES ECOSYSTEMES

De nombreuses études ont essayé de mesurer l’importance de la biodiversité et l’identité et abondance relative d’espèces dans le maintien des processus écosystémiques ces derniers années, (Hooper et al. 2005, Díaz et al. 2006a). La prévision générale est alors celle qu’une plus grande biodiversité (*sensu lato*, incluant le nombre d’espèces et de traits fonctionnels) qui aura des effets positifs sur les processus écosystémiques tels que la décomposition, la prédation ou encore, la production végétale. Ceci s’explique par des effets complémentaires des espèces utilisant différents ressources ou compartiments de l’écosystème, ce qui donne lieu à une meilleure efficacité du *biota* pour utiliser et transformer la matière et l’énergie présente (Loreau et al. 2001, Petchey and Gaston 2002, Balvanera et al. 2006, Cadotte et al. 2011). La biodiversité est censée augmenter la capacité des écosystèmes à garantir un fonctionnement stable en présence de variations environnementales et ce, grâce aux réponses différentes parmi les espèces présentes à ces variations (Peterson et al. 1997, Elmqvist et al. 2003). Contrairement à ces prévisions , il est fréquent que quelques espèces monopolisent une grande partie des ressources et de la productivité d’un écosystème (Aarssen 1997, Huston 1997). Ainsi, les relations entre biodiversité et productivité ont été parfois associées à une probabilité supérieur des communautés plus diverses à contenir des espèces plus productives (Aarssen 1997, Wardle 1999, Cardinale et al. 2006). Afin de prendre en compte les effets de la dominance mais aussi de la diversité d’espèces, les propriétés d’une communauté sont mieux synthétisées en considérant l’abondance relative des espèces comme suggéré par l’hypothèse du ratio de masse (i.e. Mass Ratio Hypothesis; Grime 1998; Garnier *et al.* 2004).

Les conséquences de la perte et de la substitution d’espèces dans la stabilité fonctionnelle des écosystèmes ne sont pas bien connues sur le long terme (Chapin et al. 2000, Lindemayer et al. 2012). Par exemple, quantifier la contribution de la biodiversité aux processus écosystémiques spécifiques ou encore identifier comment les variations dans des flux de matière et d’énergie vont affecter le nombre, l’abondance et l’identité d’espèces est encore sujet de débat. A titre d’exemple, la contribution de la diversité ou de la dominance d’espèces à différents processus écosystémiques est variable en fonction du processus et peut varier d’un écosystème à l’autre voire au cours du temps (Fargione et al. 2007, Mouillot et al. 2011). De même il n’est pas certain que les relations biodiversité – productivité soient conduites par les espèces (top-down) ou bien au contraire, que le nombre d'espèces et leur abondance soit le résultat de la disponibilité d'énergie et ressources dans un écosystème ainsi que leur stoechiométrie (bottom-up) (Gross and Cardinale 2007, Scherber et al. 2010, Carnicer et al. 2015). En fait, la productivité d'un écosystème est nécessairement liée à la quantité de ressources et énergie ce qui permet la présence d'un plus grand nombre d'individus et d'espèces (Evans et al. 2005, Cardinale et al. 2009a). Ceci peut donc engendrer une plus grande biodiversité et activité des espèces. On peut par exemple considérer un modèle classique tel que celui des relations entre proies et prédateurs. La ressource contrôle la densité des populations: les populations de proies grandissent en réponse aux ressources, ce qui aura un effet bénéfique pour les prédateurs. Cependant, une diminution de ressources va diminuer la densité de proies, ce qui affectera négativement les populations de prédateurs, et le processus de prédation sera aussi amoindri. L'intensité du processus est ainsi toujours liée à l'abondance ou à la densité de la ressource associée (Holling 1973).

En conclusion, les écosystèmes sont des entités homéostatiques et résistantes, capables d'autorégulation et de résilience (Peterson et al. 1997, Folke et al. 2004). Toutefois, en même temps ils peuvent être fragiles car la transgression de certains seuils (i.e. des modifications dans la composition d'espèces ou dans les flux biogéochimiques) peuvent perturber son équilibre, déclenchant alors un changement de régime et conduisant l'écosystème à un état différent avec des propriétés nouvelles (Naeem 1998, Folke et al. 2004, Sundstrom et al. 2012). Il est donc nécessaire de clarifier les liens entre la diversité, l'abondance relative d'espèces, la disponibilité de ressources ainsi que l'intensité et l'équilibre dans des processus écosystémiques (Hillebrand and Matthiessen 2009, Kearney et al. 2010, Thompson et al. 2012, Carnicer et al. 2015).

II. LES FOURMIS COMME MODELE D’ETUDE EN ECOLOGIE DES COMMUNAUTES ET DES ECOSYSTEMES

Les fourmis constituent *a priori* un modèle animal excellent pour des études écologiques. On peut facilement trouver un support à cette affirmation lorsqu’on s’aperçoit de l’ubiquité et de l’abondance des fourmis dans le monde comme de la facilité de leur échantillonnage (Hölldobler and Wilson 1990, Lach et al. 2010). Toutes les fourmis appartiennent à la famille des Formicidae qui est apparue sur Terre il y a entre 180 et 130 millions d’années; l’hégémonie de cette famille est restée incontestée depuis 60 millions d’années (Wilson and Hölldobler 2005, Ward 2014). Aujourd’hui, le succès écologique des fourmis est uniquement comparable à celui de notre propre espèce (Wilson 1971, Wilson and Hölldobler 2005).

En effet, les fourmis sont présentes dans la majorité des écosystèmes terrestres et représentent souvent une partie importante de la biomasse animale (Hölldobler and Wilson 1990). Egalement, les fourmis sont capables d’occuper une grande diversité de compartiments dans la majorité des écosystèmes (i.e. dans le sol, la litière, dans le troncs des arbres et même dans la canopée; Fowler & Delabie 1995; Blüthgen & Stork 2007; Ryder Wilkie *et al.* 2010). Ceci est particulièrement flagrant dans les régions les plus chaudes et les plus humides de la planète dans lesquelles la diversité écologique des fourmis semble la plus importante (Kaspari et al. 2000, Gibb et al. 2015a). A titre d’exemple, la biomasse des fourmis dans des écosystèmes tropicaux peut constituer jusqu’à la moitié du poids des animaux sur la cime des arbres, ou encore un quart du poids des animaux terrestres (Fittkau and Klinge 1973, Davidson and Patrell-kim 1996). Bien que moins importante en proportion, les fourmis semblent être très importantes aussi dans des régions plus froides (Stork 1988, Frouz and Jilková 2008).

Comme tous les arthropodes, les fourmis ont une longue histoire évolutive, des taux de reproduction rapides et une sensibilité importante aux changements chimiques (Kremen et al. 1993, Keith 1997). De plus, la majorité des espèces de fourmis possède la particularité d’habiter dans des nids ou dans des colonies sessiles, ce qui les rapproche des plantes (Andersen 1991a, López et al. 1994). Afin de nidifier, par exemple, les fourmis ont besoin de conditions du sol ou d’abris assez spécifiques ainsi que de ressources alimentaires particulières dans leur environnement (Ribas et al. 2003, McGlynn et al. 2009, Blüthgen and Feldhaar 2010, Wu et al. 2010). Egalement la durée de vie d’une colonie peut être très longue. En fonction des espèces elle peut durer plusieurs dizaines d’années, voire des centaines si de nombreuses générations occupent un même endroit (Frederickson et al. 2005, Ingram et al.

2013). En conséquence, la compétition pour des ressources de nidification ou pour des ressources alimentaires, a été souvent considérée comme un pilier de l'écologie des fourmis (Hölldobler and Wilson 1990, Parr and Gibb 2009). En effet, il est relativement fréquent d'observer des interactions agressives entre espèces de fourmis pour protéger leur territoire ou des aliments (Wilson 1971, Andersen 1992). En outre la distribution de nids de fourmis semble souvent dépendante de la distribution locale de ressources ainsi que de la présence d'autres espèces (Andersen 1991; McGlynn 2006; Parr & Gibb 2010; Arnan *et al*. 2011).

L'échantillonnage de fourmis est relativement simple et efficace du point de vue du coût et du temps (Delabie et al. 2000, Longino et al. 2002). Des méthodes standardisées existent à ce propos et sont largement appliquées dans différentes parties du monde, ce qui permet d'établir des comparaisons raisonnables entre régions et types d'habitats (Agosti et al. 2000, Underwood and Fisher 2006, Gotelli et al. 2011). La biodiversité des fourmis est modérée et leur taxonomie relativement bien étudiée (www.antweb.org). Grâce à des bases de données existantes, on peut aujourd'hui comparer plus de 15000 espèces et sous-espèces décrites, ce qui représente, d'après les estimations, environ deux tiers de la biodiversité totale de fourmis dans le monde (Agosti and Johnson 2005). En plus, les nouvelles bases de données crées à partir de coordonnées géographiques tels que *antbase* ou *Global Ant Biodiversity Informatics* (*GABI*) (*Guénard* et al. in review) constituent une ressource efficace permettant de comparer et de comprendre la distribution d'espèces de fourmis et leur variation à l'échelle du globe.

II.1 REGLES D'ASSEMBLAGES CHEZ LES FOURMIS

L'étude des règles d'assemblage chez les fourmis a souvent suivi des paradigmes spécifiques. En effet, de nombreux auteurs considèrent que la plupart des espèces de fourmis sont des généralistes, exploitant une pluralité de ressources alimentaires dans leur environnement sans une préférence nette pour l'une ou l'autre d'entre elles (Wilson 1971, Davidson 1998). Par ailleurs, l'observation fréquente de comportements agressifs liés à la nourriture ou au territoire, a mené beaucoup de chercheurs à penser que les communautés de fourmis sont principalement structurées par la « compétition par interférence », c'est-à-dire que certaines espèces en empêchent d'autres d'exploiter les ressources dont elles ont besoin (Wilson 1971, Hölldobler and Wilson 1990, Andersen 1992, Dejean et al. 2007, Blüthgen and Feldhaar 2010). En effet, beaucoup d'études ont essayé d'expliquer les communautés de fourmis comme une hiérarchie de dominance: certaines espèces, plus agressives et plus performantes dans le recrutement d'ouvrières vont exclure de leur territoire ou des ressources alimentaires de haute qualité les autres espèces subordonnées (Wilson 1971, Andersen 1991a, 1992, Parr and Gibb 2009). A titre d'exemple, la stabilité des assemblages de fourmis a très souvent été considérée comme le résultat d'un accès hiérarchique aux sources de ressources alimentaires : c'est que l'on connait comme le « compromis entre découverte et dominance ». Ce postulat défend l'idée selon laquelle les espèces subordonnées sont capables de survivre au sein du territoire d'une espèce dominante uniquement si elles sont capables de trouver les ressources alimentaires plus rapidement (Wilson 1971, Davidson 1980, 1998, Andersen 1991a, Adler et al. 2007, Parr and Gibb 2012, Cerdá et al. 2013).

Contrairement à la supposition que la majorité d'espèces de fourmis sont similaires dans leur besoins écologiques, des différences plus ou moins importantes peuvent être essentielles pour garantir la stabilité des assemblages. Par exemple, le compromis entre découverte et dominance a des effets variables en fonction d'autres facteurs environnementaux tels que la présence d'ennemis naturels, le type de microhabitat et les fluctuations environnementales spatiotemporelles (Cros et al. 1997, Sarty et al. 2006, Lebrun and Feener 2007, Feener et al. 2008, Pearce-Duvet and Feener 2010, Gibb and Parr 2010, Wiescher et al. 2011). Par ailleurs, de récentes études montrent de plus en plus que la différentiation écologique entre espèces des fourmis est un phénomène largement répandu (Retana et al. 2015). Cette différentiation écologique peut inclure une série de facteurs, tels que des variations dans le temps de fourragement et des tolérances variables à la température ambiante, des préférences de microhabitat comme la densité de matière organique dans le sol, l'utilisation de différents compartiments de l'écosystème, ou encore l'utilisation de différents ressources alimentaires (Andersen 1986, Luque and Reyes López 2007, Agarwal and Rastogi 2009, Arnan et al. 2012b).

Enfin, la partition écologique est parfois un sujet assez compliqué car de nombreuses dimensions écologiques peuvent interagir simultanément (Weiser and Kaspari 2006, Andersen 2008, Stuble et al. 2013). En conséquence, il semble nécessaire d'inclure une liste extensive des caractéristiques potentiellement importantes pour identifier pour chaque environnement et chaque région quels sont les facteurs les plus importants en relation avec la diversité des fourmis et la stabilité des assemblages (Silva and Brandão 2010, 2014, Retana et al. 2015).

II.2 REPONSE DES FOURMIS AUX GRADIENTS ENVIRONNEMENTAUX

Des changements très importants dans la composition spécifique des fourmis sont souvent observés lorsqu'on étudie différents habitats (Andersen 1997a, Agosti et al. 2000, Underwood and Fisher 2006). En effet, il est fréquent de trouver une forte fidélité de certains taxons de fourmis pour des environnements particuliers. Andersen (1995) avait proposé une classification des fourmis dans des groupes fonctionnels par rapport à leur affinité avec différents types d'habitat le long d'un gradient géographique ou climatique. Par exemple, les Dolichoderines dominantes sont particulièrement abondantes dans les milieux ouverts et chauds, les Myrmicines généralistes apparaissent dans la majorité d'habitats, les opportunistes sont caractéristiques des milieux perturbés, etc. Cette classification était développée dans des régions arides de l'Australie (Andersen 1995), mais elle a également servi à comprendre la structure des communautés de fourmis dans d'autres régions biogéographiques (Andersen 1997b, King et al. 1998, Leal et al. 2012, Arnan et al. 2012b). Le principal message de ces travaux est que certaines caractéristiques écologiques des fourmis leur permettant une adaptation à différents milieux sont conservées phylogénétiquement. Cependant, la nature discrète d'une telle classification fonctionnelle, ainsi que la nécessité d'adapter le modèle à chaque région, empêchent une compréhension plus profonde des mécanismes responsables de telles substitutions d'espèces.

L'importance des gradients environnementaux dans la diversité, la composition et la structure des communautés de fourmis a été étudiée plus récemment par plusieurs auteurs (Hill et al. 2008, Ríos-Casanova and Bestelmeyer 2008, Gibb and Parr 2010, Yates and Andrew 2011, Wiescher et al. 2011, Murnen et al. 2013). La température est probablement la variable la plus importante pour comprendre l'abondance et diversité des fourmis dans différents régions (Sanders et al. 2007, Dunn et al. 2009, Jenkins et al. 2011, Gibb et al. 2015a). Par ailleurs, même au sein d'une région, les habitats où le sol est directement exposé au soleil contiennent souvent des espèces différentes que ceux où la végétation est abondante (Luque and Reyes López 2007, Wiescher et al. 2011). En effet, la couverture végétale, a des effets, non seulement dans la température de l'air et du sol, mais également sur la complexité environnementale. L'abondance de litière, de branches et des troncs morts par exemple, va jouer un rôle important dans la capacité de différentes espèces de fourmis pour nidifier (Herbers 1989, McGlynn 2006, McGlynn et al. 2009, Murnen et al. 2013). La densité et la composition de la litière vont aussi influencer le succès de fourragement de différentes espèces (Lassau and Hochuli 2004, McGlynn 2006, Sarty et al. 2006, Gibb and Parr 2010). Les communautés de fourmis répondent souvent à des variations dans l'abondance de différents nutriments dans l'habitat (Kaspari and Yanoviak 2001, Bihn et al. 2008, Kaspari et al. 2012, Jacquemin et al. 2012, Peters et al. 2014). Finalement, le régime et l'intensité des pluies s'avèrent des variables aussi importantes pour tenir compte des patterns d'abondance et diversité de fourmis (Fergnani et al. 2010, Jenkins et al. 2011, Arnan et al. 2014).

La caractérisation des fourmis par une approche de traits en complément à des approches plus traditionnelles, tels que la comparaison taxonomique ou par le biais des groupes fonctionnels, a servi à identifier de nombreux mécanismes de remplacement d'espèces dans des gradients d'usage de la terre (Wiescher et al. 2012, Arnan et al. 2013, 2014, Yates et al. 2014). Par exemple, la « *Size grain hypothesis* » propose que la taille des fourmis et la longueur des pattes peuvent constituer une limitation pour leur déplacement dans la litière du fait de la difficulté à passer dans ces interstices (Kaspari and Weiser 1999, Gibb and Parr 2010). Par ailleurs, la résistance du couvain ou des ouvrières aux fortes températures peut déterminer quelles espèces seront présentes dans différents types d'habitats (Linksvayer and Janssen 2009, Mezger and Pfeiffer 2010, Wiescher et al. 2012). En particulier, il a été proposé que la taille des fourmis est positivement liée à leur résistance à la chaleur et à la déshydratation (Kaspari 1993, Oberg et al. 2012). Cependant, la validité de ces relations, est parfois variable, en fonction du groupe de fourmis étudié ou des régions (Oberg et al. 2012, Retana et al. 2015). L'étude des communautés de fourmis via leurs traits fonctionnels est une voie prometteuse mais qui demande d'études plus approfondies pour confirmer la généralité des relations traits-environnement.

II.3 PARTICIPATION DES FOURMIS DANS DES PROCESSUS ECOLOGIQUES

L'importance écologique des fourmis a été reconnue depuis longtemps (Petal 1978, Folgarait 1998, Crist 2009, Philpott et al. 2010, Del Toro et al. 2012). Les actions des fourmis dans les écosystèmes sont indirectes, lors de leur influence sur d'autres organismes (Handel and Beattie 1990, Schultz et al. 2000) et directes lors des activités de nidification et de collecte de ressources alimentaires (Petal 1992, Nkem et al. 2000, Bestelmeyer and Wiens 2003, Frouz et al. 2008). Les fourmis entretiennent notamment de nombreuses interaction avec les plantes (Davidson and Mckey 1993), les champignons (Chapela et al. 1994, Dauber et al. 2008), les bactéries (Currie et al. 2003, Russell et al. 2009), avec d'autres arthropodes

(James et al. 1999) ou même avec des vertébrés (Crist 2009). Tous semblent coopérer, être en compétition, manger ou être mangés par les fourmis (Schultz et al. 2000). A travers leur consommation de ressources, les fourmis remplissent d'importantes fonctions écologiques. En effet, elles exploitent une grande variété de ressources alimentaires incluant des graines, des insectes, des excréments, des carbohydrates etc. (Brown 2000, Brandão et al. 2012). Ces activités de récolte reflètent la participation des fourmis dans des processus écosystémiques, tels que la dispersion de graines (Handel and Beattie 1990, Orivel and Dejean 1999), la prédation (Philpott and Armbrecht 2006, Dejean et al. 2007), l'herbivorie (Verchot et al. 2003) ou la détritivorie (Folgarait 1998). Mais les fourmis sont aussi des alliés mutualistes des plantes (Sagers et al. 2000, Heil and McKey 2003, Orivel and Leroy 2010) et de certains insectes herbivores (Styrsky & Eubanks 2007; Stadler & Dixon 2005). Enfin, elles ont un rôle éminent dans la bioturbation et la structure physique des sols (Nkem et al. 2000), les cycles biogéochimiques (Petal 1978, Frouz and Jilková 2008) et la fixation d'azote (Verchot et al. 2003; Evans et al. 2011). Tous ces facteurs réunis font des fourmis d' importants ingénieurs de l'écosystèmes (Jouquet et al. 2006, Meyer et al. 2011).

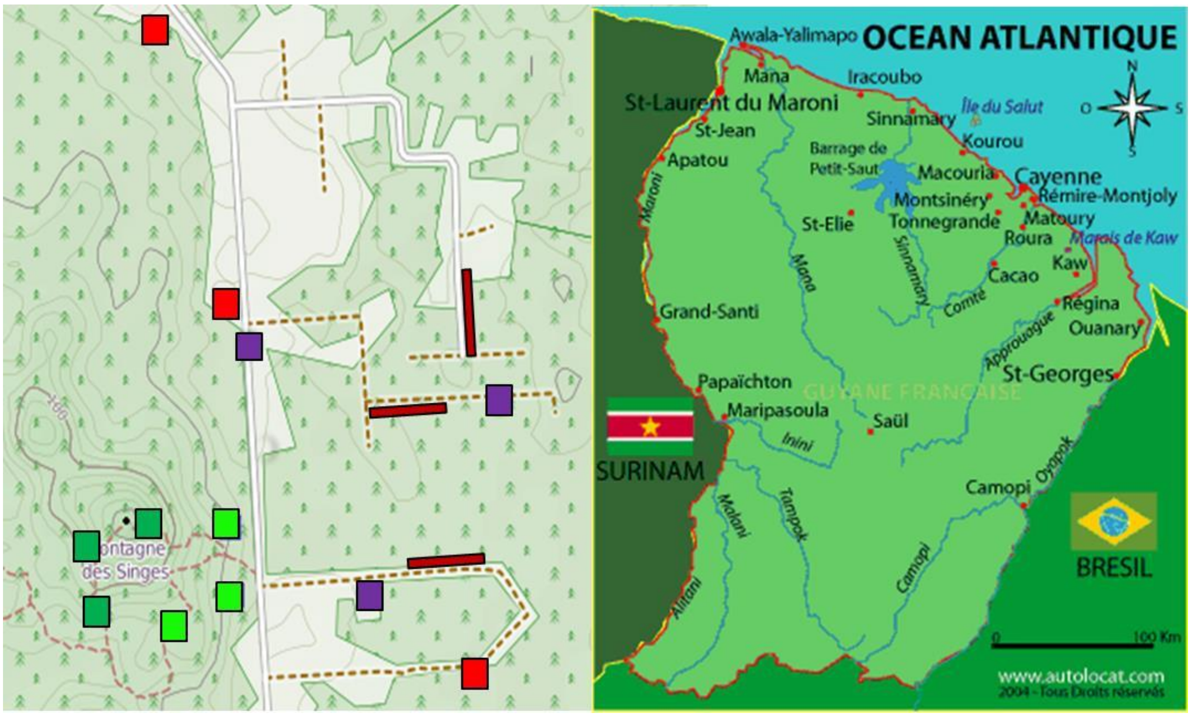
Cependant, peu d'informations existent sur les quantités de différents types d'aliments qui sont prélevés par des espèces de fourmis, ou par des communautés entières. Par ailleurs, les études se focalisent souvent sur un processus écologique en particulier, comme par exemple la prédation, la granivorie, la dispersion de graines, la protection de mutualiste ou la détritivorie (Philpott et al. 2008, Dejean et al. 2009, Fayle et al. 2010, Dominguez-Haydar and Armbrecht 2011, Warren and Giladi 2014).

Plusieurs études réalisées jusqu'à présent montrent qu'une plus grande couverture végétale peut avoir un effet positif sur la participation des fourmis à des processus tels que la prédation, la granivorie ou la fréquentation des plantes a nectar (Wolff and Debussche 1999, Philpott and Armbrecht 2006, Philpott et al. 2006, Dominguez-Haydar and Armbrecht 2011, Šipoš and Kindlmann 2013). Ces activités de fourragement peuvent avoir des effets positifs sur la dispersion des graines (Leal et al. 2007, Arnan et al. 2012a) ainsi que sur la production végétale grâce à leur influence sur des insectes herbivores (Suzuki et al. 2004, Philpott et al. 2006, Van Mele et al. 2007). Mais ces résultats ne sont pas généralisables, en effet, d'autres études ont évalué l'exploitation de proies et de charogne dans des gradients environnementaux sans trouver de différences significatives (Philpott et al. 2008, Fayle et al. 2010). Par ailleurs, si la prédation de graines est trop grande le service de dispersion peut également être bouleversé (Arnan et al. 2012a). Dans certains cas tout de même, les effets bénéfiques des fourmis sur la production végétale peuvent être inversés *via* leurs associations avec des hémiptères (Offenberg et al. 2013). Enfin, la participation d'une espèce de fourmi à différents processus écosystémiques peut être variable en fonction des conditions ou des ressources disponibles. Certaines espèces vont en effet contribuer à différents processus (prédation, granivorie ou encore élevage d'aphides) plus ou moins intensément en fonction du contexte (Crist and MacMahon 1992, Offenberg 2001, Mollot et al. 2014).

III. OBJECTIFS GENERAUX

En Guyane Française la forêt est encore bien conservée. En effet, plus de 90% du territoire (88000 Km^2) est encore couvert par des forêts en bon état (Hammond 2005). Cependant l'intensité de la déforestation grandit parallèlement à une rapide croissance démographique qui, selon les estimations, devrait doubler dans les trente prochaines années (INSEE 2011). En vue de ces changements, il s'avère important d'identifier et de comprendre les conséquences de tels impacts pour la biodiversité et le fonctionnement des écosystèmes guyanaises. Du fait de l'importance des fourmis dans les écosystèmes tropicaux (Davidson and Patrell-kim 1996) et de leur qualité comme bioindicateurs (Andersen 1997a), je me suis intéressé a ce groupe d'animaux afin d'étudier les modifications dues à l'anthropisation.

L'idée soutenue par cette thèse est la suivante : les changements d'usage des terres ont un effet dans la composition des espèces et des traits des fourmis engendrant alors des conséquences sur la participation de ces dernières aux différents processus écologiques. J'essaie de connecter, au moins en partie, les mécanismes responsables de la persistance et l'abondance relative de différentes espèces dans une série d'habitats le long d'un gradient d'anthropisation (Fig. 2) et les mécanismes responsables du maintien du rôle écologiques des assemblages de fourmis dans ces différents habitats.



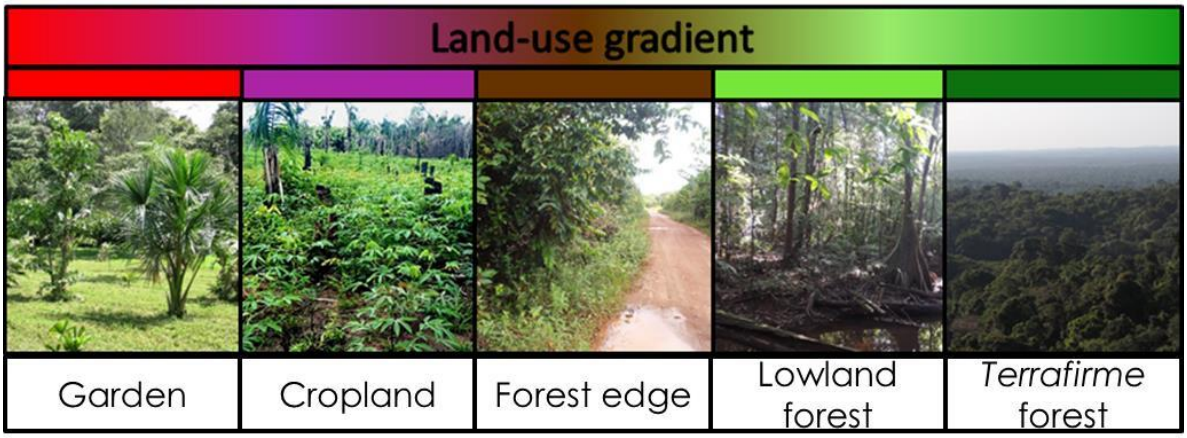


Figure 2. Site d'étude et habitats choisis pour représenter un gradient d'anthropisation. De gauche à droite, les habitats reflètent un dégrée plus important de perturbations en soustraction de biomasse végétale par rapport à l'état initiale : jardins, abattis, lisières, forêts de bas-fond et forêts de *terra-firme*.

Le questionnement principal de cette thèse est alors divisé en deux sous-parties. Premièrement je me suis intéressé à l'organisation des assemblages de fourmis en réponse à des facteurs locaux et environnementaux (Chapitre IV). Plusieurs caractéristiques fonctionnelles sont particulièrement prises en compte pour expliquer l'organisation d'espèces au sein des habitats (Articles 1 et 2) et la substitution d'espèces entre habitats (Articles 2 et 3). Je me suis ensuite intéressé aux relations entre la structure fonctionnelle des assemblages de fourmis, et la performance de ces derniers dans l'exploitation de différents types de ressources alimentaires (Articles 4 et 5). L'interprétation est alors que l'intensité d'exploitation de ces ressources reflète la contribution de ces assemblages dans les processus écosystémiques représentés.

Pour mieux comprendre les relations habitat-diversité-processus, j'ai choisi une approche de traits morphologiques et une caractérisation de l'utilisation de différentes ressources par les espèces trouvées. En effet, tenir compte de la morphologie s'avère intéressant car des liens significatifs existent entre la forme des fourmis et leur capacité à survivre et fourrager dans différents types d'habitats, ainsi qu'à exploiter différents ressources alimentaires (Weiser and Kaspari 2006, Gibb et al. 2015b). De plus, la quantification de l'utilisation de ressources alimentaires par des espèces de fourmis permet d'étudier les différences écologiques entre espèces, et d'identifier leur contribution à des processus écologiques précis. En effet, les appâts choisis pour les expériences, représentent des ressources présentes dans la nature et associés à des processus écologiques importants impliquant les fourmis. Cette approche devra me permettre d’établir un lien entre les caractéristiques fonctionnelles des espèces et leur performance dans l’exploitation de ressources et leurs réponses aux variations environnementales.

IV. REGLES D’ASSEMBLAGES ET ANTHROPISATION

Par « règles d’assemblages », on entend un ensemble de mécanismes expliquant pourquoi dans une région, les espèces apparaissent, là où elles apparaissent, et pourquoi certaines combinaisons d’espèces semblent plus probables que d’autres *vis-à-vis* de leurs caractéristiques écologiques et leurs interactions (Weiher and Keddy 1995, Hille Ris Lambers et al. 2012). En conséquence, ce chapitre porte sur l’organisation des espèces de fourmis selon les différents habitats et au sein de ces derniers. Par nécessité, j’ai divisé les mécanismes qui agissent à l’échelle locale et au niveau du type d’habitat, bien que la nature fonctionne plutôt comme un continuum.

Dans l’étude des processus locaux, je me suis consacré à l’étude des différences écologiques entre espèces, notamment, lors de leur utilisation de ressources alimentaires. En effet, bien que la littérature décrive souvent une importante compétition pour la nourriture au sein des communautés de fourmis, il n’existe que très peu d’études visant à comprendre comment les différences dans l’acquisition de ressources alimentaires sont liées à la structure des assemblages.

Dans l’étude des effets de l’habitat j’ai d’abord voulu connaitre les impacts des changements d’usage de terre sur le nombre et l’identité des espèces. J’ai ensuite essayé de comprendre comment les différences écologiques des espèces associées à ces différents milieux peuvent nous aider à prédire de telles modifications.

Trois articles sont présentés. Dans le premier, les partitions écologiques circadienne et trophique sont étudiées dans un fragment de forêt. Cette étude montre des différences interspécifiques importantes dans ces deux dimensions, qui peuvent, potentiellement expliquer la coexistence d’espèces. Dans le deuxième article, les activités de fourragement des fourmis pour différents types de ressource sont comparées entre des forêts et des abattis. Notamment on s’intéresse à des variations dans l’utilisation des appâts contenant différents types d’aliments, ainsi qu’à des différences quand un même type d’appât est présenté de plusieurs manières, pour représenter le microhabitat ou l’hétérogénéité environnementale. On trouve que les espèces utilisent différentes ressources alimentaires, et favorisent différentes conditions pour le faire, entre habitats mais aussi au sein de ces habitats. Le troisième article porte sur les variations morphologiques le long du gradient d’anthropisation étudié. Il est démontré que les fourmis associées à différents types d’habitat sont très hétérogènes quand on compare leurs morphologies, mais que la richesse d’espèces n’est pas forcement liée à l'espace morphologique occupé par les assemblages (*i.e.* la diversité de stratégies écologiques).

En somme, ces articles démontrent d'une part que les caractéristiques écologiques des espèces sont fortement dépendantes du type d'habitat, mais également, que les assemblages locaux sont composés d'espèces possédant des caractéristiques très différentes. Ces résultats suggèrent une prévalence de certains types d'espèces ou de traits en fonction de l'environnement, mais aussi que l'exclusion compétitive est un mécanisme important pour expliquer la stabilité de ces assemblages.

IV.1 PARTITION DE LA NICHE ET DETERMINISME DES ASSEMBLAGES LOCAUX

Traditionnellement, les myrmécologues ont accordé un rôle très important à la compétition dans la structure des communautés de fourmis (Parr and Gibb 2009, Cerdá et al. 2013). Ceci est lié à l'observation d'une importante activité et d'un recrutement de fourmis envers des ressources alimentaires, ainsi qu'à l'observation de comportements agressifs entre espèces (Parr and Gibb 2009). Or, nous avons démontré que l'activité de fourragement et de recrutement était très intense avec la plupart des appâts ce qui suggère que les ressources alimentaires constituent un élément limitant pour les fourmis dans les habitats étudiés. La question qui suit est alors : comment différentes espèces partageant des ressources limitantes, arrivent à coexister ?

La théorie de la niche explique la stabilité des communautés grâce à la partition écologique des espèces. En effet, c'est l'utilisation de ressources complémentaires qui va permettre à différentes espèces de coexister, et d'éviter l'exclusion compétitive. Il est donc attendu que les assemblages soient composés par des espèces complémentaires. En outre, si la partition écologique est responsable de la composition des communautés (en favorisant justement la coexistence ou cooccurrence) nous devrions pouvoir démontrer qu'un déterminisme existe dans la composition d'espèces par rapport à leurs traits.

Me basant sur Schoener (1974), je me suis focalisé sur les trois dimensions écologiques les plus importantes permettant la différentiation de niche : la partition temporelle (Article 1), la partition du régime alimentaire (Articles 1 et 2) et la partition du microhabitat (Article 2). On trouve des différences écologiques importantes entre espèces dans tous les assemblages étudiés qui s'ajustent aux prédictions de la « similarité limitante » (MacArthur and Levins 1967, Abrams 1983). En effet, dans les deux premiers articles il est montré que dans un fragment de forêt, ainsi que dans des abattis et dans des forêts, la règle est de trouver des assemblages composés par des espèces avec des régimes alimentaires très distincts. De plus, dans le premier article il est aussi montré que les variations temporelles constituent également un mécanisme de différentiation écologique important chez les fourmis. Enfin, nous avons démontré une partition des microhabitats ou des conditions privilégiés par les espèces pour obtenir leurs ressources, au moins, dans les forêts, bien que cette dimension écologique ne semble pas importante dans les abattis.

D'autres travaux ont également montré qu'une partition écologique trophique, temporelle ou de microhabitat constituent des axes de variation potentiellement liés à la coexistence d'espèces de fourmis (Andersen 1986, Fowler and Delabie 1995, Luque and Reyes López 2007). Ces résultats invitent à remettre en question la supposition d'une redondance écologique entre les espèces de fourmis (Wilson 1971, Parr and Gibb 2012). En effet, une majorité d'espèces de fourmis sont « généralistes » exploitant des carbohydrates, des lipides et des protéines sous différents formes (Blüthgen and Feldhaar 2010). Mais l'identité de ces formes, ainsi que les proportions dans lesquelles elles sont exploitées sont très importantes pour comprendre les différences entre espèces et la stabilité des assemblages. Par exemple, l'accès à des sources de nectar ou de miellat, de charogne, de proies ou de graines, changent en fonction du microhabitat ou encore du comportement ou de la morphologie des espèces (Cerdá et al. 1998a, McGlynn and Kirksey 2000, Blüthgen and Feldhaar 2010). Ainsi, une différentiation dans une voire plusieurs dimensions écologiques rend la coexistence possible, si la compétition intraspécifique, est supérieure à la compétition entre espèces (Pacala and Roughgarden 1982, Tilman 1982).

Néanmoins, il est important de prouver que les différences écologiques jouent un rôle pour expliquer la distribution des espèces (Connor and Simberloff 1979, Connell 1980). Notamment on s'attend à une exclusion d'espèces écologiquement similaires. Cette question a été examinée dans le deuxième article, dans lequel il est montré que les assemblages locaux sont non seulement constitués d'espèces très différentes, mais également, que le degré de différentiation à l'échelle de l'assemblage est plus intense que si l'on considère une extension spatiale supérieur. Ceci est cohérent avec les attendus d'une exclusion des formes écologiques similaires (Diamond 1975, Abrams 1983).

La globalité des résultats montrés illustre d'une part un fort degré de partition écologique dans les assemblages de fourmis le long de différents axes de variation. Alors que d'autre part, le fait de trouver une similarité écologique moins importante au niveau local qu'au niveau de l'habitat, constitue une preuve valable d'un certain degré de déterminisme dans la composition des assemblages. On pourra encore invoquer la stabilité dans le nombre d'espèces que nous avons échantillonné dans chaque type d'habitat (*e.g.* Article 3). En effet, les variations du nombre d'espèces entre assemblages du même type d'habitat sont assez basses, notamment, lorsqu'on considère un important degré de remplacement d'espèces même entre parcelles d'un même type d'habitat (*i.e.* forêts). Cette stabilité apparente de la biodiversité taxonomique et écologique ne peut pas être expliqué que par une contribution des interactions interspécifiques (Silva and Brandão 2010, Arnan et al. 2014, Fayle et al. 2015).

IV.2 EFFETS DE L'HABITAT SUR LES ASSEMBLAGES DE FOURMIS

Bien que de nombreuses études aient décrit des changements dans la composition d'espèces de fourmis le long de gradients environnementaux (Hoffmann 2010, Gibb et al. 2015a), peu d'entre elles ont essayé d'identifier les mécanismes responsables de ces substitutions (Wiescher et al. 2012, Arnan et al. 2014, Yates et al. 2014).

Les effets de l'habitat sur la diversité et la composition spécifique des fourmis sont évalués. Une explication de ces variations est recherchée à travers un examen des variations de caractéristiques fonctionnelles telles que les préférences alimentaires et les stratégies de fourragement (Article 2) ainsi qu'à travers les traits morphologiques (Article 3). La prévision théorique est alors que l'on trouve localement un sous-ensemble d'espèces capables de coloniser ce type d'habitat, parmi toutes les espèces présentes dans la région (Keddy 1992b). Cette capacité à coloniser et survivre dans chaque environnement dépend des caractéristiques écologiques de chaque espèce. Ainsi, dans différents habitats on peut trouver des variations du nombre d'espèces voire de l'identité de ces dernières (Fig. 3). D'une part, les changements de nombre d'espèces peuvent être issus d'une diminution de la diversité fonctionnelle viable dans un type d'habitat (Petchey and Gaston 2002). Cette « contraction de niche» peut s'expliquer par une diminution du nombre de stratégies écologiques viables dans un environnement par rapport à un autre, ce qui aurait comme conséquence la disparition des espèces possédant des caractéristiques non adaptées (Ricklefs 2012b, Lamanna et al. 2014). De plus, le remplacement d'espèces entre habitats est souvent expliqué par un changement d'identité fonctionnelle, c'est-à-dire un « déplacement de niche », expliqué par une variation dans la dominance de type d'espèces, reflété par un changement de la valeur moyenne des traits des espèces (Garnier et al. 2004, Cornwell et al. 2006).

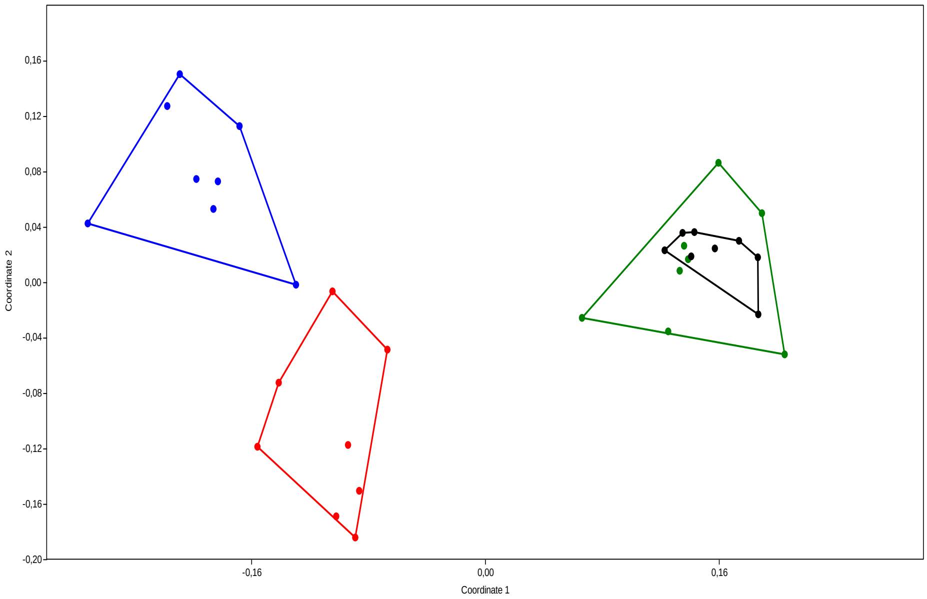


Figure 3. Relations entre filtre environnemental, diversité et identité fonctionnelle et composition d'espèces exemplifiées dans un espace fonctionnel. Les points représentent des espèces, leur position et séparation dans l'espace fonctionnel nous indiquent leurs différences écologiques. Les polygones délimitent les espèces présentes dans un même type d'habitat. L'aire de ces polygones illustre la diversité fonctionnelle des espèces présentes, tandis que leur position dans l'espace montre des changements de valeurs de traits (identité fonctionnelle)~~.~~ Les polygones bleu, rouge et verte représentent des communautés de diversité fonctionnelle similaire, mais une différence dans la composition spécifique, expliqué par des changements dans l'identité fonctionnelle de ces espèces. Les communautés noire et verte contiennent des espèces avec une identité fonctionnelle similaire, mais différent dans la diversité fonctionnelle et le nombre d'espèces.

Dans le gradient d'anthropisation étudiée on a pu constater une forte diminution du nombre d'espèces, ainsi qu'un fort changement dans la composition d'espèces. Ces changements, était notamment observables en comparant les milieux forestiers (*terrafirme* et basfonds) et les milieux ouverts (jardins et abattis). En effet, la chute de biodiversité dans les milieux ouverts est flagrante (Articles 2, 3), mais il est aussi frappant de ne pas trouver (ou presque pas) des espèces en commun avec les milieux forestiers. Les lisères uniquement, étant un milieu de transition, contenaient des communautés des espèces qui intégrait un mélange d'espèces de ces deux types d'habitats, ainsi que certaines espèces qui leur était propres (Article 3).

L'étude des communautés par le biais de leur diversité fonctionnelle a montré des différences très nuancées entre milieux. Par exemple, parmi les aspects écologiques étudiés, c'est uniquement en examinant les stratégies de fourragement, qu'on a trouvé une faible partition de niche dans les abattis en comparaison avec les forêts (Article 2). Alors que la partition de niche alimentaire semblait très importante dans ces deux types de milieux (Article 2). Enfin, d'un point de vu morphologique, les milieux ouverts contenaient un ensemble d'espèces tout aussi différentes que les milieux forestiers (Article 3). Il est donc difficile de conclure que la réduction du nombre d'espèces soit une conséquence d'un espace fonctionnel plus restreint. En revanche, lorsqu'on s'intéresse à l'identité fonctionnelle, plutôt qu'à leur diversité, les différences semblent plus nettes. En effet, des changements des valeurs moyennes des traits morphologiques importants ont été trouvés entre habitats (Article 3), ainsi que des modifications dans l'utilisation de ressources alimentaires, et même dans leurs stratégies de fourragement (Article 2).

Cependant, les traits morphologiques pour lesquels nous avons trouvé les plus grands changements, déviaient des hypothèses principales émises pour expliquer le filtrage environnemental chez les fourmis entre habitats du type forêts et habitats simplifiés/agricoles. En effet, bien que les traits les plus souvent mentionnés comme importants dans le processus de filtrage environnemental entre ces habitats soient la taille et la longueur des pattes (i.e. « *size grain hypothesis* », Kaspari & Weiser 1999; Farji-Brener *et al.* 2004), dans notre étude c'était plutôt des traits tels que la taille relative des mandibules ou des dents qui étaient les plus variables, ainsi que des traits plus « sensoriels » comme les antennes. Ces résultats semblent cohérents avec les différences observés dans l'utilisation de ressources alimentaires entre habitats. En effet, les traits mandibulaires sont en général associés à des régimes alimentaires particuliers (Weiser and Kaspari 2006, Silva and Brandão 2010, Gibb et al. 2015b). mais remarquons que d'autres études ont également trouvé une différence dans l'utilisation de ressources entre habitats (Bihn et al. 2008, Peters et al. 2014). A la vue de ces résultats, on peut suggérer, qu'un filtrage d'espèces par les ressources alimentaires disponibles est possible. Cette question, peu étudiée jusqu'à présent, mérite donc plus d'intérêt dans des études futures (Kaspari et al. 2012).

ARTICLE 1. DIETARY AND TEMPORAL NICHE DIFFERENTIATION IN TROPICAL ANTS - CAN THEY EXPLAIN LOCAL ANT COEXISTENCE?

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ABSTRACT

How species with similar ecological requirements avoid competitive exclusion remains contentious, especially in the species-rich tropics. Niche differentiation has been proposed as a major mechanism for species coexistence. However, different niche dimensions must be studied simultaneously to assess their combined effects on diversity and composition of a community. In most terrestrial ecosystems, ants are among the most abundant and ubiquitous animals. Since they display direct, aggressive competition and often competitively displace subordinate species from resources, niche differentiation may be especially relevant among ants. In a forest fragment in French Guiana, we studied temporal and trophic niche differentiation in a ground ant community. Various baits were presented during day and night to assess the temporal and dietary niches of the local species. They represented natural food resources such as sugars, carrion, excrements, seeds, and live prey. In addition, pitfalls provided a background measure of ant diversity and abundance. The communities attracted to the different baits significantly differed from each other, and even less attractive baits yielded additional species. We detected species specialised on living grasshoppers, sucrose, seeds or dead insects. Community differences between day and night were even larger than those between baits, and many species were temporally specialised. However, others did not show temporal and/or dietary specialisation. In contrast to commonness, foraging efficiency of species was correlated to food specialisation. We conclude that many ant species occupy different temporal or dietary niches. However, for many generalised species, the dietary and temporal niche differentiation brought forward through our sampling effort, cannot alone explain their coexistence.

Keywords: Functional traits; baiting; dietary specialisation; niche breadth; partitioning; temporal distribution; ants

INTRODUCTION

Even though challenged by the neutral theory of biodiversity (Hubbell 2001), which claims that much of the diversity we observe can be explained without invoking species' differences, niche differentiation is still broadly seen as the central mechanism explaining species coexistence and diversity (Chase and Leibold 2003). Indeed, the principle of limiting similarity states that competitive exclusion should prevent the stable coexistence of species with identical niches (Gause 1934b, Morrison 1996, Sanders and Gordon 2003). As a consequence, local species richness may be limited when there is little niche diversification and specialisation (Stephens and Wiens 2003). Nevertheless, in the tropics where species richness is among the highest, it is essential to understand, "how identical is 'identical'?" (May and MacArthur 1972). As Agrawal and Ackerly state, community ecology should move from mere lists of community-structuring factors (such as species-specific niche traits) to a predictive framework for where, when, and how multiple factors may work, both individually and in combination, to structure communities (Agrawal and Ackerly 2007).

Competition and exclusion have been considered a 'hallmark in ant ecology' (Parr and Gibb 2010, Cerdá et al. 2013). Many ant species effectively displace others from high-quality resources through direct interference, and some species can even displace others from their territories (Hölldobler 1983). Because ants are among the most abundant animals in tropical rainforests (Hölldobler and Wilson 1990), we should expect strong competition among ant species. Thus, the high local ant diversity in the tropics awaits explanation.

Several mechanisms have been shown to enhance ant species coexistence. Firstly, stochastic factors such as nest proximity to a resource, or the distance to nests of competing species greatly affect the chances of an ant colony to discover and/or monopolise a resource. A high variation in the success rate of colony establishment can result in a patchy distribution of dominant ant colonies with multiple gaps between their territories (Andersen 2008, Andersen et al. 2013). Secondly, trade-offs should prevent dominant species from monopolising all resources. Trade-offs, i.e. negative correlations, have been reported between behavioural dominance and resource discovery (Fellers 1987), dominance and thermal vulnerability (Cerdá et al. 1998; Bestelmeyer 2000) or dominance and parasite vulnerability (Lebrun and Feener 2007).

A third mechanism is niche differentiation in one or more dimensions (Hutchinson 1959). It can be temporal (seasons: Albrecht & Gotelli 2001; time of day: Fellers 1989; Santini et al.

2007; Segev and Ziv 2012), spatial (vertical, ecologically different strata: Tanaka et al. 2010), and/or linked to diet. Ants forage on a large range of food resources (Feldhaar et al. 2010). They are important arthropod predators (Floren et al. 2002; Philpott and Armbrecht 2006), but also utilize plant saps (Davidson et al. 2003; Hunt 2003) and seeds (Carroll and Janzen 1973). Nitrogen, which is often limited in rainforests, is usually obtained from live or dead animals, but also from faeces (Menzel et al. 2012). Besides, ants engage in mutualisms with plants and plant-sucking insects (Ness et al. 2010). Certain ants occupy highly specialised food niches, such as collembola, or even fungi (Weber 1966, Carroll and Janzen 1973, Johnson et al. 2001, Santamaria et al. 2009). Thus, dietary niche differentiation is a potentially important mechanism for local species coexistence. However, apart from studies on specific species, the relative contribution of different food types to most ant diets is unknown (Bihn et al. 2010). Moreover, the question remains how niche differentiation in the trophic, temporal or other dimensions interact. To answer this, it is crucial to simultaneously consider multiple niche aspects and measure their relative importance for species coexistence.

The high species diversity in tropical forests, concomitant with a relative rarity of most species, makes it hardly possible to study every species' niche in detail. Rather, it requires a community approach where species-specific niches are assessed simultaneously. Because of the principle of limiting similarity, dietary composition and temporal specialisation are essential functional traits in defining a species’ niche. In the present study, we analysed food and temporal niches of a tropical ant community, and additionally assessed spatial commonness of the participating species. We hypothesized that temporal and trophic niche breadth and optima should vary between different species, especially among locally co-occurring species. Moreover, we predicted that common species should have a broader food niche. In turn, specialised species that have a narrower food niche may compensate this by a broader temporal niche, and/or should be proportionally more efficient in finding their preferred resources than generalised species.

MATERIALS AND METHODS

Study site

The study was conducted on the Campus Agronomique in Kourou, French Guiana (5°09′35″N 52°39′01″W - 5.1597°N 52.6503°W). The climate is equatorial, has a mean precipitation of 3000 mm and mean humidity of 80%-90%. The study area is a continuous 16 ha forest fragment, bordered by urban grass and surrounded by residential areas. The forest type belongs to the facies *Cesalpinaceae*, *Chrysobalanaceae*, *Lecythidaceae*, of the Coastal part of French Guiana. These types of forests are characterized by high plant diversity. All sampling took place from February to March 2012 and was performed only in absence of rain, and in dry soil to avoid any bias linked to field conditions.

Choice of baits

We aimed for a complementary range of baits which reflected natural resources available to ants in a rainforest, and used the following set of baits: sucrose (20 vol.%; 3ml; the most common disaccharide in extrafloral nectar), melezitose (20 vol.%, 3ml; a trisaccharide commonly produced by trophobionts), crushed mealworms and grasshoppers (2-3g), chicken excrement (2-3g), a seed mixture (2-3g composed of ground corn and sunflower, millet, lin, soya, barley, dari, phalaris and grass seed), oleic acid (3ml; common in both dead insects and elaiosomes), living termites and living grasshoppers. Live baits have been rarely used up to now (Santamaria et al. 2009), but they may represent an important part of an ant community's diet. We selected *Anoplotermes* termites, which do not have a soldier caste and represent a small prey without chemical or morphological defences. As a second prey type, we selected grasshoppers (Caelifera: Acrididae) representing a prey which was larger (1.5-2.5 cm), more mobile and had a harder integument than termites. Overall in terms of bait attractiveness, sucrose and crushed insects are considered most attractive as they present easy foraging and highly nutrient resources (Blüthgen and Fiedler 2004a), followed by melecitoze, termites and grasshoppers, still very nutrient but harder to assimilate. Finally seeds, oleic acid and chicken excrement were assumed to be the least attractive because of low nutrient content.

Sampling design

We established four plots of 4 x 4 grid points each (16 points per square plot), i.e. a total number of 64 grid points. The grid points in the plots were separated by 10 m each all plots were less than 100 m from one another. At each grid point, we presented in total eight different baits, both during day and at night, and placed pitfalls during day and at night. However, to avoid interference between multiple baits, only one bait or one pitfall was presented at each grid point at a given time. We took care that, during each sampling session, all eight baits were presented evenly (at different grid points), in order to avoid any bias due to fluctuating weather conditions. Pitfalls were only placed when no baiting was performed on the same plot.

All ants collected were preserved in 75% ethanol. They were counted and sorted to morphospecies by Mickal Houadria and Alex Salas-Lopez, based on Bolton (1997). Voucher specimens of all species are deposited at the Institute of Zoology, University of Mainz.

Pitfalls

The pitfall traps (Ø 4cm, depth 6cm) were buried in level with the surrounding soil surface and replaced after each sampling session (into the same hole) to reduce the digging-in effect (Greenslade 1973). They were opened for 10 hours between 20h30 to 6h30 for the nocturnal traps and between 7h00 to 17h00 for the diurnal ones. For each grid point, we obtained three 10-hour replicates day and night, yielding a total of 60 sampling hours. To kill and preserve the ants, the traps were filled ca. 1.5 cm high with a 50% propylene glycol solution. This preservative is non-toxic to vertebrates at these quantities and neither attracts nor repels ants (Boonzaaier et al. 2007).

Displaying the bait

Many studies use some sort of card to expose baits (Pearce-Duvet et al. 2011, Gibb and Parr 2013). This has little effect on the ants' foraging behaviour (Fellers 1989), but makes it difficult to retrieve them. Narrow access to baits, in contrast, facilitates ant sampling, but hinders recruitment and possibly promotes bait monopolisation of one ant species against others. Therefore, we presented baits in circular plastic boxes with lids. Access to the bait was maintained as wide as possible to hamper bait monopolisation. The boxes were placed 1 cm deep in the ground and had, 6 mm above the bottom, two slit-like openings (1 cm wide and 8 cm long), level with the ground. They could be quickly retrieved by encasing into a similar box without side openings. As plastic is potentially avoided by some ants, the base of the box were covered with paper towel. A hole in the lid allowed squirting the killing solution (propylene glycol solution 70%) right after retrieval.

The liquid solutions were pipetted directly onto the paper towel in the baiting device while the solid baits were put into the centre of the devices. Live baits were harder to display. Approximately ten termites were maintained free on the paper towel and usually stayed at a small piece of termite mound which was added. To avoid that all termites would be captured before the end of the sampling approximately five further individuals were glued live on a 2 cm stick with odourless rat glue (Greenleaf Ltd., Beijing, China). For grasshoppers, in order to partly maintain their ability to jump but restrain it to the baiting device, we tethered it to a fine, 3 cm long string which was pinned to the base of the boxes.

The baits were presented for 90min during the day (between 10h00 and 15h00) and at night (between 20h00 and 23h00). Preliminary tests had shown that this time was sufficient to allow at least partial recruitment on all baits, but was not long enough to have dominant ants saturating the majority of the most attractive baits.

Data analysis

In our analyses, we used frequency and incidence data. 'Frequency' is defined here as the number of occurrences, i.e. the number of times an ant species occurred at baits (regardless of the actual number of individuals). 'Incidence', in contrast, denotes the spatial commonness, i.e. the number of grid points (out of 64) where a species was captured at all. For example, a species caught at two different baits at the same grid point will have a frequency of two, but an incidence of one.

COMPARISON OF SAMPLING METHODS AND BAITING EFFICIENCY

Exhaustiveness of the different sampling methods (eight bait types, total baits, and pitfalls) was estimated by calculating Cole's rarefaction curves. Furthermore, we estimated the expected species richness with the Chao2 species richness estimator, using EstimateS 8.20 (Colwell 2013). The respective data were pooled according to the 64 grid points. For the eight bait types, each data point (grid point) thus represents two baits (day and night, 2x90min); for total baits, it is 16 baits of 90 min each, and for the pitfall samples each data point represents six nocturnal and diurnal pitfall replicates (6 x 10 hours). Comparison between the ant communities sampled with baits and pitfalls was calculated using Bray-Curtis method where the relative abundances of the species on each sampling technique was standardised.

The ant communities at different baits and times of day (based on presence absence) were analysed using PERMANOVA (Clarke and Gorley 2006), with 'bait type' and 'time of day' as fixed factors and 'grid point' as random factor; furthermore, we tested for day/night differences for each bait type separately using PERMANOVA. Similar analyses were conducted to test for temporal differences on ant communities sampled with pitfall traps. Further analysis was conducted with PERMANOVA for grid-point-wise presence/absence data to compare pitfall and bait data, with 'time of day' and 'capturing method' as fixed and 'grid point' as random factors.

FOOD SPECIALISATION

Food specialisation was assessed based on Simpson's diversity index. Incidence was chosen over frequency to be sure that all the food choices were not from only one or two grid points, which could limit the species capacity in foraging several times the preferred resource. We chose 10 as a cut-off value for there to be a clear possibility for the species to have gone to the other seven resources. For each species n (with a frequency $\geq$ 10), we calculated its total frequency on each bait, and calculated its food specialisation as $fs_n = \sum p_i{}^2$, where p_i is the frequency of ant n on bait i divided by its total frequency.. A common species, however, is more likely to encounter different baits just by chance. Therefore, we calculated fs_n for each species 1000 times, each time based on a total frequency of species n rarefied to 10 occurrences.

FOOD PREFERENCES AND FORAGING RATIO

As used here, 'food specialisation' looks at the relative exclusiveness of a species for any resource (i.e. a measure between 0 and 1), whereas 'food preferences' provide information if, and which, resources are significantly preferred. A species specialised in one resource will prefer it, but a species with one or several preferences may or may not be highly specialised overall. For each species, we conducted 1000 permutations per species to assess on which bait the incidence was higher than expected from random (preferred bait). This was done by randomly assigning the summed incidences per bait to the five different baits; we then calculated the quantile of the real value against these null distributions, and deemed them significant if they fell outside the 95% confidence interval.

The foraging ratio (*fr*) of a species was calculated as the ratio of a species' frequency on its most preferred bait (highest frequency) divided by its overall frequency in pitfalls. A high foraging ratio implies that few scout ants (as measured by pitfall frequency) suffice to efficiently find baits, i.e. they suffice for a relatively high frequency on their favoured bait.

TEMPORAL NICHE AND SPECIALISATION

For each species n with a frequency $\geq$ 10, we calculated its temporal niche tn_n by comparing its total frequency during day and at night. tn_n was calculated as

$$tn_n = 2 \cdot \frac{fr_{day_n}}{fr_{day_n} + fr_{night_n}} - 1$$

Where tn_n is the temporal niche position, $fr_\mathrm{day,n}$ and $fr_\mathrm{night,n}$ are the total number of occurrences during day and night, respectively tn ranges from -1 (purely nocturnal) to +1 (purely diurnal).

This metric was calculated twice for each species, once based on pitfall frequencies and once based on bait frequencies. We interpret the pitfall-based *tn* as a measure of the ant's foraging activity (when the ants is actively scouting for food resources). In contrast, the bait-based *tn* measures when the ant actually succeeds in foraging and recruiting. Significance of a species' temporal specialisation was assessed with a paired Wilcoxon test for grid point-wise frequency at night and during day. Temporal specialisation was calculated as $ts = |tn|$, and ranges from 0 (no specialisation) to 1 (purely nocturnal or purely diurnal). Wilcoxon signed-ranks test was used for evaluating if a species temporal distribution significantly diverged from no specialisation, i.e if it was significantly more present at day or night. Correlations between different functional traits (*tn, fs, fr*) were done using Spearman rank correlations.

NICHE DIFFERENTIATION AND CO-OCCURRENCE

Finally, we assessed the impact of temporal and trophic niche differentiation on co-occurrence. For each pair of species, we calculated the 'absolute co-occurrence' as the number of grid points where both species had been found. We constrained this analysis to the 13 most common species, such that we included all species that co-occurred at least 10 times, since rarely co-occurring species would not require niche differentiation. 'Relative co-occurrence' was calculated by absolute co-occurrence divided by the average incidence of both species. Temporal niche differentiation was obtained as the difference between *tn* values; and dietary niche differences was calculated as the Bray-Curtis distance between the incidences of the two species on each of the eight baits. If niche differentiation explained co-occurrence, then locally co-occurring species should have higher niche differences than species that did not co-occur. We used a partial Mantel test (command *mantel.partial*) to analyse the correlation of absolute or relative co-occurrence with temporal and trophic niche distance. All analyses (if not mentioned otherwise) were conducted using R version 2.15.2 (R Development Core Team 2015).

RESULTS

Ant communities in baits and pitfalls

A total of 34 species were captured on baits and 47 in pitfalls. This yielded a total of 52 species (including 10 singletons), with 29 species captured both with baits and pitfalls. Species richness at the site was estimated as 38 species (mean Chao2 estimate; range: 35-56) captured with all baits, while 52 species could have been sampled with pitfalls (range: 48-67) (Table 1, Fig. 1). Thus, mean species estimates were close to the actual numbers we captured with all baits pooled and with pitfalls. Ant communities on baits and pitfalls were significantly different (PERMANOVA with presence/absence data: pseudo-F = 18.9, df = 1, p = 0.001), both overall and when analysed separately for day and night data (each $p \leq 0.001$). Bray Curtis distance of ant assemblages between pooled baits and pitfalls was 0.717 (standardised abundance).

Table 1: Total abundances, occurrences, and total species richness at each bait, and totals for diurnal and nocturnal baits. Estimated species richness is given as the mean of Chao2 estimator values. *For baits with high variation in abundance, the uncorrected Chao1 estimator was higher than Chao2, and therefore used as recommended by Anne Chao.

bait type	Abundance	occurrences	total species richness	estimated richness
Sucrose	6403	218	23	25.95
Melezitose	4365	188	23	32*
Crushed insects	2382	162	25	38.78
Grasshoppers	1900	97	19	19.49
Oleic acid	1371	90	16	32*
Seeds	651	95	22	47*
Termites	321	92	19	21.95
Chicken faeces	170	60	18	21*
Day	9635	517	32	-
Night	7906	485	25	-

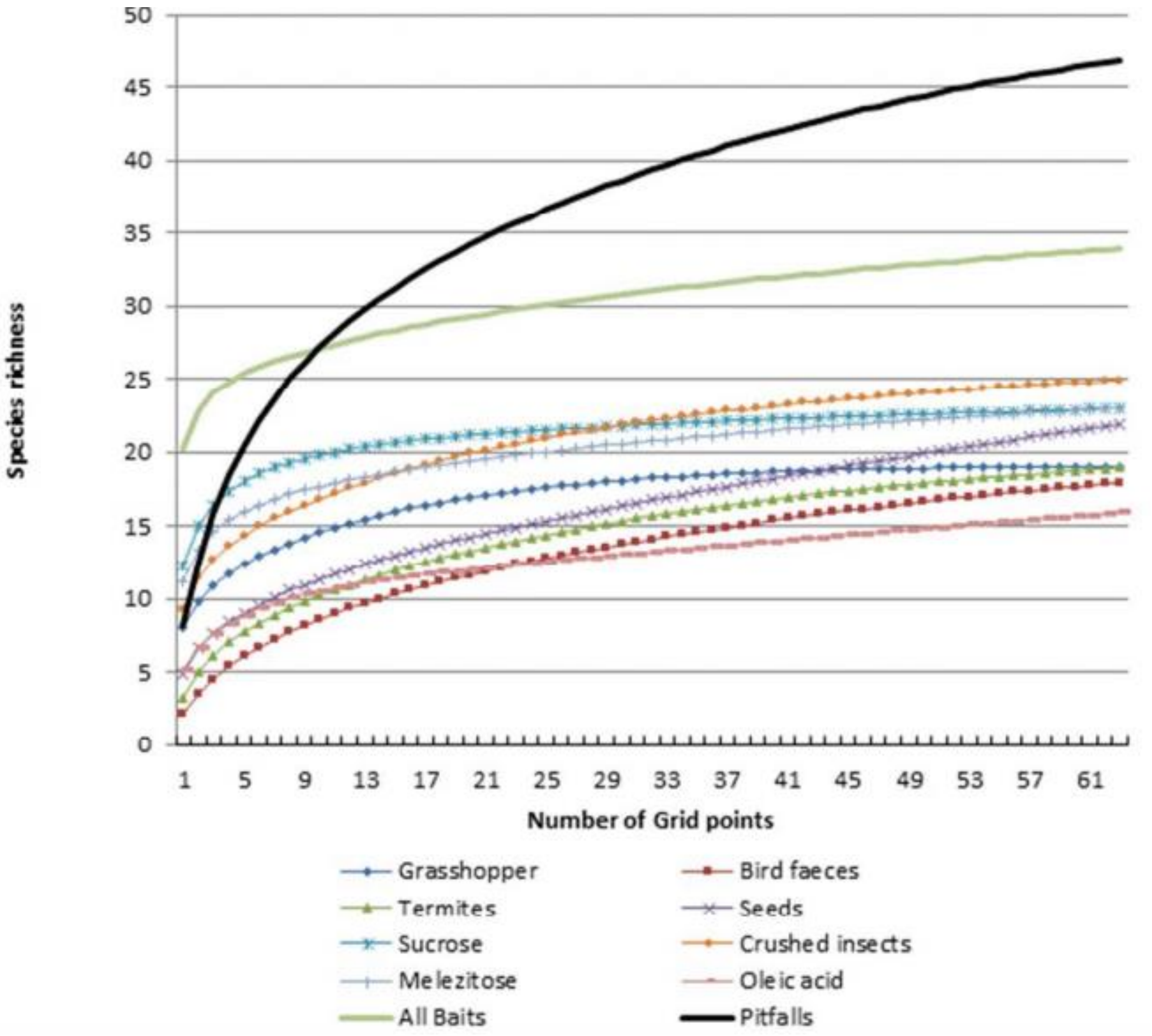

Figure 1 Rarefaction curves for the eight bait types, for pitfalls and all baits pooled. In each case, samples were pooled according to grid point, such that each rarefaction curve is based on 64 samples.

In total, 21 species were caught on at least 10 grid points using baits or pitfalls (Table 2). Ten of these were much more often caught at baits. Their incidences at baits were more than twice the incidences on pitfalls, while the opposite was only true for two species (Fig. 2). After correction for the total incidences on baits and in pitfalls, three species were caught significantly more often on baits (*Camponotus* sp. 2, *Crematogaster limata*, *Pheidole zeteki*), and three species in pitfalls (*Pachycondyla crassinoda*, *Sericomyrmex* sp. 1, *Trachymyrmex* sp. 1) (Chi² tests: all $\text{Chi}^2 > 5.6$; $p \leq 0.018$).

Table 2. The more common species (total incidence ≥ 4) with abundance, incidence, food and temporal specialisation.

Species	Abbreviation	total abundance at baits	incidence at all baits	incidence at pitfalls	**Food specialisation**		**Temporal specialisation**	
					fs	significantly preferred baits	temporal niche pitfall	temporal niche bait
Anochetus diegensis	*Ano1*	0	0	5	n/a	n/a	n/a	n/a
Atta Cephalotes	*Att1*	0	0	5	n/a	n/a	n/a	n/a
Camponotus sp.1	*Cam1*	75	11	2	0.58	Cru ***	n/a	Ns
Camponotus sp.2	*Cam2*	962	51	17	0.34	Suc ***	ns^{3}	night***^{3}
Camponotus sp.3	*Cam3*	93	12	4	0.44	Cru ***	ns^{1}	night***^{1}
Crematogaster limata	*Crem1*	702	14	2	0.42	Cru ***	n/a	Ns
Crematogaster levior complex	*Crem2*	556	10	11	0.28	ns	ns	day**
Cyphomyrmex minutus	*Cyp1*	1	1	4	n/a	n/a	n/a	n/a
Diplorhoptrum sp.1	*Dip1*	157	33	15	0.31	ns	day**^{1}	ns^{1}
Diplorhoptrum sp.2	*Dip2*	199	26	9	0.29	ns	ns	Ns
Labidus sp.1	*Lab1*	0	0	4	n/a	n/a	n/a	n/a
Nylanderia sp.1	*Nyl1*	474	23	8	0.58	Suc ***	ns	Ns
Odontomachus haematodus	*Odo1*	33	19	17	0.34	Gra **	ns	Ns
Pachycondyla crassinoda	*Pac1*	6	3	29	n/a	n/a	ns	n/a
Paratrechina sp.1	*Par1*	150	6	1	n/a	ns	n/a	Ns
Pheidole sp.1	*Phe1*	758	16	10	0.31	ns	day**	day*
Pheidole zeteki	*Phe10*	199	25	6	0.42	Suc **	ns	day***
Pheidole pugnax	*Phe11*	3294	40	33	0.33	Suc **	ns	day*
Pheidole sp.12	*Phe12*	73	15	7	n/a	ns	ns	Ns
Pheidole cf. *texticeps*	*Phe16*	235	15	12	0.41	ns	day**	Ns
Pheidole sp.17	*Phe17*	61	3	4	n/a	ns	n/a	n/a
Pheidole sp.18	*Phe18*	24	5	2	n/a	n/a	n/a	n/a
Pheidole sp.21	*Phe21*	60	10	7	0.32	ns	ns	day*
Pheidole subarmata	*Phe3*	5234	45	38	0.27	Suc *	ns	Ns
Pheidole aripoensis	*Phe5*	249	14	14	0.32	ns	day**^{2}	ns^{2}
Sericomyrmex sp.1	*Ser1*	83	5	24	n/a	ns	ns	Ns
Solenopsis sp.1	*Sol1*	3354	18	13	0.27	ns	ns	Ns
Trachymyrmex sp.1	*Tra1*	22	10	19	0.53	See ***	ns	night*

fs: food specialisation based on unrarefied frequency data. Significant food preferences were determined with randomization tests; the temporal niche was tested against an equal day-night distribution using chi^2 tests. 'Gra': live grasshoppers; 'Cru': crushed insects; 'See': seeds; 'Suc': sucrose. 'n/a': Frequencies too low (<10) for analysis. 'ns': not significant. Significant food preference, and significant temporal niches (i.e. different from an equal day-night distribution) are denoted with asterisks (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Significant differences between temporal niche from pitfalls and from baits (according to chi^2 test) are denoted with superscripts. $^{1}p < 0.05$; $^{2}p < 0.01$; $^{3}p < 0.001$. 'ns': not significant; 'n/a': too few data for estimation.

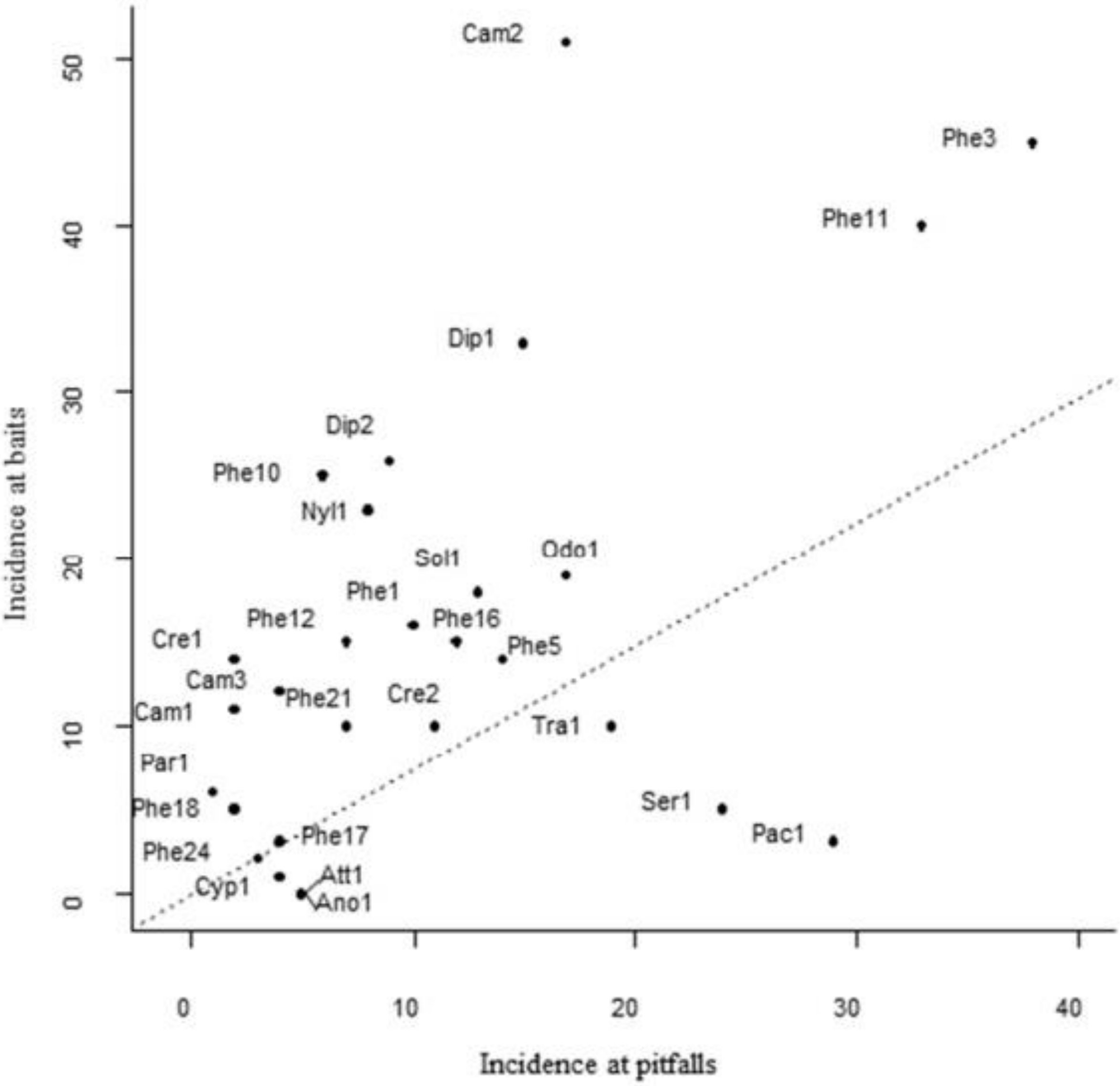

Figure 2 Incidence at baits and in pitfalls. The slope of the dotted line equals the ratio of the summed incidences at baits and in pitfalls, to correct for different capture rate of baits and pitfalls. Species abbreviations are given in Table 2.

Ant communities at different baits

The baits varied strongly in the number of individuals and occurrences but less so in total number of species attracted. The most attractive bait in terms of individuals (sucrose) attracted 37.7 times more individuals than the least attractive one (chicken faeces). However, the total number of attracted species on sucrose and chicken faeces was 23 vs. 18, respectively (Table 1). The highest number of species (25) was found on crushed insects (Table 1). Although oleic acid, chicken faeces and seeds were less attractive (as measured in number of occurrences), they attracted additional species not present at other baits. Chao's species estimations and rarefaction suggested that baiting was rather exhaustive for sucrose, grasshoppers, termites, and chicken faeces, whereas more species could have been captured with further baiting of melezitose, crushed insects, seeds, and oleic acid (Table 1, Fig. 1).

Species composition on the different baits differed greatly (PERMANOVA on presence/absence data: pseudo-F = 9.5; df = 7; p = 0.001); but the differentiation between day and night was even higher (pseudo-F = 25.8; df = 1; p = 0.001) (Fig. 3). The interaction between bait type and time of day was significant (pseudo-F = 2.9; df = 7; p = 0.001). When ant assemblages were analysed for each bait type separately, we found significant temporal differentiation for seven bait types (each $p \leq XX$) but not for oleic acid (p = 0.062). Ant assemblages in pitfalls were also significantly different between day and night (pseudo-F = 5.9; df = 1; p = 0.001). Ant assemblages on melezitose and sucrose (PERMANOVA: p = 0.061) did not differ significantly in pair-wise presence/absence comparisons, nor did those recorded on termites and grasshoppers (PERMANOVA: p = 0.625) or those between oleic acid and seeds (PERMANOVA: p = 0.085). Consequently, melezitose, termites and oleic acid were omitted from the analysis of food specialisation, and only sucrose, grasshoppers, and seeds were retained, for yielding more occurrences (Table 1). Pooling similar baits would have resulted in unequal sample numbers and thus biased further analysis. All other baits significantly differed from one another in the ant communities they attracted, even after correction for false discovery rate (Benjamini and Hochberg 1995) (all $p < 0.05$).

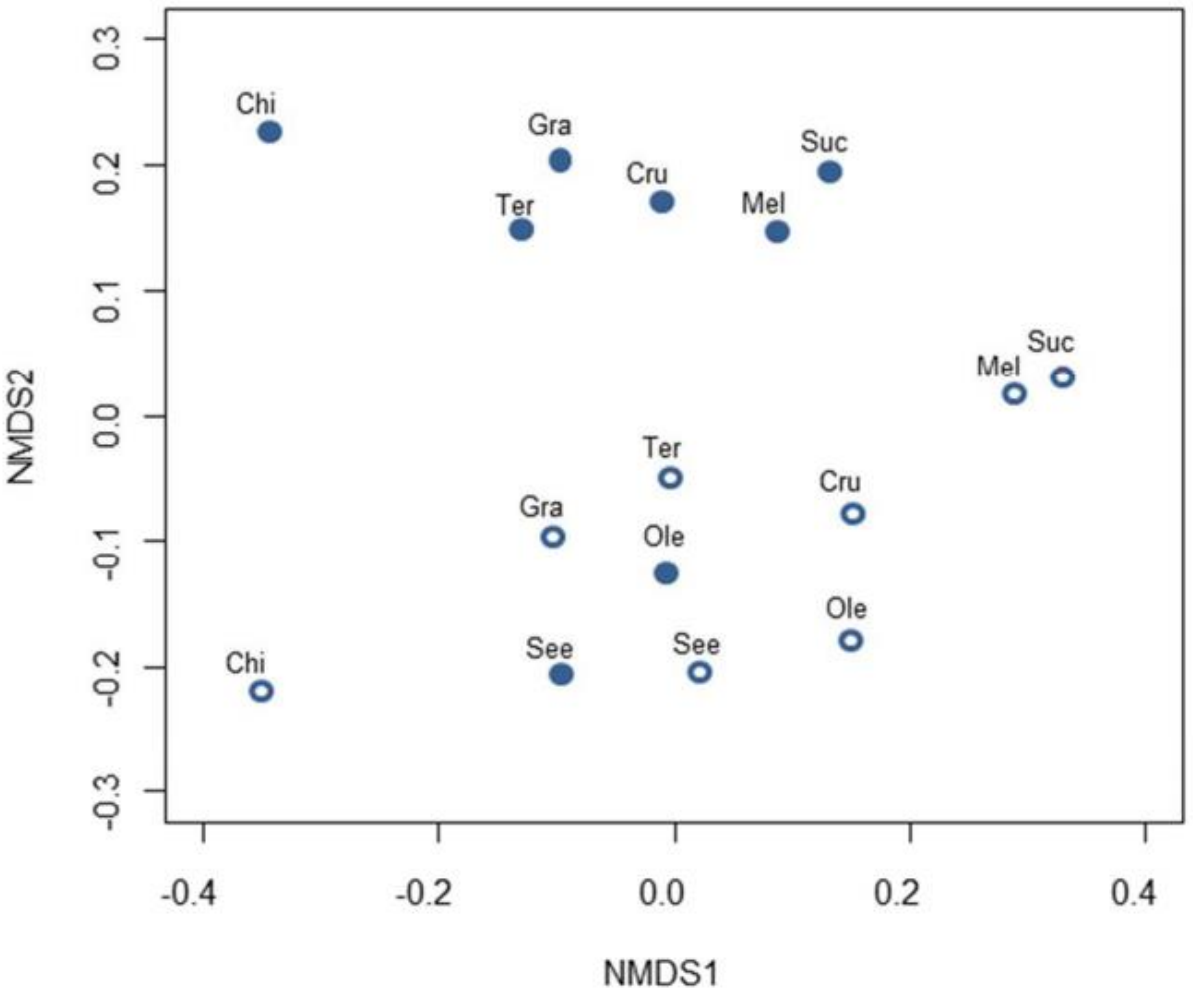

Figure 3 NMDS ordination, based on presence/absence data, for the ant assemblages attracted to the eight food baits and the two time periods. *Cru*: crushed insects; *See*: seeds; *Suc*: sucrose; *Mel*: melezitose; *Gra*: live grasshoppers; *Ter*: live termites; *Chi*: chicken faeces; *Ole*: oleic acid. Full circles represent nocturnal and empty circles diurnal baits.

Food specialisation and preferences

We calculated *fs* for 18 species with an incidence ≥ 10 at the five baits (omitting the baits melezitose, termites and oleic acid). Our results showed that no species were fully specialised or absolute omnivores, instead, that a full gradient of species with varying dietary habits existed.

Among the 18 species we analysed, only ten showed significant food preferences (Fig. 4, Table 2). Five species, including the three most abundant ones, significantly preferred sucrose over the other baits. *Camponotus* sp.1 and 3, and *Crematogaster limata* preferred crushed insects. In contrast, among the eight *Pheidole* species, none preferred crushed insects, but three of them (*Pheidole subarmata, Ph. zeteki* and *Ph. pugnax*) had a preference for sucrose. *Odontomachus haematodus* was found to prefer grass hoppers than other resources, and *Trachymyrmex* sp.1 preferred seeds.

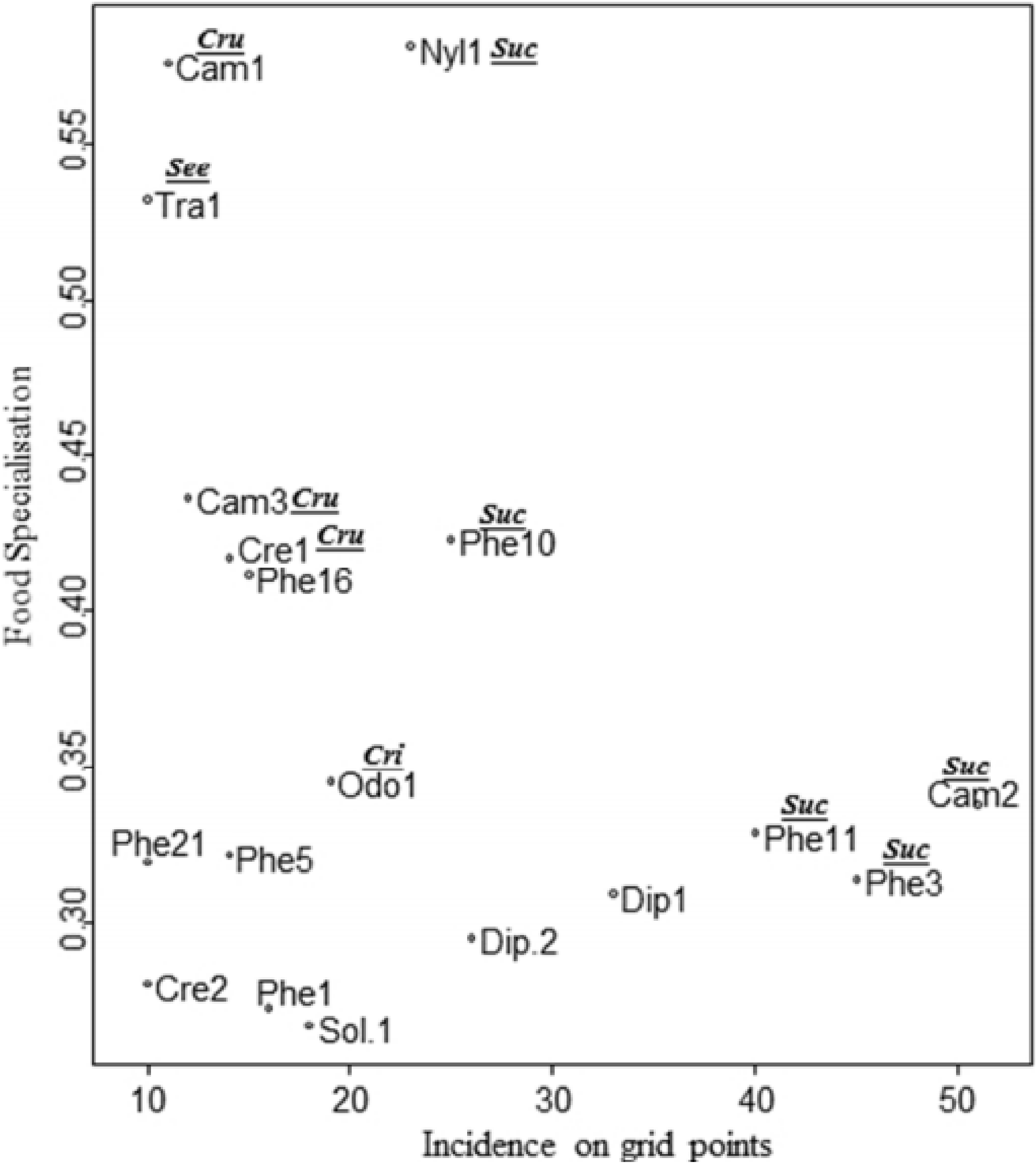

Figure 4 Rarefied food specialisation *fs* plotted against incidence at baits. This index can range from $fs_n = 5*(1/5)^2 = 0.2$ if all five bait types are used equally (with each $p_i = 1/5$), to $fs_n = 1.0$ in the case that only a single bait type is used. For species with significant food preferences, the preferred baits are given: *Cru* (crushed insects), *Gra* (grasshopper), *Suc* (sucrose), *See* (seeds). Species abbreviations are given in Table 2.

Temporal specialisation

Overall, nocturnal and diurnal ant communities differed markedly (Fig. 3), and this effect was consistent for pitfalls and baits. Total species richness at night was slightly lower (Table 1). At baits, 32 species were captured during the day and 25 at night (total species number: 34). In the pitfalls, we obtained 43 species during the day and 31 at night (total species number: 47). The species only captured at night were two *Pachycondyla* and two *Camponotus* species, and several singletons. All other species were found both at day and night although not always evenly.

One-fourth to one-third of the species showed significant temporal specialisation (4 out of 19 in pitfalls; 8 out of 21 at baits) (Fig. 5). In the pitfalls, four species were frequently more sampled during the day, but no species were primarily nocturnal. At baits, we found three significantly nocturnal and five diurnal species. Interestingly, four species showed a significant difference in their day/night distribution between pitfalls and baits (Fig. 5; Table 2): from pitfalls to baits, two shifted from no specialisation to night (*Camponotus* sp. 1 and 2), and two shifted from day specialisation to no specialisation (*Diplorhoptrum* sp. 1; *Pheidole* sp. 5). Only one species (*Pheidole* sp.1) was significantly more abundant during the day in both baits and pitfalls.

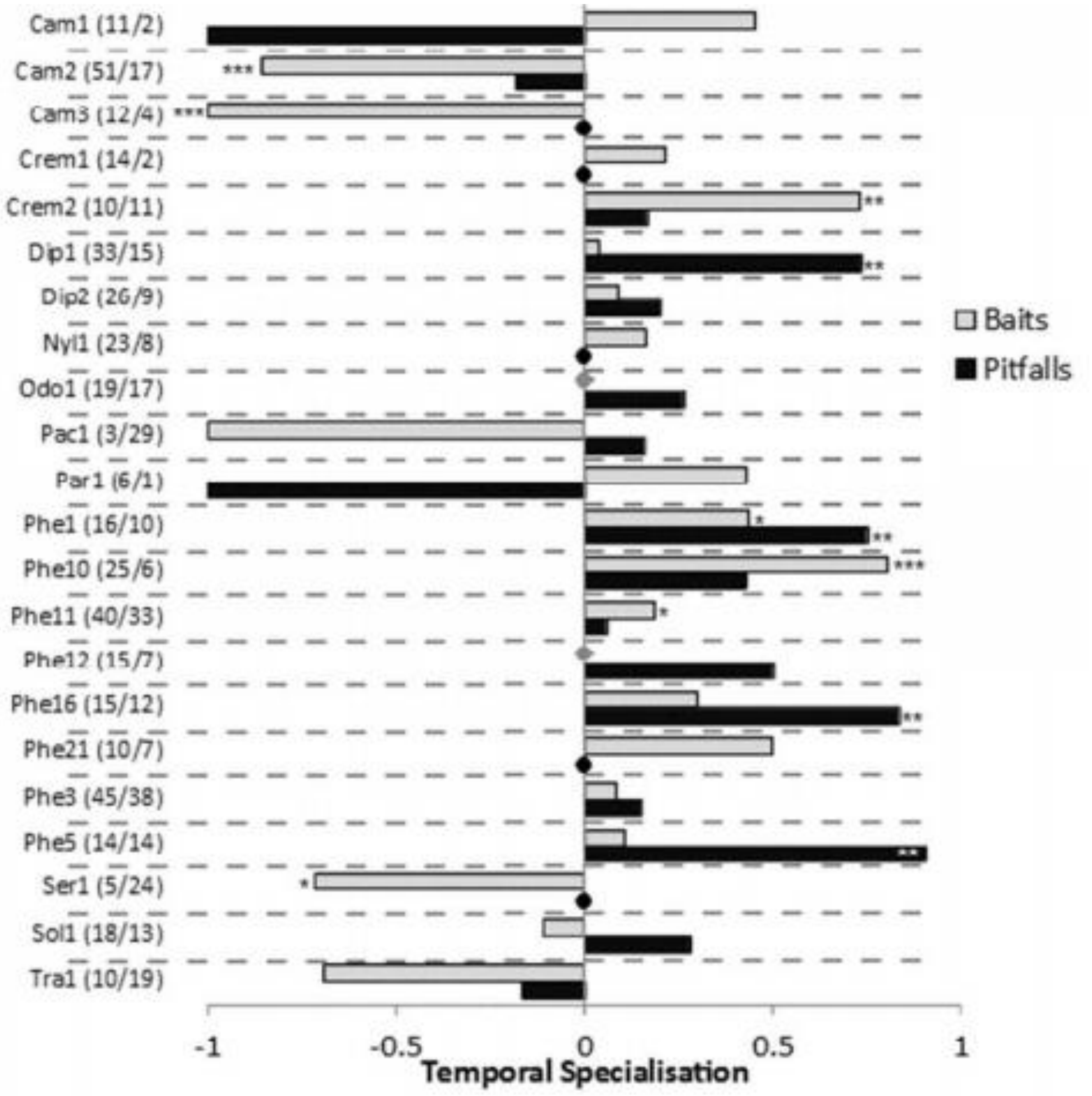

Figure 5 Temporal specialization at baits and in pitfalls, based on species frequencies. Significant temporal specialization (according to □² test) is indicated with asterisks: *p < 0.05; **p < 0.01; ***p < 0.001. Full circles indicate a temporal niche of zero. The numbers in brackets give the incidences at baits and in pitfalls, respectively.

Combining functional traits and commonness

Overall, the degree of food specialisation was not related to commonness. The food specialisation index was not correlated to incidence at baits (Spearman’s rho = -0.28, p = 0.26; Fig. 4). However, although three common species significantly preferred baits, there were no species with an *fs* value > 0.35 *and* an incidence above 25. Note that two species common in pitfalls (*Pachycondyla* sp. 1 and *Sericomyrmex* sp. 1) were too rare on baits to adequately estimate their food niche. Similarly, the degree of temporal specialisation did not correlate to incidence (for baits: Spearman’s rho = -0.32, p = 0.19; pitfalls: rho = -0.07, p = 0.78). Temporal and food specialisation were not correlated (Spearman rank correlation; temporal specialisation at baits vs. *fs*: rho = 0.021, p = 0.93; temporal specialisation at pitfalls vs. *fs*: rho = -0.46; p = 0.052). The two species with highest *fs* (Fig. 4) showed no temporal preferences for baits or for pitfalls. Finally, *fs* was positively correlated to the foraging ratio *fr* (Spearman’s rho = 0.65, p = 0.0037), implying that specialised species had a lower incidence in pitfalls compared to their incidence at baits than generalised species.

Local co-occurrence could not be explained by niche differences. For co-occurring pairs of species, the absolute or relative number of grid point-wise co-occurrences was not correlated to the temporal or trophic niche differences (absolute co-occurrences: partial Mantel test: r = -0.089; p = 0.69; relative co-occurrences: r = -0.043; p = 0.62).

DISCUSSION

Temporal and trophic niche differentiation in ant communities

The aim of this study was to simultaneously assess trophic and temporal niches of an ant community and investigate whether these functional traits explain ant coexistence. Both niche dimensions were found to influence community composition. Species assemblages of nocturnal and diurnal ant communities differed strongly. Moreover, ant communities differed between bait types for five of our eight baits (sucrose, living grasshoppers, chicken faeces, seeds, and dead insects), the ant communities varied significantly for each pair-wise comparison. However, the difference between diurnal and nocturnal communities was greater than that between communities at different bait types (Fig. 3). Temporal segregation hence seems to facilitate species coexistence more than the range of food resources our baits represented. The significant interaction between time and food type was probably related to oleic acid, which was the only resource to not differ between diurnal and nocturnal ant communities. This may be due to *Camponotus* sp. 2, which was frequent on most baits but never foraged on oleic acid. Being nocturnal and numerically dominant, this species therefore had consequences on the temporal segregation of this resource. This result matches a study on temperate ant communities, where day/night segregation among species was high and represented an important coexistence mechanism (Stuble et al. 2011, 2013). Temporal niche partitioning of dominant and subordinate ants has also been shown in Mediterranean ant communities (Santini et al. 2007, Segev and Ziv 2012) but in most cases it is difficult to show that this is an effect of competition (Andersen 1992).

The high temporal differentiation found on community level was also detectable on species level. One-third of the ant species showed temporal specialisation in pitfalls or baits. Notably, temporal segregation was high between two of the three most common species, with *Camponotus* sp. 2 being nocturnal and *Pheidole pugnax* being diurnal. This concurs with previous findings on competition between dominant species which can regulate their distribution and temporal partitioning (Andersen and Patel 1994). Two results about species-level temporal niches were unexpected: Firstly, there were more exclusively diurnal than nocturnal species, both in the pitfall and the bait samples, although one could expect a similar number of nocturnal species which avoid diurnal competitors. The pattern coincides with a slightly higher overall abundance and frequency of ants during the day, but this cannot fully explain the rarity of nocturnal specialists. Secondly, temporal specialisation in pitfalls and baits often differed. Temporal specialisation that remained the same in both sampling methods was only found for one species (*Pheidole* sp. 1). One explanation may be that pitfalls mostly capture scouts, i.e. individuals that forage on their own. Since no food resources are involved, there should be little effects of interspecific competition on the temporal niche in pitfalls. In contrast, baits reflect the ability of species to recruit to a resource and potentially withstand competing species. We therefore tentatively interpret the temporal niche at pitfalls as unaffected by competition, whereas the temporal bait niche could be influenced by competitors. Notably, from pitfalls to baits, the temporal niche either shifted from 'diurnal' to 'unspecialised', or from 'unspecialised' to 'nocturnal', but not towards diurnal. Thus, it seems possible that some species manage to evade competitors by recruiting more heavily at night. In order to clarify these temporal shifts, in addition sampling should be performed at crepuscular times, where ant communities could differ from both day and night.

Beside temporal differentiation, communities differed between different food resources. Food resources varied greatly in their attractiveness, but even less attractive items yielded additional species. Five of the eight baits attracted ant communities that differed significantly from one another. For example, living termites and grasshoppers were much less attractive than insect carcasses, but attracted a significantly different community, including a species that significantly preferred live grasshoppers to dead insects (*O. haematodus*). This emphasizes the need to include live baits in further studies, especially since they have been scarcely used up to now (Santamaria et al. 2009), and the consumption of living or dead matter cannot be distinguished by studies based on stable isotopes. Such a differentiation, and the fact that all baits together attracted more species than any single bait type (Fig. 1), shows that there is trophic niche differentiation on community level. On species level, this was reflected in species that preferred certain food items to others. For four bait types (grasshoppers, crushed insects, sucrose, and seeds), species showed significant preferences. Remarkably, the three most numerically dominant species with highest frequency and incidence (Fig. 2 and 4), significantly preferred sucrose over crushed insects. This concords with the fact that carbohydrates and proteins meet different colony needs and that colonies spend more time foraging their limiting nutrient (Kay 2002) from which we can extrapolate that numerically dominant species may have a greater need for carbohydrates and may show 'high tempo foraging' (Davidson 1997).

Interestingly, ant communities at sucrose (a disaccharide) did not differ from those at melezitose, which is a trisaccharide common in honeydew (Völkl et al. 1999). This suggests that all species in our study that use sucrose are also able to digest melezitose. Hence, the regular consumption of melezitose-containing honeydew may not represent an option to evade competition by sucrose-foraging species. In other, mostly arboreal ant communities, however, several ant species avoid feeding on melezitose and are thus unable to effectively utilize some of the honeydew sources (Blüthgen and Fiedler 2004b). Furthermore, we had expected to find different predatory ant species at grasshoppers and termites. Apparently, the same ant species could overwhelm the two prey items regardless of their size.

None of the species preferred oleic acid, only omnivore species (mostly *Pheidole*) capable of consuming pure lipids were attracted. We had not expected this since elaiosomes are assumed to contain oleic acid as attractant (Boulay et al. 2005, Bronstein et al. 2006), but see (Reifenrath et al. 2012), and the presence of a chemical food cue alone often suffices to attract specialised species (Schmitt et al. 2004). However, no information could be obtained on the diversity of elaiosome-bearing plants at the site.

To assess food niche differentiation in ants, most studies to date applied one of the two approaches: multiple artificial baits (Le Breton et al. 2006, Cerdá et al. 2012, Arnan et al. 2012b) or stable isotope analyses (Bihn et al. 2010). Artificial, highly attractive baits such as tuna or honey have often been used as a rough guide to a species' preference between carbohydrates or proteins. Our data confirmed (Table 2) that several species preferred either carbohydrates or proteins (Cerdá et al. 1989), but in many species, the food specialisation was more gradual than a crude classification would suggest (Fig. 4). Stable isotopes are a useful tool to assess the trophic position of an ant and allow to gather data for whole ant communities (Blüthgen et al. 2003), but do not allow discrimination between dietary items of the same trophic level (that is, with a similar ^{15}N signature). Stable isotope studies therefore often classify species with intermediate signature or with high intraspecific variation as omnivorous (Pfeiffer et al. 2014) but it is hardly possible to further distinguish among such species.

Despite high differentiation on community level, and the detection of species that were trophically or temporally specialised, local ant co-occurrence could not be explained by niche differences alone (as shown by partial Mantel tests). Hence, it seems likely that a finer resolution is needed to determine the niches of species that occur at the same grid points. This may include specialisation on further food items, a finer temporal differentiation, or differing seasonal foraging peaks (Albrecht and Gotelli 2001). To our knowledge, little is known about ant seasonality in the tropics, but a recent study has found flooding during the wet season and high desiccation risk during the dry season as possibly responsible for reducing abundance in ants (Baccaro et al. 2012).

Ants attracted to baits *vs*. background diversity

Baits generally attract less species than other methods like pitfalls or winkler traps (Andersen 1991b, Groc et al. 2007, Tista and Fiedler 2010). However, they present the advantage of being the fastest way to capture ants, and they can be used to obtain ecological and behavioural data. Baits have been used to assess dominance hierarchies, temporal differences of ant activity between periods and seasons (Delsinne et al. 2007, Arnan et al. 2012b) and also trophic and microhabitat differences (Kaspari and Yanoviak 2000). In our study, the baits attracted 19 out of the 22 more common species with comparable or higher incidence (Bray-Curtis distance: 0.717), and 29 out of 47 species caught with pitfalls in total. For four of the eight baits, rarefaction and Chao species richness estimators suggested that additional species may still have been sampled (Table 1). Most of the species that were captured in pitfalls, but absent or rare at baits, were predators according to literature (genus *Pachycondyla* and *Anochetus*; Dejean et al. 1999) or fungus growers (*Atta*, *Cyphomyrmex*; Mikheyev et al. 2010), other species were with very few occurrences limiting their chances in occurring on the baits. We therefore suggest that their primary food sources were absent from the set of baits or inappropriately displayed. Many ant predators are solitary foragers, specialised on certain prey types, do not recruit, and immediately retrieve the whole food item to their nest instead of feeding directly at the spot (Dornhaus and Powell 2010). Thus, the chances of capturing such species without constant bait observation are smaller compared to species that recruit massively and do not retrieve large pieces of bait. *Pachycondyla crassinoda* for instance was only found twice on crickets and once on crushed insects but had a high pitfall incidence (Fig. 2). Therefore presenting suitable live prey species in an appropriate manner may prove difficult. For future studies, the set of baits should be continuously extended or amended with complementary baits and/or specific displays, aiming to cover as many species as possible.

Are specialisation, commonness and foraging efficiency interrelated?

The relationship between food specialisation and commonness has been explored in many taxa. Commonness can be defined in terms of geographic range, local abundance, or a combination of both (Kunin and Gaston 1993, Slatyer et al. 2013). Often, specialists are less abundant than generalists (Harcourt et al. 2002, Goulson et al. 2008), but specialisation can also be positively linked to local abundance (Blüthgen et al. 2007, Boulangeat et al. 2012). Here, we reasoned that species with a broader food niche should have a greater incidence than more specialized ones. In turn, more specialized species should be more efficient foraging for their required resources. The first prediction was rejected - commonness (measured as incidence) was not related to the degree of food or temporal specialisation. There were no common food specialists, as had been expected, but rare species included generalised and specialised ones (Fig. 4). Finaly, we could show that specialised species tend to be more efficient foragers, as evidenced by the correlation between foraging efficiency (*fr)* and food specialization (*fs*).

CONCLUSIONS

The present study shows that ant communities show temporal and trophic niche differentiation. Diurnal and nocturnal assemblages differed strongly, and assemblages at five different food items were significantly different from one another, although this difference was smaller than the temporal differentiation. On species level, in our range of baits, no correlation was found between species co-occurrence and niche specialisation. Significant preferences for food items and time periods were found for one-fourth to half of the species, and this would probably increase if sampling effort is intensified. However, while many species did have temporal and/or food preferences, no species showed strict temporal or dietary exclusiveness: the niches were broad enough to allow a certain variation in food resources and temporal activity. Such variation may be especially important for subordinate species, which can modify their dietary habits in presence of dominant species (Sanders and

Gordon 2003). This niche 'plasticity' may be an important mechanism to reduce competition, and we interpret the temporal niche difference of species caught in pitfalls and at baits as evidence of such plasticity.

Future studies should aim at assessing niche differentiation in more detail. This could include different strata complimentary to ground sampling (subterranean; shrubs, tree trunks, canopy), more different baits and additional time periods. Especially for predatory species, the manner of bait display will be crucial to correctly assess their niches. It is likely that ants differ in further niche dimensions which are more difficult to assess, e.g. activity under different weather conditions. The community-based approach presented here may also be complemented by single-species assays in order to exclude the impact of competitors. We should bear in mind that niche differentiation is but one possible mechanism of species co-existence, and that the role of other factors, such as stochasticity in colony establishment success, dispersal and habitat disturbance must not be neglected (Andersen 2008, Arnan et al. 2011). Knowledge about food niches and the degrees of specialisation not only allows investigation of niche partitioning and organismal traits, but is also crucial for the study of trophic ecosystem processes, complementarity and redundancy (Blüthgen and Klein 2011).

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ARTICLE 2. HABITAT EFFECTS ON RESOURCE USE BY ANT SPECIES AND ASSEMBLAGES: EVIDENCE OF CONVERGENT COMMUNITY STRUCTURE AND ECOSYSTEM PROPERTIES

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In preparation for Ecography

ABSTRACT

Habitats are hypothetically stable environments acting as a template for species' ecological strategies. We hypothesized that the characteristic properties of a given habitat such as resource limitations, have a deterministic effect on the assembly processes (i.e. niche filtering and limiting similarity) and the resource use patterns of individual species and entire assemblages. We investigated species and assemblage level resource use patterns in five forest and four cropland assemblages in French Guiana. We devised two separate experiments using bait-traps to characterize ant species' trophic niche and their foraging strategies, reflecting their ability to obtain a same resource in varying forms. The majority of the baits offered were rapidly exploited in the two habitats suggesting significant resource limitation. In each experiment, we captured more than 60 species in the forests and more than 15 species in the croplands. Each species tended to show a consistent resource use strategy across assemblages of the same habitat. Also, species from the same habitat preferentially exploited the same resources suggesting habitat-level niche filtering, although, resource partitioning in local assemblages resulted in less resource use overlap compared to habitat level. Ant assemblages inhabiting forests and croplands differed in the proportions of resources exploited, suggesting different resource availability between the two habitats. The overall foraging activity by assemblages in the same habitat type resulted in similar resource use proportions. Our findings suggest that habitat conditions filter the ecological strategies of tropical ant species and that habitat level resource use patterns emerge as a result of both local competition and habitat-level niche filtering.

Keywords: convergent community structure, ecological niche, ecosystem properties, *Formicidae*, habitat filtering, intraspecific niche breadth, limiting similarity

INTRODUCTION

Niche theory emphasizes the role of limited resource availability on the survival, population growth and coexistence of organisms, and exposes the ecological processes related to the exploitation and the competition for these resources (Chase and Leibold 2003, Pocheville 2015). A crucial problem, is that the aggregate ecosystem properties that emerge from species interactions, and that define the ecosystem itself–remain frequently undefined in the attempt of understanding niche processes (Southwood 1977, Jax 2005). In particular, it is still uncertain how limiting resources are used and recycled by co-occurring species, ensuring the flows of material elements necessary for their growth in different types of habitats (Loreau 2010).

In this perspective, Southwood (1977) proposed that habitats provide a template for the ecological strategies of organisms, their coexistence and the resulting ecosystem properties. In particular, the author emphasized the necessity of quantifying such ecosystem level properties towards a better understanding of community dynamics. Here we attempt to provide such a characterization. We focus on food resource use as the most straightforward link between autecology, competitive interactions and habitat characteristics (Jax 2005, McGill et al. 2006, Thompson et al. 2012, Poisot et al. 2013), and we specifically address the role of food resource availability in shaping tropical ant assemblages.

Community ecology investigates the mechanisms explaining patterns of species coexistence depending on niche differences (Cody and Diamond 1975). In a given habitat, species capable of using abundant resources more efficiently are at a competitive advantage and displace others from the assemblage (Tilman 1982, McKane et al. 2002). This may result in the survival of species having common ecological strategies (a mechanism known as habitat filtering) (Keddy 1992, Mayfield and Levine 2010). Consequently, within the same habitat, species are on average more likely foraging for the same abundant/high quality resources, resulting in interspecific resource overlap (Hurlbert 1978; Fox and Vasseur 2008). Conversely, competition intensity between ecologically similar species can favour interspecific niche differentiation (aka niche partitioning), as predicted by the principle of limiting similarity (MacArthur and Levins 1967, Tilman 1982, Abrams 1983). The relative influence of these processes is scale-dependent, that is, species' niches are expected to become more similar as a result of habitat filtering among assemblages of the same habitat, but the degree of such similarity can be limited at smaller spatial scales (i.e. local assemblages) due to competitive interactions and niche differentiation (Kraft and Ackerly 2010, Algar et al. 2011). An equilibrium state of assembly composition is attained when species interactions result in an optimal use of available resources under the influence of habitat filtering and niche differentiation (Diamond 1975). We then expect assemblages undergoing the same dynamics to show similar (i.e. convergent) aggregate ecosystem properties (Southwood 1977, Jax 2005).

Central to such niche-based approach to community assembly is the delineation of distinctive resource use strategies across species. But species can accommodate environmental variations over time or between habitat types thanks to intraspecific variation in resource use strategies (Correa and Winemiller 2014, McGee and Eaton 2014), and because the interactions with other organisms influence their realized niche (Savolainen and Vepsäläinen 1988, Houadria et al. 2015). Understanding the actual role of foraging strategies in community dynamics thus requires characterizing resource availability (Yanoviak and Kaspari 2000, Peters et al. 2014) as well as the variation of resource use strategies within and among species (Bolnick et al. 2002), but it is rarely directly quantified in empirical essays. As a consequence, much controversy aroused about the actual role of habitat filtering and competition, against alternative mechanisms involving random colonization processes or the presence of natural enemies (Connor and Simberloff 1979, Connell 1980).

In applying the habitat template theory to resource use patterns in ant assemblages, we hypothesize first that habitat conditions result in predictable resource use patterns at the species and assemblage levels, and, second, that these patterns are the outcome of deterministic assembly rules for each habitat. We sampled Neotropical ants in nine plots distributed in forests and croplands, two habitat types where differences in resource availability and accessibility are expected due to differences in the vegetation and leaf litter (Gibb and Parr 2010, Mollot et al. 2014, Peters et al. 2014). In these two habitat types, we performed two separate baiting experiments first to assess food resource use differences, and, second, how the availability of the resources in terms of amount or form affected their exploitation (foraging strategies). We quantified and compared food resource use by ants at different levels of biological organization (i.e. intraspecific, interspecific, entire assemblages and across habitats). Ants represent a major part of the animal biomass in the tropics and forage actively for food resources frequently resulting in important competitive interactions (Parr and Gibb 2009). At the assemblage level, resource exploitation intensity is frequently considered a reflection of environmental limitations in nutrient availability (Kaspari and

Yanoviak 2001, Hahn and Wheeler 2002, Bihn et al. 2008, Peters et al. 2014). Within assemblages, the outcome of interactions can result in niche partitioning in terms of food preferences, temporal activity or foraging strategies (Luque and Reyes López 2007, Lanan 2014, Houadria et al. 2015). Finally, resource use patterns by the same species can change as a result of environmental limitations (Pfeiffer et al. 2014, McGee and Eaton 2014) or as a result of competition (Savolainen and Vepsäläinen 1988, Houadria et al. 2015).

We tested three major predictions concerning individual ant species, entire assemblages and assembly rules. First, if habitat had a deterministic effect on a species' actual niche, we did not expect intraspecific resource use variations to be significant. Moreover, we expected that co-occurring species may use different proportions of resources under the influence of limiting similarity. Second, we tested whether habitat has a deterministic effect on the combined resource use patterns by assemblages. If habitat filtering occurs, the assemblages in the same habitat type are expected to show comparable a comparable equilibrium composition and aggregate properties, related to comparable resource use proportions. In contrast, we expect forest and cropland assemblages to differ due to distinctive filtering. Third, to demonstrate the scale-dependence of limiting similarity and habitat filtering, we compared the extent of interspecific niche overlap at habitat scale (pooled assemblages) and at assemblage scale. High niche overlap is expected at habitat scale due to niche filtering, but can also be found in local assemblages if competitive exclusion occurs. Conversely, local niche differentiation should entail distinct niche overlap at local assemblage and habitat scales. We designed null models with scale-dependent constraints to assess the extent of filtering and limiting similarity at species, assemblage and habitat scales (Gotelli and Graves 1996).

MATERIALS AND METHODS

Study site and sampling scheme

The study area is located in the coastal part of French Guiana at *La Montagne des Singes* (5°04'19''N; 52°41'42''W). To represent local assemblages, we selected nine plots in two habitat types: five forests and four slash-and-burn croplands. Each plot represented a local ant assemblage. The forests were characterized by highly diverse vegetation dominated by the families *Fabaceae*, *Chrysobalanaceae* and *Lecythidaceae*, as is representative of the rainforests in the coastal part of French Guiana. The croplands consisted of traditional young (i.e. 3 to 5-years old) mixed crops of different plant species, mainly manioc, pineapple, sugar cane, pepper and fruit trees. The two habitats were selected to represent contrasting environmental conditions regarding vegetal diversity, litter density, shade and disturbance levels, resulting in an almost full taxonomic turnover of plants and ant species. Still, the plots representing the same habitat type shared a high fraction of species.

On each plot, 20 sampling locations separated by 10 meters across a rectangular grid (1200 m^2) were set up. The number of sampling locations was chosen based on a recommended minimum to characterize an ant assemblage (Agosti and Alonso 2000). The baits were located at these sampling points in the experiments. A distance of at least 250 m was left between the plots, and all of the plots were situated within a radius of 3 km and relatively interspersed. By doing so, we aimed to avoid spatial autocorrelation all while examining plots that were not too far away from each other so that there was no large-scale environmental variation and we could consider a single, consistent pool of species capable of reaching any of the plots. Sampling was carried out between March and October 2013, alternately in the croplands and the forests, always in the morning (8:00 am - 11:00 am) and only in dry conditions (i.e. in the absence of rain and/or flooding) to avoid, as much as possible, sampling biases linked to soil conditions and thermal stress.

Baiting experiments

We collected data on assemblage composition and interspecific niche differences at the same time. Two experiments were designed to address the resource use strategies of ants in sampled assemblages.

TROPHIC NICHE EXPERIMENT

First, we devised a food type experiment (hereafter referred to as ‘trophic niche’) to investigate ant foraging behaviour depending on the nature of the nutrient supply. Seven different food items representing some of the most frequently available sources of essential nutritional requirements for ants, including carbohydrates, proteins and lipids (see Houadria et al. 2015), were used. A mixture of sucrose and melezitose (3 ml at 25% w/w dropped onto paper towelling) constituted the main sugar source that ants obtain from plant nectar and sap-sucking insects, respectively. Insects constitute the main source of proteins and lipids for most ant species; however, insects can be differently accessible depending on their size or whether they are dead or alive. We offered dead insects (3 g of dead, crushed *Tenebrio mollitor* mealworms), small prey (at least 20 *Anoplotermes* sp. termites) and large prey (two, live 1.5 cm- and 3 cm-long mealworms). A mixture of peanuts and rice was offered to represent seeds which are highly lipidic and mainly composed of starch. Finally, excrements are exploited by some species, and we therefore used bird droppings (3 g of chicken excrement).

ACQUISITION STRATEGIES EXPERIMENT

Second, we devised a resource accessibility experiment (hereafter referred to as ‘acquisition strategies’) to investigate ant foraging behaviour depending on the different forms a resource may become available in the environment (Fig. 1). We offered dead insects (the most attractive resource considering the number of ant genera attracted and number of recruited individuals in the first experiment) in five different bait displays. These baits (3 g of dead *Tenebrio mollitor* as in the previous experiment) were presented as *i*) a standard resource on the ground leaf litter, *ii*) in interstitial soil litter (a plastic container where an open Eppendorf containing the resource was placed inside with six 0. 5 cm diameter holes providing the ants access; e.g. Sarty, Abbott & Lester 2006), *iii*) in the surrounding vegetation (presented in an open Eppendorf which was tacked to the trunks of trees at a height of 1.3 m; Kaspari & Yanoviak 2001), *iv*) as small particles (close to 0.1 g of dried mealworms ground into powder presented in Petri dishes on the ground; McGlynn & Kirksey 2000), and *v*) we also examined how rapidly a bait was discovered by placing 3 g of dead *Tenebrio mollitor* in Petri dishes on the ground, surveying the Petri dishes every 5 minutes, and closing them as soon as any ant activity was observed (Pearce-Duvet, Elemans & Feener 2011).

With the exception of the rapid discovery bait, the other bait traps were surveyed every 5 to 10 minutes to monitor ant activity (i.e. the species consuming the items were noted), and collected after 1 hour. After each sampling session, the bait traps were closed to capture the ants. The traps were then taken to the laboratory, and the specimens were killed by freezing at -20°C. The ant specimens were then counted and sorted to genera using the identification key by Bolton (2003) and then to morphospecies based on morphological differences. A reference collection was built and can be found at the UMR Ecofog, Kourou, France.

Figure 1. Bait displays. a) Standard petri box presentation, used for all the food types in the trophic assessment, and also the standard and fast retrieval baits in the resource acquisition strategies experiment. b) Paper towel with small particles of dead insects placed on the lid of a plastic container which was used to enclose the ants. c) Plastic container with access holes containing artificial litter and an eppendorf tube filled with dead mealworms. d) Eppendorf tube stuck with blue-tack to a tree trunk.

Statistical tests

We used incidence data for our analyses (e.g. the number of times species were found at a given bait type in each sampling location). Incidence data is meaningful type of ant abundance data associated to the density of ant colonies in space (Agosti and Alonso 2000). On each plot, representing a local assemblage, a species could be present at most 20 times for a given bait type (i.e. the number of sampling locations within assemblage plots). Species captured in five or more baits were retained for analysis (unless otherwise indicated). This was the minimal information needed to analyse differences in resource use patterns between two species based on a *Chi*-square (χ^2) test.

Our analyses concerned the comparison of resource use patterns among species, assemblages (set of species) or habitats (sets of assemblages). All the comparisons were based on contingency tests (hereafter 'proportionality tests') in the software Past 3.0 (Hammer et al. 2001). The procedure is based on the *Chi*-squared distribution and tests the hypothesis that the effects of the rows and columns are independent in an r x c contingency table (Brown and Rothery 1993). The data input is a matrix where the columns are resource categories and the rows are the elements compared (i.e. species, assemblages or habitats). The cells in the matrix contain the sum of the incidence data for that element and resource (e.g. when comparing species co-occurring in a plot, the score for each resource and species combination is the number of sampling locations where the species was observed at that resource). The algorithm keeps the sums in the rows and columns constant in order to account for the probability of exploitation of a given resource category for the elements compared. The confidence limits at $P < 0.05$ were computed using a Monte Carlo procedure with 10000 randomizations. A significant result in the test indicates that the resources were consumed in different proportions between the elements compared.

All of the tests were performed separately for the two data sets (i.e. trophic and resource acquisition). To resolve the problem of multiple comparisons, we used the method of false discovery rates (FDR) and the algorithms described in Pike (2011). This *post-hoc* method is based on the evaluation of the distribution of P-values to determine significance and is suitable for determining true positive results. In addition, it is also capable of detecting false negatives. In the presentation of our data, we kept the P-values provided by the original statistical tests and reported the FDR results when there was a mismatch (package *multcomp* in R).

DETERMINISTIC EFFECTS OF HABITAT ON RESOURCE USE BY SPECIES

We identified the trophic niche of species and the extent of niche differences across species. For this purpose, we examined the variation of the resource use pattern of each species among assemblages representing the same habitat type (intraspecific variations), and assessed whether species co-occurring in the same assemblage differed in resource use (interspecific variations).

Intraspecific resource use variations were only examined on species sufficiently represented in the different assemblages (we chose species for which 10 or more incidences were found for at least three plots). Based on these conditions, a total of 24 species were analysed per experiment (trophic niche or acquisition strategies). Each row indicates the species resource use in a different plot, and the columns are the different resources (note that species were associated only to one habitat).

Interspecific niche differences were tested for each plot. We retained species with an incidence of five or more within that plot for our analyses. The rows were species and the columns resources.

DETERMINISTIC EFFECTS OF HABITAT ON RESOURCE USE PATTERNS AT ASSEMBLAGE LEVEL

To compare assemblages representing the same habitat type, we summed up the incidence data for all of the species co-occurring in each plot and at each resource. The rows were then the assemblages of a given habitat type (i.e. forest or cropland), and the columns were the resources. A significant result in the test indicated that the overall resource use activity of ants differed among assemblages of the same habitat.

To compare resource use patterns between forest and cropland, we summed up the incidence data for all of the species in each habitat and at each resource. The rows were each of the two habitats, and the columns were the resources. A significant result in the test indicated that the overall resource use activity of ants differed between habitats.

DETERMINISTIC EFFECTS OF ASSEMBLY PROCESSES ON ASSEMBLAGE STRUCTURE

To investigate the influence of assembly processes, we addressed two basic hypotheses: species within the same habitat are expected to use similar resources (niche filtering hypothesis), but in local assemblages similarity may be limited by competition (limiting similarity hypothesis).

We assessed the extent of niche filtering among ant species within assemblages and habitats, based on the null expectation that species can use random proportions of resources (Gotelli and Graves 1996). We used Ecosim routines of niche overlap implemented in R at the habitat level first and then on each assemblage. We chose the RA3 algorithm and the Pianka overlap index as classical procedures for testing the resource overlap hypothesis (Gotelli and Entsminger 2001). For each test, 1000 matrices were generated by randomizing resource frequencies within each row (species), and calculating the average niche overlap among species. The observed niche overlap at different levels of organization (assemblage or habitat) was compared to the corresponding null distribution using a two-tailed statistical test. Values lower than the 2.5% quantile indicated that species differ more in their resource use than expected by chance (limiting similarity). Values over the 97.5% quantile indicated more similarity than expected by chance (functional convergence). In addition, the algorithm provides a standardized effect size measure (SES) of the deviation between the observed and the expected overlap values from the null distribution. According to the indications of the algorithm (Gotelli and Ellison 2013), the SES measure can be used to compare the strength of the effect of resource overlap between samples of different sizes (i.e. assemblages and habitat, varying in the number of species). On a SES scale, we expected the habitat-level overlap to be greater than the assembly-level overlap. Since the habitat-level overlap consisted of a single value, statistical significance was provided by comparing that value with the confidence interval based on the mean ± standard deviation of the SES for the local assemblages.

RESULTS

In the trophic experiment, we collected 81 species in the forest habitat and 26 in the cropland habitat. In the acquisition strategies experiment, 66 species were captured in the forest habitat and 15 in the cropland habitat. The percentage of baits exploited was very high for the majority of resources. Within one hour, the great majority of baits containing dead insects, sugars, seeds and termites were exploited, frequently, by several species simultaneously (Table 1).

Table 1. Resource exploitation intensity

	Resource	Percentage of exploited baits	Average number of species per bait	Average number of species per plot
Forest	Big prey	53 ± 1	0,61 ± 0,09	4,8 ± 1,9
	Termite	92 ± 1	1,34 ± 0,21	13,4 ± 1,6
	Dead T.	97 ± 4	1,93 ± 0,44	16,8 ± 3,4
	Excrement	44 ± 1	0,62 ± 0,11	9,2 ± 2,6
	Seeds	99 ± 2	2,35 ± 0,26	18,6 ± 3,3
	Sucrose	82 ± 7	1,75 ± 0,43	14,6 ± 3,6
	Melezitose	80 ± 8	1,36 ± 0,26	11,8 ± 2,7
	Big prey	92 ± 8	1,14 ± 0,19	3,5 ± 1,5
	Termite	100 ± 0	1,86 ± 0,36	6,5 ± 1,1

Cropland	Dead T.	100 ± 0	1,76 ± 0,25	8,5 ± 3,2
	Excrement	49 ± 2	0,59 ± 0,27	4,8 ± 1,3
	Seeds	96 ± 7	2,08 ± 0,2	9 ± 1,4
	Sucrose	100 ± 0	1,95 ± 0,19	9,8 ± 1,8
	Melezitose	91 ± 7	1,43 ± 0,31	7,5 ± 1,1

Intraspecific resource use constancy among assemblages of a same habitat type but interspecific differences within assemblages

Variations in resource use patterns at intraspecific level were extremely low for the two experiments performed. Out of a total of 24 tests (Table 2), significant differences were only found in the means of the resource acquisition of *Nylanderia* sp.1. This result disappeared after applying a correction for multiple comparisons (FDR adjusted-*P* = 0.16). The absence of intraspecific resource use variations provides a robust evidence of the constancy of environmental conditions and species interactions among assemblages representing a same habitat type.

Table 2. Contingency tests calculated on resource use matrices by dominant species. The number of assemblages considered (Plots) and incidence (n) are indicated. Significant differences from a random distribution are based on χ2 distribution and are indicated as follows: *, 0.01 < P < 0.05; ns, non-significant; ! , Non-significant after FDR correction.

		Trophic resource				Acquisition strategy			
Habitat	Species	Plots	n	χ^2	*P*	Plots	n	χ^2	*P*
Forest	*Wasmannia auropunctata*	5	79	22,48	0,31 ns	5	65	16,2	0,45 ns
	Ochetomyrmex neopolitus	5	69	21,53	0,6 ns	3	45	7,67	0,48 ns
	Pheidole sp.8	4	72	8,54	0,9 ns	--	--	--	--
	Pheidole sp.16	2	29	0,57	0,9 ns	5	20	12,84	0,85 ns
	Pheidole sp45	4	43	11,57	0,52 ns	5	16	16,17	0,17 ns
	Nylanderia sp.1	3	38	8,49	0,33 ns	4	27	5,6	0,90 ns
	Diplorhoptrum sp.1	5	38	23,47	0,27 ns	4	16	11,82	0,44 ns
	Crematogaster sp.2	3	31	12,08	0,48 ns	--	--	--	--

Cropland	*Solenopsis saevissima*	4	238	12,78	0,81 ns	4	195	7,88	0,8 ns
	Pheidole fallax	4	187	21,6	0,24 ns	4	77	5,08	0,96 ns
	Crematogaster sp.5	3	126	13,3	0,35 ns	4	100	18,2	0,09 ns
	Camponotus sp.3	3	28	5,67	0,68 ns	3	38	14,67	0,06 ns
	Nylanderia sp.4	3	26	9,69	0,73 ns	3	31	15,7	0,045* !

Interspecific trophic partitioning was found in all of the forest and cropland assemblages after applying a correction for multiple comparisons (Table 3). Partitioning in resource acquisition strategies was detected in all the forest assemblages after applying multiple comparisons correction, but in only one of the cropland assemblages.

Table 3. Contingency tests calculated on the trophic and on the resource acquisition strategies matrices on five forest and four cropland assemblages. At the left, the analyses correspond to the entire assemblages. At the right, only dominant species are retained. The number of species, the percentage of exploited resources and the degrees of freedom (Df) are indicated. Degrees of freedom correspond to (m - 1 * n - 1) where m is the number of resource states, and n the number of assemblages compared. Significant differences from a random distribution are based on χ2 distribution and are indicated as follows: ● significant test after FDR correction; * P <0.05; ** P < 0.01; *** P <0.001; ns, non-significant.

		Trophic resource				Resource acquisition			
Habitat	Plot	Number of spp	Df	% Expl.	χ2	Number of spp	Df	% Expl.	χ^2
Forest	For1	13	72	72.1	90.813 ●	11	40	58.2	60.73 *
	For2	12	66	79.4	186.84 ***	7	24	68.8	42.071 **
	For3	10	54	78.4	95.04 **	8	28	72.9	47.943 **
	For4	14	78	78.2	132.13 ***	8	28	68.4	38.72 ●
	For5	7	36	60.8	109.72 ***	5	16	67.0	29.73 *
Cropland	Crop1	9	48	94.2	80.816 **	6	20	87.5	38.7 **
	Crop2	8	42	95.1	98.713 ***	3	8	84.1	4.74 ns
	Crop3	5	24	86.6	49.193 **	4	12	93.1	13.965 ns

Crop4	8	42	94.0	90.291	***	6	20	91.3	27.564	ns

Resource use constancy by assemblages of a same habitat type but differences between habitats

We found no difference in the exploitation intensity of different food resources among assemblages of a same habitat type, neither for the trophic niche nor for the acquisition strategies experiments (Table 4). Significant trophic differences were found however between forests and croplands ($\chi^2 = 85.23$, $P < 0.001$). This may be explained by a more frequent exploitation of carbohydrates and especially big prey in croplands than in forests (Table 1). In contrast, no differences were found in the intensity of resource acquisition strategies between habitats (Table 4).

Table 4. Contingency tests of the resource use constancy between assemblages of a same templet condition, and between habitat types based on a χ2 distribution. The total occurrences of species (n) and the degrees of freedom (Df). Degrees of freedom correspond to (m - 1 * n - 1) where m is the number of resource states, and n the number of elements compared (assemblages/habitat).

Trait	Assemblages	Elements compared	Incidence	Df	χ^2	*P*
Trophic resource	Forest	24	953	24	27.08	0.30
	Cropland	18	836	18	26.06	0.10
	Between	6	1789	6	85.23	< 0.001
Resource acquisition	Forest	16	612	16	22.03	0.14
	Cropland	12	516	12	9.49	0.66
	Between	4	1128	4	3.62	0.45

High niche overlap at habitat and local assemblage levels

At the habitat scale (pooled assemblages), the observed trophic overlap was greater than expected by chance for forests ($\text{Pianka}_{obs} = 0.54$ *vs* $\text{Pianka}_{null} = 0.50$; $P < 0.001$) and croplands ($\text{Pianka}_{obs} = 0.65$ *vs* $\text{Pianka}_{null} = 0.57$; $P < 0.001$) (Table 5). This indicates that some types of resources were more frequently exploited than others by the majority of the species. In addition, overlap was also larger than expected in the 80 % of forest assemblages (Table 5), but only in the half of the cropland assemblages. Indeed, in croplands, the degree of deviation from the null expectation was considerably larger at habitat scale than for the average assemblage ($SES_{Habitat}$ = 5.53 *vs* a local mean of 1.39). The same result was observed in forest habitat compared to local assemblages ($SES_{Habitat}$ = 6.83 *vs* a local mean of 2.73). Considering that the standard effect size is theoretically unaffected by the sample size, these results suggest that species co-occurring in local assemblages of each habitat present a lower degree of resource overlap than the pooled set of species present in that habitat.

Table 5. Observed and expected range of trophic niche overlap measured at assemblage and habitat level. The results correspond to the observed and expected overlap range calculated as the mean Pianka index at 95% confidence interval. The P-values indicate the 2nd tail probability and the standardized effect size (SES) derived from these distributions are indicated.

		Trophic resource				Acquisition strategy			
Habitat	Plot	Obs	95% IC limits	P-value	SES	Obs	95% IC limits	P-value	SES
Forest	For1	0.609	0.526-0.603	0.012	2.726	0.590	0.553-0.639	ns	0.143
	For2	0.543	0.434-0.535	0.012	2.7	0.576	0.488-0.631	ns	0.663
	For3	0.611	0.445-0.56	0.002	4.058	0.635	0.566-0.677	ns	0.742
	For4	0.622	0.43-0.513	0.001	7.095	0.735	0.63-0.74	0.033	2.339
	For5	0.401	0.294-0.489	ns	0.558	0.610	0.544-0.712	ns	-0.048
	For $_{Habitat\ level}$	0.54	0.490-0.513	0.001	6.831	0.656	0.590-0.616	0.001	7.978
Croplands	Crop1	0.58	0.497-0.603	ns	1.386	0.733	0.687-0.803	ns	0.15
	Crop2	0.564	0.449-0.587	ns	1.809	0.919	0.88-0.967	ns	0.253
	Crop3	0.594	0.52-0.703	0.028	0.028	0.82	0.727-0.88	ns	0.841
	Crop4	0.688	0.592-0.695	0.035	0.035	0.785	0.766-0.856	ns	-0.458
	Crop $_{Habitat\ level}$	0.654	0.546-0.603	0.001	5.525	0.722	0.709-0.781	ns	0.635

In the acquisition strategies experiment, forest species overlapped more than expected by chance in the bait displays used at the habitat scale ($Pianka_{obs}$ = 0.66 *vs* $Pianka_{null}$ = 0.60, $P <$ 0.001), but this pattern was only maintained in one of the local assemblages (Table 5). Accordingly, the standardized effect size at the habitat scale was more than 3 times larger than in any of the local assemblages. In the croplands, the species presented a random pattern of resource use at the habitat and assemblage scales (Table 5).

DISCUSSION

In this study, we investigated the resource use strategies of ants at species and assemblage levels in forests and croplands, to address the deterministic effect of habitat conditions on species ecology, species interactions and overall patterns of resource use thus affecting ecosystem level properties (Southwood 1977).

Our first hypothesis was that, within each habitat type (cropland and forest, respectively), a given species should consistently use the same proportions of resources based on the idea that its niche requirements are fixed and that the environmental conditions are alike (including resource availability and competitive interactions). We tested resource use constancy at species level within each habitat against an alternative hypothesis of intraspecific resource use variation (Bolnick et al. 2002), which conversely considers that organisms can adapt their foraging effort and exploit different resources in variable environments to get maximal reward (MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977). In this case, species can shift resource use depending on resource availability or on the intensity of the competition (Durso et al. 2013, Correa and Winemiller 2014, Moleón et al. 2014). Previous studies on ants provided evidence of intraspecific resource use variations between habitats (Mollot et al. 2014, Pfeiffer et al. 2014, McGee and Eaton 2014), and depending on the presence of competitors (Savolainen and Vepsäläinen 1988, Holway 1999). Here, however, we found marked resource use constancy at species level in our experiments, thus supporting our first hypothesis. Moreover, we expected convergent assemblage structure to appear under the influence of consistent resource limitations in similar environments (Cody and Diamond 1975, Tilman 1982). In this regard, we used ant activity levels on different resources in assemblages as a proxy of local resource limitations and habitat properties, based on findings by other authors (Kaspari and Yanoviak 2001, Kaspari et al. 2012, Peters et al. 2014). We found resource use constancy among species and among assemblages of the same habitat as well. Such results provide robust evidence of the constancy of environmental conditions and species interactions among assemblages representing the same habitat type.

The second hypothesis was that habitats also determine the specific pathways of interactions between species. We report four findings which together support the key role of biotic filters in determining ant community structure in local assemblages. First, the majority of the baits were rapidly exploited, indicating resource limitations, which is the essential driver of competition. Second, we confirmed that intraspecific variations in resource use in different assemblages were minor in comparison to interspecific variations within the assemblages (Abrams 1983). This is the most basic assumption prior to accept the limiting similarity prediction: species are more limited by conspecifics than by other species due to niche overlap, thus enabling coexistence (Abrams 1983). Third, based on contingency tests, interspecific niche partitioning was the rule in all of the assemblages studied for at least one of the ecological dimensions considered (i.e. food or acquisition strategies). Finally, while there was a significant niche overlap for each experiment (i.e. trophic or acquisition strategies) at habitat level, we found substantially lower niche overlap values at assemblage level. The latter finding highlights the varying influence of niche mechanisms at different spatial scales, in particular, niche filtering and convergence was important at the habitat level, and niche differentiation predominated in local assemblages (Levine and Hille Ris Lambers 2009, Kraft and Ackerly 2010).

Distinctive resource use patterns of species between forests and croplands were likely to represent distinct environmental constraints and habitat properties between these two habitats. At the habitat level, species in the forests presented a considerable overlap for trophic niche and acquisition strategies, indicating ecological convergence for, presumably, resource use and foraging strategies providing the greatest reward in this habitat. In the croplands, an overlap existed for trophic niche, but not for foraging strategies at the habitat level. Moreover, ant assemblages in forests and croplands differed in their overall use of food resources, which suggests that these two habitats are characterized by different resource limitations (Bihn et al. 2008, Peters et al. 2014). A greater use intensity of proteinaceous resources in croplands *vs.* forests was found in previous studies (Bihn et al. 2008, Peters et al. 2014). Also, the denser litter and greater plant diversity found in the forest makes possible the use of different strategies for resource acquisition by forest ants which is not the case in the simplified environmental matrix observed in the croplands. The specialization of certain species to forage preferentially in some environments might explain the overlap in the forests and not in the croplands. For example, different foraging guilds of ants have been reported as well as their abundance variation in different environments (Brandão et al. 2012, Lanan 2014).

Our results demonstrate that forest and cropland habitats are characterized by different ecological dynamics, including ecological overlap and partitioning of species for different resources. The interactions between species likely affected the behaviour of each species and the overall use patterns by the entire assemblage. This finding supports the idea that, for a given environment, an equilibrium assemblage structure exists, which reflects how individual foraging behaviours and consistent species interactions lead to some characteristic and constant properties of the habitat.

CONCLUSION

We provide evidence of the joint influence of habitat filtering and niche differentiation on the resource use patterns and community structure of ants. Our study shows the spatially nested influence of these processes, at habitat and assemblage level, respectively, in accordance with previous studies on diverse organisms (Ackerly and Cornwell 2007, Kraft and Ackerly 2010, Algar et al. 2011, Carboni et al. 2015). Resource limitations result in the niche filtering and overlap over the spatial expansion of different habitats, but this overlap is limited by the influence of competitive exclusion in local assemblages. Future studies should aim to provide evidence of how resource availability and their variation affect ecological patterns at different biological and spatial scales, and how this relates to the ecosystem level properties characteristic of different types of habitat.

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ARTICLE 3. TURNOVER OF ANT COMMUNITIES ALONG A LAND-USE GRADIENT: FUNCTIONAL TRAITS MATTER, BUT THE MORPHOLOGICAL SPACE DOES NOT VARY

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ABSTRACT

Land-use changes frequently lead to major changes in the composition and diversity of organisms. Trait-gradient analyses should allow a better understanding of the causes of such changes. Particularly, a reduction in the range of strategies capable of surviving in a given environment (niche contraction) and changes in the average trait values of species (niche shift) may explain variations in species' number and identity. We investigated the variation in ant taxonomic composition and morphological trait diversity along a land-use gradient characterized by contrasted habitats - from gardens to forests - in French Guiana. We measured 13 core ant morphological traits on all species sampled. We then selected the set of five traits that best captured changes along the land-use gradient. Potential effects of niche contraction and niche shifts were evaluated by examining morphological traits individually as well as in combination. Niche contraction was evaluated by comparing the range of individual traits with an expected random regional pool using null models. The morphological space occupied by ant assemblages was estimated using the n-dimensional hypervolume. Niche shift was assessed by tracking changes in Community-Weighted Means (CWM) for individual traits, and using multivariate analysis for the best subset. We found that variation in taxonomic diversity was unrelated to the plot-level morphospace. Conversely, a significant shift in taxonomic composition was accompanied by changes in the average values of community traits along the studied gradient, examined both individually and in combination. We argue that morphology is a relevant proxy of niche positions and, subsequently, taxonomic turnover in ants. However, in contradiction with theoretical expectations, the morphospace is slightly affected by habitat filtering and loosely related to taxonomic changes. Examining the sensitivity of the morphospace to abiotic and biotic factors and how it reflects the total niche space available for species is thus of the utmost importance.

Keywords: community assembly, Formicidae, functional diversity, habitat filtering, gradient analysis, land-use intensification, n-dimensional hypervolume approach

INTRODUCTION

Land-use changes induced by human activity are a primary driver behind the erosion of biodiversity and the alteration of ecosystem functioning observed in most biomes worldwide (Lindemayer et al. 2012). Whereas taxonomic diversity has traditionally been used to track the effects of global change on ecosystems, it often provides insufficient information to reveal and quantify the mechanisms underlying those effects (Pereira et al. 2013). Trait-based ecology aims to provide an ecological characterization of species and entire assemblages to understand the mechanisms beyond such changes (McGill et al. 2006, Enquist et al. 2015). The theoretical expectation is that local habitat patches are occupied by a non-random subset of species among many others present in a regional pool, a process also known as “habitat filtering” (Weiher et al. 2011). At the community level, changes in species richness and composition between habitats can be explained by two mechanisms: niche contraction and niche shift (Ricotta and Moretti 2011). The niche can be understood *sensu* Hutchinson as a functional space where dimensions correspond to resources and/or traits (Hutchinson 1957). Niche contraction can be understood as a reduction in the range of options present in a given environment compared to another. A reduction in the suitable range of ecological strategies, probabilistically reduces the number of species which can survive within that habitat among those present in a region (Hutchinson 1957, Ricklefs 2012b). Moreover, a niche shift indicates changes in the average trait values in response to environmental conditions, which generally result in the substitution of some species by others and/or changes in the relative abundance of species (Grime 1998, Garnier et al. 2004).

Ants are excellent model organisms to track changes in habitat conditions due to their ecological success, diversity and ubiquity (Hoffmann 2010, Arnan et al. 2014). Ant species occupy a variety of habitats and microhabitats and use different food and nesting resources (Weiser and Kaspari 2006, Blüthgen and Feldhaar 2010). Therefore, we expect the trait patterns of ant communities to capture relevant environmental shifts as suggested by pioneering functional approaches to ant biodiversity (Andersen 1992, 1995). Applying trait-based approaches to ants could be valuable in revealing the mechanisms underlying species replacement along land-use and climatic gradients (Arnan et al. 2014, Yates et al. 2014). Morphological traits are particularly useful since they have been connected to variations in species affinity to different macrohabitats as well as food and microhabitat use within them (Weiser and Kaspari 2006, Yates et al. 2014, Gibb et al. 2015b). In this sense, several hypotheses have been put forward linking ant morphological traits and responses to environmental factors. In particular, the size-grain hypothesis proposes that body size and leg length determine foraging success in relation to litter density and structure: small ants should be more adapted to litter-dense environments thanks to a better capacity to move in the litter interstices (Kaspari and Weiser 1999, Gibb and Parr 2010). Another prominent hypothesis, the size-thermal resistance hypothesis, states that larger ants should resist higher temperatures better than do smaller ants thanks to a lower surface-to-body mass ratio (Kaspari 1993, Oberg et al. 2012). Finally, mandibular and sensorial traits (e.g. eyes, antennae) are frequently related to the food regimes and foraging modes of different species (Weiser and Kaspari 2006, Silva and Brandão 2010, Gibb et al. 2015b).

In this study, we describe the variations in the diversity and species composition of ant assemblages along a land-use gradient. We try to explain that such changes are a consequence of habitat filtering by examining changes in species morphological traits. We hypothesize that the range of each trait and average values calculated at the community level can reflect species diversity and identity in agreement with the hypotheses of niche contraction and niche shift, respectively. In addition, we carry out a multi-trait approach to niche contraction and niche shift considering a subset of five traits which best represented ant community changes between the habitats examined. Considering multiple traits simultaneously is relevant since the performance of species in their environment depends on the combination of characters and possible trade-offs (Murren 2012).

MATERIALS AND METHODS

Study site and sampling protocol

The study was carried out on the *Montagne des Singes*, Kourou, French Guiana (5°04’27”N, 52°42’03”W). The climate is equatorial and characterized by alternating dry and rainy seasons with high, constant yearly and daily temperatures (T_{year}=29±5°C) and abundant annual precipitation (i.e. more than 3000 mm/yr). Sampling took place between January and May 2014 (i.e. the rainy season). Sampling was carried out in the morning (8:00 am - 11:00 am) in dry conditions only (i.e. in the absence of rain and/or flooding) to avoid, as much as possible, sampling biases linked to soil conditions and thermal stress.

We selected five habitats representing an increasing gradient of land-use intensification: *terra firme* forest, lowland forest, forest edges, traditional croplands, and gardens. These correspond to natural and anthropogenic ecosystems frequently investigated in studies focusing on how land use influences biodiversity (Lindemayer et al. 2012). The forests (*terra* *firme* and lowland) are old-growth forests characterized by a high plant diversity, abundant organic soil matter and trees of varying sizes with the largest diameters over 1 m and a canopy higher than 30 m. Lowland forests are affected by episodes of flooding during the rainy season, resulting in a regular disturbance of the ground matrix and removal of soil litter. Forest edges are at the interface between forests and roads, and are more frequently affected by human disturbance than are forests. Agricultural areas correspond to traditional cropping based on slash-and-burn practices, and further substitution by a mixture of crops (e.g. *Manihot esculenta, Colocasia esculenta, Anana comosus,* and fruit trees). Finally, gardens are house lawns regularly mowed by their owners ensuring that the only vegetation cover is grass. For ants in particular, the decrease in the amount of litter and organic matter from forest to gardens together with a higher incidence of light can significantly affect taxonomic and trait composition (Linksvayer and Janssen 2009, Wiescher et al. 2012, Gibb and Parr 2013, Arnan et al. 2014).

We sampled three 0.12 ha plots (30 m x 40 m) per habitat. All of the plots (from all of the habitat types) were interspersed and separated by at least 200 m and were all situated within a radius of 3 km. This guaranteed that all of the plots sampled were placed within a unique climatic envelope and that they were potentially colonized by the same species originating from the regional pool. In each plot, the sampling protocol was based on a 20-point rectangular grid (10 m between each sampling point).

Sampling strategy

Ant sampling consisted of baiting trials carried out in the field which allowed us to monitor ant activity. Seven food items representing some of the resources most frequently consumed by ants (see Houadria et al., 2015) were offered in Petri dishes (5-cm diameter): two sugars - sucrose and melezitose – as proxies for nectar and honeydew, respectively; chicken excrement and dead mealworm (*Tenebrio molitor*) larvae for detritus (excrement and dead insects, respectively); live *T. molitor* larvae and termites for prey; and a mixture of grains of rice and peanuts to represent seeds. For the sugar baits, 3 ml diluted in a 25% w/w solution were dropped onto a small piece of paper towel. We used 3 g of all of the other baits. Each bait type was offered once on each grid-point.

The Petri dishes were lined with a layer of parafilm since this method had facilitated capturing the ants in our pre-sampling experiments. After 1 hour, we captured all of the individuals in the Petri dishes which were subsequently identified to species or morphospecies according to the guide published by Bolton (2003). Voucher specimens are deposited at the UMR Ecofog, Kourou, French Guiana.

Ant trait measurements and transformation

For each species, we measured morphological traits only on ant workers since they constitute the most abundant caste and are specialized in foraging for their colonies. Measurements were made on six specimens per species for monomorphic species and on 10 specimens for polymorphic ones (i.e. several species from the genera *Camponotus*, *Solenopsis* and *Crematogaster*). We considered only minor workers for the *Pheidole* genus. We initially selected a set of 13 frequently-studied morphological traits (Silva and Brandão 2014, Yates et al. 2014, Gibb et al. 2015b) (Fig. 1).

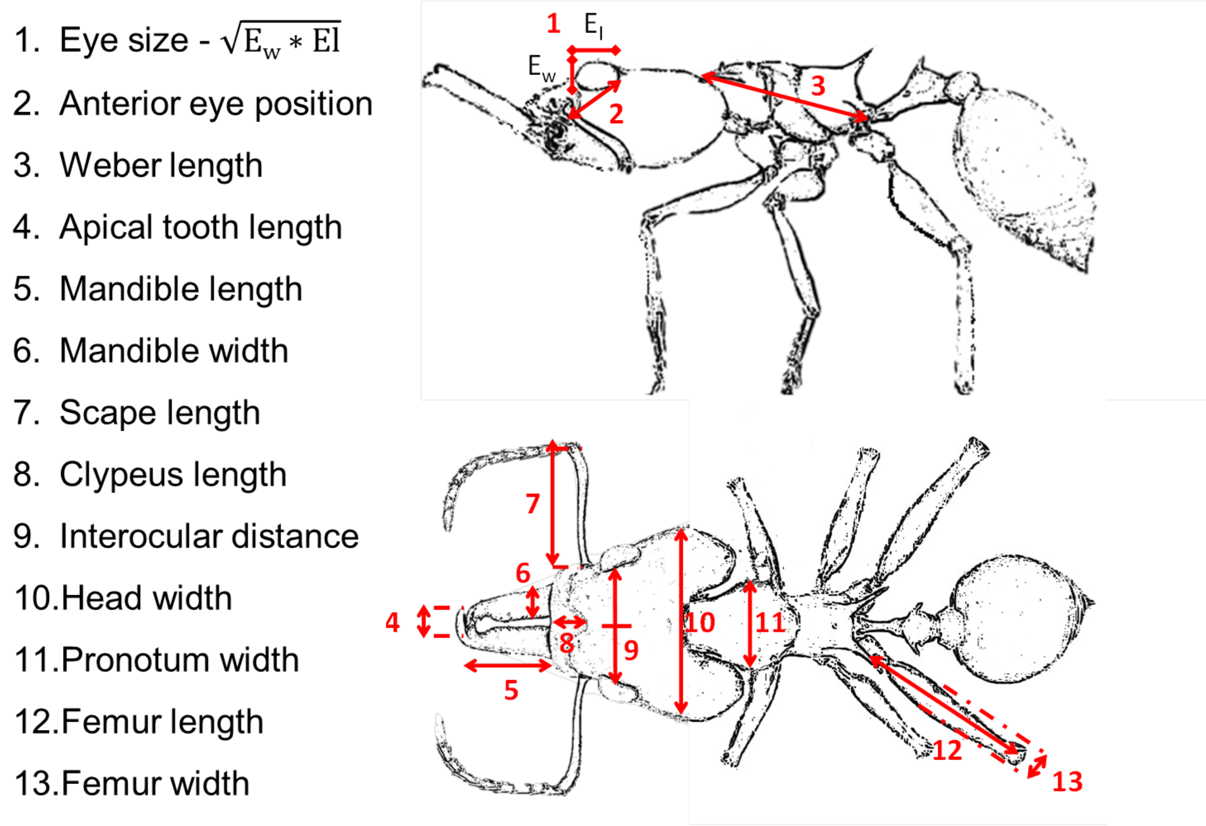

Figure 1. Set of measured morphological traits represented on a schematized ant.

Individual trait values per species were averaged to provide a single value per trait per species. A preliminary Principal Component Analysis indicated that all of the traits were highly correlated and covaried with size (Weber's length). Therefore, we primarily used the log-transformed Weber's length as a core trait and divided the other traits by it to obtain allometrical variables. Weber's length was normalized because the distribution in ant sizes was not normally distributed (Silva and Brandão 2010, Yates and Andrew 2011, Gibb et al. 2015b).

Statistical analyses

SPECIES RICHNESS AND COMPOSITION

To test for differences in species richness between habitats, we compared the mean species richness using an analysis of variance (ANOVA). To identify differences in taxonomic composition which can be related to a habitat-filtering process, the species captured at least 5 times were ordinated using a Principal Coordinate Analysis and the Bray-Curtis distance. This distance is affected by changes in the relative abundance of species (i.e. substitution of species along environmental gradients, also known as "species turnover"), and also nestedness patterns resulting from the loss of individuals and species between habitats without any species substitution (Baselga 2013). Analyses were conducted with Past 3.0 software (Hammer et al. 2001). The significance of the ordination was tested with a PERMANOVA (Anderson 2001) using "*adonis"* in the R *vegan* package.

TRAIT-BY-TRAIT TESTS OF HABITAT FILTERING

First, we examined the possible reduction of trait ranges in plots compared to the range of traits in the regional pool, which included all five habitat types combined. To that end, the difference between the maximal and minimal trait values for each plot was compared to the range of traits in randomized communities. For each comparison, we built 4,999 randomized communities composed of species drawn (without replacement) from the species pool and whose species richness is equal to the species richness observed in the plot (see also Taudiere & Violle 2015). If the range of traits in the actual plot was lower than the 5% quantile of the range of traits for the 4,999 associated randomized communities, it was considered significantly lower than expected by chance.

Then we examined changes in the average values of the traits to test the niche shift hypothesis. The Community-Weighted Mean (CWM) (Garnier et al. 2004) was calculated for each trait *j* in each plot *k* as:

$$CWM_{j,k} = \sum_{i=1}^{S} p_i x_i \qquad \text{Eqn 1}$$

where p_i is the relative frequency of species (i.e. the proportion of grid-point level incidence in each plot), and x_i the trait value of species *i*. We carried out analyses of variance (ANOVA) to test whether CWM values varied across the different habitats.

MULTI-TRAIT TESTS OF HABITAT FILTERING

Because examining individual traits may hide the importance of species allometries and eventual trade-offs between trait values in the adaptation process to the environment and competitors, it is important to consider multiple traits simultaneously; this has become known as ‘the integrated phenotype’ (Murren 2012). The most parsimonious set of traits explaining between-habitat differences were identified with the “bioenv” function in the R *vegan* package. This function enables the selection of the best subset of traits so that the Euclidean distances of scaled traits have the maximum (rank) correlation with community dissimilarities (Clarke 1993). Five traits (i.e. apical tooth length, eye size, mandible length, mandible width and scape length) were selected through this procedure. Thereafter, we examined changes in the niche space and niche position between habitats using only these five traits.

The morphological space occupied by ant assemblages in different plots was estimated using the R *hypervolume* package (Blonder et al. 2014). The hypervolume represents the functional space (unit: $sd^{number\ of\ traits}$) occupied by a set of species in a number of dimensions equal to the number of traits considered. The hypervolume provides a better estimation of niche spaces than other methods by progressively adding volume units which depend on a bandwidth parameter (Blonder et al. 2014). The bandwidth represents the size of the unitary space covered by randomly selected species within the niche space. Like other methods that quantify functional spaces, the hypervolume is sensitive to changes in species richness and their repartition within the niche space (Mason et al. 2013, Blonder et al. 2014). In particular, the addition of species increases the probability of detecting greater hypervolumes, as long as the average spacing of species within a niche space is kept constant. On the contrary, if a niche space is kept constant, the probability of an overlap between two observations increases with the density of species, with a resulting negative relationship between species richness and hypervolume. In the generation of hypervolumes we used a bandwidth of six to avoid biases related to the probability of an overlap between data points within niche spaces associated with habitats with different levels of species richness. We can then consider that a relationship between species richness and functional space is a desirable result as long as the species included are representative of the communities examined (i.e. not biased by outliers or other artifacts). To remove the effects of outlayers, for each plot, 100 hypervolumes were generated by extracting 50 random species with replacement and a probability equal to their relative incidence in the 20 sampling locations of the plot. We considered 50 draws a representative size since, on average, 2.5 species were found at a bait, and standard sampling in ants consists of 20 sampling locations (Agosti and Alonso 2000). Variations in the morphological space between habitats were compared using nested analyses of variance where the 100 hypervolumes per plot were nested within plots.

To test multi-trait niche shift, we performed a Principal Component Analysis using the CWM values for the five traits selected by the "bioenv" function to identify the major functional dimensions of the 15 plots studied.

POST-HOC ANALYSES FOR PAIR-WISE COMPARISONS BETWEEN HABITATS

For all of the statistical tests performed, pairwise comparisons between habitats were carried out using the "false-discovery rate" (FDR) (Benjamini and Hochberg 1995). This method provides corrections for multiple testing by performing a step-wise evaluation of *P*-values, which are more powerful and appropriate than through other traditional methods such as Bonferroni-based methods (Pike 2011).

RESULTS

Taxonomic changes along the land-use gradient

Significant differences in species richness were found between the majority of habitat pairs (ANOVA, $F_{4,\ 10} = 42.48$ $P < 0.001$), revealing that the number of species significantly decreased with increasing land-use intensification (Fig. 2a). Biodiversity loss was especially big in croplands and gardens compared to "forested" habitats (e.g. a lower difference for edges *vs*. croplands; ANOVA FDR, P = 0.004). Gardens and croplands did not contain a significantly different number of species (ANOVA FDR, P = 0.13). Also *terra firme* plots presented diversity levels similar to those of lowland forests (ANOVA FDR, P = 0.36) and edges (ANOVA FDR, P = 0.08), although lowland forests contained more species than did edges (ANOVA FDR, P = 0.02).

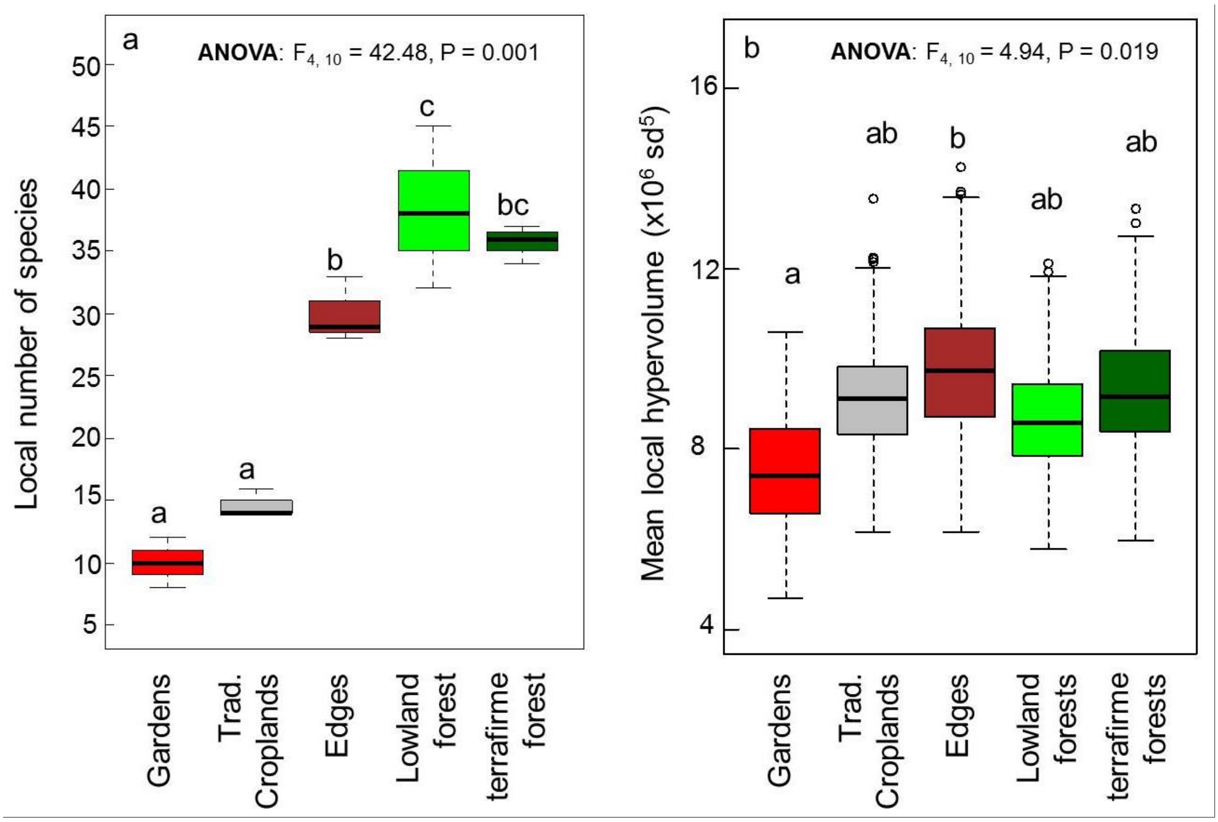

Figure 2. Plot level species richness (a) and morphospace (b) comparisons between habitats based on three replicate plots per habitat. The morphospace was calculated using five traits (choice based on the "bioenv" statistical function; see methods) using the hypervolume method (100 iterations per plot). Tests consisted of analyses of variance followed by the FDR correction.

A permutation multivariate analysis using Bray-Curtis distances indicated strong differences in species composition between habitats (PERMANOVA, $F_{4,\ 10}$ = 7.05, P = 0.001). Pairwise comparisons indicated important changes in species composition and relative species' frequencies along the land-use gradient. For instance, the ordination (Fig. 3a) indicates a Bray-Curtis distance of 1 between open habitats (i.e. gardens and croplands) and forest habitats (i.e. lowland and *terra firme* forests). Indeed, no common species (i.e. incidence greater than 5 per plot) were shared between these two types of habitats, suggesting the very important role of habitat in explaining species' turnover.

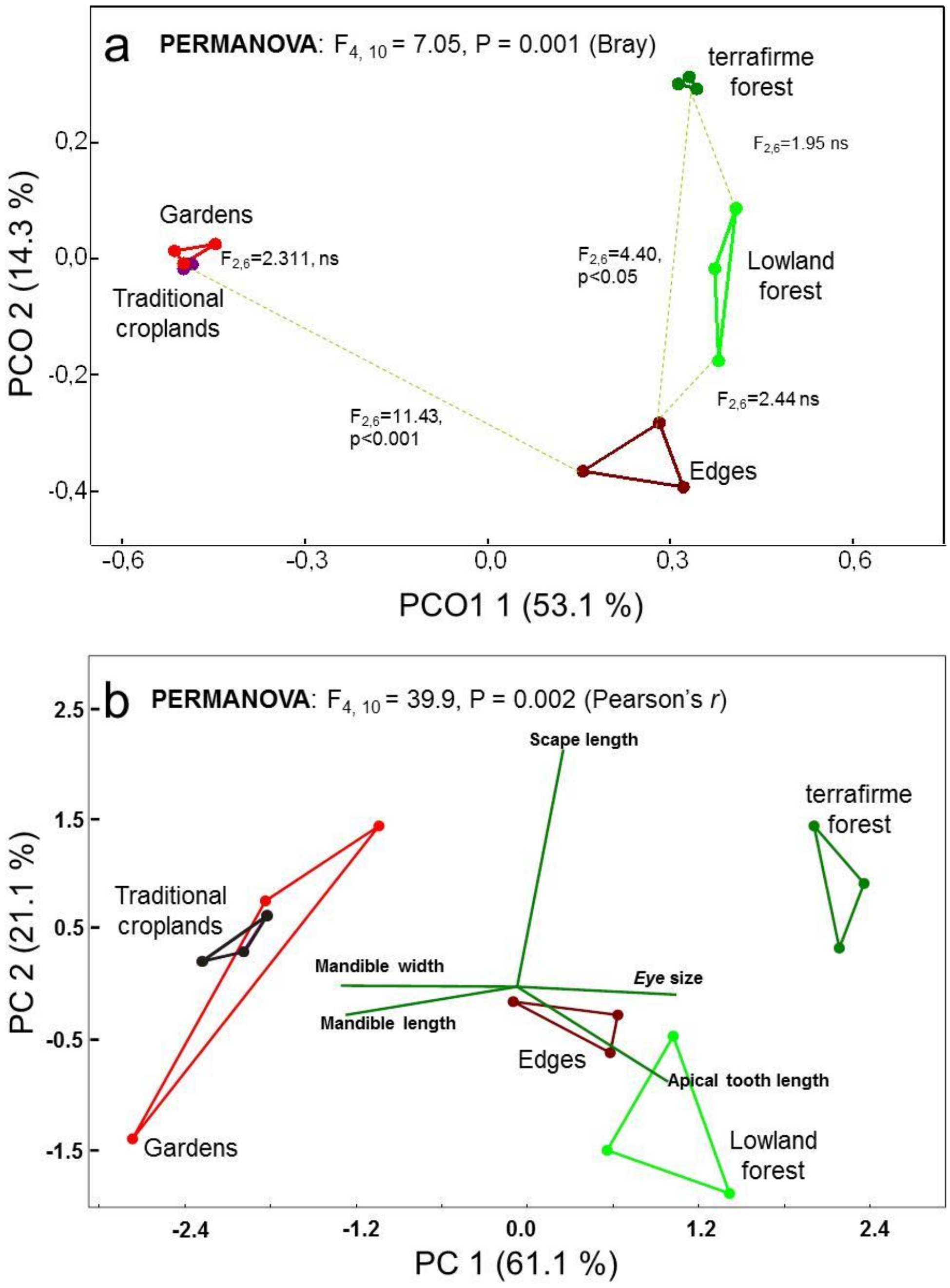

Figure 3. (a) Ant species composition in different local assemblages (arranged using Principal coordinates and the Bray-Curtis distance). Plots belonging to the same habitat are joined by convex hulls. Significant tests between habitats (PERMANOVA) are indicated by the dotted-lines joining the nearest neighbour for each group. (b) A principal component analysis using the Community-Weighted Means (CWM) for traits. Each plot is characterized by five selected traits (see text for more details). In both cases, signification tests were calculated using the FDR correction.

Croplands and gardens presented a similar species composition. Edges had a few species in common with open habitats (PERMANOVA, Bray-Curtis > 0.75, $P < 0.001$), but mostly shared species with forested habitats. For instance, the ant assemblages found in forest edges could not be distinguished from those found in lowland forests, which presented an intermediate species composition between forest edges and *terra firme* forests (no significant differences with either). Edges and *terra firme* forests were, however, inhabited by significantly different assemblages (Fig. 3a). Since species richness was not different between the edges and forests (Fig. 2a), the Bray-Curtis distance observed can only be explained by changes in the composition and relative frequency of species, rather than nestedness patterns.

Changes in species richness are not associated with changes in the morphospace

Among all of the 13 traits studied individually, only four presented significant patterns of trait-based habitat filtering after the FDR correction (Table 1). Ant communities from gardens and agricultural areas presented a narrower range of mandible sizes compared to those from the regional pool. In forested habitats (i.e. forest edges, and lowland and *terra firme* forests), the range of leg and apical tooth lengths and eye size were shorter and smaller, respectively, than expected by chance, although in different proportions depending on the habitat.

Table 1. Number of plots per habitat for which the observed range of traits is lower than for the regional pool ('null model' procedure). Only traits with significant habitat filtering signatures are displayed. Habitats are presented according to the land-use gradient: *terra firme* forest, lowland forest, forest edges, traditional croplands and gardens.

Trait	Gardens	Traditional croplands	Edges	Low-land forests	*terra firme* forests
Mandible width	1/3	2/3			
Apical tooth length			1/3	2/3	1/3
Eye size			1/3	3/3	2/3
Femur length					2/3

Despite a clear decrease in species richness along the land-use gradient (ANOVA $F_{4,\ 10} = 42.48$ $P < 0.001$), the five-trait morphospace (selected using the "bioenv" function) occupied by all of the species occurring in a plot showed little variation along the gradient (Fig. 2b).

Only the gardens and forest edges differed significantly (ANOVA $F_{1,\ 4} = 8.81$, $P = 0.04$), displaying the lowest and highest functional spaces, respectively. Forest edges presented the greatest morphological-trait space, although this pattern was not significant.

Niche shift along the land-use gradient

The examination of individual CWM traits showed that mandible width (ANOVA $F_{4,\ 10} = 6.6$, $P = 0.007$) and length (ANOVA $F_{4,\ 10} = 31.9$, $P = 0.0001$) decreased as land-use intensification increased (Fig. 4a, b; Table 2). Moreover, ants foraging in gardens and agricultural areas displayed longer apical teeth than did those nesting in forested areas (ANOVA $q_s > 10.5$, $P < 0.001$) (Fig. 4c). Eye size increased with land-use intensification (ANOVA $F_{4,\ 10} = 7.6$, $P = 0.004$), but dropped for those species nesting in gardens compared to those species nesting in traditional croplands (Fig. 4d).

Table 2. Statistical results of ANOVAs of individual trait responses across the different habitats. The symbol ¥ indicates that the community-level organization could not be interpreted for the trait under scrutiny (i.e. pairwise comparisons indicated differences only between two non-contiguous habitats without relation to the gradient examined).

Trait	DF	F	P
Total eye size	4	7.60	0.004
Mandible width	4	31.94	<0.001
Mandible length	4	6.63	<0.01
Apical tooth length	4	50.92	<0.001
Scape length	4	2.83	0.083
Clypeus length	4	4.96	0.018 ¥
Inter-ocular distance	4	3,41	0.052
Log Weber's length	4	3.13	0.065
Femur length	4	3.04	0.070
Anterior eye position	4	2.95	0.076
Pronotum width	4	2.82	0.084
Head width	4	2.03	0.165
Femur width	4	0.68	0.619

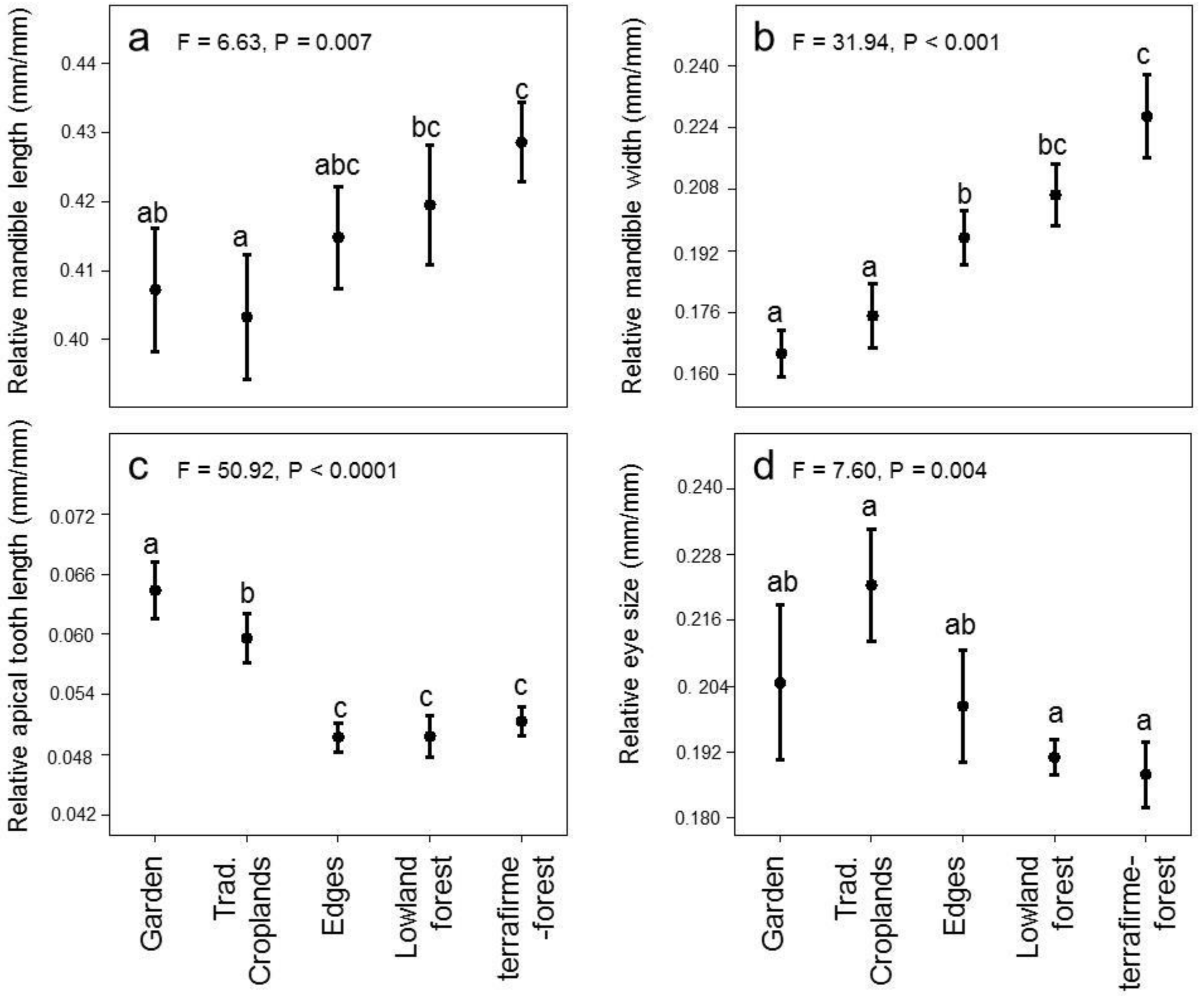

Figure 4. Variation in Community-Weighted Means (CWM) based on three replicate plots per habitat for relative mandible length (a), relative mandible width (b), relative apical tooth length (c), and relative eye size (d). FDR-corrected significant tests between habitats (ANOVA) are indicated with letters.

A Principal Component Analysis using the CWM values for the five traits selected for multi-trait analyses clearly delineated the different habitats along the first axis (PC1, 61.1%) (Fig. 3b). This axis mainly showed a negative co-variation between mandible length and width on the one side, and apical tooth length and eye size on the other. The second axis (PC2, 21%) was mainly characterized by scape length and separated species from the *terra firme* forest from those from lowland forests and forest edges.

DISCUSSION

To understand the drivers of the loss in species diversity related to human activity, there is an urgent need to identify the mechanisms behind species' adaptability to different habitat conditions as well as explain the capacity of ecosystems to bear a given number of species. Trait-based approaches have been successful in elucidating the drivers of variation of *alpha* and *beta* diversity in organisms like plants (e.g. Lamanna *et al.* 2014) and the effects of the intensification of land use on different taxa (Flynn et al. 2009). Pioneering examples concerning ants showed significant variations in the mean trait values of a community of several behavioural, morphological and life history traits along broad environmental gradients (Arnan et al. 2013, 2014, Yates et al. 2014). Here, we show a reduction in species richness in the most disturbed habitats without a reduction in the morphological space occupied by co-occurring species. This might be interpreted as the outcome of other key biotic and abiotic drivers in the continuing coexistence of local ant species. A second key finding is that the taxonomic changes observed across the land-use gradient are followed by changes in Community-Weighted Means (CWM) for morphological traits. Together, our findings illustrate the relevance of using a trait-based approach to discover the drivers behind changes in ant biodiversity within and across habitats.

Species richness and the morphological space

The observed diminution in species richness with land-use intensification could not be entirely related to the hypothesis of niche contraction. On the one hand, the range of individual traits was affected by habitat conditions, although trait-based habitat filtering varied between habitats and the traits under scrutiny. Moreover, variations in species richness between habitats were not accompanied by significant changes in the morphological space. Curiously, the forest edges plots contained a marginally lower number of species than did forested habitats, but their morphological diversity appeared greater according to the hypervolume. This may be related to the inclusion of ant species from open and forested habitats in forest edges, which were morphologically very distinct. These results considered together suggest a compensatory effect of different traits on the total morphological space occupied. Finally, the fact that the morphospace was not affected by habitat filtering and did not vary with species richness further suggests that overall niche dimensionality may be a poor driver of local ant diversity.

Several explanations can be advanced to explain the divergent responses of species richness and morphospace to land-use changes. First, because the species' mean traits were used in this study, it is still possible that the morphospace would differ between habitats by considering intraspecific variability (Violle et al. 2012) or intra-colony variations which can be greater than differences between colonies (Tschinkel et al. 2003). Moreover, from a niche-based perspective, the fact that forested habitats contain a greater number of species without changes in the plot-level morphospace may suggest that species are more tightly packed in this habitat. This might be explained by a greater abiotic filtering of morphological traits in forests or that niche differentiation is more pronounced in open habitats potentially due to more intense ant-ant interactions. This could not be confirmed, however; although we also examined the upper-tail of trait ranges, we did not find coherent trait overdispersion patterns. Another alternative hypothesis is that *Solenopsis saevissima*, both present and dominant in gardens and croplands, may outcompete several other species as has frequently been reported for fire ants (Tschinkel 2006, Dejean et al. 2015). Finally, an alternative possibility is that the use of hypervolumes in our estimation of morphological spaces reduced our ability to detect changes in the niche space. We do not believe this to be the case, however, because the accuracy of our results was evaluated through manipulations of the data set. Moreover, we also verified that relatively similar results could be obtained with other related indices (i.e. functional dispersion and Rao quadratic entropy) (Mason et al. 2013).

Furthermore, sampling methods may also affect the species captured and their associated traits. For instance, our sampling method consisted of food baits to attract ants foraging on the ground. While the diverse set of food items chosen enabled us to capture a large number of species, other species might have been captured using other sampling methods or sampling at different times of the day (Houadria et al. 2015).

Taxonomic changes are accompanied by a strong functional shift

A high level of species substitution was observed across habitats along the land-use gradient in accordance with findings from previous studies (Agosti et al. 2000, Underwood and Fisher 2006). Interestingly, species replacement between habitats was best explained by the variation in five morphological traits. Four of these traits also showed significant variations when examined individually: mandible length and width decreased with land-use intensification, whereas apical teeth length and eye size increased. These traits probably reflect changes in both food availability and the microhabitat (e.g. more or less litter accumulation) along the gradient. Mandible traits (i.e. length, width, tooth size) have indeed been linked to trophic functions and eye traits either to trophic functions and/or microhabitat (Fowler et al. 1991; Weiser & Kaspari 2006; Silva & Brandão 2010). For instance, in forests, the abundance of hypogaeic and predatory species was greater than their abundance in croplands and gardens. These species had smaller eyes and smaller body sizes and longer mandibles, respectively.

The few previous studies that focused on variations in mandibular and eye traits in relation to habitat shifts also found ants with longer apical teeth and a smaller mandible size in open habitats (Yates et al. 2014, Gibb et al. 2015b). These repeated patterns found in different regions (i.e. Neotropical and Australian), together with other findings highlighting trophic shifts at the community level between habitats, provide further evidence that trophic-related traits participate in structuring ant communities (Bihn et al. 2010, Pfeiffer et al. 2014, Gibb et al. 2015b).

According to thermal resistance-size and size-grain hypotheses, we expected ants from traditional croplands and gardens to be larger and have longer legs than those found in forested habitats. We failed, however, to find such patterns as was the case for previous studies (Parr et al. 2003, Wiescher et al. 2012, Gibb and Parr 2013). Nevertheless, we carried out sampling during the morning specifically to avoid an excessive thermal stress enabling us to capture most of the diurnal ants present, but, based on previous studies, variations could have taken place during the day or between day and night (Cerdá et al. 1998b, Houadria et al. 2015). An additional explanation might be that greater size can be costly in terms of worker production, particularly in frequently disturbed habitats like croplands and gardens, which may increase the mortality of foraging workers. Overall, this reinforces the importance of advancing our knowledge on the ‘functionality’ of these traits, as illustrated by recurrent contrasting results when testing such hypotheses (Oberg et al. 2012; Wiescher et al. 2012).

CONCLUSION

The application of trait-based approaches to invertebrate biodiversity is important (e.g. Pey et al. 2014), especially towards understanding community transitions along environmental gradients. Here, we have been able to define the niche space of ant communities based on the statistical selection of five core functional traits. While we have proven the relevance of this choice in tracking the functional responses of ant communities to land-use intensification, other studies defined the morphospace based on a slightly different set of traits (e.g. a set of six traits: clypeus length, eye length, mandible width, mesosoma length, petiole height, and femur length; in Silva & Brandão, 2010). This opens up an interesting area of research concerning the traits that should be measured as well as the number of functional dimensions needed to portray the niche space of ant species and communities (Arnan et al. 2014, Silva and Brandão 2014).

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V. ECOLOGIE DES ECOSYSTEMES : RELATIONS ENTRE BIODIVERSITE ET PROCESSUS ECOSYSTEMIQUES

L'objectif de ce chapitre est d'essayer de comprendre comment la performance des communautés de fourmis dans l'utilisation de différentes ressources alimentaires est liée à la composition et à la structure fonctionnelle de ces communautés. Il s'insère donc dans la lignée de recherche étudiant les rapports entre biodiversité et fonctionnement des écosystèmes (Hooper et al. 2005, Díaz et al. 2006a). Bien que le chapitre précédent visait à comprendre les mécanismes responsables de la composition et de la structure fonctionnelle des communautés, celui-ci va plus loin dans le but de comprendre comment cette structure est liée à l'activité combinée des espèces dans l'obtention de ressources alimentaires. En conséquence l'accent est mis sur les attributs de la communauté entière et sur les implications que cette communauté peut avoir sur le fonctionnement des écosystèmes plutôt que sur les espèces.

L'écologie des écosystèmes est principalement basée sur deux hypothèses : i) les organismes ont un effet positif sur les taux de processus écologiques via leur complémentarité (Chapin et al. 1997, Hooper 1997), ii) quelques organismes favorisés par les conditions environnementales monopolisent la majorité des ressources et vont être responsables de la plupart des processus (Aarssen 1997, Grime 1998). De plus, l'écologie des écosystèmes a pour but de prédire les relations entre organismes et fonctionnement des écosystèmes à travers des indicateurs plus simples que la quantification de l'abondance des organismes et leur contribution processus.

Ainsi, je me suis d'abord intéressé aux liens qui existent entre structure taxonomique et trophique des assemblages et leur performance dans l'exploitation de ressources dans différents conditions environnementales (Article 4). J'ai ensuite étudié les relations entre composition morphologique des communautés de fourmis et l'intensité de prélèvement de différentes ressources (Article 5). L'hypothèse était alors la suivante : la morphologie des espèces est reliée à leurs différences alimentaires, et les valeurs moyennes de traits des communautés sont des indicateurs de la performance de la communauté à prélever ces différents types de ressources.

V.1 DES DIFFICULTES POUR INFERER LA REALISATION DE PROCESSUS PAR LES FOURMIS

Nos résultats démontrent premièrement qu'une perte de diversité n'a pas entraîné une diminution dans l'activité de fourragement des fourmis. Si l'on accepte que ces activités de fourragement constituent un indicateur de la contribution des fourmis à différents processus écosystémiques, nous ne pouvons pas valider l'hypothèse sur les relations positives entre le nombre d'espèces et leur performance à réaliser des processus (Hooper et al. 2005, Díaz et al. 2006a). Cependant, et comme on l'a vu dans les sections précédentes, la diversité écologique était fortement conservée entre habitats malgré la simplification environnementale dans les milieux anthropisés/ouverts. Est-ce donc la diversité fonctionnelle qui est responsable d'une maintenance des processus écologiques (Poisot et al. 2013, Frainer et al. 2014, Gagic et al. 2015)? Nos résultats ne soutiennent pas non plus cette hypothèse, car l'examen des processus isolés, ne semblent pas confirmer un pattern de relation entre diversité fonctionnelle et activité dans des appâts (Article 4).

Bien que l'intensité des activités des organismes soit une mesure importante du fonctionnement des écosystèmes, les proportions (taux) dans lesquels ces différents processus sont réalisés constituent aussi un facteur essentiel pour comprendre leur stabilité (Cardinale et al. 2009b). En effet nous avons trouvé que les proportions de ressources utilisées par les fourmis étaient différentes en fonction de l'habitat. Ainsi, nous nous sommes penchés sur la structure trophique et/ou morphologique afin de savoir si elle(s) pouvai(en)t expliquer ces variations. On trouve alors que l'utilisation de ressources alimentaires par les espèces de fourmis semble garder un lien avec l'environnement (Article 4) mais aussi avec leurs traits morphologiques (Article 5). Ces relations sont en partie expliquées par la phylogénie des espèces (Article 5). D'une part, nous avons trouvé que la consommation de proies par les fourmis était plus importante dans les abattis et les jardins, que dans les habitats forestiers. Ceci est en accord avec d'autres travaux démontrant que les fourmis associées aux milieux ouverts consomment une proportion de ressources plus riche en protéines qu'en carbohydrates, tandis que la tendance opposée est trouvée dans les forêts (Bihn et al. 2008, Peters et al. 2014). Or nous avons également observé que la consommation d'insectes morts était tout aussi importante dans les deux types de milieu (Article 4). Dès lors, ces différences d'exploitation des ressources sont-elles donc liées à l'efficacité supérieure des espèces des milieux ouverts dans l'exploitation de proies ou sont-elles dues à la limitation de ces ressources dans les autres types d'habitats ? L'ensemble de nos observations nous empêche de privilégier une possibilité plutôt qu'une autre.

Nous avons également trouvé une relation positive entre la taille du corps, des mandibules et la capacité des fourmis à capturer des proies. Les fourmis en question appartenaient souvent aux sous-familles Ponerine et Ectatomminae. De plus les espèces exploitant le plus souvent des graines appartenaient principalement à la sous-famille Myrmicinae. Ces fourmis étaient en moyenne de taille réduite. Enfin, les fourmis exploitant majoritairement des carbohydrates appartenaient essentiellement aux familles Formicinae et Dolichoderinae qui possédaient de longues pattes et de longues antennes (Article 5).

Ces résultats suggèrent qu'on peut prédire le rôle écologique des espèces en prenant en compte leur morphologies et leur groupe taxonomique (Silva and Brandão 2010, Yates et al. 2014, Gibb et al. 2015b). Cependant, la prédiction des processus écologiques réalisés par une communauté en fonction de sa structure fonctionnelle, est une tâche plus compliquée. En effet, les résultats ne suggèrent que de manière très faible qu'on puisse employer des mesures intégratives des traits/niches des communautés pour une prédiction de leur utilisation de ressources, et donc pour prédire des processus écologiques. En effet, ce lien entre structure fonctionnelle et processus était plutôt nuancé dans l'article 4ème, car les liens étaient spécifiques à chaque environnement, une généralisation n'était donc pas possible. Dans le 5ème article, on n'a pas trouvé de liens entre les variations de traits morphologiques au niveau des assemblages, et la performance de ces assemblages dans l'exploitation de différentes ressources.

ARTICLE 4. ANT-MEDIATED ECOSYSTEM PROCESSES ARE DRIVEN BY TROPHIC COMMUNITY STRUCTURE BUT MAINLY BY THE ENVIRONMENT

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ABSTRACT

The effects of diversity and functional identity of organisms matter to maintain ecosystem processes but these can be variable in different environments. Particularly, it is uncertain whether ecosystem processes are driven by complementary effects or by dominant groups of species. We investigate how community structure (i.e. diversity and relative abundance of biological entities) and environment are related to community-level contribution of Neotropical ant communities to different ecosystem processes. Ants were attracted with food resources representing six ant-mediated ecosystem processes in four environments. These environments resulted from a crossed design combining ground and vegetation strata in cropland and forest habitats. The exploitation frequencies of the baits by species and entire communities were used to estimate species and community-level performance in exploiting such resources. The taxonomic and trophic structure of ant communities in terms of complementarity and dominance were calculated. We then used these variables to predict individual ecosystem processes and multiple processes simultaneously between and within environments. We found significant variations in taxonomic and functional composition and ecosystem processes between the four environments studied. Only trophic-based indices captured variations in ecosystem processes. Environment played the most significant role in determining the overall performance of communities exploiting resources as well as in explaining variations in taxonomic and trophic community structure. We conclude that while the trophic structure of ant communities is related to ecosystem processes, our data show that biodiversity – ecosystem functioning relationships are largely context dependent about which it is difficult to generalize.

Keywords: biodiversity – ecosystem functioning, complementarity, dominance, Formicidae, food resources

INTRODUCTION

The conversion of forests into agricultural ecosystems is one of the major causes of species loss and homogenisation worldwide (Chapin et al. 2000, Lindemayer et al. 2012). Such changes have direct consequences in the structure of ecological communities and the maintenance of ecosystem processes and functioning, which are unknown in the long term. Ecosystem processes are generally understood as fluxes of matter and energy between compartments of an ecosystem (Hooper et al. 2005, Jax 2005). Community structure refers to the diversity and abundance of organisms in a community, two attributes particularly relevant to understand community changes in environmental gradients and their effects on ecosystem processes (McGill et al. 2006). Biodiversity can refer to the number of species, but also to the functional diversity, which provides a measure of the range of ecological strategies among the species present (Hooper et al. 2005, Cadotte et al. 2011). During the last decade many studies have tried to assess the importance of species diversity, identity and relative abundance in maintaining ecosystem processes in relation to habitat conditions (Hooper et al. 2005, Díaz et al. 2006a). The general expectation is that biodiversity has a positive effect in ecosystem processes such as decomposition, predation or plant productivity via complementary effects of species using resources (Petchey and Gaston 2002, Balvanera et al. 2006, Cadotte et al. 2011). This expectation is directly drawn from the niche theory, since ecological partitioning theoretically decreases competition, increasing overall community performance in using resources (Poisot et al. 2013, Turnbull et al. 2013). In contrast, other studies suggest that a few species frequently dominate the largest fraction of available resources, and are responsible for most of an ecosystem's productivity (Aarssen 1997, Grime 1998, McKane et al. 2002). Likewise, environmental pressures may favour the competitive advantage of species with particular functional traits (Fox and Vasseur 2008, Bílá et al. 2014). Therefore, the general properties of ecological communities may better be captured by assessing the dominance structure of communities, or from a functional perspective, the average community properties as stated by the mass ratio hypothesis (Grime 1998, Garnier et al. 2004).

In opposition to the hypothesis of species-driven ecosystem processes, there is a great uncertainty on whether biodiversity – ecosystem functioning relationships are driven by species or whether species diversity or activity respond to environmental factors such as light, precipitation or chemical fertility (Gross and Cardinale 2007, Scherber et al. 2010). Furthermore, the relative abundance of different resources (e.g. ecosystem stoichiometry) may drive the number and identity of species in communities associated with different processes (Kaspari et al. 2012). Therefore, it seems relevant to understand how changes in biodiversity, and changes in community functional properties take place in relation to different ecosystem processes in different environments (Gamfeldt et al. 2008, Mouillot et al. 2011).

In this study, we investigate the relationships between species resource use, their environment and community structure in Neotropical ant communities. Neotropical forests harbour one of the richest faunas in the world, as well as one of the most endangered by the rapid forest conversion into agricultural areas in the last decades (Morris 2010). Quantifying the exploitation of different resources by co-occurring species should be helpful to understand the environmental and biotic constraints driving biodiversity relationships with ecosystem functioning (McKane et al. 2002, Poisot et al. 2013). This is particularly relevant for ants, for which these relationships have rarely been investigated (Fayle et al. 2010, Philpott et al. 2010). Ants are abundant organisms in the majority of terrestrial ecosystems, and they participate in several ecosystem processes and functions through their use of food resources (Folgarait 1998, Philpott et al. 2010, Brandão et al. 2012). For instance, some ant species play eminent roles as insect predators (Philpott and Armbrecht 2006), mutualist protectors of plants or insects while foraging for sugars (Blüthgen and Fiedler 2004a), or detritivores consuming carrion and excrements (Kaspari and Yanoviak 2001, Houadria et al. 2015). Using six food resources representing such ecosystem processes, we attracted ants foraging in two ecosystem strata (ground and vegetation) in two habitat types (forests and croplands). These four environments were chosen to represent the most common ecosystem conditions in natural and agricultural ecosystems in the geographic region studied and because we expected nutritional differences to occur between them (Kaspari and Yanoviak 2001, Peters et al. 2014). The taxonomic and trophic structure of ant communities were then compared between these four environments and used to explain community performance in exploiting resources.

Specifically, we test whether the community-level performance in exploiting individual resources (processes) and their combination in a multifunctionality index are positively affected by: (i) the number of species, (ii) the dominance of particular species, (iii) the trophic complementarity of species, (iv) the dominant trophic phenotype in the community, and/or (v) environment (habitat and strata) above any biodiversity variable. We have no clear *a priori* expectations of which of these features should govern, although we expect ant community structure to affect ant performance in mediating ecosystem processes.

MATERIALS AND METHODS

Study site and sampling protocol

The study took place in the *La Montagne des Singes* area, Kourou, French Guiana (5°04’27”N, 52°42’03”W). The climate is equatorial and affected by the Intertropical Convergence Zone, with mean precipitation about 3000 mm and a mean humidity of 80-90%. Temperatures vary between 18 and 35ºC. Sampling was performed in five forest areas and four traditional cropland areas. These habitats were chosen as representative of the most spread forest type in the coastal part of the Guianas, and the traditional farming technique. Thus we expected to capture the typical pressures that ant biodiversity (and biodiversity in general) is facing in the land-use transformation process (Lindemayer et al. 2012). All of the plots were located within a radius of 3 km and separated by at least 250 m from each other, and relatively interspersed. Forests plots belong to the same forest continuum dominated by the botanical families *Fabaceae*, *Chrysobalanaceae* and *Lecythidaceae* as is frequent in the species-rich forests in the coastal part of French Guiana. These plots were characterized by a great diversity of tree morphologies and sizes, a thick litter layer, and large amounts of wood debris. Croplands were areas where the original forest was burnt and replaced by mixed crops (e.g. banana trees, cassava, pineapple, sugar cane). The vegetation was generally young (i.e. less than 4-years and less than 3-m tall), providing an irregular shade and the absence of litter. The sampling was performed between January and July 2013, between 08:00 AM and 11:00 AM (no later than 10:00 AM in the croplands due to high temperatures) and only in the absence of rain and in dry soil conditions to avoid any bias linked to field conditions or frequently observed temporal variations (Wittman et al. 2010, Houadria et al. 2015). Sampling consisted of baiting trials where food items were placed on the ground and on the vegetation during separate sampling sessions. Habitat and strata combinations were considered as separate environmental classes (hereafter, environments) because sampling revealed major variations in taxonomic composition and differences in ecosystem processes as is to be expected due to different resource limitations between habitats and ecosystem compartments (Kaspari and Yanoviak 2001, Peters et al. 2014). Moreover, because the number of exploited baits and ant activity and diversity greatly differed between these four environments, a stratified sampling strategy was adopted to obtain sufficient species-wise information. Particularly, we limited the number of cropland plots since the species composition was very similar in all of them and the number of species was lower than in the forest plots. In addition, the number of sampling locations on trees was increased in both habitats because discovery rates were lower, and, in general, a single species was found foraging on each tree, in contrast to ground sampling locations where several species foraged simultaneously. Consequently, 20 sampling locations were distributed at ground level on a grid system of 4 x 5 grid points with a 10-m interval between the points. In addition, 40-50 trees and understory plants of various sizes were chosen in each plot, for a total of 400 plants in all forest plots combined and 165 in the croplands. Only plants on which at least one of the baits was exploited were taken into account. All the metrics used in this study are based on relative occurrences which control for any bias related to the number of samples.

Ants were attracted using six food types associated with ecosystem processes. Two sugars, sucrose and melezitose (3 ml of 25 % weight water solution) represented the use of carbohydrates which mediate ant protection of plants (e.g. sucrose in nectar) and sap-sucking insects (e.g. melezitose in honeydew). Dead mealworms (*Tenebrio molitor*) and chicken feces (3 g each) represent two different sources of detritus consumed by ants (i.e. processes of scavenging and coprophagy). These detritus differ, however, in their nutrient content; excrements contain lower amounts of proteins and other nutrients. Finally, we separated predatory function into small prey (at least 20 alive termite individuals: *Anoplotermes* sp.), and large prey (two, live 1.5-cm and 3-cm long mealworms) since prey size may determine the ability of different species to handle prey (see also Houadria et al. 2015).

At each sampling location, all of the resources were presented once. At ground level, each resource type was presented in a Petri dish (5 cm in diameter) covered with Parafilm® which was wrapped around the dish at collection time to prevent the ants from escaping. In the vegetation, the food resources were displayed in 2 ml Eppendorf ® tubes attached to branches at between 80 cm and 1.5 m in height, so that the mouth was in contact with the trunk or branch. The food baits were presented during two different sessions, with first all non-prey items and then prey items, which enabled us to survey prey capture behavior (as otherwise many of the mobile prey escaped). On the ground, the food baits were simultaneously presented in a circle surrounding the sampling location, each of the baits separated by at least 50 cm from the others. This distance was chosen after preliminary trials that confirmed it prevented several baits from being monopolized by a single recruitment trail. In the vegetation, the baits were randomly distributed to prevent monopolization by a single species. Ants attracted to the baits were collected after 1 hour by closing the Petri dishes or the Eppendorf tubes.

Biodiversity variables related to ecosystem processes

To investigate the relationships between community structure and ant-mediated ecosystem processes, four biodiversity variables were calculated for each of the 18 communities studied (see below). We used species occurrences on the different food types, organizing the data in a matrix with resource types (processes) in columns and species in rows (Appendix. 1). Cells indicate the number of times a species was found on each resource type. Standardization by rows provided an estimate of the relative use of the different resource types by the species considered and can be understood as a proxy of the species' role in the ecosystem studied. Standardization by columns enabled the assessment of the relative contribution of a species to particular processes. The few species that were present in more than one environment were considered separate species. Only species present on six or more occasions per environment were considered in the analysis, because any lower number of occurrences could not be distinguished from the random use of food types according to the *Chi*-squared distribution. The variables chosen represent major facets of community structure relevant to our understanding of ecosystem processes, namely, the diversity and dominance of the studied communities on the bases of taxonomic and trophic descriptors.

i) Effective taxonomic richness: For each of the resources tested separately and in combination (i.e. multifunctionality), the Hill numbers with diversity coefficient 1 were calculated (Shannon's entropy conversion described in Jost 2006). Effective taxonomic richness informs the real number of species consuming each resource type considering their relative abundance, thus limiting any bias related to differences in sample sizes between communities. The Hill numbers were obtained using the '*vegan'* package in R (Oksanen 2010).

ii) Dominance by particular species: The effect of individual species on processes was calculated as the percentage of baits of a resource type exploited or multifunctionality by the most abundant species (i.e. dominance index, D). This variable represented the ability of a single species to potentially ensure a given process.

iii) Trophic complementarity: To test whether resource exploitation was related to the degree of trophic complementarity, we calculated the "functional dispersion" of species according to their relative use of different food types using the R-package '*FD*' (Laliberté et al. 2014). This index provides a measure of the overall trophic space occupied by a community and the relative abundance of species distributed within that space, which is in keeping with the idea of interspecific food resource partitioning (Poisot et al. 2013).

iv) Community-weighted trophic mean: The tendency of each community to exploit the different resources was assessed using the community-weighted mean value (CWM) calculated for each plot and process (Garnier et al. 2004) as:

$$CWM = \sum_{i=1}^{S} p_i x_i \qquad (1)$$

Where p_i is the relative occurrence of species i at each of the 20 sampling points on the ground or each tree for the vegetation and x_i is the relative use of the resource by species i (standardized by rows in Appendix 1). This measure is driven by the relative abundance of species, and it is therefore associated to the dominant trophic phenotypes within communities (Grime 1998).

To provide a measure of the community-level performance in ecosystem processes, we considered the proportion of exploited baits of a given food type during the duration of the experiment (1 hour) compared to the total number of sampling locations in a given habitat. This provides an estimate of the probability of a given resource type to be exploited by any ant species within the community under examination. This is related to the fluxes or removal of these resources resulting from ant activity, which is directly related to the definition of ecosystem process (Hooper et al. 2005, Jax 2005). Ecosystem processes were examined individually and the proportions were then averaged to provide a portrait of the multifunctionality (Mouillot et al. 2011).

Statistical analyses

All of the statistical analyses were performed using the R software (R Development Core Team 2015). Analyses were performed on the bases of 108 values for each of the biodiversity variables representing community structure and resource exploitation rates. The data were derived from the six food resources tested on each of the 18 ant communities studied (five replicates for forest communities on ground and vegetation, and four replicates for cropland communities).

First, we examined variations in the four biodiversity variables selected between habitats and ecosystem processes. Each biodiversity variable was regressed against food (factor with six levels) and environment (factor with four levels), controlling for interactions between both using a 2-way type II Analysis of Variance recommended for unbalanced factorial designs. According to the nature and distribution of the data, a linear model was used to fit each of the four biodiversity variables, and a generalized linear model using a binomial distribution was used to examine the exploitation of resources where the number of exploited baits was compared to the total number of trials. Pairwise comparisons were carried out using Tukey's test or *Multcomp* package in R for linear and binomial assumptions, respectively.

To disentangle which biodiversity variables explained individual processes, we developed generalized linear models. We used the exploitation frequencies for each resource type (i.e. the number of exploited baits compared to the number of trials) as a response variable regressed against each of the biodiversity variables using a binomial distribution family. Then the same test was repeated regressing multifunctionality (the average of the six processes considered) against the effective taxonomic richness, dominance and trophic complementarity. In this case, an arcsine transformation was applied to the proportion of exploited baits and regressed against biodiversity variables using a linear model. Community-weighted means were not included in the multifunctionality model because when applied to proportions (i.e. relative food use) this provides an equal value for all the plots (i.e. 0.166). Moreover, there is no real reason to infer multiple functions from community-weighted values, as these are expected to correlate to specific functions.

Because we wanted to understand whether ecosystem processes could be explained solely by biodiversity mechanisms regardless of environmental conditions, the models were first developed using biodiversity variables alone and then including environment as a factor (with four levels corresponding to habitat and strata combinations).

RESULTS

A total of 137 species were captured in all the four studied environments combined (Appendix 1). The average number of species captured per plot was greater in forests, particularly on the ground (mean ± sd = 38.8 ± 4.0), although the number of species found foraging on vegetation was only the half (mean ± sd = 19.8 ± 3.6). As expected, the average number of species captured in cropland plots was lower, both on the ground (mean ± sd 15.5 ± 1.3) and on vegetation (mean ± sd = 12.8 ± 5.3). The percentage of baits occupied by the most abundant species (*i.e.* overall dominance) was considerably superior in croplands than in forests. For instance, *Solenopsis saevissima* occupied a third or more of the ground baits containing insects in any form. Moreover, *S. saevissima* together with *Pheidole fallax* and *Crematogaster* sp. 5 represented more than 75% of occurrences on ground baits. Baits placed on vegetation were mostly occupied by *Solenopsis saevissima* and *Camponotus novogranadensis* which together, were present in more than a third of the baits of any kind. In forests, the different resources were frequently exploited by many species, and a different species was the most abundant one on each resource type. Indeed, when considering all the baits in combination, the most abundant species on the ground (*Ochetomyrmex neopolitus and Wasmannia aurpunctata*) represented less than the 10% of the occurrences. The same happened on vegetation, where the two most frequent species at baits (*Crematogaster brasiliensis* and *Azteca* sp. 2) represented less than the 15 % of occurrences.

Community structure and variations in the community-level performance between processes and environments

The taxonomic and trophic community structure of ant communities examined greatly differed between processes (food types) and environments (Table 1, Figs. 2-4). The effective taxonomic richness varied between processes ($F_{5,\ 81}$ = 15.58, P < 0.001, Fig. 1) and environments ($F_{3,\ 81}$ = 13.19, P < 0.001), but no interactions were found between them ($F_{15,\ 81}$ = 1.34, P = 0.19). The greatest number of species was found on the ground in forest habitats (Tukey's HSD differences > 1.4, P = 0.026), and more species consumed dead insects and sugars in general, while large prey and excrements attracted fewer species (Table 1).

Table 1. Average values and standard deviation of the biodiversity variables and bait exploitation rates obtained at both the process and environmental levels. Letters indicate significant differences based on pairwise comparisons (Tukey's test and *Multcomp* package in R; see methods) after running an ANOVA.

	Effective taxonomic richness	Dominance	Trophic complementarity	Community weighted trophic mean	Bait exploitation rate
Large prey	2.75 ± 1.00 (a)	0.38 ± 0.14 (b)	1.08 ± 0.60	0.06 ± 0.03 (a)	0.44 ± 0.32 (a)
Small prey	6.05± 1.91 (b)	0.18 ± 0.09 (a)	1.47 ± 0.51	0.18 ± 0.03 (b)	0.69 ± 0.29 (b)
Dead insects	7.04 ± 2.98 (b)	0.19 ± 0.09 (a)	1.36 ± 0.34	0.25 ± 0.04 (d)	0.81 ± 0.19 (c)
Excrements	4.73 ± 2.14 (ab)	0.26 ± 0.11(a)	1.53 ± 0.62	0.09 ± 0.04 (a)	0.37 ± 0.16 (a)
Nectar	6.95± 2.01 (b)	0.17 ± 0.07 (a)	1.41 ± 0.32	0.24 ± 0.03 (c)	0.70 ± 0.25 (bc)
Honeydew	6.02± 2.23 (b)	0.20 ± 0.08 (a)	1.24 ± 0.32	0.18 ± 0.02 (b)	0.64 ± 0.25 (b)
Forest trees	8.01 ± 2.11(a)	0.23 ± 0.1 (ab)	1.22 ± 0.19 (a)	0.166 ± 0.07 (a)	0.41 ± 0.17 (a)
Forest ground	16.88 ± 2.07(b)	0.16 ± 0.11(a)	2.05 ± 0.15(c)	0.166 ± 0.08 (a)	0.75 ± 0.22 (b)
Cropland trees	7.24 ± .129 (a)	0.25 ± 0.14 (b)	1.31 ± 0.33 (a)	0.166 ± 0.08 (a)	0.40 ± 0.22 (a)
Cropland ground	7.72 ± 0.13 (a)	0.30 ± 0.12 (b)	1.78 ± 0.09 (b)	0.166 ± 0.06 (a)	0.89 ± 0.21 (b)

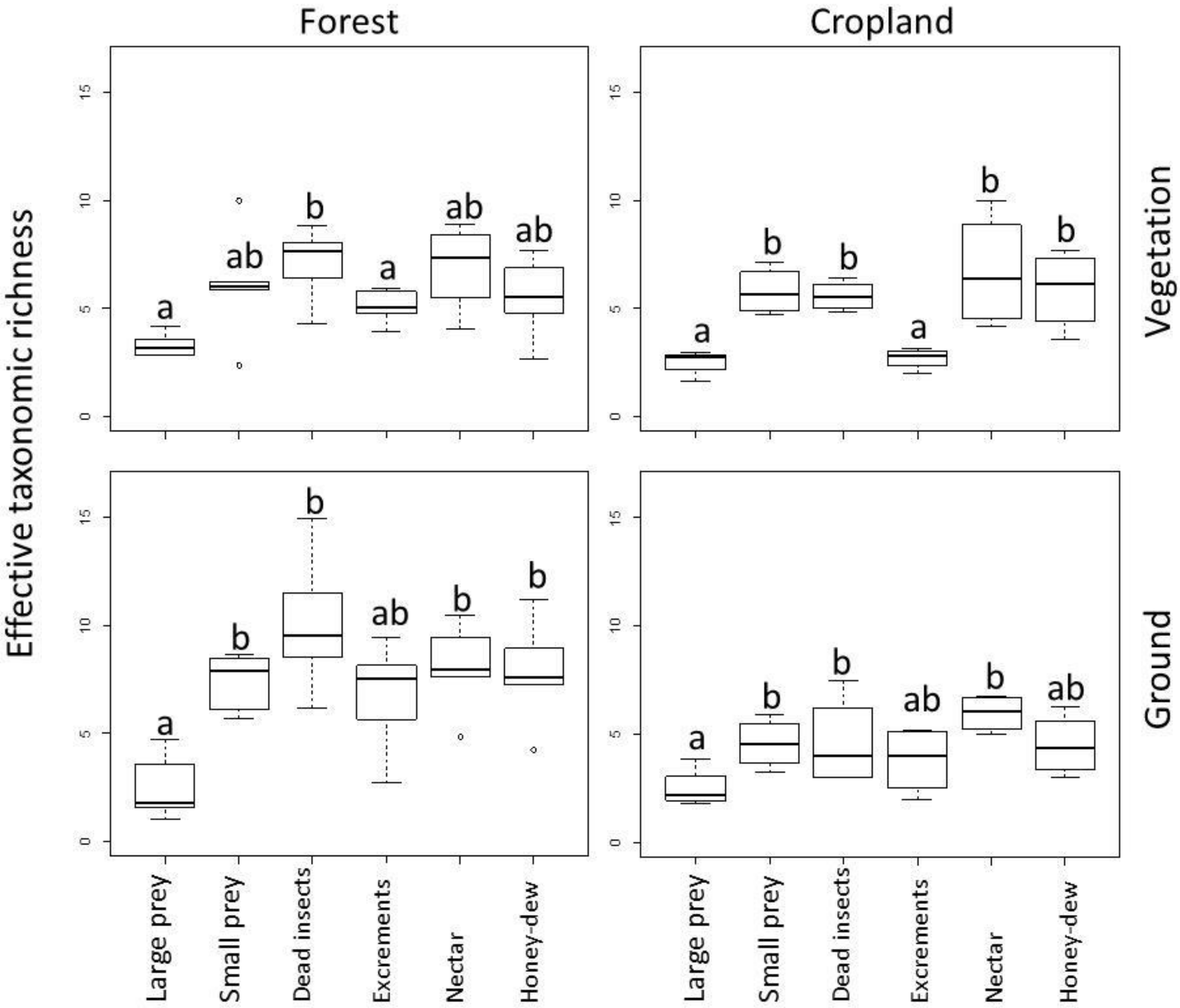

Figure 1. Box-plots of the effective taxonomic richness per food type between habitat and strata. Bold lines represent the median and whiskers account for the 95% confidence interval of the data. Outliers appear as circles. Letters indicate significant *post-hoc* differences using Tukey's test between processes within habitats.

Dominance varied between the different ecosystem processes ($F_{5,\ 84} = 14.15$, $P < 0.001$, Fig. 2) and environments ($F_{3,\ 84} = 9.52$, $P < 0.001$). No interaction existed between processes and environment ($F_{1,\ 84} = 1.03$, $P = 0.44$). Dominance values were lower on the ground in forest habitats, but significant differences were only detected between this environment and ground- and vegetation-foraging ants in the croplands (Table 1). Higher dominance values were also found for large prey compared to the other processes (Tukey's HSD all differences > 0.11, $P = 0.001$).

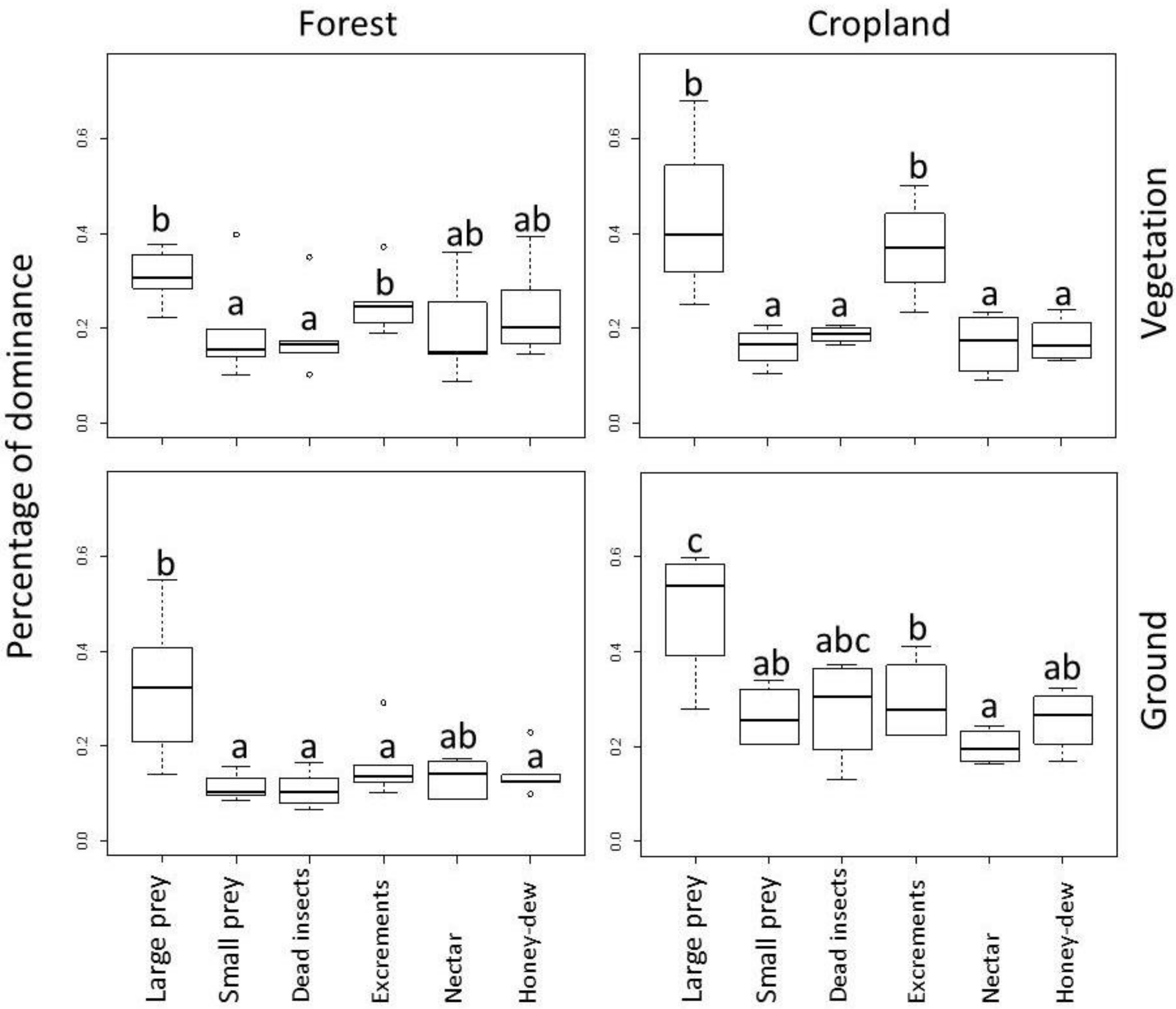

Figure 2. Box-plots of the dominance index per food type between habitat and strata. Bold lines represent the median and whiskers account for the 95% confidence interval of the data. Outliers appear as circles. Letters indicate significant *post-hoc* differences using Tukey's test between processes within habitats.

Trophic complementarity only differed between ground- and vegetation-foraging communities ($F_{3,\ 78}$ = 24.85, P < 0.001, Fig. 3) (Tukey's HSD mean difference > 0.32, P < 0.001; Table 1), and in the ground-foraging communities of the forest plots compared to the croplands (mean difference = 0.35, P = 0.003), but not between arboreal communities (mean difference = 0.015, P = 0.99). Significant variations in trophic complementarity were not detected between processes ($F_{5,\ 78}$ = 2.12, P = 0.071) and there was no interaction between environment and processes ($F_{15,\ 78}$ = 1.47, P = 0.13).

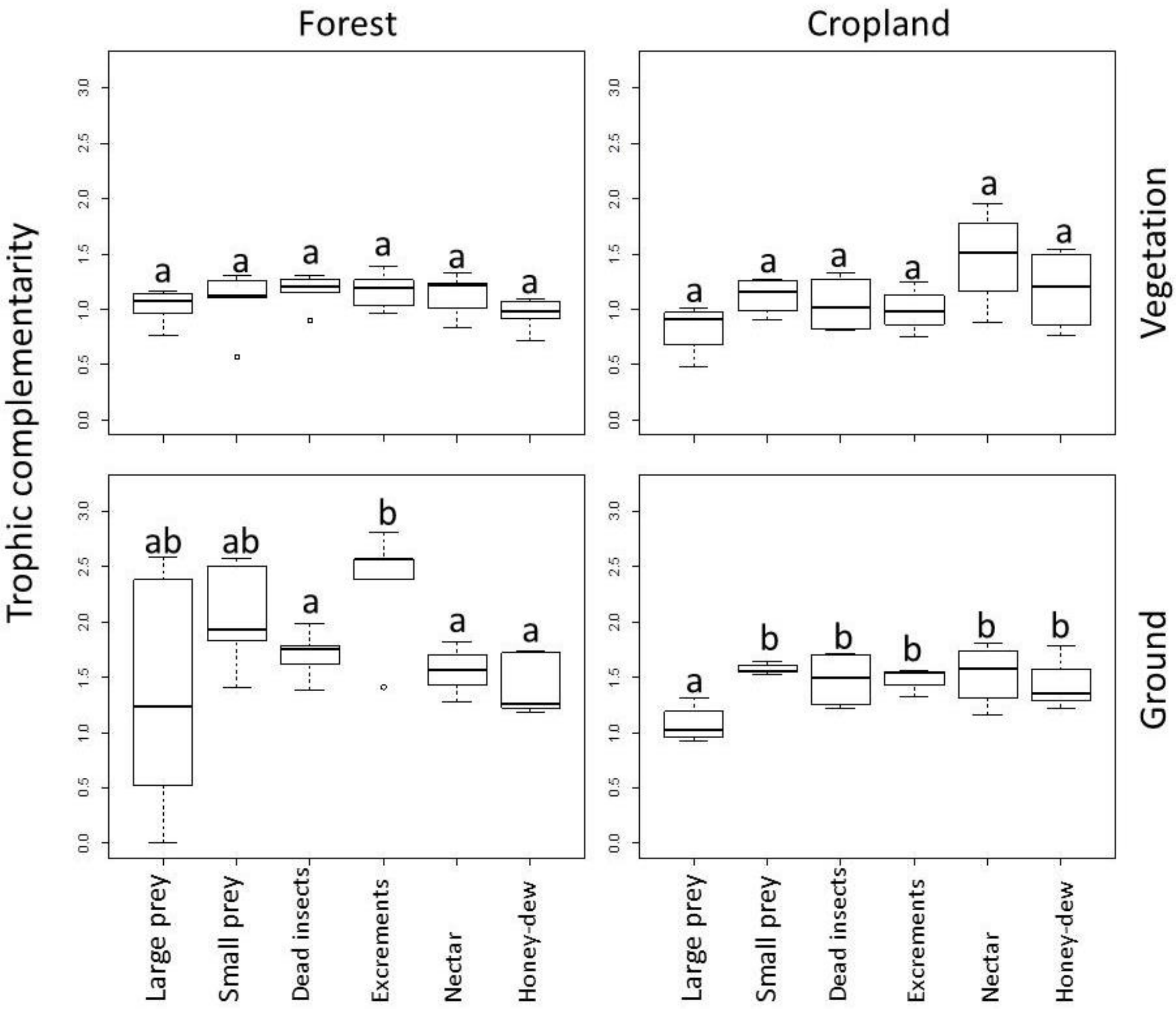

Figure 3. Box-plots of the trophic complementarity per food type between habitat and strata. Bold lines represent the median and whiskers account for the 95% confidence interval of the data. Outliers appear as circles. Letters indicate significant *post-hoc* differences using Tukey's test between processes within habitats.

The community-weighted mean values were significantly different between processes ($F_{5, 84}$ = 216.20, P < 0.001, Fig. 4), but not between environments. Dead insects were the most used resource in the four environments (Tukey's HSD minimal mean difference; Dead insects – Sucrose = 0.035, P = 0.02, Table 1). An interaction was detected between environment and process ($F_{15, 84}$ = 11.42, P < 0.001) and this is illustrated by a significant increase in the capture of large prey by ground-foraging communities in the croplands, or the consumption of excrements by arboreal-foraging communities in the forest plots compared to the other communities.

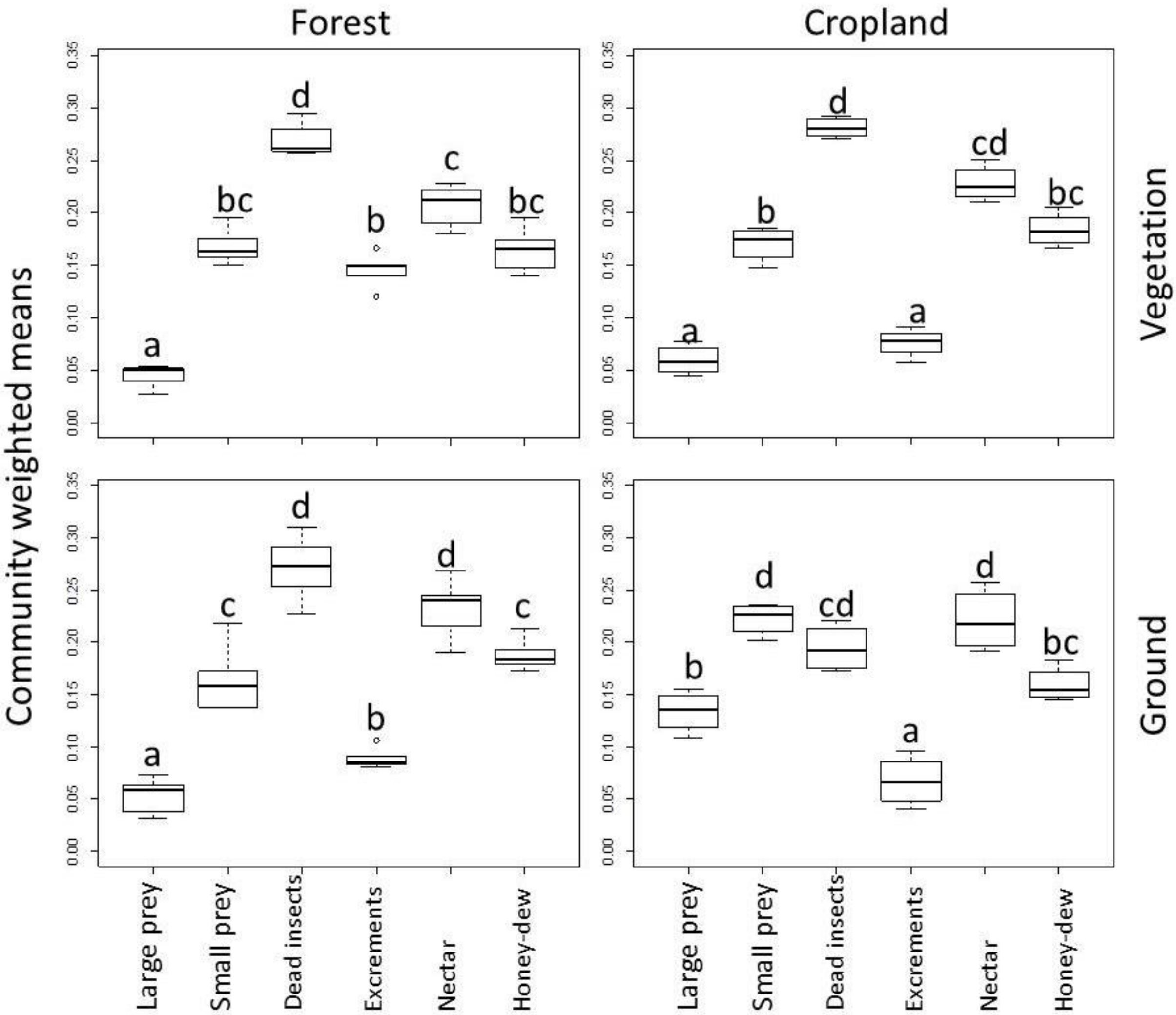

Figure 4. Box-plots of the community-weighted trophic mean values per food type between habitat and strata. Bold lines represent the median and whiskers account for the 95% confidence interval of the data. Outliers appear as circles. Letters indicate significant *post-hoc* differences using Tukey's test between processes within habitats.

Finally, the exploitation rates differed between processes (ANOVA, $\chi^2_{5,\,84} = 148.4$, $P < 0.001$) and between environments ($\chi^2_{3,\,84} = 41.07$, $P < 0.001$) but the factors were interdependent ($\chi^2_{3,\,84} = 55.38$, $P < 0.001$). Dead insects and sucrose were consistently the most exploited resources. Arboreal-foraging communities exploited the excrements relatively more frequently (Fig. 5), while the capture of insects, especially large prey, was relatively more frequent on the ground than on vegetation. Large prey baits were less frequently exploited than those representing other processes, with the exception of the excrements (Table 1). This tendency dramatically changed, however, on the ground in the croplands where the exploitation frequencies of large prey reached levels similar to other food items.

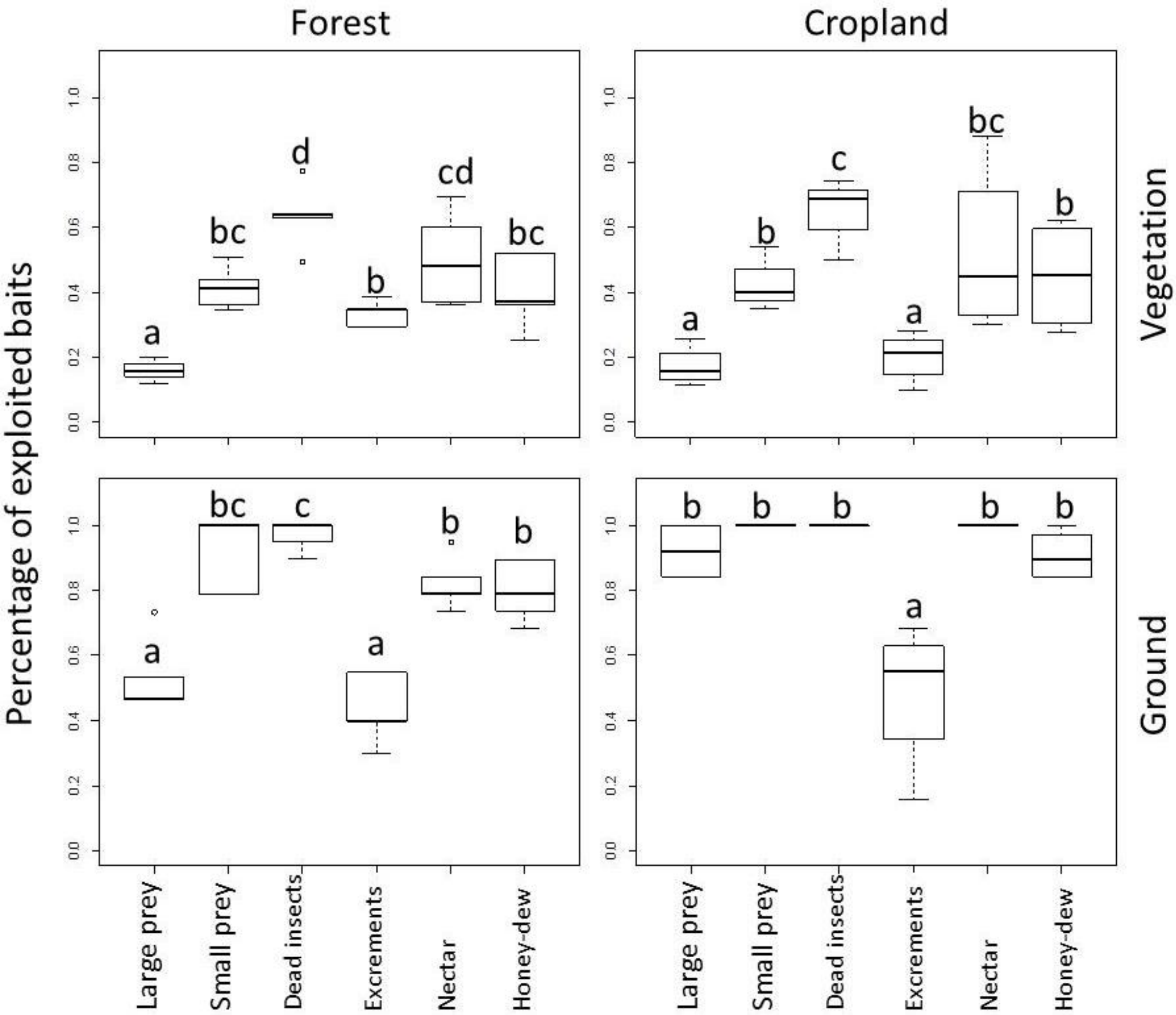

Figure 5. Box-plots of the exploitation rates of food types (i.e. ecosystem processes) between habitat and strata. Bold lines represent the median and whiskers account for the 95% confidence interval of the data. Outliers appear as circles. Letters indicate significant *post-hoc* differences using the *Multcomp* package in R between processes within habitats.

Effects of community structure and environment on ant community performance in ecosystem processes

When the effects of environment were not considered in the models, indices based on the trophic characterization of species were consistently more useful in capturing process variations between environments than were taxonomic-based indices (Table 2). For instance, the expected positive relationship between the effective taxonomic richness and community-level performance in the exploitation of food items was not found. Moreover, there was a negative correlation between the effective number of taxa and the frequency of exploitation of large prey. Particularly, it was greater on the ground in the croplands where the number of species associated with this process was the lowest ($Z = -3.4$). Dominance was positively related to the overall exploitation of small prey, indicating the key role of particular species in exploiting this resource type in some environments. The differences in the exploitation of prey resources between environments were captured by differences in trophic complementarity and also by community-weighted trophic mean (CWM). Particularly, greater levels of predation were recorded on the ground related to a greater trophic complementarity of these communities, and CWM reflected better differences between croplands and forests. The community-level exploitation of sucrose (representing nectar) was only significantly related to the CWM, and melezitose (representing honeydew) and dead insects to trophic complementarity. Finally, multifunctionality only showed a significant correlation with trophic complementarity (Table 2).

The inclusion of environment as a variable in the models highlighted the consistent effect of this factor on all of the processes with the exception of the exploitation of dead insects (Table 2). Moreover, the inclusion of environment offset the relationship between community structure and processes with only the CWM having significant relationships with the same food resources, and trophic complementarity with the exploitation of dead insects.

Table 2. Statistical tests of the relationships between biodiversity variables and individual ecosystem processes and multifunctionality. Tests were carried out both with and without environment as a factor. Asterisks indicate the level of significance after a two-tailed test. Significance codes: 0 '*' 0.001 '**' 0.01 '*' 0.05.**

Emulated Ecosystem Process	Effective taxonomic richness		Dominance		Trophic complementarity		Community weighted trophic mean		Habitat	
without environment *(n = 18)*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Large prey	12.162	***	2.845	ns	8.139	**	87.105	***	----	----
Small prey	0.092	ns	5.590	*	42.438	***	7.567	**	----	----
Dead insects	0.739	ns	0.967	ns	9.391	**	0.114	ns	----	----
Excrements	0.919	ns	0.00003	ns	0.107	ns	0.919	ns	----	----
Nectar	1.423	ns	0.035	ns	0.066	ns	10.823	**	----	----
Honeydew	1.217	ns	2.042	ns	16.097	***	2.012	ns	----	----
Multifunction	0.066	ns	0.025	ns	0.759	***	----	----	----	----
with environment *(n = 18)*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Large prey	0.481	ns	0.0183	ns	0.821	ns	4.130	*	25.115	***
Small prey	2.212	ns	0.766	ns	0.904	ns	12.279	***	17.025	***
Dead insects	0.959	ns	0.063	ns	6.066	*	2.090	ns	3.811	Ns
Excrements	1.702	ns	0.391	ns	2.484	ns	0.578	ns	10.280	*
Nectar	1.343	ns	0.006	ns	1.345	ns	7.311	**	46.777	***
Honeydew	0.383	ns	0.006	ns	0.009	ns	1.498	ns	24.600	***
Multifunction	0.0004	ns	0.0001	ns	0.001	ns	----	----	22.304	***

DISCUSSION

We report changes in the community composition and structure of Neotropical ant communities between four environments using a set of baits as attractants. The species richness levels reported here largely corresponds to those that we found in a previous study, supporting the high taxonomic and ecological diversity of the forests in the coastal part of French Guiana (Houadria et al. 2016). Our results indicate important environmental effects on the taxonomic and trophic structure of the ant communities examined as well as on their performance exploiting different food resources. Community-level use of different resources was related to the trophic structure of communities but loosely with taxonomic-based variables. In conjunction with certain authors, here we consider that resource exploitation represents the ability of ant communities to participate in ecosystem processes (Fayle et al. 2010, Šipoš and Kindlmann 2013). Other studies used baits with non-substitutable nutrients such as carbohydrates, lipids, proteins or salt, and interpreted their relative use as a consequence of resource limitations (Kaspari et al. 2012, Fowler et al. 2014, Peters et al. 2014). Nevertheless, the ecological roles of species should be rather defined by how species obtain such nutrients (Brandão et al. 2012). For example, an insect may contain proteins and lipids, but depending on whether it is dead or alive and depending on its size, different ant species are able to exploit these nutrients. This has very different implications for ecosystem functioning.

The percentage of baits exploited was greater on the ground than on the vegetation. These differences in ant activity between the two strata can be related to a lower availability of nesting habitats in trunks, resulting in a lower discovery rate of resources in the lapse of the experiments. We found no evidence of differences in the relative consumption of proteinaceous *vs* sugary resources between the ground and the vegetation in contrast to previous findings (Kaspari and Yanoviak 2001, Hashimoto et al. 2010). Nor did we find such differences when comparing croplands and forests, as did other authors studying ant communities in the Neotropics and East Africa (Bihn et al. 2008, Peters et al. 2014). Overall this might indicate that land-use changes effects in the trophic structure of ant communities may differ across biogeographical regions, or even within regions depending on environmental conditions (Arnan et al. 2014). Indeed, dead insects, which are the typical bait type representing protein limitations as well as scavenging, and baits containing sugars (here representing mutualistic protection) were well represented in the four environments studied. The percentage of captured prey was greater on the ground, particularly in the croplands, while the exploitation of excrements was considerably greater on forest trees. One possible explanation is that this increase may be due to the ability of many arboreal ants to recycle nitrogen from excrements (Cook and Davidson 2006).

We found higher levels of dominance and lower species diversity in the croplands in comparison to the forests, which is a frequent consequence of land-use changes (Fargione et al. 2007, Peters et al. 2014). The positive relationship between dominance and prey capture on the ground shows that a single species can maintain a high functional performance for specific processes (Cardinale et al. 2006, Houadria et al. 2016). Moreover, contrarily to that which is frequently expected, the number of species was not related to the execution of processes (Balvanera et al. 2006, Fayle et al. 2010, Maestre et al. 2012). Indeed, the exploitation of baits was slightly higher in the croplands, particularly on the ground. This is likely the result of the generalist foraging behaviour of many species in simplified environments (Andersen 1992, Fargione et al. 2007, Peters et al. 2014) and is corroborated by the lower trophic complementarity in croplands than in forests. Despite this finding, a positive relationship between trophic complementarity and the exploitation of several resources was found, supporting the expected positive effects of complementarity on ecosystem processes (Hooper et al. 2005, Cardinale et al. 2006, Poisot et al. 2013). This seems mostly explained by differences between the ground and the vegetation. Community-weighted trophic mean values (CWM) captured process differences between environments, and also the hierarchy of exploitation of the different resources within communities. This can be interpreted as providing evidence that ecosystem processes are largely driven by the functional identity of communities (Cardinale et al. 2006, Laughlin 2011, Bílá et al. 2014). Although, this also supports the limitation hypothesis which states that species forage more intensely for the most limited resources in their environment (Kaspari and Yanoviak 2001, Kaspari et al. 2012, Fowler et al. 2014, Peters et al. 2014). Conversely, when substitutable resources are considered (i.e. partially overlapping in their nutrient contents), species tend to specialize in the exploitation of the most abundant resources (McKane et al. 2002, Fox and Vasseur 2008). Therefore, whether differences in the CWM between environments are a consequence of resource limitations or suggest an ecological convergence towards abundant resources requires further investigation.

Finally, the inclusion of environment in the models revealed that this was the most significant factor explaining ecosystem process variations. This finding, in conjunction with the strong influence of environment on the taxonomic and trophic structure of the communities examined suggest that relationships between community structure and performance in providing processes are to a large extent, context specific (Needham et al. 2011, Frainer et al. 2014). For instance, ground foraging communities in forests and croplands presented remarkably different community structures, with none of the biodiversity variables alone presenting a clear relationship with the process rates observed for the different resources. In contrast, we found that vegetation communities in forests and croplands presented similar values in all the biodiversity variables considered, as well as their overall performance exploiting the different food resources. Moreover, the values found for CWM and effective taxonomic richness in vegetation reflected variations in the exploitation rates of different resources. Such differences between ecosystem compartments depending on the habitat could lead to very different interpretations about the consequences of land-use changes on biodiversity-ecosystem functioning relationships. Overall, complementary and dominance effects seemed to drive processes in combination, but their relative contribution was variable depending on the environment.

CONCLUSIONS

Despite the partial success of trophic biodiversity variables in predicting processes, we cannot conclude unambiguously whether these were the drivers of ecosystem processes because of the predominance of an environmental effect. Such an effect can be significant even within habitats, as illustrated by the major differences found in the community structure and the differences in the use of resources between the ground and the vegetation. Therefore, we suggest caution in the interpretation of community structure effects on ecosystem processes. Nevertheless, it can still be argued that biodiversity variables are indicators of these processes. Future studies need to consider species abundance, their ecological characteristics and performance in exploiting resources together with resource availability in different environments. Such studies would contribute to our understanding of how resource abundance affects the functional structure of biological communities, controlling the biotic and environmental components of ecosystem processes.

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Article 5. Ant morphology as a surrogate indicator of resource use: evidence at THE SPECIES AND COMMUNITY LEVEL IN A LAND-USE GRADIENT IN FRENCH GUIANA

Alex Salas López

Under revision in Ecological Indicators

ABSTRACT

I investigated whether the morphological trait values of Neotropical ants can be used to infer food resource use by individual species and by entire communities, and whether these relationships are affected by habitat type and/or by phylogeny. I attracted ants using food baits that represented different ecological processes (e.g. predation, granivory, detritivory, protection) in five habitat types along a land-use gradient (from forests to gardens). I assessed ant activity at the baits and characterized 64 species from six subfamilies according to their food use and community-level resource exploitation intensity in the different habitats. Next, I performed a Mantel test to reveal the relationships between 13 morphological measures and resource use at the species level. I then used ant clades (i.e. subfamily) and habitat to rank the ants along three axes of variation in relation to their morphology and food resource use. Finally, I used community-level morphological traits to predict the exploitation intensity of entire assemblages for such resources using a "4th-corner" analysis. Morphological traits were closely linked to the species' ability to exploit different resources. These relationships were affected by phylogeny and, to a lesser extent, by habitat type. Community-level trait characterization was not useful, however, in predicting the intensity of the exploitation of different types of resources in varying environmental conditions. I conclude that morphological traits are accurate predictors of the ecology of species, but they should be used with caution when trying to understand community-level patterns.

Keywords: biodiversity-ecosystem functioning relationships, ecosystem process, Formicidae, indicator, morphological traits

INTRODUCTION

How important is the shape of an organism in determining its ecological performance exploiting resources? The relationships between form and function have long fascinated ecologists (Darwin, 1859; Nyhart, 1995; Russell, 1916). Nature provides many examples of morphologically similar organisms living in analogous environments or using the same type of resources despite their different origins and histories (ecological convergence *sensu* McGhee, 2011). In the last decade, the morphological characterization of species from very different taxa (including terrestrial vertebrates and invertebrates, fish and plants) has been progressively applied towards understanding how ecological communities are organized so as to provide and maintain ecosystem functions *via* their use of resources (Frimpong and Angermeier, 2010; Kattge et al., 2011; Pey et al., 2014; Wilman et al., 2014). The premise is that morphological trait values directly affect the ecological performance of species in exploiting different resources, thus mediating their ecological functions (Lavorel and Garnier, 2002; Violle et al., 2007; Wainwright, 1994).

On the other hand, organisms differing in their forms can also display similar ecological functions (e.g. ants, birds and rodents consume seeds; Brown, Reichman, and Davidson 1979). Moreover, the necessity of species to adapt to their biophysical environment, to limited resources and to competitors simultaneously may result in ecological trade-offs when trait value combinations beneficial in a particular situation result in a poor performance in another (Kneitel and Chase, 2004; Raevel et al., 2012; Schuwirth et al., 2015). Finally, species with a common ancestry (i.e. clades) are frequently phenotypically similar, which is why understanding phylogenetic structure provides an alternative to relying on adaptive hypotheses to elucidate ecomorphological patterns (Losos, 2008; Mayfield and Levine, 2010). Therefore, considering the common ancestry of species may be helpful in accounting for the underlying ecological traits essential to the ecological role or the survival of species in a given environment (Barton et al., 2011; Gibb et al., 2015).

In this study, I investigated the relationships between morphology and the use intensity of different food resources by Neotropical ants in a series of habitats representative of a land use gradient. Ants are ecologically successful organisms consuming a wide variety of food resources in many types of ecosystems (Brandão et al., 2012; Folgarait, 1998). Ant species can be, *inter alia*, predators, granivores, indirect herbivores, fungus-eaters, or detritivores. (Brandão et al., 2012; Fowler and Delabie, 1995; Houadria et al., 2015). Several studies have provided evidence of the relationships between the morphology of ant species and their use of food resources and/or their survival in different habitat conditions (Arnan et al., 2012; Gibb and Parr, 2013; Gibb et al., 2015; Weiser and Kaspari, 2006). Moreover, the morphological and ecological characteristics of species such as food use and habitat preference are frequently phylogenetically conserved at greater taxonomic levels like subfamilies (Andersen, 1995; Brandão et al., 2012; Gibb et al., 2015; Weiser and Kaspari, 2006); but see (Yates et al., 2014). No studies to date have tried to examine, however, how the links between morphology and food resource use vary in different environments, or whether these relationships are affected by phylogeny. I hypothesized that morphological trait values at the species and at the community levels can be used as a surrogate of ecological function (e.g. predator, detritivore, mutualist). Because I wanted to understand the role of morphology in explaining trophic function regardless of other major drivers of morphology, I separated the influence of local resource use from that of habitat and clade (i.e. subfamily).

The following questions were particularly addressed: i) is the morphology of Neotropical ant species related to their use of food resources?, ii) are these relationships affected by habitat and subfamily?, and iii) can we use community-level trait information to predict the foraging intensity of ants for different types of food?

MATERIALS AND METHODS

Study site and sampling

The study took place at La Montagne de Singes and several agricultural areas nearby situated in the coastal part of French Guiana. The area presents a mosaic of habitat types that enabled to examine a gradient of land-use intensity representative of the landscape transformations occurring in much of the tropics (FAO and Jrc, 2012). For this purpose, I selected five habitat types: *terra firme* forests, lowland forests, forest edges, croplands, and gardens. The *terra firme* and lowland forests are old-growth forests representative of the rainforests covering a large part of the Amazon Basin. The lowland forests are seasonally flooded so that they include a greater regime of natural disturbance than do the *terra firme* forests. The forest edges run alongside paths providing access to agricultural areas. The croplands are traditional cropping systems which were 3-5 years old at the time of this study and contained a mixture of crops including, *inter alia*, manioc, pineapple, mango trees, and sugar cane. The gardens are essentially lawns surrounding houses which are frequently mowed for aesthetic reasons, and represent the most disturbed environment. I selected three representative 0.12 ha plots for each type of habitat. The plots consisted of (30 x 40 m) rectangular grids where 20 sampling locations were separated by 10 m in a grid system. In each sampling location, six food types were used to attract ants to the baits. All of the plots were within a radius of 3 km to ensure that the species present belonged to the same pool of species. In addition, to avoid spatial autocorrelation effects, the plots representing different habitat types were interspersed and a minimal distance of 200 m was respected between plots of the same kind.

The food resources used to attract ants were seeds (a mixture of seeds and peanuts ground to different sizes), dead insects (mashed *Tenebrio mollitor* mealworms), sucrose (25% w/w water solution), chicken excrements, live termites (about 20 *Anoplotermes* sp. with fragments of termite mound to induce them into staying in the Petri dish), and large prey (two differently sized, live *Tenebrio mollitor*). To avoid attraction biases related to food quantity, all of the baits contained approximately 2.5 - 3 g of food. The baits were offered in Petri dishes lined with parafilm. For each bait trap, the lid was placed next to the base to enable the Petri dish to be closed at the end of the experiment. All of the baits were presented once in each of the locations in two separate sampling sessions. In the first session, non-prey items were placed in alternative positions, encircling the sampling locations and separated by at least 50 cm from one another. In the second session, only prey items were offered. This was necessary because the prey were allowed to move in order to assess which ants were capable of capturing live insects. When the insects escaped from the baits, they were returned or replaced by another insect. For each sampling session, the ant activity at the baits was monitored for 1 hour. Each sampling location was surveyed every 5 minutes on average to record information on the ant species present and their behaviour (e.g. whether they actively exploited the items). While some ants may have been overlooked, this technique allowed to provide a more thorough general description of the ant activity in the area studied. After the experiments were completed, the ants were taken back to the laboratory and killed by freezing. Then, the specimens were counted and identified to genera using the identification guide developed by Bolton (1994) as well as other guides providing updates on ant classification (Bolton, 2003; Schmidt and Shattuck, 2014). Then genera were split into morphospecies on the basis of their morphological characters.

Morphological measures

Thirteen continuous morphological measurements were chosen to characterize the shape of the ant species studied (Table 1). The traits chosen were selected for their ecological relevance based on previous studies (Gibb et al., 2015; Silva and Brandão, 2010; Weiser and Kaspari, 2006). Measurements were carried out on six workers from monomorphic species (i.e. species with a unimodal type of worker) and ten workers for those species with several types of workers (multimodal; i.e. *Camponotus*, *Solenopsis*). In each case, I tried to encompass the variability of the workers. For species belonging to the genus *Pheidole*, the soldier caste was not considered in the measurements since this special type of ant has an ambiguous function depending on the species, and they neither forage nor participate in recruitment (Wilson, 2005). For each ant, standard linear measurements were taken using an ocular micrometer mounted on a dissecting microscope accurate to 0.01 mm.

Weber’s length (the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum; (Weber, 1938) was used as the main descriptor of body size while other traits were used to describe the shape. Allometries were obtained by dividing all of the traits by Weber’s length. Average species’ trait values were used for all of the analyses.

Table 1 Description of the functional traits examined, their abbreviations, a brief description of their functionality based on the literature and associated references.

Trait	Abb	Expected functions	References
Weber's length	WL	Related to metabolic rates, resistance and microhabitat (i.e. small ants use small spaces)	(Weber 1938, Kaspari and Weiser 1999)
Pronotum width	PW	Related to general size, related to thermal and drought resistance	(Kaspari and Weiser 1999)
Head width	HW	Related to mandible muscles, and the size of gaps through which workers can pass	(Kaspari 1993, Kaspari and Weiser 1999)
Interocular distance	IOD	Speculated to relate to microhabitat and trophic function	(Gibb and Parr 2013)
Eye size	ES	Related to visual capacity, microhabitat and trophic function	(Via 1977, Wehner 1981, Weiser and Kaspari 2006)
Anterolateral eye position	AEP	Related to microhabitat and trophic function	(Fowler et al. 1991, Silva and Brandão 2010)
Scape length	SL	Related to perception; length correlates to simplified environments	(Weiser and Kaspari 2006)
Femur length	FL	Related to foraging speed, simplified environments	(Kaspari and Weiser 1999, Pearce-Duvet et al. 2011)
Femur width	FW	Might be related to carrying capacity	
Clypeus length	ClL	Speculated to relate to liquid absorption efficiency	(Eisner 1957, Davidson et al. 2004)
Mandible length	ML	Related to trophic specialization	(Fowler et al. 1991, Weiser and Kaspari 2006, Yates and Andrew 2011)
Mandible width	MW	Related to trophic specialization	(Silva and Brandão 2010)
Apical tooth length	ATL1	Related to masticatory efficiency and granivory	(Yates et al. 2014)

Species-level foraging intensity for resources

To assess the ecological roles of ant species, I considered that two aspects were of importance: the use frequency of each of the six resources by a species, and the number of workers recruited towards these resources. To provide a balanced weight to exploitation frequency and recruitment, I applied the 4th-root transformation to the number of workers from each species found per bait. Then, the values corresponding to the 60 baits representing each type of resource and habitat were summed up (20 sampling locations in three replicate plots per habitat). Finally, the result obtained for each resource type was divided by the overall total, thus obtaining the relative foraging intensity (the values ranged from 0 to 1) for each of the six food resources tested. The observed preferences represent the relative foraging "effort" exhibited by the species considered at the different types of food resources. Only species with an incidence equal to or greater than 5 in the same habitat were retained for the statistical analyses. This amount was chosen as the minimum necessary to assess a significant food preference for some resources over others based on the *Chi*-square distribution.

The 4th-root transformation of recruitment values was suitable because, while it considerably skewed the highest values, it did not eliminate the signal of the recruitment information, which is an important feature in assessing food preferences in ants (Pearce-Duvet and Feener, 2010). This was necessary because, depending on the species' foraging strategy, recruitment patterns may change considerably as a consequence of colony size variations, the time lapse since resource discovery or in response to competitive interactions (Beckers et al., 1989; Planqué et al., 2010; Wittman and Gotelli, 2011).

Community-level foraging intensity for resources

To calculate the overall performance of ant communities in exploiting resources (i.e. resource exploitation intensity), I considered the amount of food retrieved from the baits as well as the number of workers attracted to them. I assigned a subjective value from 0 to 5 to each of the baits that increased with the amount of food retrieved during the experiment and with the number of workers observed foraging at the bait (0 when the bait was not exploited and 5 when the bait was fully retrieved or had attracted hundreds or thousands of ant workers). The plot-level exploitation intensity of each food resource was the sum of all of the 20 baits of that type divided by the maximum score possible (i.e. 100 in general, but corrected when some trials were unsuccessful or lost).

Statistical analyses

DO MORPHOLOGICAL TRAITS REFLECT THE USE OF FOOD RESOURCES BY NEOTROPICAL ANT SPECIES?

To test the correlation between ant species' morphological traits and their relative food use, I used the Mantel test (Legendre and Fortin, 2010). The null hypothesis is the absence of covariation between two distant or dissimilar matrices. In that case, I tested the Pearson correlation between two distant matrices and calculated the expected frequency distribution of the statistic for the Mantel test with 1000 randomizations. The trait matrix included 98 rows corresponding to species per habitat combinations (some species were present in more than one habitat) and the species' average for 13 morphological traits. The second matrix included the same species and their relative food preferences for the six resources examined. The ecological distance between species in relation to their morphological traits was computed using the "Euclidean" distance and using the "Horn" distance in relation to their food preferences. These two indexes of ecological distance are adequate for the two types of data analysed (i.e. continuous normally distributed variables in the case of traits and a ratio in the case of food preferences).

ARE RELATIONSHIPS BETWEEN MORPHOLOGY AND FOOD USE AFFECTED BY HABITAT AND SUBFAMILY-LEVEL CONSERVATISM?

In order to assess the effects of habitat type and subfamily on the relationships between morphology and resource use, the ecomorphological space occupied by all of the species per habitat combination was represented using a Principal Components Analysis (PCA). A PCA reduces the dimensionality of large multivariate data sets by deriving variables (principal components) which are linear combinations of the original variables. These principal components often retain most of the variability in the original traits and are useful in detecting ecomorphological pattern (Ricklefs and Miles, 1994).

The loadings of the PCA for all of the 98 species per habitat combinations for the three principal components were then explained in relation to the six subfamilies and five habitat types using an Analysis of Variance (ANOVA). Since the numbers of species in each habitat type and subfamily were unequal, a type II sum of the squares was used from the "car" package in R.

CAN WE USE COMMUNITY-LEVEL MORPHOLOGICAL TRAITS TO PREDICT RESOURCE EXPLOITATION INTENSITY BY ANT ASSEMBLAGES?

First of all, I wanted to know whether the general performance of ant communities exploiting a resource of any kind differed between habitats. For this purpose, I performed an ANOVA where the response variable was the average exploitation intensity of the six resources in each plot and habitat (a five-level factor) was used as an explanatory variable. Then, I wanted to know if the six resources used to attract ants were differently attractive depending on the type of habitat, as demonstrated by previous studies (Bihn et al., 2008; Peters et al., 2014). I performed a separate ANOVA for each the six resources using exploitation intensity as a response variable and habitat as a factor.

To test whether community-level traits were a good predictor of resource exploitation intensity in the different plots, the 4th-corner analysis was used (Legendre et al., 1997). I aimed to predict exploitation intensity as a response to species abundance, species' traits and their interactions. A 4th-corner problem requires three matrices describing environmental data; in this case: exploitation intensity (*R*), species abundances (*L*) and species' traits (*Q*) to determine how species' traits relate to the environment (*D*). The exploitation intensity matrix indicated the resource-use intensity of each resource type per plot. The trait matrix consisted of one species per trait matrix where trait values were the average value for the workers measured. The species abundance matrix contained the incidence data for species at each of the 20 sampling points. I preferred to use incidence data to measure abundance since this measurement has been shown to be related to colony density and abundance (Gotelli et al., 2011; Heatwole et al., 2013). Other ant abundance measures like the number of workers or the number of baits exploited can be affected by the type of bait or by species interactions. The RLQ model used generalized estimating equations to account for a correlation between the species observed at the sites. Forward selection and the score information criterion with a Bayesian information criterion-type penalty were used to select the most significant environment-trait interactions. I selected a generalised linear model with the negative binomial family for our 4th-corner analysis because the count data (for species incidence) were over-dispersed.

RESULTS

Morphological measurements were taken for 64 species of ants from 20 genera and six subfamilies. These species correspond to all of the species for which the incidence per habitat was equal to or greater than five, and represented 2426 incidence records (90.0%) out of a total of 2670 incidences monitored during sampling.

Do morphological traits reflect the use of food resources by Neotropical ant species?

The distance matrices of species' morphological traits and resource-use intensity were correlated to 38% based on Pearson's correlation coefficient. The Mantel statistic indicated that this correlation is highly significant ($P < 0.001$), suggesting that morphological traits are highly linked to ant trophic ecology. The correlations between morphological traits and foraging intensity for the different food types were found using a PCA (Table 2). The first three components of the PCA accounted for 63.0% of the variance in the ecological space that included morphological variables and diet-based variables (Table 2). Principal component 'I' mainly distinguished species consuming prey and those frequently consuming seeds and accounted for 30.1% of the variance. PC1 mostly reflected the greater tendency of predatory ants to be bigger and have wider mandibles than those consuming other food items, and, most particularly, seeds. Principal component 'II' accounted for 18.8% of the variance and reflected differences between ants consuming prey and/or seeds and those consuming sucrose, dead insects or excrements. PC2 indicated that ants consuming sugars and, to lesser extent, dead insects have legs and antennae that are relatively longer in comparison to their size than do ants that consume other resources. Principal component 'III' accounted for 14% of the variance and mainly reflected differences between ants consuming seeds and sucrose and other species. PC3 indicated that ants consuming seeds and sucrose were characterized by thinner heads with a shorter distance between the eyes.

Table 2. Principal component analysis. The eigen score and contribution to the variance is indicated for the first three components. The eigen score along each of these three components is indicated for the different food types and the morphological traits. With the exception of Webber's length, the relative values of morphological traits were used (divided by Webber length).

PCA table		PC1	PC2	PC3
Eigen value		0.083	0.052	0.039
% variance		30.09	18.87	14.09
Food				
	Big	**-0.305**	-0.194	0.028
	Termite	-0.228	**-0.352**	**0.332**
	Dead insect	0.097	0.262	0.299
	Excrement	-0.096	0.158	0.188
	Seed	**0.482**	-0.219	**-0.411**
	Sucrose	0.05	**0.345**	**-0.436**
Trait				
	logWL	**-0.487**	-0.101	0.016
	ATL1re	0.007	0.003	0.018
	MWre	-0.093	**-0.111**	-0.065
	MLre	0.083	-0.034	0.054
	SLre	-0.082	**0.547**	-0.047
	CLLre	0.07	0.08	0.101
	ELSre	-0.047	-0.006	0.045
	AEPre	-0.025	0.199	0.265
	IODre	**0.39**	0.012	0.33
	HWre	**0.306**	**0.101**	**0.428**
	PWre	0.124	0.053	0.141
	FLre	-0.267	**0.441**	-0.042
	FWre	0.037	0.024	-0.002

Are the relationships between morphological traits and food use affected by subfamily and habitat?

The analyses of variance revealed that the first component of the PCA was significantly driven by subfamily (SS = 4.23, F = 20.09 *P* < 0.001), but not by habitat (SS=0.04, F=0.11 *P*=0.98). PC2 was driven by subfamily (SS = 2.32, F = 15.43, *P* < 0.001) and also slightly by habitat (SS = 0.58, F = 3.02, *P* = 0.02). PC3 was not driven by subfamily (SS = 0.17, F = 0.85, *P* = 0.51) nor by habitat (SS = 0.03, F = 0.19, *P* = 0.93). The subfamilies *Ectatomminae* and *Ponerinae* contained larger species in general that consumed prey in high proportions (Table 3, PC1). The *Myrmicinae* included the smaller species that frequently consumed seeds, although this subfamily also presented the greatest variability. The families *Formicinae* and *Dolichoderinae* included ants of medium sizes but frequently with long legs and antennae. These ants frequently consumed sugars, dead insects and/or excrements. *Pseudomyrmicinae* consumed high percentages of termites and have short antennae. The ants in forested areas presented a lower general tendency to be predatory or to consume seeds, while the ants in the forests foraged more intensely for sucrose and dead insects (Table 3).

Table 3 Average scores and standard deviation of species according to their habitat and subfamily in the three principal components. Df indicates the number of species in each category.

Factor	Levels	df	PC1	PC2	PC3
Habitat					
	Forest	28	0.018 ± 0.34	-0.097 ± 0.229	0.004 ± 0.191
	Low-land f.	25	-0.032 ± 0.288	0.083 ± 0.194	-0.016 ± 0.234
	Edge	24	0.015 ± 0.283	0.065 ± 0.218	0.024 ± 0.184
	Cropland	15	-0.004 ± 0.263	-0.055 ± 0.224	-0.025 ± 0.186
	Garden	6	0.004 ± 0.17	-0.016 ± 0.277	0.014 ± 0.198
Subfamily					
	Dolichoderinae	5	-0.23 ± 0.209	0.098 ± 0.078	0.121 ± 0.255
	Ectatomminae	3	-0.471 ± 0.07	-0.178 ± 0.096	-0.093 ± 0.16
	Formicinae	12	-0.094 ± 0.177	0.289 ± 0.137	-0.008 ± 0.263
	Myrmicinae	79	0.118 ± 0.214	-0.005 ± 0.187	0.001 ± 0.189
	Ponerinae	7	-0.528 ± 0.195	-0.291 ± 0.151	-0.074 ± 0.129
	Pseudomyrmicinae	2	-0.374 ± 0.006	-0.537 ± 0.085	0.123 ± 0.094

Can we use community-level morphological traits to predict the resource-use intensity of ant assemblages?

No differences in the average resource-use intensity by ant communities in different habitats were detected (ANOVA, $F_{4,15}$ = 2.91, P = 0.08). The examination of individual processes demonstrated, however, significant habitat-level differences in the exploitation of dead insects (ANOVA, $F_{4,15}$ = 3.83, P = 0.038), excrements (ANOVA, $F_{4,15}$ = 4.10, P = 0.030), seeds (ANOVA, $F_{4,15}$ = 4.10, P = 0.030) and large prey (ANOVA, $F_{4,15}$ = 4.13, P = 0.03). The greatest variations in resource-use intensity were detected for prey items and were greater in the open habitats (i.e. croplands and gardens) compared to the forests (Table 4). Conversely, the baits containing excrements were the most exploited in the forest edges, but were consistently the least exploited baits in the rest of the habitats. The exploitation of seeds presented a pattern unrelated to the examined land-use gradient, although the ant communities associated with the *terra firme* forests and those associated with the gardens exhibited greater levels of seed use than did ant communities associated with the other habitats.

Table 4 Percentages of baits exploited for the different food resources in the studied plots in five habitat types

Habitat	Dead insects	Excrements	Seeds	Sucrose	Termites	Big prey	Average
Terra firme forest	71.6	9	87	53.8	62	19	50.4
	70	13.5	72.7	29.8	50.5	28	44.08
	62	14.5	45.6	25.6	57	37	40.28
Lowland forest	62.1	14	58	53.4	34.3	17.3	39.85
	64.8	10	58	37.5	46	22.3	39.77
	55	5.2	48.7	32	30	24.8	32.62
Edge	93.4	55.7	43.6	56.4	57	52	59.68
	83.4	27.5	42.8	53.9	76	28.2	51.97
	58.2	21.8	35.2	30.8	50	16.2	35.37
Cropland	85.6	20.5	37	38.2	66.2	52.4	49.98
	63.2	14.7	38	47.6	52.7	57.1	45.55
	78.8	8	67.9	60.2	75.9	71.7	60.42
Garden	64.2	8.5	76.8	71	80.2	72.5	62.2
	87.1	11.5	77.3	76.2	61.6	37.4	58.52
	78.4	7	38.7	19	81.5	81.4	51

The 4th-corner analysis revealed a low correlation between the morphological trait values of ant communities associated with the different habitat types and the performance of these communities in exploiting food resources. Indeed, only one trait-resource association was found to be significant, indicating that the communities where the ants have a long, apical tooth were numerous and were characterized by the exploitation of large quantities of big prey (r_{obs} *vs* $r_{expected}$ = 0.30 *vs* 2.16, $P = 0.022$). These communities were mainly associated with the gardens and, to a lesser degree, with the croplands. The rest of trait-resource associations were not found to be significant.

DISCUSSION

The aim of this study was to investigate whether the morphological trait values of ants are of use towards understanding their food use (and, therefore, their ecological function) at the species and the community levels. Moreover, I tried to understand whether form-function relationships were variable in different environments or whether they were conserved in different clades, thus limiting the suitability of using morphological traits to understand ecological function. Previous studies already investigated ant morphological traits in relation to their food regimes, although these were based either on life history observations (Brandão et al., 2012; Silva and Brandão, 2010; Weiser and Kaspari, 2006) or on isotopic signatures (Gibb et al., 2015). This is the first study to provide a link between ant morphology and relative food use for several food types observed through baiting trials, and also the first to investigate the validity of trait-function associations in different environments and across clades. Answering this question is an important step towards understanding the autoecology of species, but also, from a functional ecology perspective, towards understanding how ant communities characterized by different morphologies differ in their overall use of resources and, therefore, in their contribution to ecological processes.

Do morphological traits reflect the use of food resources by Neotropical ant species?

I found that ant morphological traits were highly related to the frequency with which species used the different food resources. In particular, the ant species that frequently foraged on prey items were larger and possessed larger mandibles. I also found that ants frequently exploiting seeds tended to be smaller, and ants consuming sucrose had longer legs and antennae. My findings are similar to a study conducted in Australia where predatory ants were larger than omnivorous ants based on their isotopic signatures (Gibb et al., 2015). Surprisingly, my results contrast with another study on Neotropical ants where predatory species were on average smaller than ants consuming other types of resources (Weiser and Kaspari, 2006). A possible explanation for these discrepancies may be that the sampling techniques used in each study influenced the types of ants captured. For instance, predatory ant species differ greatly in size depending on whether they are ground-foraging ants or subterranean ants, the former being larger (Brandão et al., 2012). In line with this hypothesis, I used baits in my study, whereas pitfall traps were used in the one carried out in Australia (Gibb et al., 2015), and Weiser and Kaspari (2006) used ant specimens coming from a museum and collected with other methods that favour litter-dwelling ants (i.e. Winkler traps).

Are the relationships between morphological traits and food use affected by subfamily and habitat?

While morphology can affect the performance of ants in the exploitation of different food resources, it can also be important in the adaptation of ants to their biophysical environments (Arnan et al., 2014; Gibb and Parr, 2013; Gibb et al., 2015; Kaspari, 1993; Weiser and Kaspari, 2006; Yates et al., 2014). Moreover, the phylogenetic conservatism of ecological features is frequent in ants, and, therefore, I also wanted to understand whether such links between shape and trophic ecology might be explained by alternative hypotheses such as adaptations to the habitat or phylogenetic conservatism (Gibb et al., 2015; Weiser and Kaspari, 2006).

Despite the conclusions by many studies that habitat conditions influence ant morphology, the effect of habitat in morphology-trophic function relationships was only moderate. Indeed, only a slight effect of open *vs* more forested habitats was found in the tendency of species to forage more frequently on prey and seeds, which are sources of proteins and lipids. Similar patterns have already been reported in other studies, although with different bait choices (Bihn et al., 2008; Peters et al., 2014). Our finding suggests that the trade-offs between adaptation to the habitat and to food resources are not very constraining in the ant communities studied (Gibb et al., 2015).

In contrast, the inclusion of phylogeny in the models importantly explained the links between form and function. In particular, the ant species mostly exploiting the prey baits belonged to the subfamilies *Ponerinae* and *Ectatomminae* and included genera such as *Odontomachus*, *Pachycondyla*, *Neoponera* and *Ectatomma*, which were the largest ants captured in this study. Likewise, the small size of the *Myrmicinae* ant species attracted to seeds can be explained by the fact that many of these species belong to the genera *Pheidole* and *Solenopsis* (*Diplorhoptrum*). Also, ants belonging to the subfamilies *Formicinae* and *Dolichoderinae* consumed larger fractions of sugar than did ants from other families and were characterized by longer legs and antennae. Our results are thus in keeping with the idea that ecomorphological traits are, to some extent, phylogenetically conserved in ants (Brandão et al., 2012; Weiser and Kaspari, 2006).

Can we use community-level morphological traits to predict the resource-use intensity of ant assemblages?

From a functional ecology perspective, the aim of trait-based approaches is to characterize species in terms of their functional traits and then determine how functional trait variation between ecosystems affects the patterns of biodiversity and ecosystem functioning (Enquist et al., 2015). Although ants are considered an important element in the maintenance of many ecosystem processes (Crist, 2009; Folgarait, 1998; Philpott et al., 2010), very few studies have assessed foraging intensity on different types of resources by ants and how this is affected by environmental conditions (Fayle et al., 2010; Peters et al., 2014; Šipoš and Kindlmann, 2013; Zelikova and Breed, 2008). Although differences were found in resource-use intensity for different food types between habitats, I was unable to infer such variations using community-level morphological traits as predictors. Thus far I can only put forth the hypothesis that other relevant aspects of ant ecology, such as colony size or foraging strategy and behaviour, may be relevant aspects to include in the equation in future studies (Lanan, 2014; Planqué et al., 2010).

In conclusion, our study indicates that morphology can be used to understand the autoecology of species, even when these come from different habitat types. Nevertheless, community-level trait characterization should be considered with caution when trying to understand the functioning of ecosystems.

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VI. DISCUSSION GENERALE

En vue d’une anthropisation qui accélère de jour en jour, identifier les effets des changements d’usage de terre sur la biodiversité et le fonctionnement des écosystèmes est une préoccupation d’extrême importance (Ojima et al. 1994, Foley et al. 2005). En Guyane, il y a jusqu’à présent peu d’études référençant l’importance de ces changements sur la biodiversité (Brosset et al. 1996, Thiollay 1997), et encore moins concernant les conséquences dans le fonctionnement des écosystèmes (Baraloto et al. 2010). On a de plus en plus recours aux fourmis en tant qu’organisme cible permettant d’étudier de telles modifications (Chapitre II). Dans le territoire guyanais, on estime qu’il existe plus de 1000 espèces de fourmis (Groc et al. 2009). Quelques études ont également mis en lumière des changements importants dans la composition de fourmis dans des communautés associées à différents milieux (Groc et al. 2009, 2014). Cette thèse complète en partie ces études, en essayant notamment de comprendre ces changements en réponse aux phénomènes d’anthropisation cités plus haut (voir aussi Delabie et al. 2009). En outre, ce travail va plus loin, en mettant l’accent sur l’identification des mécanismes responsables de ces changements d’identité des espèces présentes dans les différents types d’habitats mais aussi sur les conséquences écologiques de ces changements.

Avec ces objectifs en perspective, j’ai ainsi abordé ce sujet avec une vision hiérarchique des effets des changements d’usage de terre à différents niveaux d’organisation biologique. Dès lors, la démarche a été de partir d’une caractérisation écologique au niveau de l’espèce, pour remonter ensuite à l’échelle des communautés pour enfin considérer une perspective écosystémique.

La caractérisation a été réalisée en tenant compte des mesures morphologiques et des occurrences d’espèces dans des appâts. Cette approche présente certainement des limitations qui seront discutées plus tard, mais elle permet d’aborder des questions essentielles lors qu’on souhaite comprendre les organismes dans leur environnement, et ce même environnement en tant que conséquence de ces organismes. Quelles ressources utilisent ces espèces ? Comment ces espèces sont organisées en réponse à des conditions environnementales et à la présence d’autres espèces? Enfin, l’action combinée des espèces peut-elle donner lieu à des conditions prédictibles nous permettant une meilleure compréhension du fonctionnement des écosystèmes?

VI.1 LE ROLE DE LA COMPETITION DANS LES ASSEMBLAGES DE FOURMIS

Comme on l'avançait dans la section I.2, deux modèles existent pour expliquer des mécanismes de coexistence en présence de compétition. D'une part, les modèles basés sur les différences dans les besoins écologiques des espèces, et d'autre part les modèles basés sur la compétitivité dans l'accès à ces ressources. Dans le premier cas on fait référence au principe de la similarité limitante : si chaque espèce est limitée par une ressource différente, l'exclusion compétitive n'aura pas lieu (MacArthur and Levins 1967). Dans le deuxième cas on considère le modèle de dominance-découverte (Levins and Culver 1971): dans toute paire d'espèces, celle qui domine peut éloigner l'autre des ressources convoitées, la coexistence dépend alors de la capacité de cette deuxième espèce à coloniser ces ressources plus rapidement que le compétiteur dominant.

Parmi les myrmécologues, le modèle de compétition le plus populaire a été celui du compromis entre découverte et dominance (Davidson 1998, Parr and Gibb 2012) (voir section II.1). Malgré l'attention retenue par cette ligne de recherche, le modèle a servi à « rejeter » l'importance des effets de la compétition sur les assemblages de fourmis plutôt qu'à la démontrer (Parr and Gibb 2012, Cerdá et al. 2013). Néanmoins, nier l'importance de la compétition dans la structure des communautés de fourmis, ne semble pas cohérent vue l'intensité avec laquelle fourragent les fourmis pour les ressources alimentaires. En effet, le point de départ de ces travaux est de considérer que les espèces de fourmis ont des besoins écologiques identiques, et que les agressions constituent le mécanisme standard de coexistence (Wilson 1971, Davidson 1998). Mais ces « a priori » sont-ils vérifiés ?

Bien que moins souvent invoquée pour comprendre la stabilité des communautés de fourmis, une des choses que l'on remarque fréquemment, est que ces communautés sont souvent composées d'espèces possédant des besoins et des caractéristiques écologiques très distinctes (Brown 2000, Brandão et al. 2012, Lanan 2014). Dans les différents articles, nous avons également démontré une forte partition de niche sur différents axes de variation écologique, qui semble bien expliquer la composition d'espèces dans les assemblages. Ceci nous ramène à nouveau à la rejection de l'importance de la compétition dans la structure des communautés de fourmis (Parr and Gibb 2012, Cerdá et al. 2013). Ces deux révisions de la littérature mettent en évidence une tendance dominante à étudier les communautés de fourmis par rapport à la compétition par interférence, cependant, la confrontation directe a depuis longtemps été considérée comme une option coûteuse pour les espèces engagés (Case and

Gilpin 1974). Ainsi, il est peu probable que cette stratégie soit sélectionnée davantage, sauf si la partition écologique est impossible (Case and Gilpin 1974, Roughgarden 1983). Reprenant une citation de W. Tschinkel et E.O. Wilson : « L'abondance d'une espèce parmi d'autres dans les appâts a très souvent été considérée et de manière très convaincante, comme une évidence de compétition » « cependant une connaissance détaillée de l'histoire naturelle des espèces aura suggéré des hypothèses plus intéressantes et fondés, et avec peu de relation avec le conflit physique directe » (Tschinkel and Wilson 2014).

La partition de la niche est donc sûrement l'aspect le plus important permettant la coexistence d'espèces grâce à une limitation de la compétition par exploitation (Schoener 1974). Dès lors, il est remarquable que les aspects écologiques permettant une différentiation de niche entre espèces, puissent être variables entre habitats tel comme nous l'avons démontré (Article 2). C'est également la conclusion à laquelle arrivent d'autres auteurs (Wiescher et al. 2011, Arnan et al. 2014). Des études futures devront ainsi privilégier une identification des dimensions écologiques importantes dans la coexistence d'espèces, et leurs variations dans le temps et dans l'espace, plutôt qu'un examen de la dominance d'appâts via des agressions.

VI.2 EFFETS DE L'ANTHROPISATION SUR LES COMMUNAUTES DE FOURMIS

Les impacts de l'anthropisation sur les communautés de fourmis sont jusqu'à présent peu connus en Guyane. Les informations que nous détenons concernent d'une part les effets négatifs sur la diversité spécifique dus aux activités humaines (Delabie et al. 2009). D'autre part nous savons que les milieux anthropisés sont souvent favorables à l'installation de certaines espèces au potentiel envahissant (Pacheco and Vasconcelos 2007, Delabie et al. 2011, Talaga et al. 2015). Enfin, ces changements peuvent entrainer des modifications dans la dominance de certaines espèces avec un impact sur la stabilité des communautés (Orivel et al. 2009, Dejean et al. 2015).

Les résultats confirment le fort impact de ces changements sur la composition spécifique, et nous éclairent sur les mécanismes potentiellement responsables de ces changements. Nos résultats rejoignent en partie d'autres études, montrant qu'une perte d'espèces et une substitution des communautés de fourmis en réponse à la simplification d'habitats liée aux changements d'usage de terre (Hoffmann 2010, Gibb et al. 2015a). Le remplacement d'espèces entre types d'habitat est fortement lié à des variations de leurs caractéristiques écologiques, ce qui nous a permis de valider l'hypothèse du « déplacement de niche ». Ces résultats suggèrent alors que les différentes espèces de fourmis ont des contraintes importantes pour coloniser et survivre dans différents types d'habitat en fonction de leurs morphologies, de leurs stratégies de fourragement ou de leurs niches alimentaires. On peut ainsi spéculer que ces changements sont dus à des variations de température (moyenne et fluctuations journalières), à la sécheresse, ou tout simplement à la présence de matière organique dans le sol ou de végétation (Wiescher et al. 2012, Gibb and Parr 2013, Arnan et al. 2014, Yates et al. 2014).

En revanche, l'importance de la « contraction de niche » dans la détermination du nombre d'espèces n'était pas confirmée. Notre étude contraste ainsi avec d'autres ayant trouvé un lien entre la diminution de stratégies écologiques et le nombre d'espèces en réponse à l'anthropisation (Bihn et al. 2010, Peters et al. 2014). Nous proposons ainsi d'autres possibilités permettant d'expliquer la diminution de diversité observée dans les milieux ouverts/anthropisés (jardins et abattis) par rapport aux habitats forestiers (*terrafirme* et bas-fonds).

D'une part il est possible que la présence de litière et des microhabitats particuliers permettent à une plus grande quantité d'espèces de nidifier et de coexister grâce à une distribution hétérogène des ressources dans l'espace (Andersen 1986, Sarty et al. 2006). La faible partition écologique dans les stratégies de fourragement trouvées dans les abattis par rapport aux forêts, semblent cohérentes avec cette possibilité (Article 2).

Enfin, en introduisant les facteurs conditionnant la diversité et composition d'espèces, nous avons expliqué comment les filtres écologiques agissent dans une succession d'échelles (Götzenberger et al. 2012). La première de ces échelles, est biogéographique : le nombre d'espèces présentes est lié à l'histoire du lieu, qui aurait conditionné les évènements d'apparition et d'extinction d'espèces dans la région, et qui pourront donc coloniser les différents types d'habitat (Ricklefs 1987). Ainsi, il est fortement possible que le nombre d'espèces trouvées dans les différents types d'habitat étudiés soit directement lié à la surface des habitats favorables dans la région/réservoir. En effet, les biomes les plus représentés peuvent abriter un nombre supérieur d'espèces, qui seront potentiellement capables de coloniser les patches d'habitat locaux (MacArthur and Wilson 1967). Pour une confirmation de cette hypothèse, une meilleure compréhension de la configuration du paysage guyanais et de l'histoire de vie des espèces de fourmis présentes est nécessaire. Par exemple, la composition d'espèces associées à des abattis et des jardins, gardait quelque similarités avec la myrmécofaune répertoriée dans des inselbergs : abondance d'espèces du genre

Brachymyrmex, et une diminution d'espèces des genres *Crematogaster* et *Pheidole* (Groc et al. 2009). On remarque également une prévalence et une dominance écologique importante de *Pheidole fallax* et des fourmis de feu, telles que *Solenopsis saevissima,* souvent associés à des savanes en Guyane et dans le « Cerrado » brésilien (Pacheco and Vasconcelos 2007, Renard et al. 2012). De plus, on trouve quelques espèces de fourmis introduites par l'homme telles que *Tapinoma melanocephalum*, *Pheidole megacephala*, *Cardiocondyla emeryi*, *Monomorium floricola.* Ces espèces sont bien connues pour leur affinité avec des milieux perturbés dans des régions tropicales (Bertelsmeier et al. 2014).

VI.3 L'INTERFACE ESPECES PROCESSUS ECOSYSTEMIQUES : PLUS DE QUESTIONS QUE DES REPONSES

Tout organisme a une influence sur son environnement lors de ces activités biologiques comme, par exemple la consommation de ressources. Or, dans un groupe d'une abondance telle que celui des fourmis, il semble assez curieux que la question des relations entre diversité, composition des communautés de fourmis et processus écologiques n'aient pas suscité plus d'études (Folgarait 1998, Fayle et al. 2010, Philpott et al. 2010).

Certains auteurs ont démontré une relation positive entre diversité de fourmis et l'intensité de prélèvement de proies vivantes et mortes (Philpott and Armbrecht 2006, Fayle et al. 2010). Contrairement à ces auteurs, nous n'avons pas trouvé de variations importantes dans l'intensité de fourragement des fourmis en réponse à l'anthropisation et diminution du nombre d'espèces. En revanche, une tendance existe et va dans le sens contraire des prédictions : l'activité des fourmis était légèrement supérieure dans les milieux les plus dégradés et pauvres en espèces. D'autres études réalisées sur les fourmis semblent indiquer que ces patterns constituent un cas typique : les milieux ouverts vont souvent inclure un nombre plus faible d'espèces, sans que pour autant l'abondance de fourmis diminue (Gove 2007, Peters et al. 2014). En effet, il est fréquent que ces conditions favorisent l'abondance de certaines espèces « généralistes » qui peuvent consommer des grandes proportions d'une variété de ressources (Andersen 1992, Peters et al. 2014). Dans notre cas, il est possible que ce soit justement l'abondance d'espèces généralistes qui explique le fait que certaines ressources telles que les proies, aient été plus exploitées dans les milieux ouverts, malgré la présence de plus d'espèces « prédatrices » dans les forêts (e.g. fourmis appartenant aux sous-familles Ponerinae, Ectatomminae). Par ailleurs, il est aussi possible que l'intensité d'exploitation de ressources soit biaisée par les conditions expérimentales que l'on trouve dans les différents environnements. En effet, une densité de litière plus importante dans les forêts aurait pu ralentir la découverte et le recrutement d'espèces dans les appâts (Gibb and Parr 2010). De plus, il est également possible que l'attirance des appâts soit affecté par la disponibilité de ressources dans les différents habitats (Davidson 1997, Kaspari and Yanoviak 2001). Bien qu'on n'ait pas réalisé de mesures sur la disponibilité de ces ressources, il est très probable que ces limitations soient plus importantes dans les milieux ouverts, ce qui permettra d'expliquer une plus grande attirance des appâts, que dans des forêts (Arnan et al. 2014, Peters et al. 2014). Ceci pourra s'expliquer par une abondance et une pérennité plus grande de ressources alimentaires naturelles liées à une biomasse plus importante dans les forêts, et une plus grande fréquence de perturbations dans les milieux anthropisés (Ríos-Casanova and Bestelmeyer 2008).

Les variations dans l'intensité d'exploitation de ressources étaient plus remarquables lorsqu'on examine des processus individuels. Ainsi, nos résultats suggèrent des changements importants dans les proportions de ressources utilisés par les fourmis en fonction du type d'habitat. Ici plusieurs questions se posent. D'une part nous pourrions penser que les changements dans la composition et structure des communautés sont responsables des changements, comme il est souvent attendu (Hooper et al. 2005, Díaz et al. 2006a). Mais d'autre part, il est possible que ce soit l'abondance totale et relative de ressources qui conditionnent la communauté (Gross and Cardinale 2007). A ce propos, deux interprétations sont possibles. Premièrement, les fourmis consomment d'avantage les ressources les plus limitantes dans leur environnement (Kay 2004, Kaspari et al. 2008). Ainsi, l'intensité de consommation de certains types d'appâts plutôt que d'autres, est souvent interprétée comme une réponse inverse aux abondances de ces ressources (Davidson 1997, Yanoviak and Kaspari 2000, Kaspari et al. 2012, Fowler et al. 2014). Mais, il se peut que ce soit le contraire, si l'on considère que la faune présente dans un habitat est la faune mieux adaptée aux ressources présentes (Ríos-Casanova and Bestelmeyer 2008, Kaspari et al. 2012). Par exemple c'est dans des milieux ou des excréments sont abondants qu'on trouve des bousiers et non l'inverse. Dans des cas théoriques et empiriques il a été démontré à titre d'exemple, qu'une relation entre diversité d'espèces et abondance de ressource existe, et notamment, que les espèces les plus abondantes sont celles qui exploitent davantage ces ressources (McKane et al. 2002, Fox and Vasseur 2008). En absence d'une quantification de l'abondance réelle des espèces ainsi que des relations entre consommation et abondance des ressources, nous ne pouvons pas savoir quelle est la direction des relations entre composition des assemblages et processus écologiques.

Enfin, la quantification des activités des organismes est coûteuse en temps de collecte, ce qui n'est pas viable opérationnellement pour fournir ces informations pour chaque environnement. Dès lors, nous avons essayé de comprendre si une caractérisation morphologique des espèces et des communautés, pouvait nous permettre d'identifier leur utilisation de ressources alimentaires. Bien que nous ayons confirmé l'utilité de traits morphologiques pour inférer des rôles écologiques des espèces, nous n'avons pas réussi à trouver des patterns cohérents à niveau des communautés. Il est donc important de questionner si nos résultats confirment les autres ayant testé des relations entre morphologie et écologie trophique à niveau des écosystèmes ou s' en distinguent (Bihn et al. 2010, Gibb et al. 2015b). Lorsqu'on s'arrête à la caractérisation des espèces, on trouve un support à des travaux proposant des liens entre écologie trophique et morphologie (Weiser and Kaspari 2006, Silva and Brandão 2010). Cependant, si on se concentre sur l'activité des espèces, on rejette l'utilité des traits morphologiques pour prédire l'activité des fourmis. Comme il a été constaté auparavant, les mécanismes déterminant la structure des assemblages des fourmis peuvent être spécifiques à chaque type d'habitat (Wiescher et al. 2011, Arnan et al. 2014). Ces interactions complexes organismes-environnement rendent difficile une compréhension de leur organisation et les conséquences sur les processus écologiques dont elles participent. Ainsi nous suggérerons d'interpréter avec précaution les changements de traits comme une évidence dans des variations dans le fonctionnement des écosystèmes (Bihn et al. 2010, Gibb et al. 2015b).

VI.4 UNE ECOLOGIE MULTI-ECHELLES POUR UNE MEILLEURE COMPREHENSION DES RELATIONS ENTRE BIODIVERSITE ET FONCTIONNEMENT DES ECOSYSTEMES

Déterminer les conséquences des changements d'usage de terre sur l'abondance, la diversité des organismes et le fonctionnement des écosystèmes est un sujet complexe. En effet, ces changements peuvent être abordés à différents niveaux d'organisation biologique ou écologique qui ont été traités par différentes sous-branches de l'écologie. L'étude des besoins et du rôle écologique d'une espèce est que l'on appelle « l'autoécologie » ou encore « l'histoire naturelle» (Ricklefs 2012a). Lorsqu'on s'intéresse aux mécanismes responsables du maintien d'un ensemble d'espèces réunis dans un environnement, on fait référence à l'écologie des communautés ou des assemblages (Roughgarden 1983, Weiher and Keddy 1995). Enfin, quand l'intérêt dépasse les espèces, mais touche les effets de ces espèces sur leur environnement, on parle d‘écologie des écosystèmes (Hooper et al. 2005). Ces trois domaines d'étude, sont très souvent séparés, et considèrent uniquement des fragments d'information utiles à leur propose d'étude. Malgré cette simplification, il reste évident qu'ils gardent une relation très importante (Loreau 2010, Enquist et al. 2015).

La majorité des espèces présentent un certain degré de plasticité écologique. Ainsi, dans un environnement donné chaque espèce va davantage exploiter les ressources qui lui permettent de maximiser sa croissance populationnelle. Par conséquent, il est impossible de comprendre le rôle écologique d'une espèce en l'isolement de son environnement et des interactions qu'elle maintien avec d'autres organismes. Par exemple, des changements d'alimentation ont été démontrés pour quelques espèces de fourmis entre habitats (Pfeiffer et al. 2014, McGee and Eaton 2014), ainsi qu'en réponse aux interactions compétitives (Savolainen and Vepsäläinen 1988, Savolainen 1991, Blüthgen and Fiedler 2004a). En accord avec ces études, nous avons mis en évidence des variations entre le jour et la nuit concernant le type de ressources exploitées par certaines espèces de fourmis (Article 1). Ces variations suggèrent que l'efficacité du fourragement et la compétitivité de ces espèces change au cours de la journée. Ainsi, certaines espèces pourront exploiter des ressources complémentaires le cours du temps en fonction des compétiteurs présentes. Portés sur ce principe, nous avons émis l'hypothèse selon laquelle des conditions de fonctionnement des écosystèmes similaires, chaque espèce doit utiliser les mêmes ressources (Article 2). Nous avons confirmé que pour un même période (i.e. le matin) et type d'habitat, les espèces utilisait des proportions de ressources constantes sur différentes parcelles. Ceci suggère que ces assemblages qui représentaient un même type d'habitat étaient caractérisés par des teneurs en ressources et des interactions entre espèces similaires.

Dans une perspective d'écologie des communautés, une prémisse essentielle est que les interactions biotiques et de l'abondance de ressources expliquent la diversité et l'identité des espèces présentes dans une communauté (MacArthur and Levins 1967, Tilman 1982). Ainsi, pour qu'on puisse prévoir que les interactions entre espèces soient responsables de la structure d'une communauté (i.e. théorie de la similarité limitante), il est nécessaire de connaître le rôle de chaque espèce dans le contexte donné de ressources et des interactions (Article 2). Outre les interactions entre espèces, c'est l'abondance de ressources qui va conditionner la productivité de l'écosystème, aussi bien que l'espace fonctionnel dans lequel ces espèces coexistent (Articles 2 et 4).

Finalement, l'écologie des écosystèmes établit comme principe que l'abondance et la diversité d'organismes avec des traits complémentaires est le moteur des processus écologiques. Dans le début d'introduction de cette thèse, le concept d'habitat était entre autres choses, défini comme un état prédictible et stable, caractérisé par des taux des processus représentatives de ce type d'habitat (Southwood 1977, Jax 2005). Cependant, comme nous venons de le voir, les espèces peuvent uniquement participer à certains processus dans certaines conditions. De ce fait, il est non seulement important de connaître le potentiel d'une espèce dans l'exploitation de certaines ressources, mais aussi, de le faire dans différents conditions, dans différents périodes ou dans différents compartiments de l'écosystème (Articles 1, 2 et 4). Par conséquent, le maintien des équilibres écologiques dépend aussi d'une sorte d'équilibre dans les interactions entre espèces. En harmonie avec ce principe, nous avons trouvé premièrement, que les proportions de ressources exploitées ne subissaient pas de variations entre assemblages représentant le même habitat (voir surtout article 2, mais aussi articles 4 et 5). Deuxièmement, nous avons mis en évidence qu'un certain degré de déterminisme dans la partition trophique des assemblages de fourmis était très probablement expliqué par des interactions entre espèces (Articles 1 et 2).

Il est donc essentiel, que ces champs d'étude séparés de façon artificielle (autécologie, écologie des communautés et écologie des écosystèmes), se rejoignent et se lient afin de mieux comprendre la manière dont les ressources jouent un rôle sur les espèces présentes et leurs interactions, et comment celles-ci, à leur tour, agissent sur le fonctionnement et la stabilité des écosystèmes (Loreau 2010, Turnbull et al. 2013).

VI.5 CONCLUSIONS ET PERSPECTIVES

Nous avons émis trois prédictions quant aux effets des changements d'usage de terre sur les communautés de fourmis et leur participation aux processus écosystémiques. D'une part nous prévoyions des changements dans la diversité et dans la composition spécifique des communautés de fourmis entre habitats le long du gradient d'anthropisation étudiée. En autre, nous avions prédit des variations des traits écologiques des espèces associés à différents type d'habitat. Finalement, nous nous attendions à ce que les changements dans la composition spécifique entre habitats impactent la participation des communautés de fourmis à différents processus écosystémiques. Nous avons trouvé un support à toutes ces prédictions comme il a été discuté dans les sections précédentes, mais nous avons aussi soulevé les limites de nos résultats pour expliquer les relations entre environnement, biodiversité et fonctionnement des écosystèmes.

L'échantillonnage a été entièrement basé sur l'utilisation d'appâts. Il s'agit d'une technique fréquente pour capturer des fourmis, et conseillée pour étudier les interactions entre espèces (Bestelmeyer et al. 2000, Gotelli et al. 2011). Bien que la diversité des ressources alimentaires employées vise à couvrir les ressources les plus souvent exploités par les fourmis, il faut être conscient, que les informations obtenues concernent uniquement un sous-ensemble d'espèces parmi toutes celles présentes dans la zone d'étude. Par exemple, l'échantillonnage était réalisé en début de journée pour éviter des biais possibles (sauf dans l'article 1). A priori, cette période de la journée maximise le nombre d'espèces diurnes (car on évitait le stress thermique de midi). Cependant, un nombre d'espèces nocturnes, voire d'autres privilégiant justement les périodes les plus chaudes du jour ont certainement été ignorés (Fellers 1989, Luque and Reyes López 2007, Wittman et al. 2010). De plus, la diversité de ressources potentiellement exploitées par les fourmis est beaucoup plus grande et inclut une liste innombrable de proies, de types de graines, de nectars, miellats etc. (Blüthgen 2003, Fischer et al. 2008, Brandão et al. 2012). Par ailleurs d'autres méthodes peuvent permettre de capturer un plus grand nombre d'espèces, voire des espèces complètement différentes (Romero and Jaffe 1989, Wang et al. 2001, King and Porter 2005, Groc et al. 2007, Gotelli et al. 2011). Ceci a été observé dans le premier article : le nombre d'espèces capturées est supérieur lorsqu'on utilise des « pitfalls » (ou piège à fosse). Cependant, il a été montré que les pièges de ce type sont moins performants dans les milieux ou la litière est trop dense, et impossible à appliquer dans les milieux ou le sol est trop dur (Majer 1997, Groc et al. 2007, Sabu et al. 2011). Tout de même, les piège « winkler » permettent de capturer les espèces cryptiques et celles nidifiant dans la litière, mais il ne s'agit pas d'une méthode de capture adaptée à des milieux au sol dénudé de litière ou matière organique (King and Porter 2005, Groc et al. 2007). Ainsi, les pièges de type pitfall et winkler ont des performances variables en fonction de la quantité de litière ou du type de sol entre autres (King and Porter 2005, Groc et al. 2007). C'est pourquoi l'utilisation d'appâts constitue la méthode rapportant le moins de biais de capture en comparant des habitats différents (Majer 1997, Groc et al. 2007, Sabu et al. 2011).

Malgré les possibles limitations, l'utilisation d'appâts constitue d'une technique d'échantillonnage qui nous permet d'obtenir de manière simultanée une information de la diversité et composition spécifique, et d'autre des informations sur l'écologie des espèces capturées. Ainsi, une extension du protocole employé dans cette thèse, permet de mettre en lumière des perspectives intéressantes. Nous pouvons par exemple examiner des variations intraspécifiques dans l'utilisation de ressources. En effet, bien que ceci ait été fait en partie, un examen au niveau des colonies en absence de compétition avec d'autres espèces, permettra une comparaison des niches trophiques « fondamentale» et « réalisé ». Cette comparaison semble en effet essentielle pour une meilleure compréhension des effets de la disponibilité de ressources et des compétiteurs sur le succès de fourragement des espèces. Nous avons également étudié les préférences alimentaires des fourmis dans deux types de microhabitat (sol et végétation). L'adaptation et application de ce méthode à des fourmis d'autres compartiments écosystémiques : fourmis cryptiques de la litière, fourmis souterraines ou encore celles de la canopée, ouvre des perspectives intéressantes pour des étude sur la stœchiométrie à différents niveaux écosystémiques (Fowler and Delabie 1995, Yanoviak and Kaspari 2000, Fowler et al. 2014). De plus, afin de confirmer que ce que l'on observe dans les appâts reflète les ressources exploitées par ces espèces dans leur milieu, il sera convenable de quantifier les activités de collecte de différentes ressources (e.g. graines, nectar, miellat, proies) au niveau des colonies. Ceci permettra de valider les observations réalisées grâce à cette méthodologie en les comparant avec les rôles écologiques attribués à différents groupes d'espèces par d'autres chercheurs (Silvestre et al. 2003, Brandão et al. 2012). Enfin, l'idéal sera d'identifier le rôle trophique mesuré et quantifié avec d'autres traits de mesure directe, nécessitant uniquement des individus de fourmis, et non une série d'observations. Concrètement, des traits tels que la morphologie ou les isotopes semblent des indicateurs ayant un succès relatif (Feldhaar et al. 2009, Brandão et al. 2012, Gibb et al. 2015b). Il est possible que leur combinaison avec des informations phylogénétiques, puisse constituer un indicateur plus robuste de la niche des espèces. Cette perspective est particulièrement intéressante pour inférer une information écologique des inventaires déjà réalisés, ainsi que des inventaires futurs en employant d'autres techniques de capture.

Une deuxième limite de cette thèse est liée, comme il a été mentionné précédemment, à une méconnaissance de l'abondance réelle des espèces et de l'abondance de ressources disponibles. Sans ces informations précises, nos résultats ne peuvent que suggérer des patterns, mais on ne peut confirmer que les relations entre écologie des espèces trouvées et leur environnement soient exactes. Des études futures devront tenter de trouver des liens quantitatifs plus précis (densité de fourmilières, biomasse, quantité de ressources exploités…).

Certains études ont déjà fourni des mesures quantitatives assez précises sur l'abondance de fourmis (Petal 1992, Tobin 1994, Davidson and Patrell-kim 1996). Des auteurs ont réalisé des expériences de suppression de fourmis, afin d'identifier les impacts sur les écosystèmes (Zelikova et al. 2011, Klimes et al. 2011). Ce type de mesures et de manipulations est certainement difficile et coûteuses à mettre en place, et encore plus à maintenir dans le temps afin de pouvoir identifier les conséquences sur le long terme. Une alternative intéressante, serait alors d'étudier les variations dans la consommation de ressources voire dans la composition d'espèces suite à un enrichissement de ressources (Kay 2004, McGlynn et al. 2009, Kaspari et al. 2012, Jacquemin et al. 2012). En effet les variations quant à l'utilisation de ressources au niveau intraspécifique ou au niveau de la communauté peuvent refléter des syndromes de limitation de ressources, fournissant des éléments pour prédire des changements dans le fonctionnement des écosystèmes (Kaspari et al. 2012, Pfeiffer et al. 2014, McGee and Eaton 2014).

La troisième limite de cette étude est sans doute son caractère « local ». En effet, si le choix de se concentrer sur une zone a permis d'obtenir plus d'information concernant les espèces trouvées, nous ne pouvons pas négliger la possibilité que ces relations ne soient pas valables ailleurs. Une perspective importante serait donc d'élargir ces expériences à d'autres zones de Guyane, ainsi que dans d'autres régions biogéographiques pour confirmer que les patterns de changements dans la composition spécifique, fonctionnelle et écologique, sont robustes, stables, et généralisables. A ce caractère local on peut également ajouter un manque important de connaissances sur les dynamiques populationnelles des espèces en général en Guyane. Actuellement, une série d'études visent justement à répertorier la biodiversité de différents organismes sur le territoire guyanais, afin de fournir des bases fonctionnelles sur les effets des gradients environnementaux sur ces communautés (DIADEMA 2013). Les fourmis font partie de ces organismes.

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ANNEXES

ANNEXE 1. MATRICE D'UTILISATION DE RESSOURCES PAR LES FOURMIS ASSOCIEES A LA VEGETATION ET AU SOL DANS DES FORETS ET DANS DES ABATTIS

Appendix 1. Article 4. Resource-use matrix used to assess differences in the relative use by species and quantify ant participation in ecosystem processes. Six columns of resource categories are shown that represent relevant-ant mediated ecosystem processes. The habitat and strata where the species were collected is indicated. Cells indicate the number of species occurrences for each combination of resource habitat and strata. A blue-to-red 'heat' map, indicating lower to higher relative rates of occurrence at different baits, provides a sense of the relative contribution of the different resources to the species' diets. The columns are standardized for a given plot and community, and provide the relative contribution to a process by each species. For comparison purposes each of the species has been associated to a functional group according to the Functional Group classification developed by Andersen (1995).

Tree foraging communities

Habitat	**Morphospecies or species**	Nectar	Honey-dew	Large prey	Small prey	Dead ins.	Excrement	Andersen FFG classification 1995
Cropland	Azteca sp.7	1	1	1	1	2	2	Dominant Dolichoderine
Cropland	Brachymyrmex sp.1	3	1	0	0	2	0	Opportunist
Cropland	*Camponotus cf. fastigatus sp.1 Roger, 1863*	2	2	0	2	4	1	Subordinate Camponotini
Cropland	*Camponotus novogranadensis Mayr 1870*	12	2	10	18	24	15	Subordinate Camponotini
Cropland	Crematogaster sp.11	1	1	0	1	3	1	Subordinate Camponotini
Cropland	Crematogaster sp.5	3	7	0	10	13	2	Generalised Myrmicinae
Cropland	*Monomorium floricola (Jerdon 1851)*	10	10	0	5	15	1	Generalised Myrmicinae
Cropland	Nylanderia sp.4	4	4	0	2	2	0	Opportunist
Cropland	*Paratrechina longicornis (Latreille 1802)*	5	1	0	2	1	0	Opportunist
Cropland	*Pheidole fallax Mayr (Wilson 1963)*	10	11	4	7	12	1	Generalised Myrmicinae
Cropland	Pheidole sp.20	4	3	0	2	2	0	Generalised Myrmicinae
Cropland	Pseudomyrmex sp.1	6	6	0	7	8	1	Tropical climate specialist
Cropland	Solenopsis sp.1	3	3	1	2	4	0	Generalised Myrmicinae
Cropland	*Solenopsis saevissima Smith, 1855*	15	13	8	11	22	7	Generalised Myrmicinae
Cropland	*Solenopsis geminata Fabricius, 1804*	2	3	0	0	2	1	Generalised Myrmicinae
Cropland	*Tapinoma melanocephalum Fabricius, 1793*	14	9	0	0	2	1	Tropical climate specialist
Forest	Azteca sp.1	6	3	4	6	7	7	Dominant Dolichoderine
Forest	Azteca sp.2	7	9	10	20	18	12	Dominant Dolichoderine
Forest	Brachymyrmex sp.3	4	2	0	0	4	1	Opportunist
Forest	*Camponotus cf. fastigatus sp.2 Roger, 1863*	7	4	2	9	9	13	Subordinate Camponotini
Forest	Camponotus femoratus (Fabricius, 1804)	3	1	1	3	7	2	Subordinate Camponotini
Forest	*Cephalotes atratus (Linnaeus, 1758)*	0	0	0	0	3	4	Tropical climate specialist
Forest	Crematogaster sp.2	7	6	0	3	4	0	Generalised Myrmicinae
Forest	*Crematogaster limata Forel, 1904*	24	23	2	13	26	14	Generalised Myrmicinae
Forest	*Crematogaster longispina (Wheeler, 1925)*	13	13	0	11	12	2	Generalised Myrmicinae
Forest	Crematogaster sp.6	12	8	1	9	21	5	Generalised Myrmicinae
Forest	*Crematogaster brasiliensis Mayr, 1978*	16	17	1	23	28	15	Generalised Myrmicinae
Forest	Crematogaster sp.8	4	3	0	0	3	2	Generalised Myrmicinae
Forest	Crematogaster sp.9	1	0	0	2	2	2	Generalised Myrmicinae
Forest	Dolichoderus attelaboides (Fabricius, 1775)	6	2	0	1	5	12	Opportunist
Forest	*Dolichoderus bispinosus (Olivier, 1792)*	9	2	2	9	18	21	Dominant Dolichoderine
Forest	*Ectatomma tuberculatum (Olivier, 1792)*	3	5	2	4	2	1	Opportunist
Forest	Nylanderia sp.1	3	3	0	0	1	0	Opportunist
Forest	*Ochetomyrmex neopolitus Fernandez 2003*	20	18	7	10	19	5	Generalised Myrmicinae
Forest	Pheidole sp.11	7	3	1	4	4	0	Generalised Myrmicinae
Forest	Pheidole sp.16	3	1	0	0	3	0	Generalised Myrmicinae
Forest	Pheidole sp.25	2	2	0	1	2	0	Generalised Myrmicinae
Forest	Solenopsis sp.8	2	4	6	10	10	3	Generalised Myrmicinae
Forest	*Wasmannia auropunctata (Roger, 1863)*	25	19	0	9	28	5	Generalised Myrmicinae

Ground foraging communities

Habitat	**Morphospecies or species**	Nectar	Honey-dew	Large prey	Small prey	Dead ins.	Excrement	Andersen FFG classification 1995
Cropland	Brachymyrmex sp.1	19	7	0	0	1	1	Opportunist
Cropland	*Camponotus novogranadensis Mayr 1870*	2	0	4	8	6	7	Opportunist
Cropland	Crematogaster sp.5	18	19	0	24	32	15	Generalised Myrmicinae
Cropland	*Dorymyrmex pyramicus (Roger, 1863)*	2	3	0	2	6	0	Opportunist
Cropland	*Monomorium floricola (Jerdon 1851)*	2	4	0	0	6	0	Generalised Myrmicinae
Cropland	Nylanderia sp.4	8	4	0	3	3	2	Opportunist
Cropland	*Pheidole fallax Mayr (Wilson 1963)*	46	32	22	26	15	4	Generalised Myrmicinae
Cropland	*Pheidole megacephala (Fabricius, 1793)*	15	12	2	8	7	1	Generalised Myrmicinae
Cropland	Pheidole sp.20	7	5	0	5	3	0	Generalised Myrmicinae
Cropland	Pheidole sp.23	3	1	0	4	1	2	Generalised Myrmicinae
Cropland	*Pseudomyrmex termitarius (Smith, 1855)*	1	1	0	6	0	0	Tropical climate specialist
Cropland	*Solenopsis saevissima Smith, 1855*	18	14	54	55	45	12	Generalised Myrmicinae
Cropland	*Solenopsis geminata Fabricius, 1804*	3	1	5	4	1	0	Generalised Myrmicinae
Forest	Azteca sp.2	0	0	0	1	5	0	Dominant Dolichoderine
Forest	*Camponotus cf. fastigatus sp. 2 Roger, 1863*	1	1	0	1	0	3	Subordinate Camponotini
Forest	Camponotus femoratus (Fabricius, 1804)	1	0	0	2	6	2	Subordinate Camponotini
Forest	*Crematogaster cf. flavosensitiva Longino, 2003*	1	1	0	2	2	1	Generalised Myrmicinae
Forest	Crematogaster sp.2	6	8	1	8	12	1	Generalised Myrmicinae
Forest	*Crematogaster limata Forel, 1904*	1	4	0	5	8	4	Generalised Myrmicinae
Forest	*Crematogaster longispina (Wheeler, 1925)*	2	0	0	3	3	1	Generalised Myrmicinae
Forest	*Crematogaster brasiliensis Mayr, 1978*	5	8	0	7	9	6	Generalised Myrmicinae
Forest	Diplorhoptrum sp.1	6	4	0	1	10	1	Cryptic species
Forest	Diplorhoptrum sp.3	0	2	0	0	4	3	Cryptic species
Forest	Diplorhoptrum sp.4	6	1	0	6	8	0	Cryptic species
Forest	Dolichoderus attelaboides (Fabricius, 1775)	1	0	0	1	0	7	Opportunist
Forest	*Dolichoderus bispinosus (Olivier, 1792)*	0	0	2	0	2	6	Dominant Dolichoderine
Forest	*Ectatomma ruidum*	3	1	4	1	0	0	Opportunist
Forest	*Ectatomma edentatum*	0	0	2	2	2	0	Opportunist
Forest	*Neoponera verenae*	0	0	4	2	0	0	Generalist predator
Forest	Nylanderia sp.1	9	9	0	0	13	0	Opportunist
Forest	Nylanderia sp.2	20	17	0	1	9	2	Opportunist
Forest	*Ochetomyrmex neopolitus Fernandez 2003*	14	5	6	19	14	6	Generalised Myrmicinae
Forest	*Odontomachus haematodus (Linnaeus, 1758)*	0	0	11	5	4	0	Generalist predator
Forest	*Odontomachus scalptus Brown 1978*	3	0	7	5	0	0	Generalist predator
Forest	*Odontomachus chelifer (Latreille, 1802)*	0	0	5	5	1	0	Generalist predator
Forest	Pheidole sp.1	10	2	0	0	6	0	Generalised Myrmicinae
Forest	Pheidole sp.11	5	1	0	5	3	1	Generalised Myrmicinae
Forest	Pheidole sp.12	3	2	0	0	1	0	Cryptic species
Forest	Pheidole sp.16	6	5	0	2	4	0	Generalised Myrmicinae
Forest	Pheidole sp.2	5	7	0	2	8	2	Generalised Myrmicinae
Forest	Pheidole sp.26	1	2	0	2	1	0	Cryptic species
Forest	Pheidole sp.27	2	3	0	0	1	0	Cryptic species
Forest	Pheidole sp.29	4	4	0	3	5	0	Generalised Myrmicinae
Forest	Pheidole sp.32	2	1	0	2	2	0	Cryptic species
Forest	Pheidole sp.33	5	7	0	4	4	0	Generalised Myrmicinae
Forest	Pheidole sp.34	3	0	0	3	1	0	Cryptic species
Forest	Pheidole sp.37	9	8	0	2	13	2	Generalised Myrmicinae
Forest	Pheidole sp.4	4	2	0	0	1	1	Generalised Myrmicinae
Forest	Pheidole sp.5	2	2	0	2	3	0	Generalised Myrmicinae
Forest	Pheidole sp.8	17	10	0	6	17	3	Generalised Myrmicinae
Forest	Pheidole sp.9	3	4	0	2	1	2	Generalised Myrmicinae
Forest	Trachymyrmex sp.2	0	4	0	0	0	4	Tropical climate specialist
Forest	*Wasmannia auropunctata (Roger, 1863)*	13	14	0	10	16	2	Generalised Myrmicinae

ANNEXE 2. INCIDENCE DES DIFFERENTS ESPECES PAR HABITAT ET MESURES MORPHOMETRIQUES REALISEES

Appendix 1. Article 5. Incidence data in the five habitat types and morphological measures for the considered species.

Species name	Forêts de *terrafirme*	Forêts de bas-fond	Lisières	Abattis	Jardins	Wl mesuré	Wl log+1	ATL 1re	MW re	ML re	SL re	CLL re	ELS re	AEP re	IOD re	HW re	PW re	FL re	FW re
Azteca sp. 1	0	3	1	0	0	0,840	0,265	0,081	0,020	0,085	0,304	0,192	0,057	0,059	0,159	0,521	0,495	0,578	0,142
Azteca sp. 2	3	2	0	0	0	1,115	0,325	0,055	0,009	0,065	0,238	0,152	0,043	0,059	0,160	0,430	0,407	0,447	0,149
Azteca sp. 4	1	0	2	0	0	1,005	0,302	0,045	0,009	0,072	0,278	0,164	0,045	0,057	0,142	0,405	0,374	0,411	0,142
Brachymyrmex sp. 1	0	0	0	22	39	0,452	0,162	0,035	0,011	0,060	0,384	0,213	0,066	0,073	0,192	0,636	0,531	0,487	0,155
Camponotus fastigatus	3	2	13	1	1	2,016	0,480	0,082	0,007	0,061	0,281	0,190	0,050	0,098	0,250	0,461	0,434	0,477	0,154
Camponotus sp. 10	0	0	1	0	0	1,799	0,447	0,120	0,023	0,119	0,282	0,165	0,060	0,123	0,213	0,390	0,455	0,513	0,144
Camponotus sexguttatus	0	0	2	0	0	2,016	0,479	0,072	0,004	0,027	0,189	0,113	0,034	0,061	0,099	0,176	0,197	0,307	0,103
Camponotus sp. 14	0	0	1	0	0	2,040	0,483	0,060	0,005	0,035	0,097	0,064	0,030	0,060	0,061	0,103	0,246	0,498	0,127
Camponotus femoratus	0	8	4	0	0	1,707	0,433	0,081	0,008	0,059	0,290	0,171	0,046	0,098	0,209	0,416	0,445	0,517	0,145
Camponotus novogranadensis	0	1	0	13	3	2,131	0,496	0,104	0,007	0,047	0,215	0,141	0,051	0,085	0,158	0,299	0,351	0,441	0,115
Cardiocondyla emeryi	0	1	0	0	0	0,503	0,177	0,033	0,012	0,073	0,245	0,130	0,056	0,034	0,081	0,448	0,346	0,305	0,077
Cardioncondyla obscurior	0	0	0	0	1	0,490	0,173	0,035	0,012	0,071	0,246	0,106	0,036	0,034	0,104	0,465	0,315	0,262	0,075
Cardiocondyla minutior	0	0	0	1	1	0,510	0,179	0,035	0,010	0,054	0,220	0,085	0,033	0,042	0,111	0,421	0,300	0,259	0,073
Cre. cf flavosensitiva	1	6	7	0	0	0,987	0,298	0,066	0,012	0,095	0,539	0,263	0,036	0,052	0,338	0,874	0,470	0,429	0,120
Crematogaster limata	8	17	2	0	0	0,967	0,294	0,057	0,011	0,099	0,563	0,277	0,039	0,066	0,411	0,906	0,493	0,454	0,121
Crematogaster sp. 3	0	13	24	0	0	0,693	0,229	0,028	0,006	0,059	0,325	0,208	0,057	0,078	0,255	0,557	0,367	0,430	0,121
Crematogaster longispina	0	8	27	0	0	0,840	0,265	0,056	0,007	0,043	0,306	0,155	0,045	0,073	0,223	0,539	0,373	0,465	0,134
Crematogaster sp. 5	0	0	0	47	18	0,613	0,208	0,061	0,016	0,082	0,333	0,170	0,074	0,101	0,274	0,642	0,397	0,346	0,094
Crematogaster brasiliensis	11	2	0	0	0	0,814	0,259	0,050	0,010	0,064	0,322	0,171	0,047	0,076	0,245	0,588	0,398	0,440	0,124
Crematogaster sp. 8	1	0	0	0	0	0,829	0,262	0,067	0,012	0,063	0,343	0,157	0,046	0,089	0,265	0,577	0,404	0,501	0,128
Cyphomyrmex sp. 1	0	1	4	0	0	0,923	0,284	0,037	0,009	0,088	0,218	0,132	0,056	0,065	0,154	0,360	0,285	0,360	0,127
Cyphomyrmex sp. 3	0	1	0	0	0	0,750	0,243	0,030	0,009	0,082	0,211	0,117	0,048	0,067	0,161	0,443	0,371	0,333	0,102

Diplorhoptrum sp. 1	17	13	15	6	1	0,333	0,125	0,015	0,009	0,090	0,255	0,108	0,024	0,022	0,130	0,565	0,377	0,275	0,086
Diplorhoptrum sp. 4	22	5	5	0	2	0,367	0,136	0,020	0,009	0,076	0,289	0,072	0,012	0,016	0,106	0,602	0,386	0,301	0,086

Species name	Forêts de *terrafirme*	Forêts de bas-fond	Lisières	Abattis	Jardins	Wl measuré	Wl log+1	ATL 1re	MW re	ML re	SL re	CLL re	ELS re	AEP re	IOD re	HW re	PW re	FL re	FW re
Dolichoderus bispinosus	4	5	0	0	0	3,914	0,691	0,146	0,009	0,068	0,211	0,110	0,019	0,026	0,063	0,124	0,130	0,292	0,068
Dolichoderus attelaboides	5	3	0	0	0	1,998	0,477	0,062	0,005	0,055	0,232	0,168	0,048	0,070	0,221	0,733	0,650	0,543	0,147
Dorymyrmex pyramicus	0	0	0	3	1	1,106	0,324	0,096	0,012	0,051	0,287	0,123	0,037	0,057	0,082	0,215	0,268	0,258	0,051
Ectatomma ruidum	2	5	0	0	0	3,324	0,636	0,116	0,009	0,099	0,225	0,082	0,024	0,038	0,090	0,172	0,181	0,350	0,096
Ectatomma edentatum	3	0	0	0	0	3,699	0,672	0,099	0,007	0,113	0,240	0,060	0,020	0,047	0,092	0,200	0,194	0,320	0,074
Ectatomma tuberculatum	1	0	12	0	0	3,945	0,694	0,137	0,011	0,140	0,251	0,087	0,028	0,040	0,093	0,193	0,180	0,306	0,069
Ectatomma bruneum	0	0	0	1	0	3,472	0,651	0,116	0,007	0,079	0,207	0,089	0,030	0,046	0,130	0,299	0,275	0,364	0,081
Technomyrmex vitiensis	0	0	0	1	0	0,850	0,267	0,028	0,006	0,062	0,244	0,139	0,047	0,053	0,105	0,323	0,310	0,365	0,134
Gnamptogenys sp. 1	1	0	0	0	0	1,699	0,431	0,067	0,008	0,068	0,237	0,134	0,027	0,039	0,140	0,264	0,225	0,339	0,088
Gnamptogenys sp. 3	0	2	0	0	0	1,305	0,363	0,055	0,010	0,099	0,259	0,168	0,036	0,041	0,159	0,325	0,274	0,381	0,115
Linepithema sp. 1	0	0	6	0	0	0,797	0,255	0,038	0,007	0,052	0,226	0,082	0,024	0,038	0,069	0,249	0,293	0,318	0,083
Megalomyrmex leoninuns	0	0	8	0	0	1,757	0,440	0,086	0,007	0,055	0,288	0,073	0,021	0,040	0,062	0,172	0,184	0,354	0,088
Monomorium floricola	0	0	0	10	2	0,456	0,163	0,020	0,007	0,055	0,202	0,104	0,026	0,033	0,147	0,454	0,326	0,247	0,064
Neoponera apicalis	2	1	0	0	0	3,704	0,673	0,190	0,015	0,120	0,269	0,150	0,066	0,052	0,057	0,140	0,172	0,316	0,090
Neoponera verenae	3	1	0	0	0	4,460	0,737	0,240	0,019	0,150	0,241	0,124	0,051	0,051	0,069	0,149	0,168	0,288	0,083
Nylanderia sp. 1	3	22	18	0	0	0,915	0,282	0,038	0,004	0,037	0,328	0,161	0,036	0,033	0,061	0,217	0,264	0,443	0,153
Nylanderia sp. 2	1	29	10	0	0	0,690	0,228	0,031	0,006	0,051	0,369	0,188	0,040	0,052	0,115	0,308	0,324	0,430	0,142
Nylanderia sp. 3	0	5	5	0	0	0,823	0,261	0,038	0,006	0,044	0,344	0,206	0,045	0,054	0,103	0,265	0,285	0,460	0,162
Nylanderia sp. 4	0	0	0	15	5	0,698	0,230	0,037	0,009	0,061	0,362	0,209	0,054	0,057	0,109	0,321	0,340	0,431	0,142
Ochetomyrmex semipolitus	22	17	3	0	0	0,570	0,196	0,040	0,016	0,113	0,278	0,106	0,043	0,047	0,157	0,604	0,411	0,316	0,098
Ochetomyrmex neopolitus	4	1	0	0	0	0,727	0,237	0,050	0,014	0,093	0,285	0,168	0,062	0,052	0,160	0,565	0,371	0,340	0,100
Odontomachus haematodus	2	13	11	0	0	3,309	0,634	0,134	0,016	0,165	0,308	0,028	0,006	0,027	0,072	0,244	0,191	0,262	0,087
Odontomachus scalptus	8	5	0	0	0	3,180	0,621	0,164	0,023	0,208	0,372	0,094	0,020	0,028	0,082	0,308	0,252	0,336	0,102
Odontomachus chelifer	5	0	0	0	0	4,802	0,764	0,326	0,033	0,242	0,390	0,079	0,014	0,025	0,073	0,223	0,175	0,304	0,098
Odontomachus laticeps	3	0	0	0	0	2,663	0,564	0,174	0,028	0,186	0,302	0,088	0,017	0,023	0,078	0,277	0,210	0,267	0,088
Odontomachus sp. 5	2	0	0	0	0	3,060	0,609	0,370	0,056	0,221	0,352	0,079	0,014	0,016	0,056	0,243	0,191	0,281	0,094

Pheidole sp.x+1	16	6	8	0	0	0,445	0,160	0,024	0,012	0,102	0,312	0,101	0,032	0,030	0,107	0,600	0,388	0,322	0,113
Pachycondyla sp. 1	0	0	0	1	0	4,610	0,749	0,180	0,018	0,222	0,274	0,087	0,025	0,034	0,082	0,233	0,208	0,271	0,094
Species name	Forêts de *terrafirme*	Forêts de bas-fond	Lisières	Abattis	Jardins	Wl measuré	Wl log+1	ATL 1re	MW re	ML re	SL re	CLL re	ELS re	AEP re	IOD re	HW re	PW re	FL re	FW re
Pachycondyla sp. 2	6	0	2	0	0	2,440	0,537	0,100	0,012	0,119	0,256	0,089	0,019	0,014	0,044	0,204	0,181	0,253	0,082
Pachycondyla sp. 5	1	1	0	0	0	2,800	0,580	0,070	0,010	0,154	0,206	0,064	0,018	0,017	0,059	0,334	0,272	0,270	0,080
Neoponera villosa	0	0	1	0	0	5,100	0,785	0,260	0,024	0,212	0,276	0,120	0,032	0,026	0,088	0,356	0,295	0,323	0,087
Paratrechina longicornis	0	0	0	0	2	0,944	0,289	0,045	0,005	0,031	0,321	0,196	0,038	0,058	0,083	0,163	0,183	0,399	0,147
Pheidole sp.1 groupe *flavens*	14	20	6	0	0	0,393	0,144	0,017	0,008	0,087	0,341	0,090	0,028	0,038	0,138	0,725	0,484	0,355	0,081
Pheidole sp.2 groupe *flavens*	0	0	14	0	0	0,386	0,142	0,029	0,019	0,128	0,323	0,126	0,047	0,032	0,095	0,610	0,487	0,316	0,085
Pheidole sp. 1	8	2	0	1	1	0,881	0,274	0,042	0,009	0,072	0,363	0,144	0,031	0,044	0,102	0,263	0,212	0,370	0,139
Pheidole sp. 10	0	1	5	0	0	1,157	0,334	0,047	0,011	0,118	0,380	0,216	0,041	0,036	0,128	0,365	0,265	0,408	0,134
Pheidole sp. 11	3	10	15	1	0	0,975	0,296	0,047	0,012	0,117	0,378	0,122	0,025	0,035	0,118	0,370	0,256	0,409	0,139
Pheidole sp. 12	1	4	0	0	0	0,857	0,269	0,043	0,011	0,090	0,348	0,145	0,033	0,045	0,144	0,431	0,306	0,380	0,118
Pheidole sp. 13	0	3	0	0	0	0,765	0,247	0,045	0,014	0,101	0,359	0,137	0,036	0,056	0,166	0,493	0,357	0,403	0,136
Pheidole bilimeki	9	3	0	0	0	0,593	0,202	0,034	0,013	0,103	0,420	0,187	0,041	0,038	0,125	0,447	0,306	0,405	0,143
Pheidole sp. 16	18	4	0	0	0	0,510	0,179	0,028	0,015	0,115	0,266	0,118	0,041	0,036	0,120	0,546	0,382	0,346	0,109
Pheidole sp. 17	0	1	0	0	0	1,010	0,303	0,035	0,007	0,068	0,306	0,131	0,029	0,047	0,120	0,288	0,245	0,410	0,138
Pheidole fallax	0	0	1	49	41	1,144	0,331	0,072	0,015	0,093	0,363	0,159	0,034	0,039	0,097	0,268	0,205	0,374	0,144
Pheidole sp. 19	0	0	2	6	0	0,596	0,203	0,032	0,012	0,110	0,340	0,141	0,038	0,037	0,134	0,491	0,318	0,323	0,125
Pheidole sp. 2	9	11	1	0	0	0,712	0,234	0,035	0,013	0,104	0,343	0,139	0,029	0,036	0,111	0,345	0,248	0,381	0,144
Pheidole megacephala	0	0	3	28	4	0,765	0,247	0,027	0,006	0,063	0,307	0,135	0,034	0,035	0,089	0,335	0,248	0,345	0,114
Pheidole sp. 21	0	0	0	3	0	0,786	0,252	0,030	0,007	0,071	0,373	0,151	0,037	0,047	0,111	0,335	0,243	0,396	0,143
Pheidole sp. 23	0	0	0	8	1	1,255	0,353	0,080	0,012	0,066	0,238	0,105	0,027	0,037	0,099	0,243	0,193	0,345	0,144
Pheidole sp. 24	3	1	0	0	0	0,750	0,243	0,057	0,015	0,087	0,349	0,139	0,036	0,054	0,173	0,522	0,373	0,396	0,128
Pheidole sp. 25	1	0	0	0	0	0,745	0,242	0,035	0,007	0,059	0,365	0,176	0,042	0,055	0,146	0,371	0,275	0,358	0,131
Pheidole sp. 26	4	2	0	0	0	0,883	0,275	0,040	0,009	0,073	0,350	0,132	0,032	0,047	0,108	0,299	0,247	0,396	0,133
Pheidole sp. 29	7	10	0	0	0	0,915	0,282	0,032	0,007	0,065	0,299	0,161	0,033	0,036	0,085	0,223	0,186	0,369	0,146
Pheidole sp. 29.cf.	0	6	0	0	0	1,033	0,308	0,047	0,009	0,076	0,345	0,156	0,033	0,043	0,107	0,273	0,226	0,427	0,161
Pheidole sp. 29.cf.2	0	1	0	0	0	0,848	0,267	0,042	0,010	0,081	0,328	0,135	0,031	0,043	0,105	0,251	0,210	0,378	0,131

Pheidole sp. 3	0	4	1	0	0	0,923	0,284	0,043	0,011	0,101	0,300	0,156	0,034	0,032	0,125	0,416	0,297	0,365	0,159
Pheidole sp. 31	2	0	0	0	0	0,911	0,281	0,044	0,011	0,101	0,387	0,120	0,021	0,032	0,119	0,357	0,254	0,383	0,124
Species name	Forêts de *terrafirme*	Forêts de bas-fond	Lisières	Abattis	Jardins	Wl measuré	Wl log+1	ATL 1re	MW re	ML re	SL re	CLL re	ELS re	AEP re	IOD re	HW re	PW re	FL re	FW re
Pheidole sp. 32	5	0	1	0	0	0,547	0,189	0,022	0,009	0,107	0,313	0,153	0,037	0,029	0,116	0,502	0,322	0,326	0,105
Pheidole sp. 4	6	4	1	0	0	0,570	0,196	0,045	0,018	0,100	0,289	0,110	0,031	0,031	0,118	0,525	0,374	0,371	0,123
Pheidole sp. 41	0	1	2	0	0	0,810	0,258	0,047	0,014	0,100	0,356	0,178	0,042	0,042	0,113	0,354	0,270	0,351	0,114
Pheidole sp. 44	0	0	3	0	0	0,820	0,260	0,050	0,015	0,100	0,386	0,176	0,040	0,056	0,172	0,462	0,313	0,424	0,135
Pheidole sp. 5	0	7	1	0	0	1,435	0,387	0,070	0,009	0,068	0,336	0,124	0,022	0,030	0,070	0,160	0,141	0,381	0,146
Pheidole sp. 6	0	1	0	0	0	0,840	0,265	0,050	0,014	0,105	0,357	0,164	0,041	0,053	0,175	0,500	0,357	0,402	0,121
Pheidole sp. 7	0	1	0	0	0	0,820	0,260	0,040	0,011	0,096	0,369	0,130	0,034	0,054	0,138	0,408	0,308	0,407	0,132
Pheidole sp. 8	29	11	0	0	0	0,496	0,175	0,025	0,011	0,087	0,243	0,099	0,032	0,022	0,067	0,415	0,295	0,262	0,095
Pheidole sp. 9	2	7	0	0	0	0,745	0,242	0,043	0,010	0,071	0,348	0,122	0,032	0,047	0,117	0,354	0,271	0,354	0,119
Pseudomyrmex gracilis	0	0	0	7	0	1,860	0,456	0,095	0,009	0,055	0,117	0,070	0,091	0,047	0,046	0,278	0,255	0,272	0,095
Pseudomyrmex cf *pallidus*	0	0	1	0	0	1,350	0,371	0,070	0,008	0,045	0,088	0,019	0,036	0,072	0,042	0,172	0,200	0,167	0,060
Pseudomyrmex sp. 5	5	0	3	0	0	1,858	0,456	0,080	0,006	0,041	0,095	0,041	0,068	0,048	0,032	0,183	0,199	0,242	0,100
Trachymyrmex sp. 1	0	1	1	0	0	1,782	0,444	0,059	0,008	0,111	0,215	0,075	0,022	0,022	0,087	0,391	0,302	0,371	0,098
Sericomyrmex sp. 2	2	1	0	0	0	1,489	0,396	0,085	0,017	0,152	0,358	0,149	0,033	0,031	0,144	0,623	0,567	0,690	0,116
Solenopsis cf *geminata*	1	1	0	0	0	0,950	0,290	0,056	0,008	0,048	0,213	0,063	0,017	0,034	0,119	0,401	0,279	0,312	0,090
Solenopsis sp. 8	5	1	0	0	0	0,407	0,148	0,019	0,009	0,084	0,254	0,103	0,023	0,023	0,129	0,539	0,361	0,282	0,087
Solenopsis saevissima	0	0	14	58	52	1,089	0,320	0,060	0,007	0,053	0,258	0,052	0,013	0,035	0,122	0,381	0,256	0,317	0,091
Solenopsis globularia	0	0	1	6	24	0,600	0,204	0,043	0,011	0,062	0,219	0,091	0,028	0,029	0,106	0,452	0,338	0,270	0,075
Solenopsis geminata	0	0	0	0	1	0,954	0,291	0,057	0,008	0,056	0,248	0,063	0,017	0,034	0,119	0,398	0,276	0,309	0,088
Tapinoma sp. 2	0	0	0	0	1	0,640	0,215	0,030	0,011	0,103	0,355	0,152	0,035	0,038	0,102	0,352	0,297	0,363	0,161
Trachymyrmex sp. 2	5	5	0	0	0	1,092	0,321	0,047	0,010	0,097	0,249	0,100	0,026	0,027	0,100	0,390	0,292	0,337	0,092
Trachymyrmex sp. 3	2	1	1	0	0	1,619	0,418	0,070	0,012	0,127	0,245	0,091	0,024	0,021	0,083	0,370	0,258	0,353	0,099
Wasmannia auropunctata	26	22	21	0	0	0,488	0,173	0,020	0,007	0,077	0,278	0,126	0,045	0,040	0,132	0,689	0,503	0,394	0,109