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REVIEW

Effects of Habitat Conversion on Ant Functional Groups: A Global Review

Roberta J Santos[1,4], Pavel Dodonov[2], Jacques Hubert C Delabie[3,4]

1 - Universidade Estadual de Santa Cruz, Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, Campus Soane Nazaré de Andrade, Ilhéus-BA, Brazil
2 - Universidade Federal da Bahia, Laboratório de Ecologia Espacial, Instituto de Biologia, Campus de Ondina, Salvador-BA, Brazil
3 - Universidade Estadual de Santa Cruz, Departamento de Ciências Agrárias e Ambientais, Campus Soane Nazaré de Andrade, Ilhéus-BA, Brazil
4 - Laboratório de Mirmecologia, Centro de Pesquisa do Cacau (CEPEC/CEPLAC), Ilhéus-BA, Brazil

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Corresponding author
Roberta de Jesus Santos
Laboratório de Mirmecologia
Centro de Pesquisa do Cacau, CEPEC/CEPLAC - Caixa Postal 7, CEP: 45600-970
Itabuna, Bahia, Brasil.
E-Mail: beta.biologia@gmail.com

Abstract

Conversion of natural to anthropogenic environments affects biodiversity, and the understanding of these impacts may be improved by assessing how different functional groups respond to such land conversion. We studied land conversion impacts on ant functional groups, as ants are ecologically important and respond well to various environmental changes. We hypothesized that conversion of natural to anthropogenic environments modifies the composition of functional groups, fostering generalist and opportunistic groups over specialist ones, with more responses of this type in tropical than in temperate regions. We recovered 412 papers from ISI Web of Science, of which we selected 17 studies, published between 1993 and 2018, that addressed our study's question. We assessed whether each functional group responded positively or negatively to conversion of natural habitat into anthropogenic land uses and used Monte Carlo tests to assess significance. Ants were affected by natural habitat conversion into monoculture and polyculture and by the conversion of savannas and of tropical and subtropical forests. Land conversion affected six of the 13 functional groups assessed here. In the temperate zone, cryptic species, predators, subordinate Camponotini, cold-climate specialists and tropical-climate specialists were impaired, whereas hot-climate specialists were favored. In the tropics, land conversion negatively impacted fungus-growers and predators. In both climatic zones, several functional groups, mainly those with broad ecological niches, did not respond to land conversion. Our results corroborate that land conversion effects vary among ant functional groups and indicate that the ant fauna of temperate ecosystems may be more susceptible than that of tropical regions.

Introduction

Human dependence on natural resources is continuously increasing and aims to meet our immediate needs for food, fiber, water, and shelter. Since the Industrial Revolution, there has been an intensification in land use change and habitat conversion (which we define here as the conversion of natural habitats into anthropogenic land uses, mainly agricultural ones), which has resulted in the global degradation of environmental conditions (Foley et al., 2005; Millennium Ecosystem Assessment, 2005; Ellis et al., 2013). The effects of such land use change range from altering the structure and functioning of ecosystems to modifying the dynamics of interactions between ecosystems and atmosphere, water bodies and the surrounding lands (Vitousek et al., 1997; Foley et al., 2005). In addition, land use changes,

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especially the conversion of natural and complex landscapes into anthropized environments, have led to the simplification, loss, and fragmentation of native habitats, contributing to the disappearance of biodiversity and consequently its functions and ecosystem services (Pimm & Raven, 2000; Hansen et al., 2004; Haines-Young, 2009; Almeida et al., 2016).

Negative impacts caused by habitat conversion and intensification have already been documented for several taxonomic groups, such as birds (Donald et al., 2001, Rittenhouse et al., 2012), mammals (Sauvajot et al., 1998; Sotherton, 1998; Riffell et al., 2011; Seki et al., 2017), insects (Vasconcelos, 1999; Philpott et al., 2008; Winfree et al., 2011), and plants (Philpott et al., 2008; Meers et al., 2010). Thus, assessing the effects of habitat conversion on biological communities helps to understand how environmental changes affect biodiversity, ecosystem functions and ecosystem services (Haines-Young, 2009; Luck et al., 2009; Geijzendorffer & Roche, 2013).

For several taxa, a commonly used functional approach is the classification of species in a community into functional groups (FGs), with functionally similar species being included in the same group (Cummins, 1974; Cianciaruso et al., 2009; Laureto et al., 2015). Species classification into FGs can be either *a priori*, according to a classification based on species characteristics or similarities, or *a posteriori,* with multivariate analysis techniques (Petchey, 2004; Calaca & Grelle, 2016). The classification into FGs has been widely used in recent studies of biotic communities, including ants (Hymenoptera: Formicidae) (Andersen, 1995; King et al., 1998; Delabie et al., 2000; Ottonetti et al., 2006; Underwood & Fisher 2006; Crist, 2009, Leal et al., 2012; Lawes et al., 2017; Assis et al., 2018). Such groupings are based on taxonomic affinities, morphological patterns, and niche dimensions such as diet, nest location, foraging behavior, and habitat preference or environmental tolerance (Andersen, 1990, 1995, 1997; Hoffmann & Andersen, 2003; Silvestre et al., 2003; Andersen & Majer, 2004; Weiser & Kaspari, 2006; Silva & Brandão, 2010; Brandão et al., 2012; Koch et al., 2019).

The classification of ants into FGs is useful in studies of habitat conversion, as such classifications permits to infer how community structure and function are affected by disturbances and environmental changes (Andersen & Majer, 2004; Underwood & Fisher, 2006). Considering the importance of the ant fauna for the provision of important ecosystem supporting and regulating services, such as nutrient cycling, seed dispersal, population control of other arthropods, and formation and structuring of soil superficial layers (Hölldobler & Wilson, 1990; Folgarait, 1998; Del Toro et al., 2012), the understanding of habitat conversion effects on different ant FGs is essential to better understand the impacts of environmental changes on biodiversity.

Since the first sketches of ant classification into FGs, with the Greenslade's (1978) pioneer study in Australia, the FGs scheme has been modified and adapted to classify ant communities from other biogeographic regions (Majer et al., 2004). One of the best known functional schemes developed from ant communities of Australian savannas classifies the groups according to the ants' relationship with climate, soil, vegetation, and disturbances, and the main FGs are: (i) Dominant Dolichoderinae; (ii) Subordinate Camponotini; (iii) Generalized Myrmicinae; (iv) Opportunists; (v) Climate Specialists; (vi) Cryptic species and (vii) Specialist Predators (see Table 1) (Andersen, 1995, 1997, 2000; King et al., 1998; Hoffmann & Andersen, 2003; Andersen & Majer, 2004; Andersen et al., 2007).

Another important functional classification, based on the nutrition and bioecological aspects of the ants, was developed for the Neotropical region, and resulted from information in previous studies (Delabie et al., 2000; Silvestre et al., 2003; Brandão et al., 2009, 2012; Silva & Brandão, 2010). This classification includes ant guilds or groups organized around ant nutritional requirements and/or feeding habits: (i) Generalist predators; (ii) Specialists; (iii) Arboreal predator ants; (iv) Generalists; (v) Fungus growers; (vi) Legionary ants; (vii) Dominant arboreal ants associated with carbohydrate-rich resources or domatia; (viii) Pollen-feeding arboreal ants, and; (ix) Subterranean ants (see Table 1 and Brandão et al., 2009, 2012).

In general, habitat disturbance and conversion affect ant communities directly, by reducing the availability of resources and removing colonies, and indirectly, through changes in habitat structure, nesting site availability, temperature, and humidity (Andersen, 2000; Philpott et al., 2010). In addition, habitat changes promoted by agriculture, logging, grazing, mining, etc., may lead to the exclusion of sensitive groups and the advent of groups tolerant to disturbances, which can replace or compete with those present before the disturbance (Andersen, 1995, 2000; Hoffmann & Andersen, 2003; Andersen & Majer, 2004; Ottonetti et al., 2006; Crist, 2009; Leal et al., 2012; Parui et al., 2015; Assis et al., 2018; Amaral et al., 2019). Highly specialized FGs, such as cryptic species, tend to be sensitive to changes in habitat due to their preference for forested environments and nesting and foraging in soil and litter (Hoffmann & Andersen, 2003). On the other hand, other groups of ants, often called opportunists, are ruderal with low competitiveness and wider environmental tolerance and may be predominant in disturbed environments (Andersen, 1997; King et al., 1998; Andersen & Majer, 2004).

In addition, the effects of habitat conversion may affect ant FGs in different ways throughout the globe, as aspects associated with species richness, such as habitat heterogeneity and physical environment, differ between tropical and temperate zones. Habitat heterogeneity is related to the variety of resources in the environment, with a greater availability of resources permitting a better partitioning of niche space and greater specialization (MacAthur & MacAthur, 1961, Pianka, 1966; Brown & Lomolino, 1998). Therefore, it is possible that conversion of native habitats to anthropogenic land use promotes greater loss of the original habitat heterogeneity in more structurally diverse and complex areas, impacting specialized FGs associated with native habitats, and may therefore be more significant in the tropics than in temperate regions.

In order to assess the effects of habitat conversion on different ant FGs in tropical and temperate zones of the globe, we conducted a literature review to: i) identify how habitat conversion (conversion of native habitats to anthropogenic

Table 1. Details of functional groups scheme of Australian ants based on their relationships to the climate, soil, vegetation, and disturbance*, and functional classification for ants of Neotropical region based on their nutritional and bioecological aspects**.

Functional groups of Australian ants

Group	Subdivision	Characteristics
Dominant Dolichoderinae		Species of the Dolichoderinae subfamily, with dominant behavior and preference for hot and open habitats.
Subordinate Camponotini		Ants tend to be behaviourally submissive to dominant dolichoderines, and have large body size, nocturnal foraging, and/or arboreal habits.
Generalized Myrmicinae		Group with subdominant behavior to Dominant Dolichoderinae from a global perspective, and with high tolerance to disturbance.
Opportunists		Group that is dominant in disturbed environments in which other groups lose their relative importance.
Climate specialists	Hot-Climate Specialists Cold-Climate Specialists Tropical-Climate Specialists	Climate specialists that have specific habitat tolerance, with preferences related to temperature and humidity.
Cryptic species		Species that can hide in their habitat and occur preferentially in forests and forage within soil and litter.
Specialist Predators		Ants specialized in diet and sensitive to disturbance.

Functional groups of Neotropical region

Group	Subdivision	Characteristics
Generalist predators	Epigaeic generalists predators	Ants with large and medium-sized predators that forage on the soil surface or above the litter.
	Hypogaeic generalist predators	Medium and small-sized ants that forage within the leaf litter.
Specialists (with specialized morphology and biology)	Predation in mass and/or nomadism	Ants with hunting strategy in groups of workers in columns/ mass in predation or nomadic behavior in predation of certain preys.
	Dacetini predators	Possess specialized jaws with morphology and mechanism different from other Mymicinae.
Arboreal predator ants		Species which forage in vegetation and prey on a range of arthropods.
Generalists	Generalized Myrmicines Generalized Formicines, Dolichoderines and some Myrmicines Small-sized hypogaeic generalist foragers	Ants with a wide ecological niche.
Fungus growers	Leaf cutters	Use live or dead plant substrate for rearing their symbiotic fungus.
	Litter-nesting fungus growers	Cryptobiotic Attina ants living in the leaf litter and using a variety of substrates (e.g. leaves, flowers, fruits, seeds, feces, lichen, and carcasses of arthropods) to rear the symbiotic fungus or yeast.
Legionary ants (army ants)		Ants with behavioral and reproductive syndrome, with nomadism, dicthadiiform reproductive females (wingless queens) and mandatory collective foraging.
Dominant arboreal ants associated with carbohydrate-rich resources or domatia		Ants picking up liquid food resources (as nectar produced by floral or extrafloral nectaries, carbohydrate-rich exudates sucking hemipterans, and exudates of some Lepidoptera larvae) or species living in association with myrmecophytes that present specialized structures aiming ant nesting (such as domatia) and provide food (nectaries and Mullerian or food bodies).
Pollen-feeding arboreal ants		Components of the Neotropical Cephalotini tribe that remove anemophilous pollen deposited on the vegetation surface, an important item in the diet of these ants.
Subterranean ants		Ants that live in the deeper layers of soil.

*Andersen, 1995, 1997, 2000; King et al., 1998; Hoffmann & Andersen, 2003; Andersen & Majer, 2004; Andersen et al., 2007; **Brandão et al., 2009, 2012.

land uses, especially agricultural areas) affects ant FGs; ii) assess whether these effects can be observed in different types of native habitats and anthropogenic land uses; and iii) verify how the different ant FGs respond to habitat conversion in the tropical and temperate zones. We hypothesized that: a) FGs in general are negatively affected by the conversion of natural to anthropogenic environments; b) opportunistic and generalist ants and ants with a preference for disturbed sites respond positively to habitat conversion; c) specialist ants respond negatively to such changes; and d) in tropical zones, more FGs of ants would have negative responses as compared to groups in temperate climatic zones.

Methods

Literature search

This study addresses the effects of converting natural to anthropic environments on ant FGs based on a literature review and statistical significance tests (Fig 1). The studies were identified through a comprehensive search (last updated in July 2018) in the ISI Web of Science database, using the following terms: "(ants OR *ant* OR Formicidae) AND (land cover OR land use) AND (functional)' in TOPIC, 'DocType=All document types, Language=All languages', from all databases". The research resulted in 412 published studies.

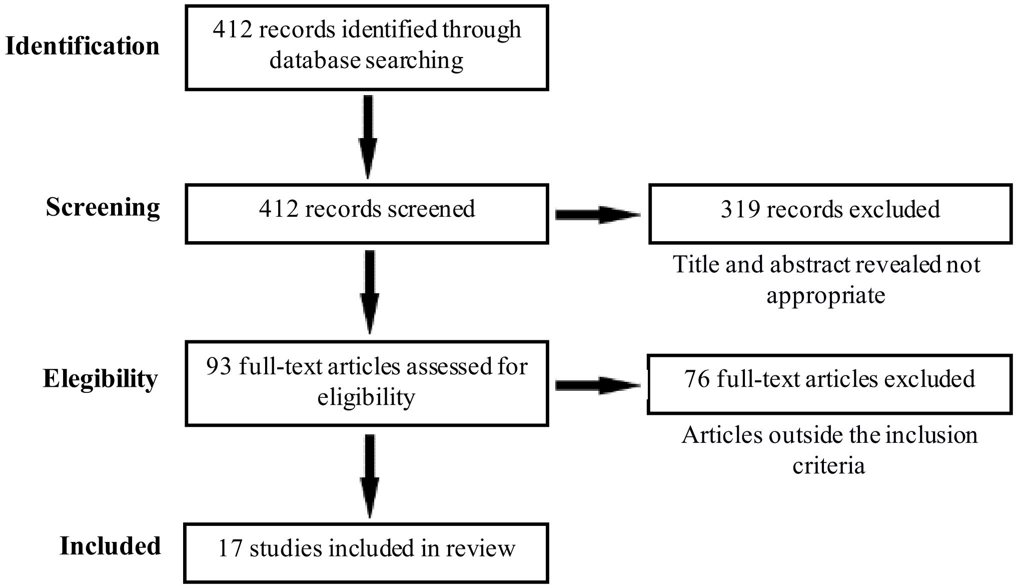

Fig 1. The flow diagram showing an overview of the study selection process according to the PRISMA (Preferred reporting items for systematic reviews and meta-analyses) guidelines. Adapted from Moher et al. (2009).

Selection criteria

After the first period dedicated to literature search, we selected studies that evaluated directly or indirectly, explicitly or implicitly, the effects of habitat conversion (natural to anthropogenic) on ant FGs and that sampled ant fauna in areas with native vegetation (control) and in converted areas. We understand conversion as the integral transformation of a natural environment into an anthropogenic environment (Coppin et al., 2004), excluding uses such as selective logging, which only partially alter the natural environment, but including agroforestry. Titles and abstracts were carefully examined to determine whether the paper met the criteria for inclusion in the review. Then, the following criteria were used to select the studies for full reading: a) we included only studies on native vegetation that was completely converted to human activities for economic purposes and maintained for such purposes throughout the study; b) we excluded studies on fire ecology (burned vs. unburned areas), studies comparing non-grazed vs. grazed areas or studies comparing different logging managements in native areas; c) we excluded converted areas that were in natural regeneration, rehabilitation or succession; and d) we only included studies that included functional classification of species and figures or tables that permitted to compare the response of ant FGs between native vegetation (control) and converted areas. A study carried out in a deactivated mining region was excluded because it was the only study with this type of land use among the selected studies. Thus, in our final dataset we had comparisons of natural areas with areas converted to monoculture, polyculture, pasture, and agroforestry.

We did not perform a meta-analysis because many published studies did not provide information such as mean and standard deviation or correlation or regression coefficients, which are necessary to calculate effect sizes (Borenstein et al., 2009). Thus, we devised a new simulation-based approach, based on the general recommendations for Monte Carlo statistical tests (Manly, 2007). As most of the studies reported responses in the absence of formal statistical significance tests, we first defined the type of response through visual analysis of figures and tables. Our assessments of the responses of different FGs in any particular study are therefore necessarily qualitative. For each study, we assessed whether the response of FGs to habitat conversion was positive, negative or neutral by comparing the occurrence of different FG in native vegetation (control) and in converted areas. When the mean values reported for each FG in the two environments did not differ or differed slightly (e.g. difference in relative presence was less than 4%; difference in mean less than 0.25; or overlapping points in the scatter plot for FGs in native and anthropogenic habitat), we considered the effect as neutral. Otherwise, we considered habitat conversion to have positive effects when the values were greater in the converted environment and negative effects when they were greater in the natural habitat. This approach is similar to that used by Hoffmann & Andersen (2003).

Due to the small number of studies that we included in the analysis according to the inclusion criteria above, it was not possible to characterize richness, frequency and abundance separately; we therefore combined these measures into a single response variable (Table 3). Thus, a positive effect may indicate a positive outcome on abundance, frequency and/or richness of a functional group, without differentiating between these measures.

Study characteristics

Our final selection included 17 papers published between 1993 and 2018, corresponding to studies carried out in several continental regions present in the tropical climatic zone [Africa (2), Asia (2), Oceania (2), and South America (3)] and temperate zone [Europe (1), North America (1), and Oceania (6)]. The selected studies employed 11 methods of ant sampling: Pitfall traps (15), Winkler for leaf litter samples (3), baits (2), hand collection (2), baited arboreal pitfall traps (1), baited pitfall traps (1), baited subterranean traps (baited Eppendorf's tubes) (1), soil monolith method (1), quadrat sampling (insect vacuum and mouth aspirator) (1), sweep netting and foliage shaking (1), and Tullgren funnels with leaf litter and surface soil samples (1) (Table 3) (for a general review of sampling ants methods, see Delabie et al., 2021). These methods were used for ant sampling in different strata (arboreal, leaf litter, soil, and subterranean). The anthropic land uses included in the studies were agroforestry (e.g. cocoa plantations with native woody plant or mixture of different crop plants), monoculture (e.g. coffee, sugarcane, *Eucalyptus* plantation), pasture (e.g. alien grasses, grazing or managed areas), and polyculture [including crop rotation, mixed-crop fields, cultivated fields (cereals), and farmland].

Table 2. Functional groups and variations in nomenclature of some functional groups present in the studies which met the selection criteria of this review.

Group	Variations in nomenclature of some functional groups that occur in the studies
Arboreal	Arboreal ants, arboreal nesting dominant, territorially dominant arboreal species, non-dominant arboreal species
Army ants	
Cryptic species	
Dominant Dolichoderinae	
Fungus-growers	Attina, fungus-growing, fungivore/surface
Generalists	Omnivore, omnivore/surface
Generalized Myrmicinae	
Opportunists	
Predators	Other predators, predator/surface, predator/litter, specialized predators, specialist predators, generalist predators, large, solitary predators
Subordinate Camponotini	
Cold-climate specialists	
Hot-climate specialists	
Tropical-climate specialists	

The classification of ants into FGs of these papers was according to functional schemes such as those of Andersen (1990, 1995, 1997), Delabie et al. (2000), Silvestre et al. (2003), and Weiser & Kaspari (2006) (Table 3 and see appendix 1). The classifications used in the selected articles are based on a particular functional grouping as previously mentioned and, in some cases, the authors of these articles made modifications and/or used literature with relevant information to group ants into ecological groups. We recognize the variety and specificity of the functional classifications of the set of studies selected in this review and, therefore, we made a broader and more general classification allowing us to analyze the extracted data. Most papers (17) classified ants into FGs and only two classified ants into functional guilds based on feeding and foraging guilds (Appendix 1). 13 FGs were used for the whole study while some FGs with differences in nomenclature were combined into a single group to facilitate data interpretation (Table 2).

Table 3. Details of the articles selected for this review.

Reference	Number of independent case studies (i.e., observation)	Continent	Habitat type and land use	Sampling method	Sampled stratum	Metrics used	References used for functional classification
Assis et al., 2008	3	South America	Tropical and subtropical rainforest vs. Monoculture Tropical and subtropical rainforest vs. Pasture	Pitfall traps	Soil	Relative presence (%)	Delabie et al., 2000
Lawes et al., 2017	1	Oceania	Tropical and subtropical rainforest vs. Pasture	Pitfall traps/ Baited subterranean traps (Baited Eppendorf tubes)/ Baited Arboreal pitfall traps/ Leaf litter samples - Winkler	Soil, arboreal, subterranean and leaf litter	Frequency of occurrence	Andersen, 1995
Pacheco et al., 2017	2	South America	Savanna vs. Polyculture	Baited pitfall traps and Baited subterranean traps (Conventional pitfall traps)	Soil and subterranean	log-transformed mean numbers of ants per trap	Silvestre et al., 2003
Saad et al., 2017	2	South America	Tropical and subtropical rainforest vs. Monoculture	Pitfall traps, Berlese (Soil samples) and Tullgren funnels (Soil samples)	Soil and subterranean	Total species richness	Weiser & Kaspari, 2006
Lu et al., 2016	1	Asia	Tropical and subtropical rainforest vs. Agroforestry	Pitfall traps/ Sweep netting and foliage shaking	Soil and arboreal	Mean functional group - relative contribution (%)	Andersen, 1990, 1995
Parui et al., 2015	2	Asia	Tropical dry forest vs. Monoculture	Pitfall traps	Soil	Relative abundance (%)	Andersen, 1995
Kuate et al., 2015	1	Africa	Tropical and subtropical rainforest vs. Polyculture	Pitfall traps/ Quadrat sampling (Insect Vacuum and mouth aspirator)/ Bait	Soil and leaf litter	Relative occurrence (%)	Delabie et al., 2000; Andersen, 2010
Kone et al., 2012	4	Africa	Tropical and subtropical rainforest vs. Agroforestry	Leaf litter samples - Winkler/ Pitfall traps/ Monolith method/ Hand collection	Leaf litter, soil and subterranean	Relative abundance	Lévieux, 1983; Majer, 1983; Andersen, 1995, 1997; King et al., 1998; Hoffmann et al., 2000; Read & Andersen, 2000; Andersen & Majer, 2004; Dejean et al., 2007; Bolton & Fisher, 2008
Franklin, 2012	12	North America	Scrub, heath and shrublands vs. Pasture	Pitfall traps	Soil	Relative abundance	Andersen, 1995, 1997
House et al., 2012	12	Oceania	Grassland vs. Pasture Grassland vs. Polyculture Woodland vs. Pasture Woodland vs. Polyculture	Pitfall traps	Soil	Percentage occurrence (%)	Greenslade, 1978; Andersen, 1997; Brown, 2000
Gollan et al., 2011	2	Oceania	Woodland vs. Pasture	Pitfall traps	Soil	Relative abundance	Andersen, 2001
Yates & Andrew, 2011	2	Oceania	Grassland vs. Monoculture Woodland vs. Monoculture	Pitfall traps	Soil	Number of ant species	Andersen, 1995
Nakamura et al., 2007	2	Oceania	Tropical and subtropical rainforest vs. Pasture	Pitfall traps, Tullgren funnels (Leaf litter and surface soil samples)	Soil and leaf litter	Mean frequency	Andersen, 2000
Schnell et al., 2003	2	Oceania	Woodland vs. Monoculture Woodland vs. Pasture	Pitfall traps	Soil	Relative abundance (%)	Andersen, 1990
Gómez et al., 2003	4	Europe	Scrub, heath and shrublands vs. Pasture Scrub, heath and shrublands vs. Polyculture Woodland vs. Pasture Woodland vs. Polyculture	Pitfall traps	Soil	Mean abundance	Andersen, 1995, 1997a (Bestelmeyer & Wiens, 1996; Andersen, 1997b, 2000; Read & Andersen, 2000; Brown, 2000)
King et al., 1998	2	Oceania	Tropical and subtropical rainforest vs. Pasture	Pitfall traps/ Leaf litter samples - Winkler/ Baits	Soil, leaf litter and arboreal	Abundance	Andersen, 1995
Lobry De Bruyn, 1993	2	Oceania	Scrub, heath and shrublands vs. Polyculture Woodland vs. Polyculture	Pitfall traps/ Hand collection	Soil	Percentage abundance (%)	Greenslade & Greenslade, 1984; Andersen, 1986, 1987

Most studies had more than a single land use or sampled in contrasting landscapes (i.e., different locations) or different years or sampled in different strata and/or with different traps, as well as having more than a single type of native vegetation. Thus, when a study showed more than a single combination of native vegetation type *versus* converted environment, each combination was considered as a separate data set, i.e., independent case studies (hereafter observations), so that some papers corresponded to more than a single case study. Studies with paired comparisons in different climatic zones were excluded. Therefore, our review summed a total of 56 observations (Table 3) for the analyses.

Statistical analysis

Due to the nature of our data, assuming values of -1, 0, and 1 (for negative, neutral, and positive responses, respectively – see below), we chose to use a Monte Carlo approach to calculate significance by comparing our observed results to simulations of the null hypothesis. Monte Carlo method works by comparing a test statistic with a large number of random samples generated under a given model, which often represents the null hypothesis (Manly, 2007). One advantage of this test is its flexibility in defining the statistics and the model used for the simulation, permitting it to be adapted for specific study questions (Manly, 2007). Thus, we developed Monte Carlo test specifically to address our study questions and to test our null hypotheses.

As we classified each response as negative, neutral, or positive, our statistical null hypothesis was that these values (-1, 0, +1) were randomly assigned to each response. We thus developed a simulation (Monte Carlo) model specifically to test this null hypothesis. We used this new Monte Carlo test to test whether the responses of ant FGs are significantly positive or negative (i.e. deviate significantly from what would be expected under our null hypothesis) and how these responses vary among the types of native vegetation, types of conversion, FGs, and climatic zone. Due to sampling size limitation, we considered observations from the same study as independent.

We coded each response (observation) as -1 (negative response, i.e., decreased FG richness or abundance in converted environment), 0 (neutral, i.e., no difference between natural and converted environments), or +1 (positive, i.e., increased FG richness or abundance in the converted environment). We then performed analyses separately for each 1) type of converted environment, 2) type of native vegetation, 3) climatic zone, 4) FG, and 5) FG separated by climatic zone (temperate and tropical); for analyses 1 to 3 we grouped all FGs due to insufficient sampling size for separate analyses.

In each analysis, we calculated the average response for each level of the explanatory variable by summing the responses (coded as -1, 0, and 1) and dividing this sum by the number of responses assessed. Thus, this index varies from -1 to 1. A value near -1 means that group most responses were negative, whereas a value close to 0 can mean that most response were neutral or that positive and negative responses were equally common and a value close to 1 means that most responses were positive.

We then simulated the distribution of this index under the null model to assess whether the average responses differ significantly from zero. We are unaware of previous studies using exactly this type of simulation but, considering the flexibility of Monte Carlo test to adapt to specific research questions and nonstandard situations (Manly, 2007), we believe that this approach is valid. The null model used for these simulations was that positive, negative, and neutral responses were all equally probable, i.e., that a study could have observed a negative (-1), neutral (0), or positive (1) response for a give FG with the same probability. Thus, in each simulation, we randomly assigned a value of -1, 0, or 1 to each response (observation), simulating the null hypothesis that the responses were random, and calculated the average response with the randomized data. We repeated this procedure 9,999 times, thus obtaining a distribution of average responses under the null model, and calculated significance (p-value) as the proportion of times that the simulated absolute value was greater than or equal to the real absolute value; the real data were included as one of the possible results of the simulation (Manly, 2007). Following a traditional line of null hypothesis significance testing, we rejected the null hypothesis for $p \leq 0.05$. All analyses were performed in R (R Core Team, 2018) and the scripts used are available as Supplementary Material 2 and at https://github.com/pdodonov/publications.

Results

When the FGs were combined, the responses were either positive or neutral. Thus, monoculture and polyculture had negative effects ($p<0.007$), whereas agroforestry and pasture did not have statistically significant effects ($p \geq 0.07$) (Table 4). The only habitats in which habitat conversion effects were consistently negative ($p<0.007$) were savanna and tropical and subtropical rainforests, and habitat conversion did not have statistically significant effects for other types of native habitats ($p \geq 0.09$). When combining the vegetation types, negative effects were observed both in the temperate and tropical zones ($p<0.01$).

Concerning the FGs, when combining the climate zones, six groups (cryptic species, fungus-growers, predators, subordinate Camponotini, cold- and tropical-climate specialists), responded negatively ($p<0.02$) to habitat conversion, whereas the other groups did not respond ($p \geq 0.08$) (Table 5). The cold- and tropical-climate specialists, as well as predators, cryptic species, and subordinate Camponotini, responded negatively ($p<0.02$) in the temperate zone too. In the tropical zone, however, only the fungus-growers and predators were negatively affected ($p<0.008$) by habitat conversion, with the other groups having neutral responses (p≥0.07). The only significant positive effect (p=0.04) of habitat conversion was observed for hot-climate specialists in the temperate zone. Finally, arboreal ants, army ants, dominant Dolichoderinae, generalists, generalized Myrmicinae, and opportunists were not affected (p ≥0.07) by habitat conversion.

Table 4. Average response values of ant functional groups and significance for disturbed habitat and native habitat. Significant results (P < 0.05) are in bold.

Disturbed Habitat	Number of observation	Number of studies	Number of observations considering the FGs	Response	Significance
Agroforestry	5	2	30	-0.2	0.4324
Monoculture	9	5	49	-0.3111	**0.0057**
Pasture	29	9	149	-0.119	0.0702
Polyculture	13	5	75	-0.2667	**0.006**
Native Habitat	**Number of observation**	**Number of studies**	**Number of observations considering the FGs**	**Response**	**Significance**
Grassland	7	2	35	-0.2	0.1809
Savanna	2	1	12	-0.6667	**0.007**
Scrub, heath and shrublands	15	3	68	-0.0441	0.7154
Tropical and subtropical rainforest	16	8	89	-0.2969	**0.0025**
Tropical dry forest	2	1	16	-0.2857	0.1653
Woodland	14	6	83	-0.1471	0.0925

Discussion

Negative effects habitat conversion to monocultures and polycultures were observed, as well as a lack of effect of conversion to agroforestry and pastures. These changes were observed in both the temperate and the tropical zones, with more FGs affected in temperate ecosystems. In general, the more specialized FGs (e.g. predators and cryptic species) responded negatively whereas more generalist groups did not respond to the habitat conversion. These results are partially consistent with our hypotheses and highlight the sensitivity of more specialized FGs to land use changes, especially in the temperate zone.

Conversion to monoculture and polyculture can thus affect both the taxonomic and functional ant diversity (Philpott et al., 2008; Fayle et al., 2010; Liu et al., 2016; Groc et al., 2017; Saad et al., 2017; Rivera-Pedroza et al., 2019). This may be due to the intensive management of some of these land uses, in which, in addition to removing vegetation cover and soil preparation, the use of fertilizers and pesticides impacts the ant fauna (Lobry de Bruyn, 1999; Matlock & de La Cruz, 2003; Steinbauer & Peveling, 2011; Queiroz et al., 2012; Nickele et al., 2013). Additionally, the loss of diversity and simplification of vegetation structure that results of these processes modifies important habitat characteristics for ants, such as microhabitat structure, supply of nesting sites, temperature, availability/access to resources, as well as competitive interactions (Andersen, 1995, 2000; Hoffmann & Andersen, 2003; Philpott & Foster, 2005; Armbrecht et al., 2006; Pacheco et al., 2009; Amaral et al., 2019). In turn, agroforestry had a neutral effect, possibly due to land uses such as shade cocoa and coffee plantations that maintain a fraction of the native vegetation and have microclimates similar or close to those of natural vegetation, increasing the availability of food, nesting sites, and hiding places to the ants and other arthropods (Perfecto et al., 1997; Philpott & Armbrecht, 2006; Delabie et al., 2007; Groc et al., 2017; Amaral et al., 2019). Although pastures did not have significant effects, this result should be treated with caution, as pastures are open areas with sun exposure and cattle trampling, with limited food resources and nesting sites that directly impact on the ant fauna (Neves et al., 2012; Cantarelli et al., 2015). Still, it is possible that the lower intensity of management practices (e.g. the low rate of application of agricultural inputs) compared to monocultures, as well as the growth of shrubs and the occurrence of scattered trees, may result in smaller differences in ant FGs between pastures and native habitats (Dias et al., 2008; Neves et al., 2012; Frizzo & Vasconcelos, 2013; Queiroz et al., 2017).

The negative effects were prominent in the conversion of tropical and subtropical rainforest and savanna. These environments are structurally and compositionally complex, and the reduction of this complexity likely affects the availability of resources and conditions necessary for ants, impacting the abundance and composition of several FGs in these habitats (Andersen, 1995, 2000; Hoffmann & Andersen, 2003). On the contrary, the conversion of tropical dry forest, scrub, heath and shrublands, grassland, and woodland to anthropogenic land uses, show non-significant effects on ant FGs. Although this may be due to idiosyncrasies of the evaluated studies, it is possible that environments such as

Table 5. Average response values of ant functional groups for climatic zone, functional group and functional group by climatic zone. Significant results (P<0.05) are in bold.

Climatic Zone	Number of observations	Number of studies	Number of observations considering FGs	Response	Significance
Temperate	38	8	198	-0.1386	**0.0177**
Tropical	18	9	105	-0.3125	**0.0002**

Functional Groups	Number of observations	Number of studies	Response	Significance
Arboreal	14	4	-0.3	0.3359
Army ants	6	3	-0.5	0.215
Cryptic species	17	9	-0.5625	**0.0072**
Dominant Dolichoderinae	44	12	-0.1053	0.3879
Fungus-growers	7	3	-0.8333	**0.0064**
Generalists	11	4	-0.1429	0.8198
Generalized Myrmicinae	45	13	0.0588	0.6491
Opportunists	49	14	0.2174	0.0871
Predators	28	11	-0.6818	**0.0001**
Subordinate Camponotini	29	10	-0.6316	**0.0001**
Cold-climate specialists	9	4	-0.6667	**0.0202**
Hot-climate specialists	37	8	0.1923	0.1288
Tropical-climate specialists	7	4	-1	**0.0013**

Functional Group in Temperate zone	Number of observations	Number of studies	Response	Significance
Cryptic species	8	3	-0.875	**0.0032**
Dominant Dolichoderinae	38	8	-0.1351	0.2829
Generalized Myrmecinae	38	8	0.0714	0.6256
Opportunists	38	8	0.1579	0.2817
Predators	6	3	-0.8	**0.019**
Subordinate Camponotini	24	6	-0.8571	**0.0001**
Cold-climate specialists	8	3	-0.75	**0.0147**
Hot-climate specialists	34	6	0.2917	**0.0451**
Tropical-climate specialists	4	2	-1	**0.0257**

Functional Group in Tropical zone	Number of observations	Number of studies	Response	Significance
Arboreal	14	4	-0.3	0.3411
Army ants	6	3	-0.5	0.2147
Cryptic species	9	6	-0.25	0.518
Dominant Dolichoderinae	6	4	1	0.0739
Fungus-growers	7	3	-0.8333	**0.0089**
Generalists	11	4	-0.1429	0.8193
Generalized Myrmecinae	7	5	0	1
Opportunists	11	6	0.5	0.1286
Predators	22	8	-0.6471	**0.0008**
Subordinate Camponotini	5	4	0	1
Cold-climate specialists	1	1	0	1
Hot-climate specialists	3	2	-1	0.0753
Tropical-climate specialists	3	2	-1	0.0748

scrublands, heathlands, and grasslands select predominantly generalist species adapted to more stressful environmental conditions (such as the species of ants of Dominant Dolichoderinae, Generalized Myrmicinae, Opportunists in relation to the habitat and/or diet generalists), thus being less affected by habitat conversion. On the other hand, a lack of effect could also have been observed if some groups (probably more specialized) were harmed while others (generalists) were favored, generating a substitution of FGs (Andersen, 1997, 2000; Hoffmann & Andersen, 2003; Underwood & Fisher, 2006).

As expected, the conversion of habitat as a whole (without separating between natural and anthropogenic land uses) negatively impacted several FGs of ants, with this effect being more pronounced in temperate habitats. Although disturbance impacts tend to be greater in habitats that are structurally complex (Arcoverde et al., 2018), it is possible that ant FGs of temperate native habitats are more vulnerable to conversion, as more groups have been affected in this zone (cryptic species, predators, subordinate Camponotini, cold- and tropical-climate specialists) than in the tropics (fungus-growers and predators). This suggests that the loss of structural heterogeneity and complexity, as well as the typical habitat conditions and resources in anthropogenic land uses, has more significant consequences for ant FGs in temperate native (Andersen, 1995, 1997; Gómez et al., 2003; Underwood & Fisher, 2006; Gollan et al., 2011; Castillo-Guevara et al., 2019). Finally, it is possible that, as tropical areas are generally more species-rich, this high species richness results in greater resistance or resilience to habitat conversion (Tilman et al., 2014).

The most affected FGs were cryptic species, fungus-growers, predators, subordinate Camponotini, cold- and tropical-climate specialists. Such effects were also observed when evaluating temperate ecosystems separately, with the exception of hot-climate specialists, which were favored, and fungus-growers, which had significant losses recorded only in the tropics, similarly to the predators. In general, these groups are more specialized than those that were not affected. The response of predators and cryptic species to conversion may be due to their specificities to their own habitat conditions and high specialization of requirements, being especially sensitive to disturbances (Andersen & Majer, 2004; Underwood & Fisher, 2006; Kone et al., 2012). This could also be the case of subordinate Camponotini, which also tend to occur in complex, heterogeneous and shaded habitats with abundant leaf litter for nesting and foraging (Andersen, 1997; Hoffmann & Andersen, 2003; Hill et al., 2008; Parui et al., 2015; Assis et al., 2018).

The FGs cold- and tropical-climate specialists are composed of ants that have important restrictions in habitat tolerance, such as variation in temperature and humidity (Andersen, 1995, 1997; Castillo-Guevara et al., 2019). In temperate regions, the occurrence of cold-climate specialists in native habitats, such as oak forests, is favored by the microclimate conditions of low temperature and sun exposure (Cuautle et al., 2016; Castillo-Guevara et al., 2019); in addition, ant species richness and overall abundance of this FG may decrease as land use intensifies (Gómez et al., 2003). It is possible that the same explanation applied to tropical-climate specialists. The FGs hot-climate specialists, in turn, were favored by habitat conversion in temperate regions. This may be due to increased temperatures in converted areas (see Gómez et al., 2003; Schnell et al., 2003; Gollan et al., 2011). Still, some studies observed this group only or mostly in native vegetation (see Gómez et al., 2003; Yates & Andrew, 2011; House et al., 2012).

Although studies suggest that some fungus-growers (e.g. leaf-cutting ants) are favored by agricultural land uses, deforested areas, edges and disturbed environments (Jonkman, 1979; Vasconcelos & Cherrett, 1995; Wirth et al., 2007; Siqueira et al., 2017), we found a negative effect on this group in the tropics. Fungus-growers ants form a peculiar FG, with habits associated with fungal gardening, for which they use residues from arthropods and carcasses and/or live or dead plant material to grow their symbiotic fungus or yeast (Delabie et al., 2000; Mehdiabadi & Schultz, 2010). Forest habitat loss has been related to decreased abundance of this group in Argentina (González et al., 2018). The impacts of habitat conversion in fungus-growers FGs probably occurred because some land uses, with intensive management, in addition to homogenizing the habitat, affect strongly the ant fauna through the use of pesticides and soil preparation with effects on the structure of the nests, as well as the availability of the organic substrate for cultivation of the fungus (Lobry de Bruyn, 1999; Queiroz et al., 2012; Nickele et al., 2013). Our results show that, although some species may be favored by habitat conversion, fungus-growers ants in general are negatively impacted by it.

Some FGs were not affected by the conversion of native habitats, including dominant Dolichoderinae in temperate and tropical ecosystems, which can be explained by their environmental tolerance, being favored mainly by warmer conditions and open habitats (Andersen, 1995, 1997; Hoffmann & Andersen, 2003). Similarly, the lack of response of generalized Myrmicinae is probably due to their broad environmental tolerance allowing them to predominate in environments with moderate levels of disturbance and shaded habitats (King et al., 1998; Hoffmann & Andersen, 2003; Andersen & Majer, 2004). Opportunists also had a neutral effect on conversion, as it is a group with broad habitat tolerance that can occur in a range of environments, generally favored in disturbed sites and with low productivity (Andersen, 1990, 1995, 1997).

Arboreal ants, army ants, and cryptic species also had neutral responses (in general or in one of the climatic zones), probably due to the existence of negative and positive responses of these FGs in different observations. The neutral response of arboreal ants is possible because some land uses still maintain trees that provide nesting sites, a limiting factor for this FG (Majer & Delabie, 1999; Schonberg et al., 2004; Kone et al., 2012). Army ants, in turn, are harmed in highly disturbed habitats (Matsumoto et al., 2009) by the lack of adequate bivouac sites, unfavorable microclimate and few organisms living in leaf litter and fallen logs (Roberts et al., 2000; Peters et al., 2011). However, the active search for preys associated with the nomadic behavior (Gotwald, 1995), the environmental tolerance and broader diet of some army ant species, may allow the occurrence of this FG in anthropic environments (Perfecto, 1992; Roberts et al., 2000; Delabie et al., 2007; O'Donnell et al., 2007; Matsumoto et al., 2009; Schleuning et al., 2011; Assis et al., 2018). Cryptic species are more diverse and abundant in forest habitats, associated with tree cover (Majer et al., 2004; Dalle Laste et al., 2019), and in our study they were negatively affected by the conversion of habitat except in the tropical zone. It is then possible that in tropical environments some components of this group have plasticity that allows their occurrence in land uses beyond the forest.

The neutral response of cold-climate specialists to conversion in the tropical region may not reliable as there were only two observations from a single study, for this group. Generalist ants did not respond to habitat conversion, probably because of this group's ability to use different sites for nesting and food sources (i.e., broad ecological niche), permitting their occurrence in native habitats (Kone et al., 2012; Pacheco et al., 2017; Saad et al., 2017) as well as in anthropogenic land uses (Kone et al., 2012; Assis et al., 2018), with survival and even dominance in homogeneous and simplified environments (García-Martínez et al., 2015; Assis et al., 2018). In the tropical region, habitat conversion did not affect subordinate Camponotini even though this group is usually associated with complex and shaded habitats (Parui et al., 2015), suggesting a broader flexibility to their occurrence in this region.

Our results highlight that habitat conversion plays an important role in the loss of biodiversity. Although we have not detected the effect of habitat conversion for all FGs of ants considered in the review, we have evidenced, in general, a negative impact on part of the groups, where polyculture and monoculture have stronger impacts than pastures and especially agroforestry. These effects are especially evident on the more specialized groups. In addition, although some groups were not affected by habitat conversion, positive effects were seldom observed. In addition, we found more observations in the temperate than in the tropical regions, indicating that further studies in tropical regions are needed to better understand these impacts. In general, our study points out the importance of remnants of native habitats for the shelter and protection of specialized organisms, while also ensuring the ecosystem services mediated by them – especially compared to more managed systems, like monocultures and polycultures.

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Authors' Contributions

All authors conceived this study. RJS collected and organized the data. PD developed the R scripts and RJS and PD performed the statistical analyses. All authors contributed to the writing, discussed the results and commented on the manuscript. This manuscript is part of RJS's PhD research, supervised by JHCD and cosupervised by PD.

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