Influence of human land use and invasive species on beta diversity of tropical ant assemblages

PRONOY BAIDYA[1] and SUMANTA BAGCHI[1,2]   [1]Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India and [2]Divecha Centre for Climate Change, Indian Institute of Science, Bengaluru, India

Abstract. 1. Understanding how biodiversity is distributed is increasingly becoming important under ongoing and projected human land use. Measures of beta diversity, and its partitions, can offer insights for conservation and restoration of biodiversity.

2. We ask how different species, functional groups, and land use contribute to beta diversity, and whether invasive species have a negative influence on beta diversity. We address these questions using ant assemblages (Hymenoptera: Formicidae) at 277 sites distributed across five geomorphic land use types in Goa, India.

3. We recorded 68 species (35 genera, 7 subfamilies) of which 5 were invasive. We classified them into eight functional groups. *Oecophylla smaragdina*—a common tropical arboreal species, and *Anoplolepis gracilepis*—a globally significant invasive, contributed the most to beta diversity. Large-bodied omnivores which may influence soil functions contributed more to beta diversity than small-bodied predators. Lateritic plateaus contributed most to beta diversity, whereas human-influenced plantations contributed the least. Beta diversity across sites was related to species turnover, whereas nestedness was more prominent for functional groups. This indicates how species replace one another with change in land use, but functional roles are lost despite such turnover. Sites with human land use had higher incidence of invasive species, and invaded sites contributed less to beta diversity than non-invaded sites.

4. Human land use strongly influences diversity and distribution of ant assemblages. Land use may spare local species richness, but not functional groups. A small number of invasive species exert negative influence even in very speciose communities.

Key words. Agro-ecosystems, Formicidae, Hymenoptera, myrmecology, nestedness, species distribution, species turnover.

Introduction

An understanding of how biodiversity is distributed across space and time can offer insights into the processes underlying community structure, macroecology, and biogeography (Gaston *et al*., 2000). This primary goal of ecology has gained more importance in the light of land use change and other forms of human influence on biodiversity, alteration of community composition, accelerated rates of species invasion and extinction (Beckmann *et al*., 2019). Species richness has traditionally been used as a metric to describe the size and structure of communities across space. Scale-dependent metrics of species richness—

locally as alpha diversity, and aggregated regionally as gamma diversity—have well-known applications such as the identification of biodiversity hotspots (Myers *et al*., 2000). Both alpha and gamma diversity concepts capture inventory information, and they differ in the spatial extent over which information is recorded (Jurasinski *et al*., 2009). Beta diversity, on the other hand, goes beyond inventory data to explain compositional variation between inventories at different scales (Mori *et al*., 2018) to help address macroecological patterns under human-influences and global change.

The concept of beta diversity was initially introduced to quantify compositional differences between two or more samples, either in space or in time (Whittaker, 1960). Over the past decades, there have been important advances on how beta diversity is interpreted in terms of its constituent components. One aspect has been the ability to partition beta diversity into

Correspondence: Sumanta Bagchi, Centre for Ecological Sciences, Indian Institute of Science, Bengaluru 560012, India. Email: sbagchi@iisc.ac.in

the contribution of individual species or sites (Legendre & Cáceres, 2013). Species contribution to beta diversity (SCBD) explains the relative importance of each species in overall beta diversity patterns, while local contributions to beta diversity (LCBD) represents the uniqueness of a site relative to all other sites. These partitions can aid management decisions in a variety of ways (Socolar *et al.*, 2016). In parallel, another major advancement has been the ability to partition beta diversity into nestedness and turnover components (Baselga, 2010; Carvalho *et al.*, 2013). Nestedness quantifies how the loss (or gain) of species causes the poorest assemblage to become a strict subset of the richest one. Whereas, turnover occurs when species replace each other across sites (Baselga, 2010).

Studies on beta diversity and its components have generally focused on taxonomic levels of diversity. But beta diversity across functional groups (Chao *et al.*, 2019) can offer a better understanding of ecological processes than taxonomic levels alone (Zarabska-Bożejewicz & Kujawa, 2018). Functional groups help conceptualise how resources or other ecological components are processed by different species to result in ecosystem services or functions (Blondel, 2003). Understanding diversity at functional group levels can aid ecological interpretations since it may be a stronger determinant of ecosystem processes than species richness (Díaz *et al.*, 2007; Clark & Singer, 2018; Ortega-Ramos *et al.*, 2020). Loss or gain of a species with a particular functional trait may impact a specific ecosystem process, and different processes are affected by different functional traits. Advances in analytical frameworks for classifying species into functional groups based on traits (Brousseau *et al.*, 2018; Wong *et al.*, 2019; Sosiak & Barden, 2021) have offered opportunities to answer several questions on biodiversity and its connections with underlying ecological processes and functions (Petchey & Gaston, 2006).

Here, we study beta diversity and the components of beta diversity at both taxonomic and functional levels in ant communities (Hymenoptera: Formicidae) across a wide range of land use categories that differ in degree of human interference. Ants as a model system are particularly interesting since they are often referred to as ecosystem engineers and keystone groups. They participate in diverse ecological processes, such as pedoturbation, nutrient cycling, and seed dispersal, in addition to predation, herbivory, material, and energy flow along with their role in several symbiotic relationships (Folgarait, 1998). Therefore, beta diversity of ant assemblages, at taxonomic and functional levels, is expected to characterise broad and general aspects of a wide spectrum of ecosystem functions. Species diversity of ants has been studied extensively in various environmental settings (Sanders, 2002; Dunn *et al.*, 2007, 2009; Vasconcelos *et al.*, 2010). However, functional diversity of ants has generally been studied either along broad environmental gradients such as elevation, climate, and productivity (Chase, 2010; Polato *et al.*, 2018), or at local scales for intact and human modified habitats (Bihn *et al.*, 2010; Arnan *et al.*, 2018). Studies across a wide spectrum of human influence at broad spatial scales are still rare (however, see Ferenc *et al.*, 2014; Mammola *et al.*, 2019) and constitute a knowledge gap. Furthermore, it is also likely that ecosystems respond to human land use indirectly when native ant communities experience invasion by exotic species (Holway *et al.*, 2002; Holway & Suarez, 2006; Bos *et al.*, 2008), but the consequences for beta diversity remain unclear.

Specifically, we ask:

1. How ant species, functional groups, and sites contribute to beta diversity across different land use?
2. Whether partitions of beta diversity vary between taxonomic and functional levels across land use? and
3. Whether invasive species have a negative influence on beta diversity?

Previous studies have found that species turnover is a major component of beta diversity (Bruhl *et al.*, 1999; Longino & Colwell, 2011; Kaltsas *et al.*, 2018), and this can be attributed to variation in micro-climatic conditions, resource availability, and anthropogenic stressors that lead to species filtering (Gutiérrez-Cánovas *et al.*, 2013; García-Llamas *et al.*, 2019). Unlike species, beta diversity of functional groups is expected to be driven by nestedness (Nunes *et al.*, 2017; de Castro *et al.*, 2020) since functional diversity could shrink under human influence such that only particular suites of traits occur in specific environmental conditions (Stevens *et al.*, 2003). We also expect sites which are under human influence to contribute less to beta diversity because of shrinkage in the community size due to environmental filtering and exclusion of species (Staude *et al.*, 2018), which could reduce functional diversity more strongly than loss of species richness, indicating a disproportionate effect on ecosystem functioning (Flynn *et al.*, 2009). We expect sites with invasive species to make lesser contributions to beta diversity in comparison to non-invaded sites (Holway & Suarez, 2006) because invasive species can outcompete native species to homogenise biotic assemblages (Holway *et al.*, 2002).

Materials and methods

Study site

We sampled ants throughout the state of Goa, at the western coast of India (14°53′ to 15°48′N, and 73°40′ to 74°20′E; Fig. 1a). The region experiences tropical monsoon climate with a mean annual temperature of 27°C. Majority of 3500 mm average annual rainfall occurs between June and August. About 60% of the state is under tree cover (forests and plantations), and other major geomorphic land use classes are lateritic plateaus, agricultural fields, and wetlands. Most forests have a prior history of logging, and have native trees such as *Macaranga peltata*, *Terminalia paniculata*, *Vitex altissima*, *Olea dioica* and *Aporosa lindleyana*. Plateaus are indurated platforms of iron-rich laterite where ephemeral herbaceous vegetation dominates during the wet monsoon period with isolated clusters of trees such as *Artocarpus hirsutus*, *Garcinia indica*, *Holigarna arnottiana*, *Xylia xylocarpa* and *Terminalia* spp (Joshi & Janarthanam, 2004). Plantations are monocultures of betelnut *Areca catechu*, coconut *Cocos nucifera* or cashew-nut *Anacardium occidentale* that are regularly managed. Wetlands are reservoirs constructed for irrigating agricultural fields where the dominant crop is paddy.
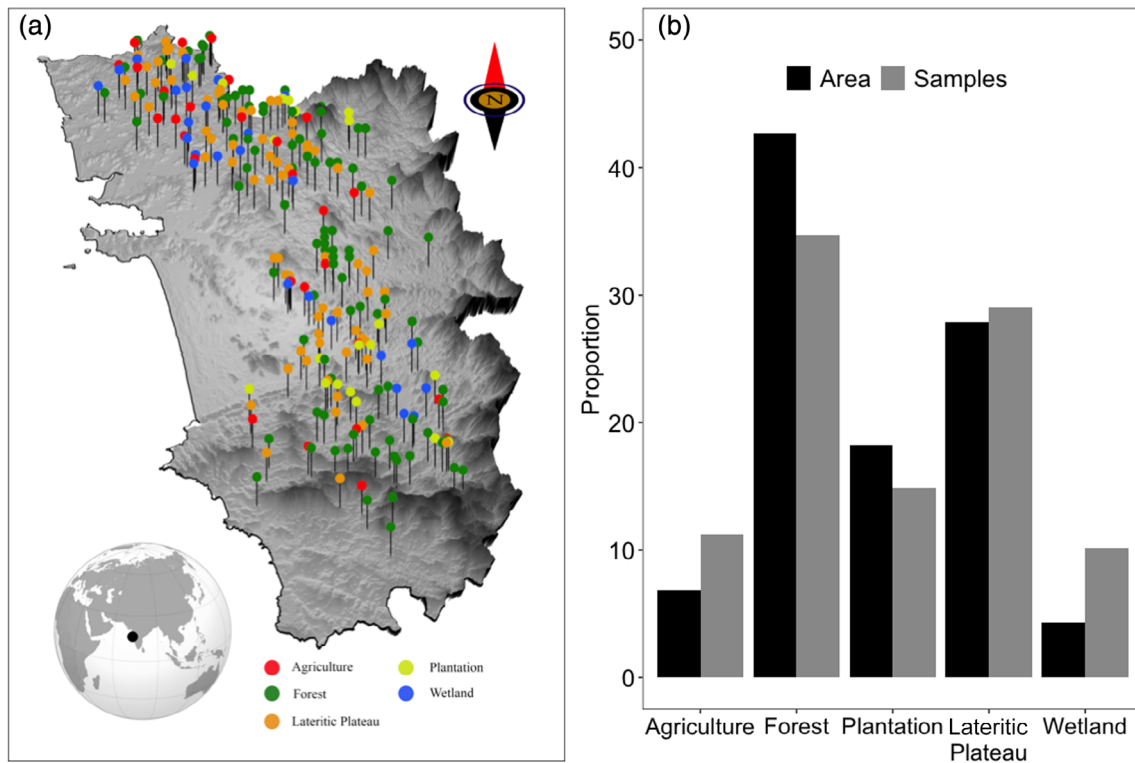
Fig 1. Study area and sampling locations (*n* = 277) across five land use categories in Goa, India (a). Number of samples relative to the area under each land use category (b).

We sampled *n* = 277 sites within an elevation gradient of 0–150 m, across the major land use and geomorphic categories covering an area of ∼2500 km^2 spanning 35 km longitudinally and 70 km latitudinally at the widest (Fig. 1a). The number of sites within each land use category was approximately proportional to their area to ensure representative sampling from all land uses in the landscape (Fig. 1b).

Sampling of ants

Ant communities can be studied using different field sampling protocols, and each method has its own advantages and drawbacks. For example, Winkler sacks of leaf litter is a preferred method in forests (Ivanov & Keiper, 2009); however, this method is less suitable in grasslands, agricultural habitats and wetlands. Similarly, pitfall traps are appropriate for epigeal ants, but may underrepresent other types of species (Gotelli *et al.*, 2011). Hand sampling is an efficient method to obtain replicated presence–absence data over large spatial scales for ant species across a wide range of habitats, provided the sampling area and effort is standardised (Gotelli *et al.*, 2011). Hence, we deployed the standardised hand sampling method to cover many sampling locations as it is well-suited to infer beta diversity from survey data (Vasconcelos *et al.*, 2008; Salata *et al.*, 2020).

Standardised hand-sampling consists of two components—uniform and consistent effort at each sampling location followed

by active search for species (Gotelli *et al.*, 2011). At each site, sampling was done along 100-m-long transect path where we laid six quadrats, each 25 m^2 in area. These quadrats were at 20 m intervals along the 100 m path (Fig. S1). For each 25 m^2 quadrat, we standardised our hand sampling protocol followed by searching in a fixed area (25 m^2) for a fixed amount of time (10 min) by the same person (all sampling was done by the first author). Ants were collected with an aspirator and a net from soil, leaf litter, understory vegetation, and from tree trunks. We recorded ant presence–absence data during peak ant activity hours (1100–1600 h) between September–November of 2015 and 2016. Data from the six quadrats were pooled to represent ant community of a given site (Fig. 1a). Total area sampled was 6 × 25 × 277 = 41 550 m^2, and total time effort was 6 × 10 × 277 = 16 620 min. In this way, presence–absence data were collected with search effort of 0.25 m^2 min^{-1} which compares favourably against similar studies (Vasconcelos *et al.*, 2008; Salata *et al.*, 2020). We did not find any ants at one sampling location. To assess sampling efficiency and adequacy, we compared the number of observed species against two rarefaction estimators—Chao 2 and Jack-knife 2 (Colwell *et al.*, 1994). Given the likelihood of encountering singletons and rare species, rarefied theoretical estimates are expected to be higher than empirical species counts (Fisher, 1999). Indeed, as in other studies (King & Porter, 2005; Vasconcelos *et al.*, 2010), theoretical species richness was higher than observed richness (Fig. S2). Frequency of occurrence revealed

11 singletons—rare species that were recorded only once (Fig. S3); these were also behaviourally cryptic in nature. So, it is likely that we recorded the common species adequately but may have missed few rare ones. This may not hinder broad inference from the data since common species play a greater role in beta diversity than the exceedingly rare ones (Brasil *et al.*, 2020).

Ants were stored in 70% ethanol and identified later in the laboratory based on taxonomic keys (Bingham, 1903) and global databases (AntWeb, 2021; AntWiki, 2021). During lab work, one new species was described as *Protanilla flamma* Formicidae: Leptanilinae (Baidya and Bagchi, 2020). All voucher specimens collected from the study were deposited at the museum of Centre for Ecological Sciences, Indian Institute of Science (species names and abbreviations in Table S1).

Traits for functional classification

For classifying ant species into functional groups, we measured a suite of morphological and ecological traits related to metabolic characteristics, resource use, life history, foraging habit, navigation, diet, thermoregulation, and habitat affinity (Fowler *et al.*, 1991; Andersen, 1995; Franks *et al.*, 1999; Weiser & Kaspari, 2006; Fayle *et al.*, 2015) (see Table 1 for more details). This covers multiple traits relevant for functional classification (Petchey & Gaston, 2006) in order to infer functional roles of classified groups (Toro *et al.*, 2015). Continuous trait variables were Webber's length, eye length, scape length, mandible length, hind leg length, and number of spines on the body which are most informative in differentiating among ecologies (Sosiak & Barden, 2021). We measured three randomly selected minor workers of each species with a Leica MC 120 HD digital camera mounted on a Leica 205 C stereomicroscope and LAS EZ 3.4 Leica Acquire V2.0 software. Discrete or categorial trait variables were polymorphism, integument sculpture, dominant colour (head, thorax, and abdomen, separately), nest site, diet, invasiveness, and behavioural response to stress and disturbance traits (Table 1). For quantification of traits, we followed established guidelines of The Global Ants Trait Database that standardises trait measurement of ants and facilitates comparisons between studies (Parr *et al.*, 2017). Behavioural response to stress and disturbance was based on Andersen (1995). Trait information on nesting site and diet was derived primarily from field observations wherever possible. However, for a few rare species we referred to available literature (Bingham, 1903; Narendra *et al.*, 2011; AntWiki, 2021). Following established methods for standardisation (Májeková *et al.*, 2016), we divided the continuous trait variables by Webber's length (Table S1).

Functional group analysis

We followed three steps to identify and assign ant species to their respective functional groups (Toro *et al.*, 2015). First, we assembled the species × traits table and transformed it into a dissimilarity matrix of Gower distance as this can combine categorical and continuous traits (Podani, 1999). For this we used *dbFD*

function in R package 'FD'. Next, we performed hierarchical cluster analysis of this distance matrix with Ward's method. Finally, the number of parsimonious functional groups was identified based on dendrogram height of ≤1 (Toro *et al.*, 2015). Once the groups where classified, we inferred functional roles for each group based on our natural history observations in field and from observations noted in Bingham (1903) (Table 2). We assigned functional groups names to reflect the ecomorphospace consisting of diet, nesting, and foraging behaviour (Sosiak & Barden, 2021), and inferred broad functional roles from the likely consequences of these traits (Toro *et al.*, 2015).

Beta diversity analysis

To quantify the contribution of individual species and functional groups to beta diversity, we calculated SCBD, at taxonomic level. For uniqueness of ant communities across land use types, we calculated LCBD, at taxonomic level (Legendre & Cáceres, 2013). SCBD depends on the number of sites a species occurs. If a species is recorded from about half of the sites sampled, then it makes higher contributions to beta diversity than other species that may be either more widespread, or rarer. To test our data with this theoretical expectation, we fitted two regression models: linear and quadratic, and compared their goodness of fit by evaluating R^2 and RMSE. Contribution of functional groups to beta diversity was calculated from average contribution of species within their respective functional groups. We used Hellinger transformation of the data as it provides asymmetrical treatment of double zeros and is well-suited to compare SCBD and LCBD between groups (Legendre & Borcard, 2018). Since values of SCBD are bounded between 0 and 1 (Legendre & Cáceres, 2013), we used beta-regression to test for differences between mean contribution of species to beta diversity by functional groups and land use. To test the effect of our sampling size on LCBD for generality, we did a resampling based accumulation analysis from each habitat. We used the *beta.div* function in R package 'adespatial' (Dray *et al.*, 2019) for SCBD and LCBD calculations and *gam* function in R package 'mgcv' (Wood, 2017) for beta regression.

To address the question of how partitions of beta diversity vary between taxonomic and functional levels across land use, we partitioned beta diversity into richness difference or nestedness, and into replacement or turnover components (Carvalho *et al.*, 2013). For this, we used the *beta* function in R package 'BAT' (Cardoso *et al.*, 2015) to calculate beta diversity as pairwise dissimilarity. As above, we used beta-regression to test for differences between land use, followed by Tukey's post hoc comparisons (adjusted $\alpha = 0.05$). We used beta diversity as response variable and land use as the predictor variable. All analyses were performed in R environment version 3.6.2 (R Core Team, 2019).

Results

We recorded 68 ant species from 35 genera representing seven subfamilies. Of these, 7 species are endemic to India, and 18 are additions to the ant fauna of Goa (Table S1). *Oecophylla*

Table 1. List of standardised morphological and ecological traits as suggested by *GlobalAnts* database, their measurement type, hypothesised functions, and unit of measurements.

Trait	Measure	Unit	Description of measurement	Hypothesised trait function or environmental response
Morphological				
Weber's length/ mesosomal length (MSL)	Continuous	mm	Taken in lateral view from the anterodorsal margin of the pronotum to the posteroventral margin of the mesosoma	Commonly used metric of body size, and correlates strongly with metabolic characteristics, resource use, and life history traits (Fayle *et al.*, 2015)
Relative eye length (REL)	Continuous	mm	Measured along longest axis of eye and divided by MSL	Suitable metric to represent how the organism orients and navigates to forage (Weiser & Kaspari, 2006)
Relative scape length (RSL)	Continuous	mm	From antennal socket to distal margin of scape and divided by MSL	Longer scapes help in better chemoreception and improved ability to navigate, sense, and move through its surroundings (Schneider, 1964; Yates *et al.*, 2014)
Relative mandible length (RMAL)	Continuous	mm	From point of clypeal insertion to apical-most tooth of mandible and divided by MSL	Varies with dietary preference (Fowler *et al.*, 1991; Weiser & Kaspari, 2006)
Relative hind leg length (RLL)	Continuous	mm	Measured from articulation point with trochanter to distal tip of the metafemur	Suitable metric of efficiency of locomotion, foraging, and response to habitat complexity (Franks *et al.*, 1999)
Sculpturing	Ordinal	1 = cuticle appears completely smooth, often shiny; 2 = shallow wrinkles/pits; 3 = surface heavily textured with ridges, grooves or pits		Thickened, structured cuticles may increase dehydration tolerance (Parr *et al.*, 2017)
Number of spines	Count	Number on mesosoma and petiole		Spines may act as an anti-predation mechanism (Michaud & Grant, 2003)
Dominant colour		Based on colour wheel and RGB codes as in (Parr *et al.*, 2017) separately for head, mesosoma and gaster		Cuticle colour provides support for melanism-desiccation hypothesis and the photo-protection hypothesis (Law *et al.*, 2020)
Polymorphism	Categorical	1 = monomorphic; 2 = dimorphic; 3 = polymorphic		Different worker castes perform different tasks within the colony, allowing greater specialisation (Wilson, 1953)
Ecological				
Nest site	Categorical	1 = hypogaeic; 2 = epigeic; 3 = under stones; 4 = dead wood; 5 = arboreal; 6 = litter; 7 = woven leaves; 8 = sand		
Diet	Categorical	1 = generalist predator; 2 = generalist; 3 = seed harvester; 4 = sugar feeder + generalist; 5 = seed harvester + generalist; 6 = specialist predator; 7 = fungivore		
Invasive	Categorical	Invasive, Native		
Behavioural response to stress and disturbance	Categorical	CS = cryptic species, GM = generalised myrmicinae, HCS = hot climate specialist, OS = opportunists, SC = subordinate camponotini, SP = specialised predator and TCS = tropical climate specialist		Behavioural responses of ants at biogeographical-scale to environmental stress and disturbance (Andersen, 1995)

Table 2. Description of traits and inferred functional roles of eight functional groups described in the study. The 68 species were clustered into functional groups based on their standardised morphological and ecological traits. 'Trait description' in the table specifies the traits that describes the respective functional group and are based on Sosiak & Barden (2021), inferred functional groups are assigned following Toro *et al.* (2015).

| Group	Trait description	Inferred functional role	Example taxa
1	Omnivorous- ground nesting- epigaeic foraging	Invasive species + decomposers	*Anoplolepis gracilepis, Solenopsis geminata, Trichomomyrmex destructor*
2	Small bodied- specialist predators- subterranean nesters	Soil invertebrate community regulators	*Dorylus orientalis, Protanilla flamma, Oocerea biroi*
3	Large bodied- omnivorous species	Decomposers, invertebrate community regulators	*Camponotus compressus, C. radiatus, Oecophylla smaragdina*
4	Large bodied- generalist predators	Soil invertebrate community regulators	*Harpegnathos saltator, Bothroponera sulcata, Odontomachus similimus*
5	Granivorous/omnivorous- ground nesters	Soil movers, seed dispersers, decomposers	*Pheidole sharpi, P. grayi, Myrmicaria brunnea*
6	Phytophagus/omnivorous- carton nesting- arboreal	Movement of organic matter	*Polyrhachis illaudata, P. exercita, P. tibialis*
7	Trophobiotic/phytophagus- arboreal	Arboreal invertebrate community regulators	*Tetraponera rufonigra, Catulacus taprobane, T. allaborans*
8	Large bodied- specialist predators	Soil invertebrate community regulators	*Diacamma indicum, D. rugosum, D. ceylonense*
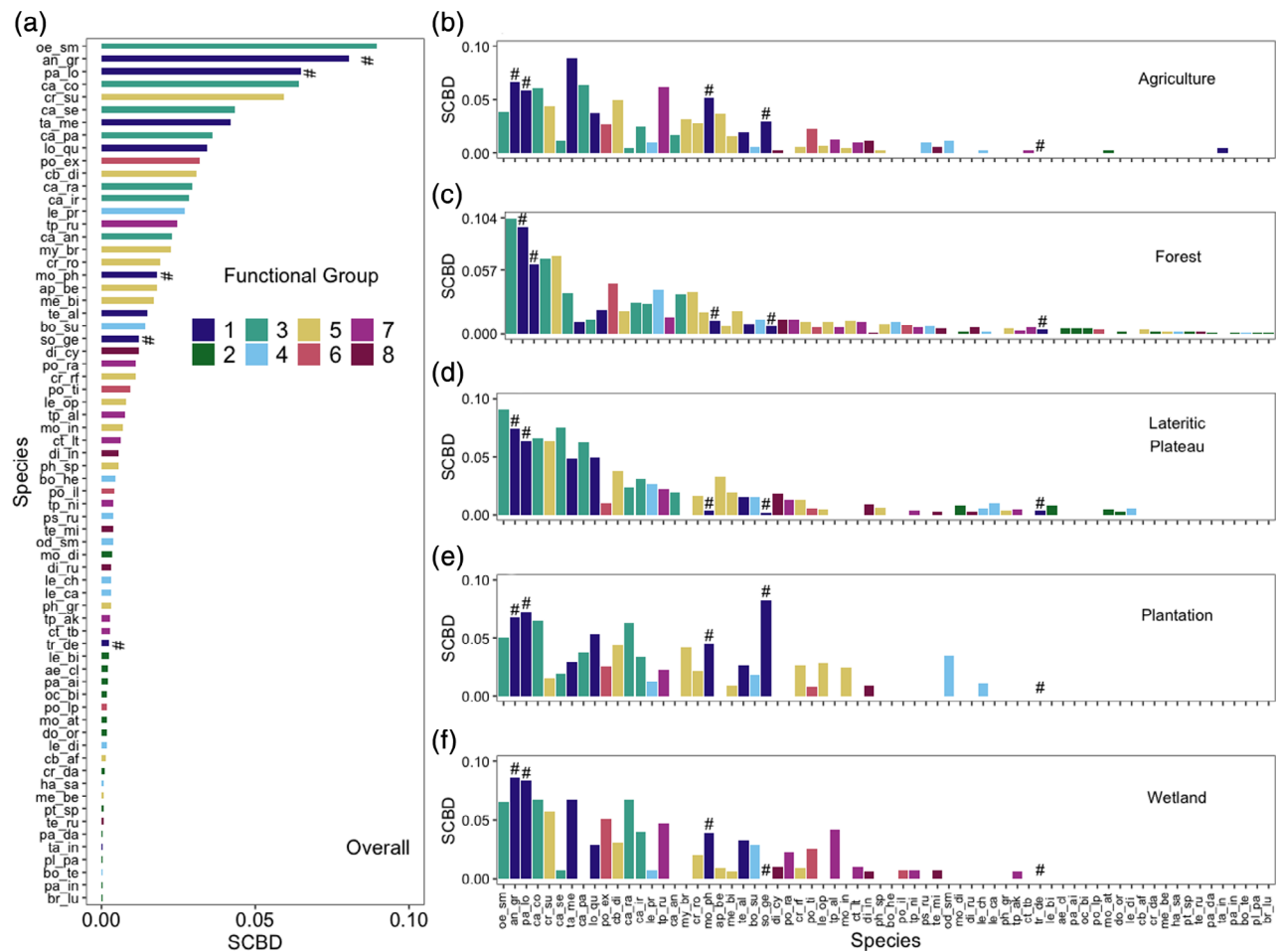
Fig 2. SCBD, for *n* = 68 species (a). Variation in SCBD of these 68 species across five land use categories (b–f). Species in all panels are coloured according to their membership in eight functional groups, and # symbol indicates an invasive species. Species abbreviations are mentioned in Table S1.
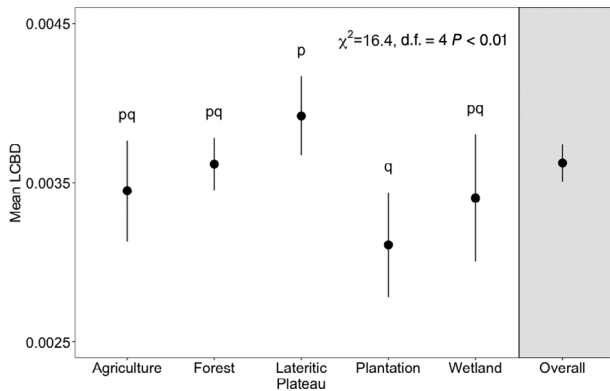
Fig 4. LCBD, of $n = 277$ sites across five land use categories (mean and 95% CI). Sites in lateritic plateaus contribute more to beta diversity than plantations, with intermediate contributions from forests, agriculture, and wetlands ($\chi^2 = 16.4$, d.f. = 4, $P < 0.01$). Different letters indicate statistically significant differences in Tukey's post hoc comparisons ($P < 0.05$). Overall LCBD (grey background) is shown separately from the five land use categories.

smaragdina (Fabricius, 1775)—a common arboreal species of the tropics—was the most frequently recorded species (188 sites), followed by the globally important invasive *Anoplolepis gracilepis* (Smith, 1857) (143 sites; Fig. S3). Mean species richness (alpha diversity) was 4.6 ± 0.15 SE (median = 4), and it was higher in agriculture than in other sites (Fig. S4; $F_{4,271} = 3.76$, $P < 0.01$). These 68 species were classified into eight functional groups (Table 2; Fig. S5).

Species and local contributions to beta diversity

SCBD across 68 species was 0.0147 ± 0.0199 (mean $\pm$ SE), and it ranged between 0.0004 and 0.0897 (Fig. 2a). Overall, the frequently recorded arboreal ant *O. smaragdina* contributed the most to beta diversity, while behaviourally cryptic, solitary-foraging and predatory Ponerines such as *Brachyponera luteipes* (Mayr, 1862), *Bothroponera tesseronoda* (Emery, 1877) and the newly described Leptanillinae *P. flamma* contributed the least (SCBD = 0.0004 for each; Fig. 2a). SCBD also varied across land use (Fig. 2b–f). Species which contributed most to overall
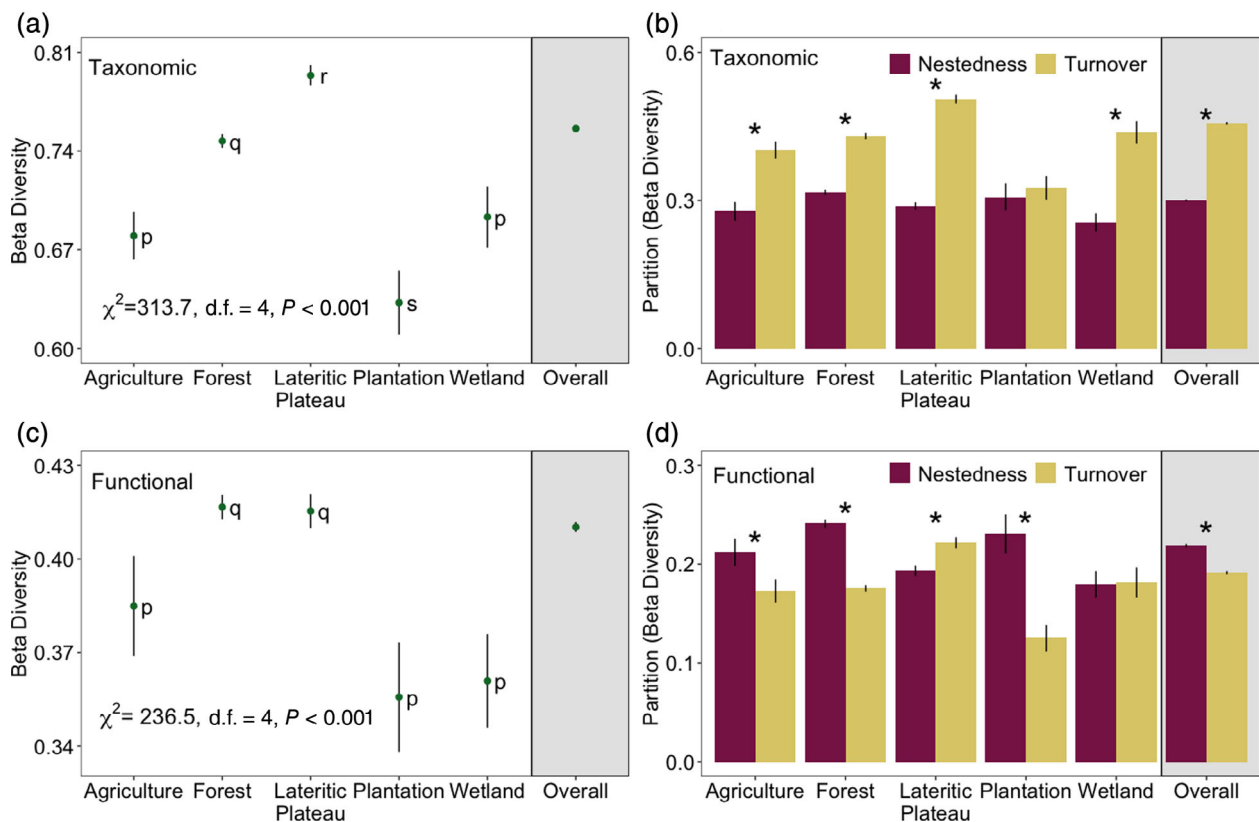

Fig 5. Beta diversity and its components due to nestedness and turnover at taxonomic and functional group levels (mean and 95% CI). At the taxonomic level, differences between land use categories ($\chi^2 = 313.7$, d.f. = 4, $P < 0.01$) suggests high beta diversity sites in lateritic plateaus compared to plantations (a). Components of beta diversity at the taxonomic level show greater influence of turnover than nestedness (b). At the functional level, differences between land use categories ($\chi^2 = 236.5$, d.f. = 4, $P < 0.001$) suggests higher beta diversity in forests and lateritic plateaus than other sites (c). Components of beta diversity at the functional level show a greater influence of nestedness than turnover (d). Different letters indicate statistically significant differences in Tukey's post hoc comparisons ($P < 0.05$). Overall pattern (grey background) is shown separately from the five land use categories.
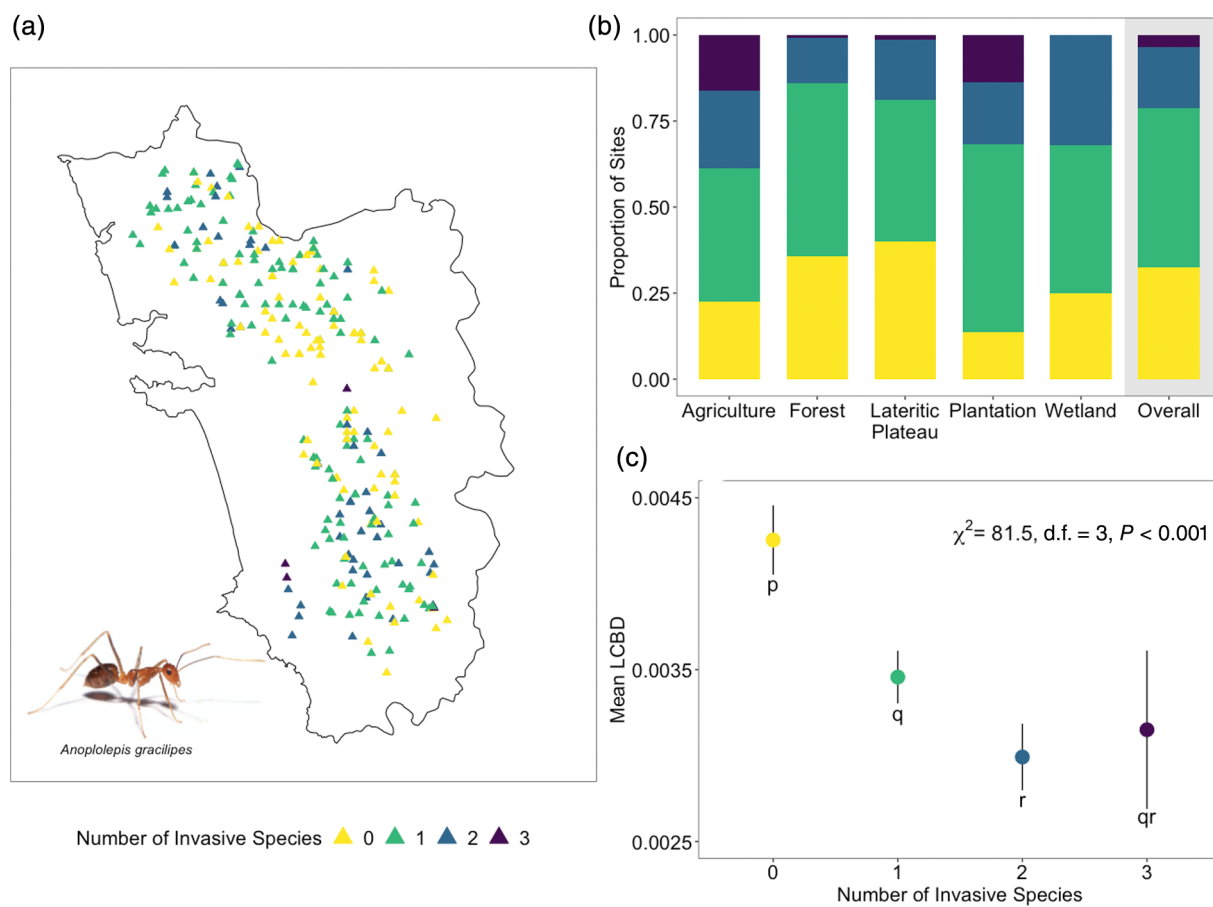
Fig 6. Variation in number of invasive species (such as *A. gracilipes*) across $n = 277$ sites (a). Proportion of sites showing 0–3 invasive species across different land use categories (b). Variation in LCBD (mean and 95% CI), with number of invasive species (c). Non-invaded sites contributed more to beta diversity than those with invasive species ($\chi^2 = 81.5$, d.f. = 3, $P < 0.001$). Different letters indicate statistically significant differences in Tukey's post hoc comparisons ($P < 0.05$).

beta diversity—*O. smaragdina*, *Anoplolepis gracilipes*, *Paratrechina longicornis* (Latreille, 1802), and *Camponotus compressus* (Fabricius, 1787) did so in all the land uses, but other species like *Tapinoma melanocephalum* (Fabricius, 1793) and *Solenopsis geminata* (Fabricius, 1804) contributed the maximum in agriculture and plantations respectively (Fig. 2b–f). SCBD showed a curvilinear relationship with the number of sites occupied by each species (Fig. S6; RMSE = 0.284, $R^2 = 0.979$, $P < 0.001$).

Average contribution to beta diversity for species within their respective functional group showed that large bodied omnivores (group 3) and omnivorous ground nesting epigaeic species (group 1) contributed most to beta diversity overall (Fig. 3), and this pattern was consistent across all land uses as there was no significant interaction between functional groups and land use (functional group: $\chi^2 = 37.7$, d.f. = 7, $P < 0.001$, land use: $\chi^2 = 0.01$, d.f. = 4, $P = 0.99$, interaction: $\chi^2 = 20.0$, d.f. = 28, $P = 0.863$).

Through resampling, we found that the average as well as variation in LCBD could be reliably estimated with our sampling effort (Fig. S7). LCBD across all sites was $0.0036 \pm 5.9 \times 10^{-5}$

(mean $\pm$ SE), ranging between 0.002 and 0.006 (Fig. 4). Sites from lateritic plateaus contributed more to beta diversity than sites in plantations (Fig. 4; $\chi^2 = 16.4$, d.f. = 4, $P < 0.01$).

Nestedness and turnover components of beta diversity

Sites in agriculture, plantation, and wetland were similar to each other while sites in forests and lateritic plateaus had higher beta diversity (Fig. 5a; $\chi^2 = 313.7$, d.f. = 4, $P < 0.001$). At the taxonomic level, the turnover component of beta diversity was larger than the nestedness component (Fig. 5b; $\chi^2 = 8513$, d.f. = 1, $P < 0.001$), and this was seen in all land uses except plantations (Fig. 5b). Beta diversity at the functional level was also low in agriculture, plantation, and wetland sites compared to natural land uses (Fig. 5c; $\chi^2 = 236.5$, d.f. = 4, $P < 0.001$). However, for functional groups, the nestedness component was larger than turnover (Fig. 5d; $\chi^2 = 616.9$, d.f. = 1, $P < 0.001$), and this pattern was seen in agriculture, forest, and plantation sites (Fig. 5d).
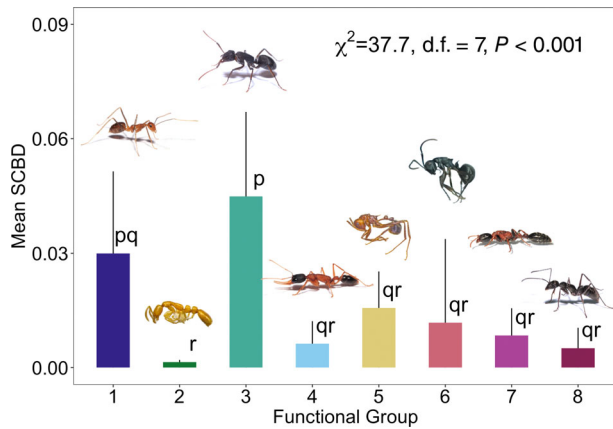
Fig 3. Contributions to beta diversity by species from eight functional groups [mean and 95% confidence interval (CI)]. Difference between functional groups ($\chi^2 = 37.7$, d.f. = 7, $P < 0.01$) suggests large bodied omnivores (group 3) contributed most to beta diversity followed by omnivorous, ground-nesting, epigaeic foraging species (group 1). Different letters indicate statistically significant differences in Tukey's post hoc comparisons ($P < 0.05$). Description of functional groups is in Table 2.

Invasive species and beta diversity

Five out of the 68 species were alien invasives. These included the globally significant invasive *A. gracilipes*, along with *P. longicornis*, *Monomorium pharaonis* (Linnaeus, 1758), *S. geminata*, and *Trichomyrmex destructor* (Jerdon, 1851). Invasive species were broadly distributed across the landscape (Fig. 6a) and at least one invasive species was recorded in 186 out of the 277 sites (67%). Invasive species were more common in human land uses (agriculture and plantations), compared to the natural land uses (Fig. 6b). Sites with invasive species contributed less to beta diversity than non-invaded sites (Fig. 6c; $\chi^2 = 81.5$, d.f. = 3, $P < 0.001$).

Discussion

These data show how ant species, functional groups, and sites contribute to beta diversity across regional spatial scales. Simultaneously, they also address how invasive species can have a negative influence on beta diversity. Data over broad spatial scales that address both aspects (human land use and invasive species) of ant communities are rare, as previous studies have generally addressed these inter-related aspects in isolation (Holway & Suarez, 2006; Bos *et al.*, 2008).

Species and local contributions to beta diversity

Identifying which species and sites contribute most to beta diversity is an important step for understanding how biodiversity is distributed across large spatial scales, and how these are impacted by human land use. Since ants are an integral part of

nearly all terrestrial ecosystems, their contribution to beta diversity at the level of species and functional groups are important determinants of many ecological processes. We find that *O. smaragdina*, *A. gracilipes*, and *P. longicornis* contribute most to beta diversity across the study area as well as in different geomorphic land use categories (Fig. 2). We also find that sites in natural land use contribute more to beta diversity, and this is low for plantations (Fig. 4). Land use change is known to cause biotic homogenisation (Arnan *et al.*, 2018) and our data are consistent with this form of human influence. Large-bodied omnivores (functional group 3) which are inferred to facilitate decomposition of organic matter, and omnivorous ground-nesting epigaeic species with invasive characteristics (group 1), contributed most to beta diversity overall and across most land use, followed by granivorous and omnivorous ground-nesters (functional group 5) which are inferred to help in pedoturbation and seed dispersal (Fig. 3). Species from these functional groups were also common (Fig. S3), and their roles may be important for ecological function across habitats. Consistent with theoretical expectations (Gaston *et al.*, 2006), we find a non-monotonic curvilinear relationship with commonness and rarity (Fig. S6), such that the commonest as well as rare species may not have a strong influence on beta diversity (Brasil *et al.*, 2020). Previous studies have interpreted such covariation as monotonic and linear (Gavioli *et al.*, 2019), even though data are expected to be curvilinear and non-monotonic.

The data also indicate that site-level uniqueness of ant community composition (LCBD) may be driven by human influence as it can alter availability of resources and environmental factors (Rubiana *et al.*, 2015). Sites in plantations contributed the least to beta diversity; these are unlike natural habitats and undergo active management that alters the understory, canopy and microclimate—all of which can affect ants. In addition, a low LCBD of sites in plantations also indicates homogeneity of ant communities due to habitat filtering (Arnan *et al.*, 2018). Sites in lateritic plateaus were most unique in their ant assemblages, and several such sites are locally threatened by land use conversion as they are seen as 'wastelands' (Department of Land Resource Government of India, 2019) that can be diverted for industrial development. Such development goals do not account for biodiversity and our data emphasise the importance of lateritic plateaus. Future management decisions for development can centre around promoting heterogenous landscapes in lateritic plateaus by adopting the concepts of land-sharing and land-sparing (Socolar *et al.*, 2016).

Nestedness and turnover components

Partitioning beta diversity into turnover and nestedness components reveals likely mechanisms that cause variation in biodiversity. It also affords comparisons across studies and insights into conservation management (Baselga, 2010). At the taxonomic level, beta diversity across land uses was influenced primarily by turnover, rather than nestedness (Fig. 5b). However, nestedness was more important for functional groups (Fig. 5d). This suggests loss of functionally unique species can be more common than loss of functionally redundant species, and that

loss of functions can outpace loss of species (Flynn *et al.*, 2009). Another possible mechanism could be the differential responses of ant communities to anthropogenic stressors in comparison to natural stressors (Gutiérrez-Cánovas *et al.*, 2013). Contrasts between taxonomic and functional beta diversity (Villéger *et al.*, 2012) also indicate that human land use can lead to loss of functions even though it spares local richness (i.e., alpha diversity Fig. S4). Thus, local richness may be insufficient to fully understand how human impacts affect ant communities.

Invasive species and beta diversity

Whether and how invasive species influence beta diversity, and by how much, is an important dimension of biotic homogenisation that affects a wide variety of assemblages. We found that while invasive species were widely distributed, they were more frequent in human land use than in natural sites (Fig. 6b). Consistent with biotic homogenisation hypothesis (Holway *et al.*, 2002), invaded sites contributed less to beta diversity (Fig. 6c). However, the contribution of individual invasive species themselves to SCBD varied across land use (Fig. 2). Contribution from *S. geminata* to beta diversity was highest in plantations (Fig. 2e). This species is native to the Neotropics and is known to outcompete other arthropods for resources due to its generalist nature of resource utilisation and aggressiveness (Risch & Carroll, 1982). *Anoplolepis gracilepis* can be detrimental to landscapes because of their agnostic behaviour towards other arthropods and this can take extreme forms of even changing the composition and structure of a forest (O'Dowd *et al.*, 2003). *Paratrechina longicornis* is known to outcompete and displace several arthropod species by their aggressive behaviour and their ability to monopolise resources (Wetterer *et al.*, 1999). *Monomorium pharonis* is another invasive species with a global footprint that appears to be a human commensal and is also known to pose potential health risk to humans by carrying several pathogenic germs (Wetterer, 2010). Although *T. destructor* is a globally important invasive, it does not seem to have great impact on natural ecosystems (Wetterer, 2009) and does not contribute much to beta diversity in our study (Fig. 2).

In conclusion, our study shows that human land use can greatly alter ant communities. While local richness remains relatively uninfluenced, land use change can alter functional diversity and raise the influence of invasive species. Further land use intensification can have detrimental effects by homogenising the community, making them progressively nested, and strengthen the negative influence of invasive species, which can all have cascading effects on important ecosystem functions performed by ants.

Acknowledgements

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

Data available on request from the authors.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting Information.
Fig. S1: Schematic showing sampling design at each location ($n = 277$ replicates).
Fig. S2: Rarefaction estimates of species richness.
Fig. S3: Species occupancy across sampled sites.
Fig. S4: Mean species richness across land use types.
Fig. S5: Cluster dendrogram of eight functional groups.
Fig. S6: Species occupancy and species contributions to beta diversity.
Fig. S7: Resampling based analysis of LCBD.
Table S1: Summary data for species codes, status, and traits.

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Editor: Raphael Didham and Associate Editor: Jerome Orivel