Assembly mechanisms of dung beetles in temperate forests and grazing pastures

Ilse J. Ortega-Martínez1, Claudia E. Moreno1*, Cecilia Lucero Ríos-Díaz1, Lucrecia Arellano2, Fernando Rosas1 & Ignacio Castellanos1

The role of deterministic and stochastic mechanisms in community assembly is a key question in ecology, but little is known about their relative contribution in dung beetle assemblages. Moreover, in human modified landscapes these mechanisms are crucial to understand how biodiversity can be maintained in productive agroecosystems. We explored the assembly mechanisms driving dung beetle assemblages in forests and grazed grassland patches, and assessed the role of dung availability, soil hardness and moisture, elevation and land use heterogeneity as environmental predictors of functional diversity. To determine the underlying assembly mechanisms, we estimated functional diversity metrics (functional richness, evenness and divergence) and their departure from the predicted values by null models. We also used GLMs to assess the influence of environmental variables on functional diversity. In most cases, stochastic processes prevailed in structuring dung beetle assemblages and, consequently, environmental variables were not good predictors of dung beetle functional diversity. However, limiting similarity was found as a secondary mechanism with an effect on dung beetle assemblages in grasslands. Our results highlight the importance of stochastic processes that may reflect a metacommunity dynamic. Therefore, restoring landscape connectivity might be more important than habitat quality for the conservation of these functionally diverse beetle assemblages.

Community assembly theory provides a conceptual foundation about the mechanisms that determine species composition of local assemblages1,2, and this background becomes especially relevant for studies concerning the ecological consequences of environmental contemporary changes. For example, results from a recent study have made it possible to improve our understanding of biological invasions, a global issue that is critical in ecology and conservation1. However, an important remaining issue is to unravel how current anthropogenic changes to the environment, such as land use change and agricultural production can modify the assembly mechanisms that shape the structure and composition of local communities3. Human activities have contributed substantially to the loss of species and degradation of ecosystems4,5, generating impacts on ecological communities6. Therefore, identifying the drivers of community assembly in human modified landscapes is an urgent challenge.

Both deterministic and stochastic mechanisms are important in assembling biological communities. The main deterministic mechanisms driving community assembly are limiting similarity and environmental filtering8–10. If the local community is formed by non-redundant species, its trait diversity will be high (trait overdispersion) as a result of strong ecological interactions, and community assembly is considered to be driven by a limiting similarity mechanism due to competition8. On the contrary, the environmental filtering mechanism (the abiotic filter) structures local communities through environmental restrictions10 producing sets of species with similar traits (trait clustering)8,11,12. Besides environmental filtering sensu stricto, recent advances in coexistence theory have shown that there are other mechanisms that may lead to trait clustering13, such as competitive ability differences (average fitness differences)13, mutualism14 or facilitation10. Therefore, if trait clustering is found in empirical studies, a clear framework should be followed to discern between environmental filtering sensu stricto and ecological interaction mechanisms10. In a different way, the stochastic assembly of communities relies on the dispersal of individuals across space, regardless of their traits, so the structure and composition of communities is limited by ecological drift and the species’ dispersal capacity, a process related to the neutral theory15.

1Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Mineral de la Reforma, Hidalgo, Mexico. 2Red de Ecoetología, Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico. *email: cmoreno@uaeh.edu.mx
Several environmental conditions may change the relative influence of limiting similarity, environmental filtering and stochastic mechanisms on community assembly, particularly if those conditions alter dispersal, arrival, and niche availability. Therefore, our ability to understand the relative importance of these not mutually exclusive assembly mechanisms is critical, as they can have high impacts on the conservation of local biodiversity and ecological functions. For example, a poor knowledge about the drivers of community assembly limit our capacity to predict the consequences of land-use change on diversity, and to devise useful management interventions in man-made landscapes.

An effective quantitative approach for understanding community assembly mechanisms is the use of functional trait-based diversity metrics. For example, recent studies on ground-dwelling beetles have incorporated the analysis of functional traits to assess forest-grassland gradients and community assembly rules. Because they are related to species’ niches, the variability of those traits within communities (i.e., functional diversity) is assumed to reflect the imprint of assembly mechanisms such as environmental filtering or competitive interactions. To disentangle the relative contributions of assembly mechanisms, we can measure the deviation of the observed functional diversity estimates from their expected distribution under a random model of assembly. Such differences are then interpreted in the light of theoretical frameworks and the most likely assembly mechanism is inferred (e.g., Liu & Wang). If the functional diversity of coexisting species is higher than expected by chance, we would infer a mechanism of limiting similarity that produces over-dispersion in functional traits. On the contrary, if the functional diversity of coexisting species is lower than expected by chance, we would expect an environmental filtering mechanism, producing under-dispersion in functional traits (i.e., functional convergence). Finally, if the observed functional diversity is not different from the expected in a null model of random assembly, stochastic processes are assumed.

Dung beetles (Coleoptera: Aphodiinae, Geotrupinae and Scarabaeinae) use vertebrate dung (mainly that of large and medium sized mammals) for food and nesting. They perform several ecosystem functions, including dung decomposition through their burial and nutrient recycling. These primary functions have consequences on secondary functions such as bioturbation, secondary seed dispersal and greenhouse gases control. Studies on dung beetle functional diversity have shown changes across different land uses and livestock production systems. Moreover, a recent study based on the functional diversity of dung beetles suggests that the environment restricts species dispersion or establishment along an elevation gradient, thus a niche filtering mechanism would be structuring these communities. Likewise, Audino et al. found that niche-based processes drove the assembly of dung beetle assemblages following active restoration, mainly by the influence of environmental filters. However, it is unlikely that a single process would be responsible of the assemblages’ structure. Hence, to understand the assembly mechanisms of dung beetle assemblages in landscapes with human impacts, it would be relevant to assess the combined effects of deterministic and stochastic mechanisms. By estimating functional diversity metrics and their departure from expected values of null distributions, we evaluate assembly mechanisms structuring dung beetle assemblages in forests and grassland patches where livestock graze in a mountain landscape. Additionally, we assess the influence of environmental variables (dung availability, soil hardness and moisture, elevation and land use heterogeneity) over functional diversity metrics. Due to the contrasting environmental conditions between forest and grasslands, and the availability of food resources that reduces competition, we expect that locally coexisting species will have similar traits due to an environmental filtering mechanism. According to this, functional diversity will be explained by environmental conditions.

Results
We recorded 3,639 individuals belonging to 23 species of subfamilies Aphodiinae, Geotrupinae and Scarabaeinae. Overall, dung beetles were more abundant and diverse in grazed grasslands (2,590 individuals of 19 species) than in forest sites (1,049 individuals of 14 species). The most abundant species in both conditions were *Onthophagus mexicanus* Bates, 1887 (*n* = 1,544 individuals), *Onthophagus opisihius* (Bates, 1887) (*n* = 1,057), *Onthophagus chevolati* Harold, 1869 (*n* = 341), *Phanaeus palliatus* Sturm, 1843 (*n* = 139) and *Copris armatus* Harold, 1869 (*n* = 139). From the total number of individuals, 64% are tunnellers, 34% are dwellers, while only 2% are rollers (Supplementary Table S1).

Assembly mechanisms. The SES values for the three FD metrics used (FRic, FEve and FDiv) were not statistically different between forest and grassland (*P* > 0.05, Fig. 1). Most of the sites had SES values within the randomly expected null interval, thus stochastic processes are assumed to be the main forces structuring these dung beetle assemblages. Nevertheless, SES.FRic values from one forest and two grassland sites (low elevation), were greater than 1.96, indicating limiting similarity.

When we pooled the data from all sampling sites of each environmental condition, the SES values of the three FD metrics were negative for the pine-oak forest, but not lower than the randomly expected values. However, for grassland the SES.FRic value was higher than expected by chance, indicating that limiting similarity shapes dung beetle assemblages in these grazed grasslands (Fig. 1).

Environmental predictors of functional diversity. For functional richness the best-fitted model included elevation and dung availability as predictor variables when all the sites were considered, but only elevation had a significant negative relationship (Table 1). However, when the forest and grassland sites were analyzed separately, any of the environmental variables had a significant relationship with functional richness. Similarly, none of the environmental predictors had a significant relationship with functional evenness.
Finally, the best-fitted model showed that functional divergence values increased with higher soil moisture when we considered all the sites, while for grassland sites we detected a negative relationship between functional divergence and dung availability (Table 1).

**Discussion**

Contrary to our expectation, stochastic processes prevail in structuring the studied dung beetle assemblages. Accordingly, environmental variables were not good predictors of dung beetle functional diversity. These results reflect some degree of ecological equivalence among coexisting dung beetle species, given the lack of clear trends of functional divergence (over-dispersion) or convergence (under-dispersion)\(^9\). Therefore, the dynamics of dung beetle assemblages may depend on processes related to species’ dispersion and demographic stochasticity\(^31,32\). A similar pattern has also been detected for ground beetles (Carabidae) in urban and suburban areas, where communities are randomly assembled as a result of stochastic mechanisms\(^33\).

---

**Figure 1.** Standardized effect size (SES) of functional richness (a), functional evenness (b), and functional divergence (c) of dung beetle assemblages in forest and grassland sites, and the total cumulative data of each environmental condition. The localities have been ordered from lowest (to the left) to highest (to the right) elevation (Supplementary Table S2). The red dotted lines include the values that are not statistically different from a distribution expected by chance, according to null models (−1.96 to 1.96 interval). Values of t tests comparing forest and grassland sites are included.
From the point of view of the spatial dynamics of community ecology, our samples of beetles in both habitats are part of a regional metacommunity, thus the set of local assemblages may be connected by dispersion. In this scenario, despite their contrasting differences in tree coverage, food availability and environmental conditions, the grassland patches could be so small that may represent a continuous environment with the forest matrix, allowing the existence of a neutral dynamic for dispersal. Such a neutral dynamic assumes that, given random changes in their abundance, species have the same competitive capacity in both habitats, thus their coexistence depends on the ecological drift (an equilibrium between immigration and extinction processes). A similar pattern has been recently described for ground beetles in grasslands embedded within a forest matrix in the northern Hungarian mountains, where a random assembly structure is explained by the considerable asymmetrical species flow from adjacent forests. Although in our study area dung beetle species richness, abundance and diversity are higher in grasslands than in forest interior, 41% of the species have been caught in both habitats (Rios-Díaz et al., unpublished data). This indicates that there is a significant flow of individuals and species between habitats probably because forests can be used by some species as habitat, and they move to the adjacent grasslands for feeding. Therefore, in order to test the metacommunity hypothesis, we would require detailed information on population’s movements.

Dispersal capacity varies among dung beetle species. Some of them can move 50 to 100 m in few days or even up to 1.5 km, although this depends on their physiological (reproductive) condition or sex. In open environments some generalist species show high vagility, while specialist species are less vagile. Also, large species move more frequently in grasslands than small species. However, as far as we know, the spatial movements of dung beetles have not been assessed in temperate mountainous landscapes similar to our study area, therefore capture-recapture experiments or remote sensing devices will be required to describe their movement patterns.
Besides their biological restrictions, landscape elements also have differential impacts on the dispersal capacity of species. For example, open areas may act as barriers for the dispersal of some forest specialist species28,38,41–44, because temperature and moisture conditions change45. However, some forest patches and other landscape elements such as live fences and isolated trees promote spatial heterogeneity and can increase functional connectivity, reducing the effects of isolation38,46. In our study area, grassland patches include several Agave fences that may act as corridors for insects. Also, the dispersal dynamics of dung beetles, as well as their opportunity to get food, may be related to the movement and density of livestock47.

Again, contrary to our expectation, we found that one forest, two grassland sites, and the complete set of grassland species, showed functional over-dispersion, which is assumed to be a result of limiting similarity processes. This suggests that, despite the availability of food resources (mammal dung), coexisting dung beetle species are functionally different in some grasslands. This could represent a secondary factor that contributes simultaneously with the stochastic process to the observed functional structure. Ecological theory would expect ecological competition to be a result of low resource availability48–50, and strong competitive interactions are expected to produce functional divergence in coexisting species4. In temperate forests of Northern Europe, competitive interactions influence the structure of dung beetle assemblages due to the limited availability and size of dung49. However, this does not seem to be the case in our study, as we even found a negative relationship between dung availability and functional divergence in grassland sites. Therefore, in the grasslands of our study region, we still need to assess other characteristics of dung, beyond its frequency on the ground. For example, traditional livestock movement may result in a complex spatial mosaic of dung with different degrees of quality and freshness. Moreover, the composition of dung beetle assemblages in grasslands may be also influenced by the intensity and history of grazing32.

It has been proposed that dung beetle assemblages in tropical forests are structured by their niche space (environmental filtering), while the influence of limited dispersal and random colonization are discarded28. This suggests that the arrival and establishment of species depends on environmental factors29,32, and could result in ecological redundancy in dung beetle assemblages28,34,55. Also, in tropical forest the degradation and loss of natural habitats decreases the functional diversity of dung beetles26,27,34, which has consequences on their ecosystem functions.57. However, in our study we lack the difference in functional diversity metrics between forest and grassland sites suggest that functional diversity of dung beetle assemblages is not affected by grazing in grassland patches. A similar situation has been found in scrub habitats near our study area28, and in the Cerrado biome in Brazil, where functional diversity does not change among vegetation types58.

In summary, our results indicate that in a temperate forest landscape, dung beetle assemblages are mainly determined by stochastic processes, and to a lesser extent by the deterministic process of limiting similarity. Therefore, these processes are not mutually exclusive, and may be acting jointly in structuring beetle communities under metacommunity dynamics associated to the traditional pastoral activities in the small grasslands of this montane landscape.

Future research will be required to know if these dynamics vary with increasing land use change or more intensive livestock management. In such cases, dung beetle assemblages could be facing the opposite processes: ecological disassembly mechanisms due to species loss. Therefore, better knowledge on assembly mechanisms might be useful to develop appropriate restoration policies. For example, Wearn et al.5 suggest that if environmental filtering is the dominant driver of assembly, then steps to restore habitat quality may be important. Alternatively, if dispersal limitation dominates assembly, then restoring landscape connectivity might be more important. However, determining specific conservation practices will require complementary information, such as data on alpha and beta taxonomic and phylogenetic diversity, and temporal dynamics of dung beetle species.

Materials and Methods

Study area. The study was carried out at the UNESCO Global Geopark Comarca Minera59 located in the state of Hidalgo, central Mexico, in the Mexican Transition Zone (Supplementary Method: Study area and location of sampling sites; Supplementary Fig. S1). In this mountainous area, livestock production is based on small flocks of sheep and goats that are guided by a shepherd in open grassland patches embedded in a forest matrix. Vegetation is characterized by pine-oak forest where Pinus teocote, P. montezumae, P. patula, Quercus laurina, Q. crassifolia and Q. rugosa are the most frequent tree species.

Data collection. Ten localities separated each other by at least 1 km were selected at the study region. At each locality we set two sampling sites: one in a grazed grassland and the other in the contiguous pine-oak forest. The minimum distance between the two sampling sites within each locality was 300 m, and each site was at least 100 m from the forest edge in order to avoid edge effects, as they may have strong influence on beetle species composition28,51. Sites ranged from 2,200 to 2,726 m a.s.l. (Supplementary Table S2).

As our research question is not related to temporal variation in the studied assemblages, we did not take into account seasonal or annual dynamics. Instead, dung beetles were sampled during the rainy season (August and September 2016), when they are most active, to maximize capture success. Previous studies in our study area have proven that intensive sampling during this limited period may be enough for recording dung beetle assemblages properly45. Moreover, we assessed the completeness of our samples to represent dung beetle assemblages at each sampling site (see below).

We used baited pitfall traps made of a plastic container (1 litre) buried at soil level, with ethylene glycol diluted in 10% water (250 ml) to break the surface tension and to preserve the beetles. Each pitfall trap was baited with a mixture (3:1) of sheep and horse dung (ca. 250 g). All this sampling methodology has been successfully used in the region for sampling dung beetles, as big native mammals are extremely scarce, thus, livestock is the main source of dung51. At each sampling site, we set up nine pitfall traps separated 50 m (following Larsen & Forsyth50). Although other authors have suggested larger distances for pitfall trapping, we set this distance as we are not using
trait data. To calculate functional diversity (FD) metrics, we selected behavioural, dietary and morphological traits of species, as these have been proposed as key characteristics in the response of terrestrial invertebrates to environmental change, and that may affect ecosystem processes. The traits considered in this paper are: 1) food relocation behaviour, 2) activity period, 3) diet type, 4) morphological measurements (body length, body width, dorso-ventral length, clypeus length, head length, pronotum length, abdomen length, forelegs length and hindlegs length), 5) wing loading, and 6) biomass (see details in Supplementary Method: Functional traits of dung beetle species; Supplementary Table S4).

Community parameters. As a preliminary analysis, we calculated the sample coverage to assess the completeness of our samples to represent dung beetle assemblages at each sampling site. In general, the estimates of sampling coverage were higher than 0.91 in all but in one forest site (0.85), indicating that the sampling effort was enough to achieve a good representation of assemblages. However, for the following analyses one forest site was omitted because of its low richness and abundance (Supplementary Table S1).

Although there are several indices of functional diversity, we selected three (FRic, FEve, FDiv) proposed by Villéger et al., that have been suggested as the most appropriate metrics to assess assembly mechanisms. Functional richness (FRic) represents the functional space (volume in the N dimensional space) that is occupied by the species in the community. Functional evenness (FEve) measures the uniformity of the distribution of species and their abundance in the functional space, while functional divergence (FDiv) represents how abundance is distributed within the volume of functional trait space occupied by species. We calculated FRic, FEve and FDiv for each sampling site and for the cumulative data of each environmental condition. These indices are based on the functional space defined by the species’ traits. To achieve this, a Principal Coordinates Analysis (PCoA) is produced to discard potentially correlated traits and reduce dimensionality. The resulting PCoA axes are used as the new standardized traits to compute the functional diversity indices, avoiding redundancy and biases. All the analyses were done using the dbFD function in the FD package in R 3.5.1.

Null models. Null models are commonly used to prove if observed patterns in ecological communities are significantly different from values expected by chance. Therefore, we calculated expected values of FRic, FEve and FDiv indices by constructing null models to detect the relative contribution of different assembly mechanisms in structuring dung beetle assemblages.

To generate null models, we shuffled the names of species on the trait data matrix to produce random combinations from the species pool: the set of species present in the region due to biogeographical and historical processes. Then, we constructed null models using FD in R and picante packages in R 3.5.1, following Swenson. We created 999 random assemblages by randomizing the trait data while maintaining the community. Randomizations were carried out for the whole set of forest and grassland sites, considering that they might have the same species regional pool. Then, we used the observed and null expected values to quantify the standardized effect size (SES) of each index. This calculation removes any directional bias associated with the decrease in variance in the expected values with increasing species richness. To calculate the SES, we subtracted the mean value of the null distribution (mean expected value) from the observed value of functional diversity, and then divided it by the standard deviation of the null distribution.

SES values can be positive or negative, and their statistical significance at P < 0.05 is assumed when the SES value falls outside the range of −1.96 to 1.96, assuming a normal distribution of deviations. On one hand, a SES value greater than 1.96 indicates that there is functional over-dispersion due to a limiting similarity mechanism. On the other hand, SES values lower than −1.96 indicate that there is functional under-dispersion, which means that an environmental filtering mechanism occurs. When SES values fall within the range of −1.96 to 1.96, mechanistic processes cannot be proved, and then stochastic processes are assumed as the observed values cannot be distinguished from random values. SES values were calculated for each sampling site, and for the cumulative data of each environmental condition (forest and grassland).

Environmental variables. We measured soil hardness, soil moisture and dung availability, at each sampling site, as these variables are related with beetles’ dung removal. To measure soil hardness and moisture we took nine values per site, near to each pitfall trap. Soil hardness was measured with a graduated penetrometer (scaled 0 to 5) and soil moisture with an analogic soil moisture meter (scaled 0 to 10). We measured dung availability in four 20 m long transects at each site. Along each transect we located 1 m² plots separated 1 meter and counted the frequency of dung occurrence in the 40 plots. We also measured elevation and land use heterogeneity surrounding pitfall traps. For this latter, we used aerial images taken with a drone (Phantom 3 advanced model, 12-megapixel camera, GPS + GLONASS) and measured the proportion of each land use type in a 100 m buffer around the pitfall traps (see details in Supplementary Method: Method used to characterize the heterogeneity of land uses surrounding the sampling sites; Table S5). Then, we calculated the exponential of the Shannon-Wiener index to estimate the effective number of land uses as a proxy of land use heterogeneity at each site.

Statistical analyses. First, we checked for spatial autocorrelation of each functional diversity metric using Moran I correlograms, and none spatial autocorrelation was detected (Moran’s I = −0.03, −0.11, and 0.16 for SES.FRic, SES.FEve and SES.FDiv, respectively, P > 0.05 in all cases). Then, we performed t tests to assess
differences in the mean SES values of each functional diversity metric between forest and grassland sites, as these variables passed normality tests (Shapiro-Wilk tests, SES.FRic: $W = 0.92$, $P = 0.16$; SES.FEve: $W = 0.94$, $P = 0.29$; SES.DFir: $W = 0.93$, $P = 0.18$).

To assess the relationships between the SES values of FD metrics (response variables) and environmental variables (predictors) we used generalized linear models (GLMs). We used gaussian distributions as the response variables were normally distributed (see above). As predictors we included all possible combinations of the environmental variables (soil hardness, soil moisture, dung availability, elevation and land use heterogeneity). We first ran the models for all the sites, and then separately for each environmental condition (forest and grassland). The candidate models were compared using the Akaike information criterion (AIC)$^{92}$. Models with the lowest AIC values were selected as the best models$^{97}$. All analyses were done in R 3.5.1$^{99}$.

**Data availability**

All data generated during this study are included in this published article (and its Supplementary Information files online).

Received: 25 September 2019; Accepted: 16 December 2019;
Published online: 15 January 2020

**References**

1. Weih, E. A primer of trait and functional diversity (ed. Magurran, A. E. & McGill, B. J.) 175–193 (University Press, 2011).
2. HilleRisLambers, J., Adler, B. P., Harpole, W. S., Levine, J. M. & Mayfield, M. M. Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* 43, 227–48, https://doi.org/10.1146/annurev-ecolsys-100411-160411 (2012).
3. Pearson, D. E., Ortega, Y. K., Eren, O. & Hierno, J. L. Community assembly theory as a framework for biological invasions. *Trends Ecol. Evol.* 33(5), 313–325, https://doi.org/10.1016/j.tree.2018.03.002 (2018).
4. Wearn, O. R. et al. Land-use change alters the mechanisms assembling rainforest mammal communities in Borneo. *J. Anim. Ecol.* 88(1), 125–137, https://doi.org/10.1111/1365-2656.12903 (2018).
5. Isbell, F. et al. Linking the influence and dependence of people on biodiversity across scales. *Nature* 546, 65–72, https://doi.org/10.1038/nature22899 (2017).
6. Johnson, C. N. et al. Biodiversity losses and conservation responses in the Anthropocene. *Science* 356(6335), 270–275, https://doi.org/10.1126/science.aam9317 (2017).
7. Harrison, S. P., Gornish, E. S. & Copeland, S. Climate–driven diversity loss in a grassland community. *PNAS* 112(28), 8672–8677, https://doi.org/10.1073/pnas.1502074112 (2015).
8. Mouillot, D., Dumas, O. & Tomassini, J. A. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Eur. Coast. Shelf Sci.* 71(3–4), 443–456, https://doi.org/10.1016/j.ecss.2006.08.022 (2007).
9. Mouchet, M.A., Villéger, S., Mason, N. W. & Mouillot, D. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24(4), 867–876, https://doi.org/10.1111/j.1365-2435.2010.01695.x (2010).
10. Kraft, N. J. B. et al. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29(5), 592–599, https://doi.org/10.1111/1365-2435.12345 (2015).
11. Weih, E. & Reddy, P. A. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74(1), 159–164 (1995).
12. Hobbs, R. J. & Norton, D. A. Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly (ed. Temperton, V. M., Hobbs, R. J., Nottle, T. & Halle, S.) 72–95 (Island Press, 2004).
13. Mayfield, M. M. & Levine, J. M. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13, 1085–1093, https://doi.org/10.1111/j.1461-0248.2010.01599.x (2010).
14. Sargent, R. D. & Ackerly, D. D. Plant–pollinator interactions and the assembly of plant communities. *Trends Ecol. Evol.* 23, 123–130, https://doi.org/10.1016/j.tree.2007.11.003 (2008).
15. Hubbell, S. P. The unified neutral theory of biodiversity and biogeography (MPB-32) (Princeton University Press, 2001).
16. McGill, B. J. & Enquist, B. J., Weiher, E. & Westoby, M. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21(4), 178–185, https://doi.org/10.1016/j.tree.2006.02.002 (2006).
17. Perronne, R., Munoz, F., Borgy, B., Reboucl, X. & Gaba, S. How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. *Perspect. Plant Ecol. Evol. Syst.* 25, 29–44, https://doi.org/10.1016/j.ppse.2017.01.004 (2015).
18. Magura, T. Ignoring functional and phylogenetic features masks the edge influence on ground beetle diversity across forest-grassland gradient. *For. Ecol. Manage.* 384, 371–377, https://doi.org/10.1016/j.foreco.2016.10.056 (2017).
19. Magura, T. & Love, G. L. Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. *Insect Sci.* 26, 154–163, https://doi.org/10.1111/1744-7917.12504 (2019).
20. Liu, X. & Wang, H. Contrasting patterns and drivers in taxonomic versus functional diversity, and community assembly of aquatic plants in subtropical lakes. *Biodivers. Conserv.* 27(12), 3103–3118, https://doi.org/10.1007/s10531-018-1590-2 (2018).
21. Halffter, G. & Edmonds, W. D. The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutionary approach (Instituto de Ecología, 1982).
22. Slade, E. M., Mann, D. J., Villanueva, J. F. & Lewis, O. T. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *J. Anim. Ecol.* 76(6), 1094–1104, https://doi.org/10.1111/1365-2664.2007.01296.x (2007).
23. Nichols, E. et al. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141(6), 1461–1474, https://doi.org/10.1016/j.biocon.2008.04.011 (2008).
24. Griffiths, H. M. et al. Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. *Ecology* 96(6), 1607–1619, https://doi.org/10.1890/14-1211.1 (2015).
25. Slade, E. M., Riutta, T., Roslin, T. & Tuohtisto, H. The role of dung beetles in reducing greenhouse gas emissions from cattle farming. *Sci. Rep.* 6(1), 18140, https://doi.org/10.1038/srep18140 (2016).
26. Barragan, F., Moreno, C. E., Escobar, F., Halflter, G. & Navarrete, D. Negative impacts of human land use on dung beetle functional diversity. *PLoS ONE* 6(3), e17976, https://doi.org/10.1371/journal.pone.0017976 (2011).
27. Gómez-Cifuentes, A., Munevar, A., Gimenez, V. C., Gatti, M. G. & Zurita, G. A. Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. *J. Insect Conserv.* 21(1), 147–156, https://doi.org/10.1007/s10841-017-9964-4 (2017).
33. Magura, T., Lövei, G. L. & Tóthmérész, B. Conversion from environmental filtering to randomness as assembly rule of ground beetle assemblages along an urbanization gradient. *Sci. Rep.* **8**(1), 16992, doi.org/10.1038/s41598-018-35293-8 (2018).

34. Leibold, M. A. et al. The metacommunity concept: a framework for multiscale-community ecology. *Ecol. Lett.* **7**(7), 601–613, doi.org/10.1111/j.1461-0248.2004.00608.x (2004).

35. Biwas, S. R. & Wagner, H. H. Landscape contrast: a solution to hidden assumptions in the metacommunity concept? *Landscape Ecol.* **27**(5), 621–631, doi.org/10.1007/s10463-012-9732-5 (2012).

36. Larsen, T. H. & Forsyth, A. T. Spacing and Transect Design for Dung Beetle Biodiversity Studies. *Biotropica* **37**(2), 322–325, https://doi.org/10.1111/j.1744-7429.2005.00042.x (2005).

37. da Silva, P. G. & Hernández, M. I. M. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PloS ONE* **10**(5), e0126112, https://doi.org/10.1371/journal.pone.0126112 (2015a).

38. Arellano, L., León-Cortés, J. L. & Ovaskainen, O. Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. *Landscape Ecol.* **23**(1), 69–78, https://doi.org/10.1007/s10980-007-9165-8 (2008).

39. Cultid-Medina, C. A., Martínez-Quintero, B. G., Escobar, F. & Chacón-Ulloa, P. Movement and population size of two dung beetle species in an Andean agricultural landscape dominated by sun-grown coffee. *J. Insect Conserv.* **19**(4), 617–626, https://doi.org/10.1007/s10841-015-9784-3 (2015).

40. Roslin, T. & Koivunen, P. Distribution and abundance of dung beetles in fragmented landscapes. *Oecologia* **127**(1), 69–77, https://doi.org/10.1007/s004420000565 (2001).

41. Roslin, T. Dung beetle movements at two spatial scales. *Oikos* **91**(2), 323–335, https://doi.org/10.1034/j.1600-0706.2000.910213.x (2000).

42. Escobar, F. & Chacón-Ulloa, P. Distribución espacial y temporal en un gradiente de sucesión de la fauna de coleópteros coprófagos (Scarabaeinae, Aphodiinae) en un bosque tropical montano, Nariño-Colombia. *Rev. Biol. Trop.* **48**(4), 961–975 (2000).

43. Hosaka, T. et al. Impacts of Small-scale Clearings due to Selective logging on Dung Beetle Communities. *Biotropica* **46**(6), 720–731, https://doi.org/10.1111/btp.12158 (2014).

44. da Silva, P. G. et al. Patch and landscape effects on forest-dependent dung beetles are masked by matrix-tolerant dung beetles in a montane tropical rainforest archipelago. *Sci. Total Environ.* **651**, 1321–1331, https://doi.org/10.1016/j.scitotenv.2018.09.195 (2019).

45. Guerra-Alonso, C. B., Zurita, G. A. & Bellocq, M. I. Livestock areas with canopy cover sustain dung beetle diversity in the humid subtropical Chaco forest. *Insect Conserv. Divers.* **12**(4), 296–308, https://doi.org/10.1111/icad.12340 (2019).

46. Sánchez-de-Jesús, H. A., Arroyo-Rodríguez, V., Andresen, E. & Escobar, F. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. *Landsc. Ecol.* **31**(4), 843–854, https://doi.org/10.1007/s10980-015-0293-2 (2016).

47. Finn, J. A. & Gettings, T. A. review of competition in north temperate dung beetle communities. *Ecol. Entomol.* **28**(1), 1–13, https://doi.org/10.1111/j.1365-2311.2002.00487.x (2003).

48. MacArthur, R. & Levins, R. The limiting similarity, convergence, and divergence of coexisting species. *Amer. Naturalist.* **101**(921), 377–385, https://doi.org/10.1086/282503 (1967).

49. Brown, J. H., Reichman, O. J. & Davidson, D. W. Granivory in desert ecosystems. *Annu. Rev. Ecol. Syst.* **10**(1), 201–227, https://doi.org/10.1146/annurev.es.10.111979.012221 (1979).

50. Connor, E. F. & Simberloff, D. The assembly of species communities: chance or competition? *Ecology* **60**(6), 1132–1140, https://doi.org/10.2307/19366961 (1979).

51. Lobo, J. M., Hortal, J. & Cabrero-Sahudo, F. J. Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Divers. Distrib.* **12**(1), 111–112, https://doi.org/10.1111/j.1366-5936.2006.00194.x (2006).

52. Alvarado, F., Escobar, F., Williams, D. R., Arroyo-Rodriguez, V. & Escobar-Hernández, F. The role of livestock intensification and landscape structure in maintaining tropical biodiversity. *J. Appl. Ecol.* **55**(1), 185–194, https://doi.org/10.1111/1365-2664.12957 (2017).

53. PeerJ. Peer. *Dung beetle assemblages to characteristics of rain forest edges. Ecotropica* **14**, 49–62 (2008).

54. da Silva, P. G. & Hernández, M. I. M. Scale-dependence of processes structuring dung beetle metacommunities using functional and community reconstruction approaches. *PloS ONE* **10**(3), e0123030, https://doi.org/10.1371/journal.pone.0123030 (2015b).

55. Beiroz, W. et al. Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. *Ecol. Indic.* **95**, 518–526, https://doi.org/10.1016/j.ecolind.2018.07.062 (2018).

56. Beiroz, W. et al. Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. *Ecol. Indic.* **49**, 216–227,https://doi.org/10.1016/j.ecolind.2014.09.043 (2015).

57. Santos-Heredia, C., Andresen, E., Zárate, D. A. & Escobar, F. Dung beetles and their ecological functions in three agroforestry systems in the Lacandona rainforest of Mexico. *Biodivers. Conserv.* **27**, 2379–2394, https://doi.org/10.1007/s10531-018-1542-x (2018).

58. Correa, C. M., Braga, R. E., Puker, A. & Korsakai, V. Patterns of taxonomic and functional diversity of dung beetles in a human-modified variegated landscape in Brazilian Cerrado. *J. Insect Conserv.* **21**(2), 89–99, https://doi.org/10.1007/s10888-018-00118-6 (2019).

59. UNESCO. Ubívědou en, http://www.unesco.org/new/en/natural-sciences/environment-earth-sciences/unesco-global-geoparks/list-of-unesco-global-geoparks/mexico/comarca-minera-hidalgo/. October, 21 (2017).

60. Magura, T., Lövei, G. L. & Tóthmérész, B. Edge responses are different: natural versus anthropogenic influence: a meta-analysis using ground beetles. *Ecol. Evol.* **7**, 1009–1017, https://doi.org/10.1002/ece3.2722 (2017).

61. Martínez-Falcón, A. P., Zurita, G. A., Ortega-Martínez, I. I. & Moreno, C. E. Populations and assemblages living on the edge: dung beetle responses to forests–pasture ecotones. *Peel.* **6**, 6148, https://doi.org/10.7717/peerj.6148 (2018).

62. Barragán, F., Moreno, C. E., Escobar, F., Bueno-Villegas, J. & Halflter, G. The impact of grazing on dung beetle diversity depends on both biogeographical and ecological context. *J. Biogeogr.* **41**(10), 1991–2002, https://doi.org/10.1111/j.1365-2324 (2014).

63. Zúñiga, M. & Halffter, G. Análisis taxonómico, ecológico y biogeográfico de un grupo americano de *Onthophagus*. *Museo Regional de Ciencias Naturales Torino Monografía.* 9, 1–211 (1988).
64. Edmonds, W. D. Revision of *Phanaeus* Macleay, a New World genus of Scarabaeinae dung beetles (Coleoptera, Scarabaeinae). Revisión de *Phanaeus* Macleay, un género del Nuevo Mundo de escarabajos estercoreros (Coleoptera, Scarabaeinae). *Contrib. Sci. 443*, 1–105 (1994).

65. Delgado, L., Pérez, A. & Blackard, J. Keys for determining the generic and supergeneric taxa of Scarabaeoidea Latreille, 1802 (Coleoptera) of Mexico. *Folia Entomol. Mex.* **110**, 33–87 (2000).

66. Howden, H. F. & Génier, F. Seven new species of *Onthophagus* Latreille from Mexico and the United States (Coleoptera: Scarabaeidae, Scarabaeinae). *Fabriesia* **29**(1), 53–76 (2004).

67. Peraza, L. N. & Deloya, C. Una nueva especie mexicana de *Dichotomius* Hope (Coleoptera: Scarabaeidae) y clave para la identification de las especies del grupo *carolinus*. *Neotrop. Entomol.* **35**(5), 629–631 (2006).

68. Cabrero-Sañudo, F. J., Dellacasa, M., Martínez, I., Lobo, J. M. & Dellacasa, G. Distribución de las especies de Aphodiinae (Coleoptera, Scarabaeoidea, Aphodiidae) en México. *Acta Zool. Mex.* **26**(2), 323–399 (2010).

69. Vaz-de-Mello, F. E. Z., Edmonds, P. A. D., Ocampo, F. C. & Schoolmeesters, P. A. Multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* **2854**(1), 1–73 (2011).

70. Edmonds, W. D. & Zidek, J. Taxonomy of *Phanaeus* revisited: Revised keys to and comments on species of the New World dung beetle genus *Phanaeus* Macleay, 1819 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Insecta Mundi* **0271–0276**, 1–108 (2012).

71. Halfter, G., Rivera-Cervantes, L. E. & Halfter, V. Diversificación del grupo *Humecus* del género *Canthon* (Coleoptera: Scarabaeidae: Scarabaeinae) en el occidente de México. *Acta Zool. Mex.* **31**(2), 208–220 (2015).

72. Moretti, M. et al. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Funct. Ecol.* **31**(3), 358–567, https://doi.org/10.1111/1365-2435.12776 (2017).

73. Chao, A. & Jost, L. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**(12), 2533–2547, https://doi.org/10.1890/11-1952.1 (2012).

74. Villerger, S., Mason, N. W. & Moullot, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**(8), 2290–2301, https://doi.org/10.1890/07-1206.1 (2008).

75. Mason, N. W., Moullot, D., Lee, W. G. & Wilson, J. B. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **111**(1), 112–118, https://doi.org/10.1111/j.0030-1299.2005.13886.x (2005).

76. Villerger, S., Miranda, J. R., Hernández, D. F. & Moullot, D. Contrasting changes in functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* **20**(6), 1512–1522, https://doi.org/10.1890/09-1310.1 (2010).

77. Laliberté, E., Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305, https://doi.org/10.1890/08-2244.1 (2010).

78. Laliberté, E., Legendre, P. & Shipley, B. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. *R package version* 1.0–12 (2014).

79. R Core Team. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, ISBN 3-900051-07-0, URL, http://www.R-project.org (2018).

80. Swenson, N. Functional and phylogenetic ecology in R (*Springer*, 2014).

81. Gotelli, N. J. Null model analysis of species co-occurrence patterns. *Ecology* **81**(9), 2606–2621, 10.1890/0012-6588(2000)081[2606:MNMAOC]2.0.CO;2 (2000).

82. Gotelli, N. J. & Colwell, R. K. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**(4), 379–391, https://doi.org/10.1046/j.1461-0248.2001.00230.x (2001).

83. Gotzenberger, L. et al. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biol. Rev.* **87**(1), 111–127, https://doi.org/10.1111/j.1469-185X.2011.00187.x (2012).

84. Rickles, R. E. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* **7**(1), 1–15, https://doi.org/10.1111/j.1461-0248.2003.00554.x (2004).

85. Hardy, O. J. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *J. Ecol.* **96**(5), 914–926, https://doi.org/10.1111/j.1365-2745.2008.01421.x (2008).

86. Chalmandrier, L. et al. A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns. *J. Veg. Sci.* **24**(5), 853–864, https://doi.org/10.1111/j.1365-2745.2013.01301.x (2013).

87. Kemnel, S. W. et al. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464, https://doi.org/10.1093/bioinformatics/bttq166 (2010).

88. Gotelli, N. J. & Rohde, K. Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecol. Lett.* **5**(1), 86–94, https://doi.org/10.1046/j.1461-0248.2002.00288.x (2002).

89. Estrada, A., Anzuero D. A. & Coates-Estrada, R. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. *Am. J. Primatol.* **48**(4), 253–262, 10.1002/(SICI)1098-2345(1999)48:4<253::AID-AJP1>3.0.CO;2-D (1999).

90. Dabrowski, J., Venter, G., Truter, W. F. & Scholtz, C. H. Dung beetles can tunnel into highly compacted soils from reclaimed mined sites in Kgalahani, South Africa. *Appl. Soil Ecol.* **134**, 116–119, https://doi.org/10.1016/j.apsoil.2018.10.015 (2019).

91. Bivand, R. S., Pebesma, E. & Gómez-Rubio, V. Applied spatial data analysis with R (*Springer*, 2013).

92. Akaie, H. A new look at the statistical model identification. *IEEE Transactions on Automatic Control.* **19**(6), 716–723, https://doi.org/10.1109/TAC.1974.1100705 (1974).

93. Burnham, K. P. & Anderson, D. R. Model selection and multimodel inference: a practical information-theoretic approach (*Springer Science & Business Media*, 2003).

**Acknowledgements**

We thank Dr. Fidel Pérez Moreno for allowing us to use an ultra-micro analytical balance in the Centre for Research in Materials and Metallurgy (CIMyM) of the Universal Autónoma del Estado de Hidalgo (UAHE), and Fernando Escobar and to Pablo Minor-Montiel for helping us to identify beetles. We also thank Iriana Zuria for her advice on the procedures to measure land use heterogeneity. This contribution was generated with funds from the Basic Science project 222632 of the Secretaría de Educación Pública and Consejo Nacional de Ciencia y Tecnología (SEP-CONACYT). This paper is part of the doctoral thesis of IJOM in Biodiversity and Conservation at the UAHE, with a scholarship from CONACYT No. 247511.

**Author contributions**

I.J.O.-M., L.A., F.R., I.C. and C.E.M. conceived the ideas and designed methodology; I.J.O.-M. and C.L.R.-D., collected the data; I.J.O.-M., C.L.R.-D. and C.E.M. analysed the data; I.J.O.-M. and C.E.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**Competing interests**

The authors declare no competing interests.
