Older forests recover faster: leaf litter arthropods reveal post-perturbation recolonization dynamics

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ABSTRACT

Understanding how ecological communities recover from disturbance is central to predicting ecosystem resilience, particularly in tropical forests where biodiversity and ecosystem functioning are tightly linked. Such landscapes are dominated by secondary forests that have experienced, and continue to experience, disturbances of varying intensity. Leaf litter arthropods play a crucial role in decomposition and nutrient cycling, making it important to understand their recovery dynamics within these heterogeneous, regenerating systems. Here, we investigated the recolonization of leaf litter arthropod communities by combining a forest chronosequence, ranging from active agriculture to old-growth forests, with a controlled perturbation-recovery experiment (PREX) in the lowland Ecuadorian Chocó. Using a litterbag approach, we assessed how mesofauna colonized the new resource over time, and how alpha and beta diversity responded to small-scale disturbances across forest ages, reflecting broader disturbance histories.

Alpha diversity showed weak responses to forest age, with only a marginally significant quadratic trend. In contrast, beta diversity increased significantly along the successional gradient, indicating greater similarity to old-growth communities in older forests. Experimental perturbations reduced both alpha and beta diversity. Effects on alpha diversity were consistent across forest ages and sampling times, but recovery patterns in beta diversity strongly depended on forest age. Older forests exhibited faster convergence toward old-growth community composition, particularly at later stages following disturbance. Indicator species analysis revealed distinct recolonization trajectories upon small-scale disturbance. Communities more similar to old-growth forests showed a gradual shift from early colonizers, such as ants and predatory beetles, to more diverse mesofaunal assemblages, including Collembola and predatory and oribatid mites, reflecting increasing trophic complexity.

Conversely, low-similarity plots remained associated with specific oribatid mite assemblages, suggesting the persistence of alternative community states under disturbed conditions.

Our results demonstrate that recovery trajectories are strongly shaped by forest age, with older forests exhibiting higher resilience and faster compositional recovery.

KEYWORDS

Ecuadorian Chocó; leaf litter arthropods; recolonization; litterbags; disturbance; natural forest regeneration

1. INTRODUCTION

Tropical forests host a major share of global terrestrial biodiversity and provide key ecosystem functions, many of which are mediated by soil and leaf litter arthropods (Basset et al. 2012; de Groot et al. 2002). These communities play a crucial role in nutrient cycling, soil formation and litter transformation, thereby supporting forest regeneration and overall ecosystem resilience (Cole et al. 2016). Structurally, leaf litter arthropod communities are organized into complex trophic networks, including detritivores, microbivores, and predators, whose interactions regulate decomposition processes and energy flow through the system (Wise and Lensing 2019; Anderson 1975). Because leaf litter arthropods respond rapidly to environmental changes (Ashford et al. 2013; Sayer et al. 2010; Blankinship et al. 2011), they can serve as sensitive indicators of community reassembly following disturbance (Uehara-Prado et al. 2009; Gergócs and Hufnagel 2009). Disturbances such as deforestation and agricultural land use profoundly alter forest structure, microclimate and biodiversity, making the recovery of ecological communities a key component of ecosystem resilience (Chazdon 2014; Lennox et al. 2018).

Recovery processes operate across multiple temporal scales (Poorter et al. 2021; Willig et al. 2007; Hamer and Hill 2000). Over longer timescales, forest succession drives gradual changes in habitat structure and resource availability (Ghazoul and Chazdon 2017; Fayle et al. 2015), which in turn shape arthropod community composition (Meloni and Varanda 2015). However, in addition to these long-term processes, local small-scale disturbances strongly influence leaf litter arthropod dynamics (Uehara-Prado et al. 2009). Forest floor perturbations, such as understory clearing or reduced activity of larger animals, can disrupt microhabitats, alter microclimatic conditions, and modify trophic interactions (Sayer et al. 2020; Tuo et al. 2024).

Recovery following disturbance (recolonization) depends on both dispersal and persistence mechanisms (Nardi et al. 2022; Huebner et al. 2012). Recolonisation is driven by immigration from surrounding habitats, including adjacent vegetation and the canopy (Schowalter 2016), as well as survival in refugia, as shown in studies of post-forest fire community reassembly (Wikars and Schimmel 2001; Huebner et al. 2012). Dispersal may be further constrained by the surrounding matrix, particularly for ground-dwelling arthropods lacking adaptations for long-distance movement (Meloni and Varanda 2015), and varies strongly among taxa, as illustrated by Oribatida, a key decomposer taxon (Behan-Pelletier and Lindo 2023). Oribatid mites disperse via multiple pathways, such as wind, litter, and soil, but their colonization success ultimately depends on their motility and reproductive capacity (Lehmitz et al. 2012).

At the same time, not all organisms are removed during disturbance events. While leaf litter removal eliminates much of the aboveground habitat, components of the forest floor community, such as microbial feeders (e.g. Collembola), small detritivores, and other soil-dwelling microarthropods, may persist in the upper soil layer and act as a residual species pool facilitating early recolonisation. Using Oribatida as a consistent example, resilience to forest floor disturbances associated with agricultural land use has been linked to species that feed on fresh macrophyte detritus and that have short generation times, enabling rapid recovery (Prinzing et al. 2002). The structural buffering capacity of the forest further mediates disturbance impacts by maintaining microclimatic stability (Sayer 2006; Lohbeck et al. 2015). In small-scale disturbances, intact canopy cover and continuous litter input from the surrounding forest matrix help maintain shading, moisture, and resource supply, preserving suitable microhabitats and potentially facilitating rapid recolonisation (Tartara et al. 2026). Therefore, recovery dynamics are shaped by the relative contributions of internal (soil-based) persistence and external (dispersal-driven) inputs (Cours et al. 2023).

Recolonisation dynamics are often taxon-dependent, especially along forest regeneration gradients. In some cases, organisms are restricted to specific ecosystems and are mainly found in later successional stages, reflecting their adaptation to these conditions. In others, no clear colonisation sequence is observed; for example, ant communities recovering after complete litter removal do not show a consistent set of pioneering species (Paolucci et al. 2010). Nevertheless, communities generally become more similar to reference conditions as recovery progresses, both after large-scale disturbances (Meloni and Varanda 2015) and small-scale perturbations (Uehara-Prado et al. 2009).

While both successional dynamics and smaller-scale disturbance responses have been widely studied, these processes are typically examined in isolation (Sagarin and Pauchard 2010). Previous studies have either focused on changes in arthropod diversity along forest regeneration gradients (Meloni and Varanda 2015) or on short-term responses to experimental disturbances (Uehara-Prado et al. 2009; Paolucci et al. 2010), but few have explicitly integrated both temporal scales (Fayle et al. 2015). As a result, it remains unclear how short-term perturbations interact with long-term successional processes to shape community reassembly.

In this study, we evaluate leaf litter arthropod recovery in a lowland tropical forest by integrating a forest chronosequence (Escobar et al. 2025) with a controlled perturbation-recovery experiment (PREX; Tartara et al. 2026) in the Ecuadorian Chocó. Using a litterbag experiment (mesh 0.5 cm), we investigated the colonizing mesofauna community under different treatments and time points following disturbance. Because litterbags represent small, standardized patches of substrate rather than natural forest floor conditions, they allow controlled comparisons of colonisation dynamics, although they may not fully capture the complexity and heterogeneity of natural litter inputs.

By integrating these approaches, our study aims to assess how long-term succession and short-term disturbance jointly shape litter arthropod communities in tropical forests. Specifically, we addressed three complementary questions: (i) how do arthropod diversity patterns (alpha and beta) vary along the forest age gradient, and in response to experimental treatments and time since perturbation? (ii) how does the magnitude of treatment effects relative to control conditions change across forest successional stages and over time, providing insight into recovery dynamics? (iii) which arthropod families characterize communities that converge toward or diverge from old-growth conditions during regeneration?

We hypothesized that: (i) early successional forests are dominated by a few highly abundant taxa, whereas older forests support more even and diverse communities; (ii) community composition converges toward old-growth conditions with increasing forest age; (iii) small-scale disturbances have stronger and more persistent effects in younger forests, leading to slower and more variable recovery compared to older, structurally complex stands.

2. MATERIAL AND METHODS

Study design

This study forms part of the Reassembly research unit, which explores tropical forest recovery along a forest regeneration gradient in the lowland Ecuadorian Chocó (Escobar et al. 2025). The chronosequence is located across the Canandé and Tesoro Escondido reserves, as well as in the nearby villages of La Yuca and Hoja Blanca (province of Esmeraldas). Reassembly's space-for-time experiment covers study plots ranging from active cacao plantations and cattle pastures to secondary forests up to 39 years old. For this study, we used a subset of 21 plots (50 × 50 m) including two active cacao plantations (one organic agroforestry system and one conventional), two active pastures, 12 regenerating forests (six each with cacao and pasture legacies), and five old-growth forests used as undisturbed references (historical information provided by Jocotoco Foundation). We defined forest age as years since land-use abandonment. Forest age and study plots' altitude were evenly distributed across the different land-use histories (Table S1).

Within this study design, we carried out a perturbation-recovery experiment (PREX) to investigate how understorey communities and processes respond to small-scale disturbance at various stages of forest succession (as described in Tartara et al. 2026). In March 2023, we established four treatment subplots: (1) Perturbation (P): complete forest floor clearing and deforestation of understory plants with a stem circumference < 25 cm at breast height; (2) Fence (CF): exclusion of large animals by enclosing the subplot with a 1 m high shade-cloth fence; (3) Perturbation + Fence (PF): combined vegetation removal and fencing; and (4) Control (C): an undisturbed and unfenced control.

Litterbag experiment

To assess the potential for arthropod mesofauna recolonisation and activity in the study plots, we employed a full-factorial litterbag experiment with local leaf litter (details in Tartara et al. 2026). Each bag (20 × 20 cm, 0.5-cm plastic mesh) contained a standardized litter mixture of five common tree species, representing a range of leaf traits across the chronosequence. Leaves were cut into 5 × 5 cm pieces, frozen at -18 °C for 30 days for defaunation, and then mixed in equal mass per species (30 g total). In March 2023, on the same day of the PREX establishment in each plot, we deployed the first set of litterbags, one in each PREX treatment. After 45 days (first collection round) the bags were collected, and after further 45 days (hence 90 days from disturbance) we deployed new ones, which were eventually retrieved 135 days post-disturbance (second collection round). In total, our study employed 168 litterbags across the 21 study plots.

Arthropod sampling

After collection, litterbags were carefully emptied inside Berlese funnels and arthropods were extracted at constant temperature (65 °C) for 60 h and collected in 90 % ethanol. Following the exclusion of 4 lost bags (first collection round, plot OG39), 164 litterbags were retained for analysis.

All extracted arthropods were counted under a stereoscopic microscope and identified to the lowest possible taxonomic level. Adult individuals were generally classified to family level and, where possible, further resolved to genus or species. Specimens that could not be reliably identified to species were grouped into morphospecies based on consistent morphological differences (Krell 2004; Oliver and Beattie 1996). Throughout this study, the term “species” is used to include both formally identified species and morphospecies.

Taxonomic identification was based on a combination of regional, order-specific keys and multiple complementary resources, including published identification literature (Appendix A) and a locally curated reference collection of previously barcoded arthropods obtained from *in situ* leaf-litter sampling (Tartara unpublished data). As part of a parallel pilot study, selected taxa (Oribatida, Hymenoptera, Staphylinidae, and Diplopoda) were subjected to molecular identification, and the resulting dataset therefore integrates both morphological and molecular approaches. Barcode sequences are publicly available on the BOLD platform (project: ARTA, https://portal.boldsystems.org/).

Statistical analysis

All statistical analyses were conducted in R v.4.3.1 (R Core Team 2023). We defined individual sampling units as unique combinations of plot, treatment, and collection round and calculated all diversity metrics at this level. We computed total abundance as the sum of individuals per sampling unit. We quantified within-community diversity (alpha diversity) using the Shannon entropy index (H), calculated with the *vegan* package (Oksanen et al. 2001), as well as Hill numbers for orders q = 0, 1, and 2 (species richness, exponential of Shannon diversity, and inverse Simpson index), estimated with the iNEXT framework (Hsieh et al. 2016). To assess community similarity along the regeneration gradient, we calculated beta diversity metrics relative to old-growth reference communities. For each sampling unit, we performed pairwise comparisons of the chronosequence plots with old-growth control plots from the same collection round, and subsequently averaged these values to account for the natural variation within the reference forest system (Metz et al. 2026). We quantified classical beta diversity using Bray-Curtis dissimilarity based on relative abundances and expressed it as similarity (1 - dissimilarity). In addition, we calculated Hill-based similarity metrics for q = 0, 1, and 2, corresponding to Jaccard (presence-absence), Horn (abundance-weighted), and Morisita-Horn (dominance-weighted) similarities, respectively (Chao et al. 2014). Prior to modelling, total abundance was log-transformed to improve normality and homoscedasticity.

To evaluate how diversity metrics varied along the forest age gradient, among PREX treatments, and between collection rounds, we fitted linear mixed-effects models (GLMMs) using the *lme4* package (Bates et al. 2015). We modelled each diversity metric separately and restricted analyses to regenerating plots, excluding old-growth reference sites. We included land-use legacy, treatment, and collection round as categorical fixed effects and forest age as a continuous predictor. We specified plot identity as a random intercept to account for repeated measurements. To test for non-linear responses along the regeneration gradient, we compared models including linear and quadratic terms of standardized forest age using likelihood ratio tests fitted with maximum likelihood. We retained quadratic terms when they significantly improved model fit; otherwise, we used linear terms. Although we initially evaluated interactions among predictors, we simplified the final models to additive structures because interactions were not significant. We assessed model assumptions through visual inspection of residuals versus fitted values and normal Q-Q plots. We evaluated model performance using marginal and conditional R^2 values. We estimated fixed effects using the *lmerTest* package (Kuznetsova et al. 2017) and assessed their significance using type II analysis of variance (ANOVA) with F-tests implemented in the *car* package (Fox and Weisberg 2018). For visualization, we refitted the models with standardized forest age, and we calculated estimated marginal means (EMMs) contrasts using the *emmeans* package, comparing each level of categorical predictors to their respective reference levels (Legacy = Cacao, Treatment = Control and Collection round = After 45 days).

To examine whether PREX treatment effects varied across forest successional stages and to assess recovery following disturbance, we quantified treatment effects relative to control subplots within each plot and collection round. For each sampling unit, we calculated treatment effects as log-response ratios (LRR):

$$\mathrm{LRR} = \log\left(\frac{\text{Metric Treatment}}{\text{Metric Control}}\right) \qquad \text{(Eq. 1)}$$

where Metric represents either the Shannon index (alpha diversity) or Bray-Curtis similarity to old-growth control (beta diversity), and Treatment corresponds to Fenced (CF), Perturbed (P), or Perturbed-fenced (PF) subplots. We selected these metrics as representative of alpha and beta diversity based on their consistent behaviour across analyses. Using LRR allowed us to standardize treatment effects while accounting for differences in baseline diversity among plots. To reduce the influence of unbalanced sampling and to include old-growth plots, we represented forest age as an ordinal variable based on its rank. We fitted separate linear mixed-effects models for alpha and beta diversity, with LRR as the response and treatment, collection round, and forest age (factor) as fixed effects, including all two-way interactions among these predictors. We included plot identity as a random effect to account for repeated measurements within plots. We excluded land-use legacy from these analyses because it showed no detectable effect in previous models. We evaluated fixed effects using type III ANOVA with χ^2 tests (*car* package). Model diagnostics and performance assessment followed the same procedures described above.

To identify families characterizing communities that converge toward or diverge from old-growth conditions, we conducted indicator species analysis (ISA) linking taxonomic composition to variation in Bray-Curtis similarity to old-growth reference communities. Following the procedures described above, we aggregated arthropod abundances per sampling unit to construct a site × family community matrix and calculated beta diversity metrics. We then restricted the analysis to regenerating plots and classified them into "high" and "low" similarity groups based on the median Bray-Curtis similarity to old-growth reference communities. We conducted indicator taxa analysis with the *indicspecies* package (De Cáceres et al. 2010), using both presence-absence data (PA) and relative abundance data (RA) to capture differences in occurrence and dominance patterns across collection rounds. We omitted treatment as a further grouping variable because it showed no detectable effect in the previous model. We applied the group-equalized correlation coefficient (r.g.), a Pearson correlation-based metric that quantifies the strength of association between taxa and groups. For presence-absence data, r.g. reflects fidelity (i.e. the consistency of occurrence within a group), whereas for relative abundance data it reflects differences in dominance among groups (Dufrêne and Legendre 1997). Statistical significance was assessed using permutation tests with 999 permutations, and taxa with $p < 0.05$ were considered significant indicators.

3. RESULTS

Diversity across forest age, time since perturbation and treatment

Alpha and beta diversity showed consistent patterns across most metrics, with the exception of the Shannon index. Therefore, we report classical diversity metrics here, while Hill-based metrics are provided in the Supplementary Information (Table S2 and S3).

Alpha and beta diversity varied along the forest regeneration gradient and among PREX subplots (Figure 1, Table 1). Although Hill-based alpha diversity showed no significant trend with forest age, Shannon index exhibited a marginally significant quadratic pattern (ANOVA: F(2, 12) = 3.62, p = 0.059), with lower diversity in mid-chronosequence (forest age^2: estimate = 0.16, low CI = 0.03, high CI = 0.28, p = 0.019; forest age = -0.16, low CI = -0.28, high CI = -0.04, p = 0.011). Beta diversity exhibited a strong positive relationship with forest age (estimate = 0.04, low CI = 0.02, high CI = 0.05, p < 0.001), indicating increasing similarity to old-growth communities in older forests.

Table 1. Results of type II ANOVA (F test) testing the significance of forest age, land-use legacy, treatment and collection round on alpha (Shannon index) and beta (Bray-Curtis similarity to old-growth communities) diversity; test statistics, degrees of freedom and p values are reported and significancy is highlighted in bold font.

Diversity	Metric	Term	Statistic	df	Df residual	p value
Alpha	Shannon index	**Forest age (^{2})**	3.615	2	12	**5.90E-02**
		Legacy	0.120	1	12	7.35E-01
		Treatment	14.599	3	108	**4.76E-08**
		Collection round	3.319	1	108	7.13E-02
Beta	BC similarity to old-growth	**Forest age**	19.678	1	13	**6.72E-04**
		Legacy	1.607	1	13	2.27E-01
		Treatment	6.112	3	108	**7.02E-04**
		Collection round	92.745	1	108	**3.23E-16**

Experimental treatments significantly affected both diversity metrics (ANOVA: alpha F(3, 108) = 14.60, $p < 0.001$; beta F(3, 108) = 6.11, $p < 0.001$), with disturbed treatments reducing average chronosequence diversity relative to controls (EMMs in treatments < EMMs in control, Figure 1 and Table S2). Collection round had a strong effect on beta diversity, suggesting temporal changes in community composition following perturbation (ANOVA: F(1, 108) = 92.75, $p < 0.001$). In contrast, land-use legacy did not significantly influence any diversity pattern (Table 1 and S3).

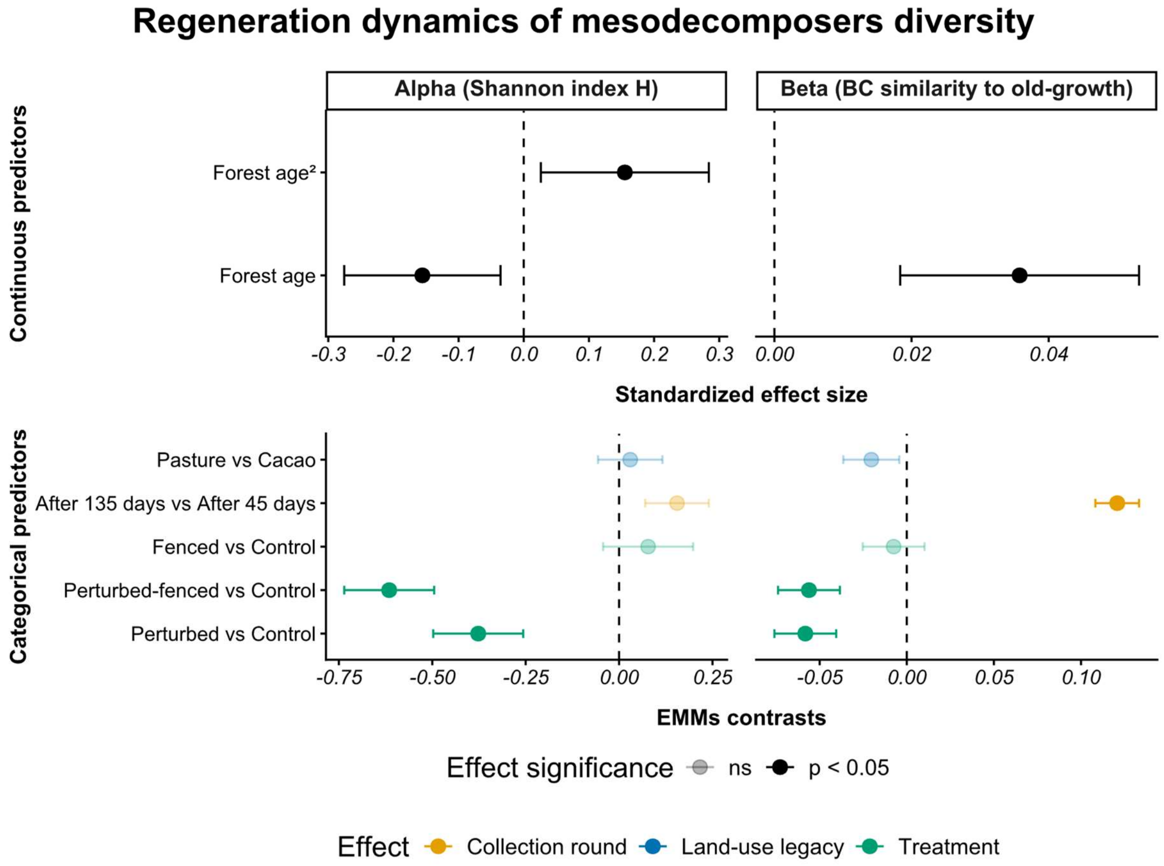

Figure 1. Regeneration dynamics of arthropod alpha and beta diversity described as the effects of forest age, land-use legacy, PREX treatment and time since perturbation on Shannon index H and Bray-Curtis similarity to old-growth forest; dots represent standardized effect sizes of forest age and EMMs contrasts along the chronosequence within each factor's levels with respect to the reference; the lines represent the respective standard error (SE); solid colouring stand for statistical significance as opposed to transparency; black/grey is

forest age, yellow is collection round (time since perturbation), blue is land-use legacy and green is PREX treatment.

Treatment effect

Treatment effects, quantified as log-response ratios (LRR, Table S4), did not vary significantly among treatments or across forest ages for alpha diversity (Table 2). Similarly, no interaction between treatment and collection round was detected, indicating that short-term recovery of alpha diversity was consistent across treatments.

Table 2. Results of type III ANOVA testing the significance of PREX treatment, collection round and forest age (factor) on treatment effects (LRR) for alpha and beta diversity; test statistics, degrees of freedom and p values are reported and significancy is highlighted in bold font.

Diversity	**Term**	**χ^2**	**Df**	**p value**
Alpha	Treatment	2.032	2	3.62E-01
	Collection round	1.242	1	2.65E-01
	Forest age (factor)	5.061	9	8.29E-01
	Treatment x Collection round	0.172	2	9.17E-01
	Treatment x Forest age (factor)	15.516	18	6.26E-01
	Collection round x Forest age (factor)	11.360	9	2.52E-01
Beta	Treatment	0.274	2	8.72E-01
	Collection round	3.450	1	**6.33E-02**
	Forest age (factor)	15.747	9	**7.24E-02**
	Treatment x Collection round	3.409	2	1.82E-01
	Treatment x Forest age (factor)	21.529	18	2.54E-01
	Collection round x Forest age (factor)	23.259	9	**5.64E-03**

For beta diversity, however, recovery dynamics marginally depended on forest age (ANOVA: $\chi^2 = 15.75$, df = 9, p = 0.072) and collection round (ANOVA: $\chi^2 = 3.45$, df = 1, p = 0.063). The interaction between collection round and forest age was significant (ANOVA: $\chi^2 = 23.26$, df =

9, p = 0.006), indicating that changes in similarity to old-growth communities over time differed among successional stages. In particular, treatment effects were reduced at the later collection round in older forest, suggesting faster recovery of community composition compared to younger regenerating sites (Figure 2).

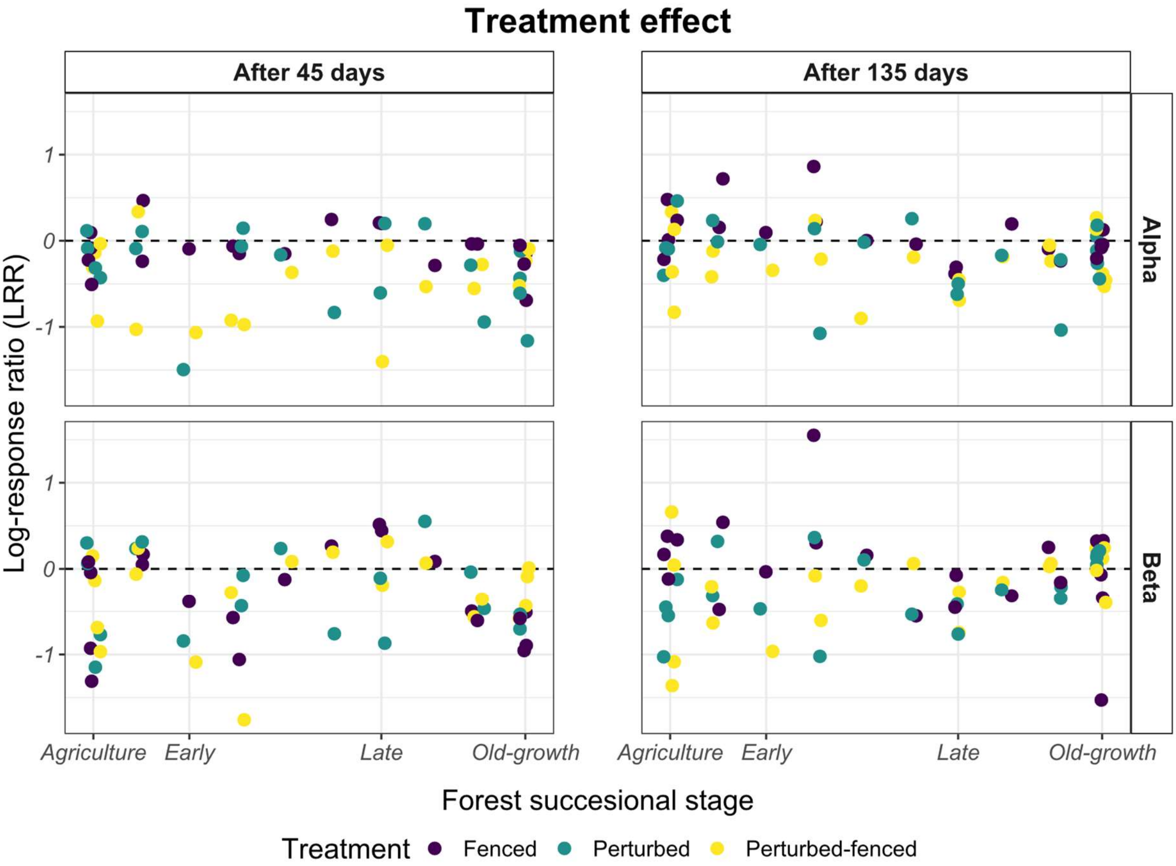

Figure 2. Treatment effects (LRR) on alpha and beta diversity across forest successional stages, PREX treatments and collection rounds; the dots represent each individual sampling unit; the colour stands for the three different experimental treatments: purple is fenced (CF), turquoise is perturbed (P) and yellow is perturbed-fenced (PF); the dashed black line at LRR = 0 indicates no effect of CF, P nor PF hence when diversity in the treatment was the same as the control, LRR < 0 when diversity in the treatment was less than the control, LRR > 0 when diversity in the treatment was higher than the control.

Family-level indicator analysis

Indicator species analysis revealed distinct arthropod families associated with high versus low similarity to old-growth communities in each collection round (Figure 3, Table S5). Patterns were largely consistent between presence-absence and relative abundance data, although indicator values were generally higher in the latter, reflecting differences in taxon dominance rather than occurrence alone. Patterns also shifted with similarity to old-growth, but remained consistent across collection rounds. After 45 days, high-similarity plots were primarily characterized by early colonizers such as Formicidae (PA r.g. = 0.408; RA r.g. = 0.414), Staphylinidae (PA r.g. = 0.333), and Campodeidae (PA r.g. = 0.391; RA r.g. = 0.303). By 135 days, some of these families remained important indicators (Staphylinidae: RA r.g. = 0.353; Campodeidae: PA r.g. = 0.388; RA r.g. = 0.310), but high-similarity plots were additionally characterized by a broader set of mesofauna. This included Collembola (RA r.g. = 0.730), Ptiliidae (RA r.g. = 0.392), Veigaiidae (RA r.g. = 0.276), and several oribatid mite families (Oppiidae: RA r.g. = 0.341; Ceratozetidae: RA r.g. = 0.266; Oribatida spp.: PA r.g. = 0.346; RA r.g. = 0.312).

In contrast, low-similarity plots were consistently associated with different oribatid mite families. After 45 days, these included Malaconothridae (PA r.g. = 0.324; RA r.g. = 0.255), Trhypochthoniidae (RA r.g. = 0.347), Nothridae (RA r.g. = 0.266), and Haplozetidae (RA r.g. = 0.309). After 135 days, Trhypochthoniidae remained a key indicator of low similarity (PA r.g. = 0.301; RA r.g. = 0.335), together with Scheloribatidae (PA r.g. = 0.453) and Formicidae (RA r.g. = 0.461).

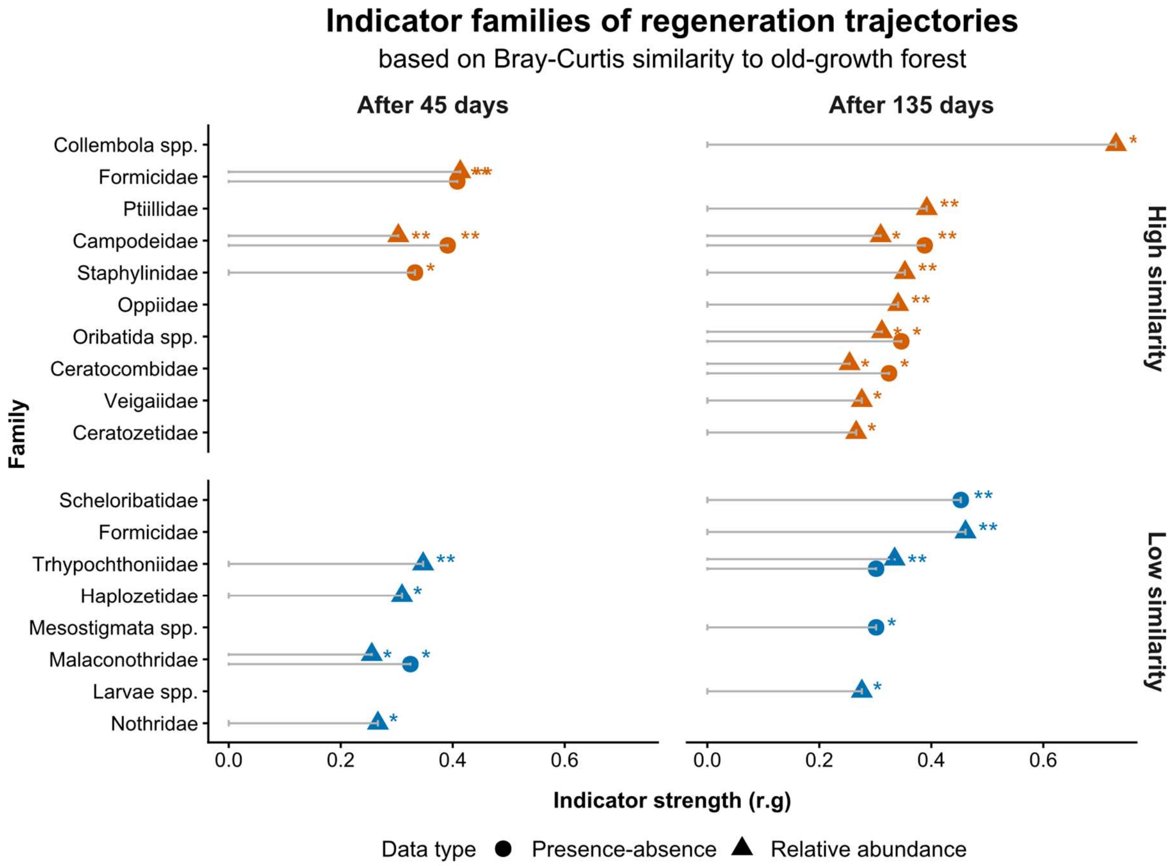

Figure 3. Indicator families associated with high or low similarity to old-growth communities across collection rounds; results are shown for presence-absence (PA, circles) and relative abundance (RA, triangles) data; the colour of each symbol indicates the group: orange = high similarity, blue = low similarity; the error bar reflects the indicator strength (r.g.), with longer bars representing stronger associations; only significant associations ($p < 0.05$) are shown and the significancy level is reported next to the symbol; families are plotted on the y-axis, grouped by similarity to the old-growth and collection round.

4. DISCUSSION

Community responses to disturbance are driven by beta rather than alpha diversity

Anthropogenic disturbances are widely known to affect community composition more strongly than species richness or diversity, making beta diversity a more sensitive indicator of ecological change (Uehara-Prado et al. 2009; Barlow et al. 2007; Maaß et al. 2014). Our results support this general pattern, as also found in a multi-taxa study along the same chronosequence (Metz et al. 2026). While alpha diversity showed only marginal responses across the forest regeneration gradient, beta diversity exhibited strong and consistent variation with forest age, experimental disturbance, and time since perturbation (Table 1, S2 and S3). This highlights that, rather than diversity *in se*, changes in community composition are the primary signal of recovery in leaf litter arthropod communities.

Convergence toward old-growth communities (beta diversity) across spatial and temporal scales

Across the chronosequence, beta diversity increased significantly with forest age (estimate = 0.036, $p < 0.001$; Table S2), indicating progressive convergence toward old-growth community composition. This pattern is consistent with previous findings from the same system (Metz et al. 2026) and supports the general view that successional dynamics lead to increasingly structured and similar communities over time. In early successional stages, communities are likely shaped by stochastic colonisation processes, resulting in high variability among sites (Meloni and Varanda 2015). As succession proceeds, continued species arrival combined with environmental filtering promotes convergence toward a more stable and constrained community state (Wardle and Peltzer 2007).

Simultaneously to these long-term dynamics, small-scale disturbances significantly altered community composition. Both perturbation treatments (P and PF) reduced overall similarity to old-growth communities relative to controls (Figure 1; Table S2), indicating that forest floor disturbance disrupts community structure across all successional stages. However, recovery trajectories remained parallel across treatments, as reflected by the non-significant forest age × treatment interaction, suggesting that localised forest floor clearance did not alter the overall direction of successional change but rather shifted communities to lower similarity levels (EMMs in disturbance < EMMs in control). Importantly, these disturbance effects were transient. Beta diversity increased significantly over time following small-scale disturbance: (collection round effect: $F = 92.75$, $p < 0.001$; Table 1), indicating ongoing compositional recovery.

Moreover, recovery rates depended on forest age, supporting our initial hypothesis. The significant interaction between collection round and forest age ($\chi^2 = 23.26$, $p = 0.006$; Table 2) indicates that communities in older forests recovered more rapidly than those in younger stands. In fact, similarity values approached those of control plots (LRR ≈ 0) after 135 days primarily in late successional and old-growth forests (Figure 2), highlighting their higher resilience. This pattern likely reflects stronger structural buffering, more stable microclimatic conditions, and closer proximity to source communities in mature forests (Sayer 2006; Lohbeck et al. 2015).

In contrast, exclusion of large animals (CF) had no detectable short-term effect on community composition. This suggests that mesofauna recolonisation is primarily driven by microhabitat conditions and passive dispersal rather than vertebrate activity within the timeframe considered. Consistent with this, a parallel litterbag decomposition study conducted in the same system found no effect of the CF treatment on decomposition rates, further indicating that large vertebrates had no direct influence on this processes and its respective community (Tartara et al. 2026).

Non-linear and weaker responses of alpha diversity along succession

In contrast to beta diversity, alpha diversity showed only a marginal and non-linear response to forest age ($p = 0.059$; Table 1), with lower values in mid-successional stages (Figure 1). This pattern suggests that species richness and evenness alone may not fully capture the complexity of successional dynamics in leaf litter communities, further reinforcing that compositional changes are more sensitive indicators of responses to large-scale disturbance.

Higher diversity and abundance (Table S2) observed in early successional and actively managed systems may reflect transient increases in resource availability, microhabitat heterogeneity, and colonization by opportunistic taxa (Connell 1979). However, despite this elevated diversity, these communities differed markedly in composition from those of mature forests, as indicated by the strong beta diversity patterns. As succession progresses, communities undergo substantial compositional turnover and restructuring, which may be accompanied by temporary declines in both diversity and abundance.

Importantly, ecosystem functioning does not necessarily track taxonomic diversity. Previous studies have shown that decomposition processes can recover more rapidly than the arthropod communities that mediate them (Cole et al. 2020). However, results from our system indicate that this relationship may not be entirely asynchronous. In fact, the parallel decomposition experiment conducted in the same system (Tartara et al. 2026) revealed a significant quadratic pattern in litter mass loss, with reduced decomposition rates at mid-successional stages. This decline coincides with the observed dip in arthropod diversity, suggesting a potential coupling between community structure and ecosystem functioning during forest regeneration.

Taxonomic drivers of beta diversity and recovery during recolonization

Indicator species analysis provided further insight into the mechanisms underlying community reassembly. Our results revealed consistent patterns across both presence-absence and relative abundance data, linking specific taxa to communities with high versus low similarity to old-growth conditions.

Communities with low similarity to old-growth were consistently associated with a distinct set of oribatid mite families, including Trhypochthoniidae, Nothridae, Haplozetidae, and Scheloribatidae (Figure 3, Table S5). These taxa likely indicate altered microhabitat conditions or shifts in resource availability following disturbance, reflecting communities adapted to simplified or perturbed environments. Supporting this interpretation, species of Scheloribatidae, particularly *Scheloribates laevigatus* and *S. latipes*, have been repeatedly reported as dominant in disturbed, open, or polluted habitats, while remaining less abundant in forest systems (Murvanidze et al. 2013; Iglesias et al. 2019). Their relatively short generation times (Pfingstl and Schatz 2021) and higher mobility compared to other oribatids further suggest an ability to rapidly establish populations.

In contrast, high-similarity communities were characterized by a broader and more functionally diverse assemblage, particularly at later stages of recolonisation from small-scale disturbance (collection round = after 135 days). Early colonization (after 45 days) was dominated by more mobile and opportunistic taxa such as Formicidae, Staphylinidae, and Campodeidae. Over time, these communities incorporated a wider range of mesofauna, including Collembola, predatory mites and multiple oribatid mite families distinct from those found in low-similarity plots. This shift reflects a progressive re-establishment of trophic interactions and functional complexity typical of mature forest systems, consistent with the observed recovery of treatment effects on community composition (Figure 2, Table S4).

However, not all indicator families of low-similarity communities are strictly linked to disturbance. Nothridae and Haplozetidae are not consistently associated with early-successional conditions (Lehmitz 2014), and their occurrence here likely reflects context-dependent responses to unmeasured microenvironmental factors (such as litter composition, moisture, or decomposition stage). Likewise, Trhypochthoniidae does not exhibit uniform ecological preferences at the family level; rather, species within this group occupy a wide range of niches across soil, litter, moss, and arboreal habitats (Norton and Ermilov 2024). Therefore, the occurrence of these taxa in low-similarity communities may also reflect species-specific tolerances and habitat affinities rather than a generalist strategy at the family level.

Finally, while the persistence of these taxa across collection rounds suggests a sustained treatment effect, their role in delaying convergence toward old-growth composition remains uncertain. One possible explanation is that their overall high abundance in early-successional plots may increase competition for resources, potentially further delaying the establishment of later-successional species. However, this hypothesis requires further investigation.

Some taxa showed context-dependent patterns. For instance, Staphylinidae were more prominent in communities with high similarity to old-growth, in line with findings from Meloni and Varanda (2015), while different oribatid families were associated specifically with either high- or low-similarity communities. Ants (Formicidae) occurred both as early indicators in high-similarity communities and as later indicators in low-similarity plots. This pattern likely reflects the ecological diversity within the group: ants include species that respond differently to disturbance, and some act as ecosystem engineers that modify microhabitats, potentially facilitating recovery (Hoenle et al. 2023). Previous work supports this variability, showing that litter ant assemblages do not follow a consistent colonisation sequence and lack clearly defined pioneer species (Paolucci et al. 2010), while studies in the same system have identified distinct taxa associated with different successional stages (Hoenle et al. 2022).

These patterns suggest that recovery is driven by an overall combination of dispersal ability, persistence in the soil, and sensitivity to microhabitat conditions. Rather than following a simple trajectory from generalist to specialist taxa, community reassembly appears to involve the replacement or coexistence of distinct functional groups, leading either to convergence toward old-growth conditions or persistence in alternative states.

CONCLUSIONS

Our study demonstrates that recovery of leaf litter arthropod communities following small-scale disturbance is strongly influenced by forest successional stage. Older forests exhibited faster convergence toward old-growth community composition, while younger regenerating sites showed slower, more variable trajectories. Recovery was driven primarily by compositional shifts rather than changes in species richness, with distinct indicator taxa characterizing high- versus low-similarity communities. We revealed that low-similarity plots were dominated by possibly disturbance-tolerant oribatid mites, whereas high-similarity communities progressively incorporated a broader mesofauna, including mobile predators, Collembola, and multiple oribatid families. These patterns underscore the role of dispersal, persistence in soil, and microhabitat conditions in shaping recolonisation pathways.

From an ecological perspective, our results highlight that structurally complex, late-successional forests provide critical microhabitats and source populations that facilitate faster community recovery, supporting both biodiversity and associated ecosystem functions such as litter decomposition. From a conservation perspective, maintaining forest structural complexity and connectivity is essential not only for preserving biodiversity but also for enhancing resilience and recovery potential in regenerating tropical landscapes.

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Older forests recover faster: leaf litter arthropods reveal post-perturbation recolonization dynamics

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Supporting Information

Table S1. Study plots with respective geographic coordinates, age since last human use and legacy.

Successional stage	Legacy	Plot	Latitude	Longitude	Forest age
Active agriculture	Cacao	CA62 (Conventional)	0.511049	-79.212168	0
		CA64 (Agroforestry)	0.543444	-79.154546	0

	Pasture	PA55	0.497629	-79.224517	0
		PA57	0.511013	-79.209140	0
Forest regeneration	Cacao	CR02	0.501487	-79.225953	3
		CR09	0.472487	-79.229596	7
		CR10	0.477183	-79.199574	25
		CR11	0.477902	-79.205066	32
		CR13	0.488969	-79.226125	2
		CR14	0.49816	-79.138483	39
	Pasture	PR19	0.552739	-79.174801	7
		PR26	0.526454	-79.204663	23
		PR31	0.479072	-79.210071	25
		PR33	0.489268	-79.228412	2
		PR34	0.493511	-79.137927	39
		PR36	0.51652	-79.143061	10
Old-growth		OG39	0.521561	-79.195372	NA
		OG41	0.529896	-79.188508	NA
		OG45	0.477783	-79.203704	NA
		OG46	0.478053	-79.194703	NA
		OG49	0.531384	-79.147979	NA

Table S2. Summary of linear mixed-effects models for alpha and beta diversity, including estimates, confidence intervals and significance of forest age, as well as estimates, standard error (SE) and significance of EMMs contrasts for land-use legacy, treatment, and collection round.

Diversity	Metric	Term	Contrast	Estimate	Low CI	High CI	SE	p value
	Total abundance (log)	**Forest age**		**-0.326**	-0.592	-0.059		**2.05E-02**
		Treatment	Fenced vs Control	-0.203			0.204	7.52E-01
		Treatment	Perturbed vs Control	-0.254			0.204	6.01E-01
		Treatment	Perturbed-fenced vs Control	-0.248			0.204	6.19E-01
		Legacy	Pasture vs Cacao	0.174			0.246	4.91E-01
		Collection round	**After 135 days vs After 45 days**	**0.694**			0.144	**4.84E-06**

Alpha	Shannon index	**Forest age**		**-0.156**	-0.276	-0.036		**1.15E-02**
		Forest age^2		**0.155**	0.026	0.284		**1.88E-02**
		Treatment	Fenced vs Control	0.078			0.120	9.17E-01
		Treatment	**Perturbed vs Control**	**-0.377**			0.120	**1.19E-02**
		Treatment	**Perturbed-fenced vs Control**	**-0.615**			0.120	**8.33E-06**
		Legacy	Pasture vs Cacao	0.030			0.086	7.35E-01
		Collection round	**After 135 days vs After 45 days**	**0.155**			0.085	**7.13E-02**
	q0	Forest age		0.002	-0.031	0.035		9.05E-01
		Treatment	Fenced vs Control	0.020			0.038	9.52E-01
		Treatment	**Perturbed vs Control**	**-0.112**			0.038	**2.17E-02**
		Treatment	**Perturbed-fenced vs Control**	**-0.164**			0.038	**2.24E-04**
		Legacy	Pasture vs Cacao	-0.009			0.030	7.79E-01
		Collection round	After 135 days vs After 45 days	0.007			0.027	7.98E-01
	q1	Forest age		0.001	-0.034	0.036		9.55E-01
		Treatment	Fenced vs Control	0.025			0.042	9.36E-01
		Treatment	**Perturbed vs Control**	**-0.122**			0.042	**2.21E-02**
		Treatment	**Perturbed-fenced vs Control**	**-0.179**			0.042	**2.59E-04**
		Legacy	Pasture vs Cacao	-0.014			0.033	6.80E-01
		Collection round	After 135 days vs After 45 days	0.005			0.030	8.54E-01
	q2	Forest age		0.000	-0.037	0.036		9.79E-01
		Treatment	Fenced vs Control	0.029			0.044	9.10E-01
		Treatment	**Perturbed vs Control**	**-0.127**			0.044	**2.46E-02**
		Treatment	**Perturbed-fenced vs Control**	**-0.183**			0.044	**3.77E-04**
		Legacy	Pasture vs Cacao	-0.020			0.033	5.69E-01
		Collection round	After 135 days vs After 45 days	0.004			0.031	9.11E-01
Beta	BC similarity to old-growth	Forest age		**0.036**	0.018	0.053		**6.72E-04**
		Treatment	Fenced vs Control	-0.008			0.018	9.74E-01
		Treatment	**Perturbed vs Control**	**-0.058**			0.018	**7.44E-03**
		Treatment	**Perturbed-fenced vs Control**	**-0.056**			0.018	**1.07E-02**
		Legacy	Pasture vs Cacao	-0.020			0.016	2.27E-01
		Collection round	**After 135 days vs After 45 days**	**0.121**			0.013	**3.23E-16**
	q0	Forest age		0.005	-0.003	0.012		2.17E-01
		Treatment	Fenced vs Control	-0.005			0.008	9.25E-01
		Treatment	Perturbed vs Control	-0.015			0.008	2.18E-01
		Treatment	Perturbed-fenced vs Control	-0.018			0.008	1.15E-01
		Legacy	Pasture vs Cacao	-0.001			0.007	9.45E-01
		Collection round	**After 135 days vs After 45 days**	**0.055**			0.006	**6.79E-17**
	q1	**Forest age**		**0.062**	0.020	0.103		**6.60E-03**
		Treatment	Fenced vs Control	-0.005			0.033	9.99E-01
		Treatment	**Perturbed vs Control**	**-0.092**			0.033	**2.74E-02**
		Treatment	**Perturbed-fenced vs Control**	**-0.079**			0.033	**7.74E-02**
		Legacy	Pasture vs Cacao	-0.044			0.038	2.70E-01

		Collection round	**After 135 days vs After 45 days**	**0.160**			0.023	**2.99E-10**
	q2	**Forest age**		**0.068**	0.022	0.113		**6.60E-03**
		Treatment	Fenced vs Control	0.000			0.036	1.00E+00
		Treatment	**Perturbed vs Control**	**-0.104**			0.036	**2.43E-02**
		Treatment	Perturbed-fenced vs Control	-0.083			0.036	1.03E-01
		Legacy	Pasture vs Cacao	-0.053			0.042	2.31E-01
		Collection round	**After 135 days vs After 45 days**	**0.155**			0.025	**1.73E-08**

Table S3. Results of type II ANOVA (F test) testing the significance of forest age, land-use legacy, treatment and collection round on total abundance (log-transformed), alpha (Hill q0, q1 and q2) and beta (Hill q0, q1 and q2) diversity; test statistics, degrees of freedom and p values are reported and significancy is highlighted in bold font.

Diversity	Metric	Term	Statistic	df	Df residual	p value
	Total abundance (log)	Forest age	6.955	1	13	**2.05E-02**
		Legacy	0.502	1	13	4.91E-01
		Treatment	0.688	3	108	5.62E-01
		Collection round	23.175	1	108	**4.84E-06**
Alpha	q0	Forest age	0.015	1	13	9.05E-01
		Legacy	0.082	1	13	7.79E-01
		Treatment	10.710	3	108	**3.21E-06**
		Collection round	0.066	1	108	7.98E-01
	q1	Forest age	0.003	1	13	9.55E-01
		Legacy	0.179	1	13	6.80E-01
		Treatment	10.741	3	108	**3.10E-06**
		Collection round	0.034	1	108	8.54E-01
	q2	Forest age	0.001	1	13	9.79E-01
		Legacy	0.342	1	13	5.69E-01
		Treatment	10.564	3	108	**3.78E-06**
		Collection round	0.013	1	108	9.11E-01
Beta	q0	Forest age	1.680	1	13	2.17E-01
		Legacy	0.005	1	13	9.45E-01
		Treatment	2.294	3	108	8.20E-02
		Collection round	98.569	1	108	**6.79E-17**
	q1	Forest age	10.420	1	13	**6.60E-03**
		Legacy	1.330	1	13	2.70E-01
		Treatment	4.445	3	108	**5.51E-03**

	Collection round	48.213	1	108	**2.99E-10**
q2	Forest age	10.419	1	13	**6.60E-03**
	Legacy	1.576	1	13	2.31E-01
	Treatment	4.605	3	108	**4.51E-03**
	Collection round	37.146	1	108	**1.73E-08**

Table S4. Treatment effects on alpha and beta diversity, calculated as log-response ratios (LRR) relative to control conditions (Eq. 1).

Plot	**Treatment**	**Collection round**	**LRR (Alpha)**	**LRR (Beta)**
CA62	CF	After 45 days	0.095	-0.928
	CF	After 135 days	0.479	0.379
	PF	After 45 days	-0.140	-0.136
	PF	After 135 days	0.335	0.661
	P	After 45 days	-0.429	-0.769
	P	After 135 days	0.463	-0.123
CA64	CF	After 45 days	-0.507	-1.31
	CF	After 135 days	0.011	-0.118
	PF	After 45 days	-0.933	-0.687
	PF	After 135 days	-0.830	-1.085
	P	After 45 days	0.117	0.301
	P	After 135 days	-0.401	-1.027
CR02	CF	After 45 days	-0.094	-0.382
	CF	After 135 days	0.095	-0.034
	PF	After 45 days	-1.066	-1.088
	PF	After 135 days	-0.343	-0.964
	P	After 45 days	-1.496	-0.843
	P	After 135 days	-0.043	-0.47
CR09	CF	After 45 days	-0.148	-1.058
	CF	After 135 days	0.220	0.303
	PF	After 45 days	-0.973	-1.758
	PF	After 135 days	-0.213	-0.604
	P	After 45 days	0.146	-0.076
	P	After 135 days	-1.075	-1.022
CR10	CF	After 45 days	0.209	0.516
	CF	After 135 days	-0.307	-0.074
	PF	After 45 days	-1.403	-0.19
	PF	After 135 days	-0.692	-0.272
	P	After 45 days	-0.605	-0.109
	P	After 135 days	-0.621	-0.413
CR11	CF	After 45 days	-0.287	0.086
	CF	After 135 days	0.196	-0.315
	PF	After 45 days	-0.532	0.068
	PF	After 135 days	-0.185	-0.158

	P	After 45 days	0.198	0.552
	P	After 135 days	-0.169	-0.247
CR13	CF	After 45 days	-0.238	0.05
	CF	After 135 days	0.155	-0.477
	PF	After 45 days	-1.029	-0.062
	PF	After 135 days	-0.120	-0.633
	P	After 45 days	-0.090	0.236
	P	After 135 days	0.235	-0.316
CR14	CF	After 45 days	-0.036	-0.495
	CF	After 135 days	-0.093	0.25
	PF	After 45 days	-0.554	-0.562
	PF	After 135 days	-0.236	0.063
	P	After 45 days	-0.943	-0.464
	P	After 135 days	-1.037	-0.212
OG39	CF	After 135 days	-0.044	-0.339
	PF	After 135 days	-0.383	0.121
	P	After 135 days	0.052	0.047
OG41	CF	After 45 days	-0.147	-0.508
	CF	After 135 days	0.127	0.328
	PF	After 45 days	-0.227	-0.433
	PF	After 135 days	0.136	0.238
	P	After 45 days	-0.435	-0.533
	P	After 135 days	-0.261	-0.018
OG45	CF	After 45 days	-0.691	-0.895
	CF	After 135 days	-0.049	-0.069
	PF	After 45 days	-0.523	-0.578
	PF	After 135 days	-0.457	-0.395
	P	After 45 days	-0.120	-0.559
	P	After 135 days	-0.112	0.137
OG46	CF	After 45 days	-0.270	-0.954
	CF	After 135 days	-0.204	0.323
	PF	After 45 days	-0.094	0.011
	PF	After 135 days	-0.530	0.244
	P	After 45 days	-0.609	-0.703
	P	After 135 days	-0.442	0.21
OG49	CF	After 45 days	-0.053	-0.58
	CF	After 135 days	-0.080	-1.529
	PF	After 135 days	0.268	-0.09
	P	After 45 days	-1.161	-0.018
	P	After 135 days	0.180	0.173
PA55	CF	After 45 days	-0.085	-0.043
	CF	After 135 days	0.237	0.337
	PF	After 45 days	-0.307	0.151
	PF	After 135 days	-0.361	-1.362
	P	After 45 days	-0.087	0.063
	P	After 135 days	-0.082	-0.449
PA57	CF	After 45 days	-0.224	0.08
	CF	After 135 days	-0.216	0.168
	PF	After 45 days	-0.035	-0.967

	PF	After 135 days	0.132	0.043
	P	After 45 days	-0.315	-1.148
	P	After 135 days	-0.095	-0.548
PR19	CF	After 45 days	-0.062	-0.571
	CF	After 135 days	0.862	1.551
	PF	After 45 days	-0.924	-0.279
	PF	After 135 days	0.235	-0.08
	P	After 45 days	-0.065	-0.433
	P	After 135 days	0.141	0.364
PR26	CF	After 45 days	0.247	0.265
	CF	After 135 days	-0.039	-0.551
	PF	After 45 days	-0.120	0.194
	PF	After 135 days	-0.191	0.061
	P	After 45 days	-0.833	-0.759
	P	After 135 days	0.256	-0.532
PR31	CF	After 45 days	0.201	0.443
	CF	After 135 days	-0.382	-0.451
	PF	After 45 days	-0.052	0.316
	PF	After 135 days	-0.452	-0.745
	P	After 45 days	0.201	-0.869
	P	After 135 days	-0.499	-0.762
PR33	CF	After 45 days	0.467	0.168
	CF	After 135 days	0.719	0.541
	PF	After 45 days	0.337	0.239
	PF	After 135 days	-0.418	-0.208
	P	After 45 days	0.108	0.314
	P	After 135 days	-0.012	0.319
PR34	CF	After 45 days	-0.038	-0.605
	CF	After 135 days	-0.235	-0.159
	PF	After 45 days	-0.276	-0.355
	PF	After 135 days	-0.052	0.028
	P	After 45 days	-0.283	-0.038
	P	After 135 days	-0.221	-0.345
PR36	CF	After 45 days	-0.151	-0.124
	CF	After 135 days	0.003	0.158
	PF	After 45 days	-0.368	0.084
	PF	After 135 days	-0.901	-0.198
	P	After 45 days	-0.164	0.236
	P	After 135 days	-0.018	0.104

Table S5. Indicator families associated with high or low similarity to old-growth plots in each collection round, based on median Bray-Curtis similarity. Values show r.g indicator strength and significance; results are given for presence-absence (PA) and relative abundance (RA) data.

Collection round	**Group**	**Data type**	**Family**	**Indicator value**	**p value**
After 45 days	High similarity	PA	Formicidae	0.408	0.006
			Staphylinidae	0.333	0.013
			Campodeidae	0.391	0.004
		RA	Formicidae	0.414	0.003
			Campodeidae	0.303	0.002
	Low similarity	PA	Malaconothridae	0.324	0.033
		RA	Haplozetidae	0.309	0.017
			Malaconothridae	0.255	0.042
			Trhypochthoniidae	0.347	0.003
			Nothridae	0.266	0.023
After 135 days	High similarity	PA	Oribatida spp.	0.346	0.02
			Campodeidae	0.388	0.007
			Ceratocombidae	0.324	0.032
		RA	Collembola spp.	0.730	0.001
			Veigaiidae	0.276	0.039
			Staphylinidae	0.353	0.003
			Ptiillidae	0.392	0.001
			Ceratozetidae	0.266	0.01
			Oppiidae	0.341	0.004
			Oribatida spp.	0.312	0.022
			Campodeidae	0.310	0.017
			Ceratocombidae	0.254	0.05
	Low similarity	PA	Mesostigmata spp.	0.301	0.026
			Scheloribatidae	0.453	0.001
			Trhypochthoniidae	0.301	0.027
		RA	Formicidae	0.461	0.001
			Larvae spp.	0.276	0.018
			Trhypochthoniidae	0.335	0.006

Appendix A

Order / Higher taxa	**Family**	**Lowest taxa**	**Morpho species**	**ID Key Source**
Oribatida				A Manual of Acarology, 3rd Edition
Prostigmata				A Manual of Acarology, 3rd Edition
Mesostigmata				A Manual of Acarology, 3rd Edition
Coleoptera	Staphylinidae	Oxytelinae	M5-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Oxytelinae	M6-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Oxytelinae	M15-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Oxytelinae	M27-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Oxytelinae	M35-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Scaphydiinae	M1-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Paederinae	M7-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Paederinae	M10-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Paederinae	M28-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Paederinae	M29-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Paederinae	M45-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Mycetoporinae	M22-Staphy	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Staphylinidae	Pselaphinae	M2-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Pselaphinae	M4-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Pselaphinae	M12-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Pselaphinae	M14-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Pselaphinae	M24-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Pselaphinae	M36-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Pselaphinae	M41-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Osoriinae	M18-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Osoriinae	M19-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Osoriinae	M20-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Osoriinae	M21-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)

Coleoptera	Staphylinidae	Osoriinae	M34-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Osoriinae	M38-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Tachyporinae	M8-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Scydmaeninae	M13-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Staphylinidae	Scydmaeninae	M26-Staphy	Lucid Key to Staphylinidae Subfamilies | Experiment (NORTH AMERICA ONLY BUT FOR SUBFAMILIES OKAY)
Coleoptera	Curculionidae	*Anchonus* sp.	M1-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	*Anchonus* sp.	M5-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	*Anchonus* sp.	M11-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	Scolytinae	M2-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	Scolytinae	M3-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	Scolytinae	M6-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	Scolytinae	M7-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	Cossoninae	M4-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	Cossoninae	M8-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Curculionidae	*Cactophagus personatus*	M9-Curcu	Marvaldi, A., & Lanteri, A. A. (2005). Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea)
Coleoptera	Scarabaeidae	*Ataenius* sp.	M1-Scara	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Scarabaeidae	Ateuchini	M2-Scara	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Scarabaeidae	Scarabaeinae	M3-Scara	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Ptiliidae	NA	NA	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Carabidae	Bembidiini	M6-Cara	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Carabidae	Bembidiini	M7-Cara	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Carabidae	*Anchonoderus* sp.	M8-Cara	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Histeridae	Haeteriinae	M1-Hist	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)

Coleoptera	Histeridae	Haeteriinae	M2-Hist	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Tenebrionidae	*Anaedus* sp.	M1-Tene	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Dytiscidae	*Copelatus* sp.	M1-Dyti	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Monotomidae	*Leptipsius* sp.	M1-Mono	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Leiodidae	Cholevinae	M1-Leio	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Erotylidae	*Myceporthus* cf. *pauperculus*	M1-Ero	https://doi.org/10.1649/0010-065X-72.2.305
Coleoptera	Phalacridae	*Olibrus* sp.	M2-Phala	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Dryopidae	*Sosteamorphus* sp.	M1-Dryo	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Dryopidae	*Parygus* cf. *erichsoni*	M2-Dryo	http://dx.doi.org/10.11646/zootaxa.4755.1.4
Coleoptera	Nitidulidae	NA	M1-Hydr	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Limnichidae	Limnichinae	M1-Limn	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Aderidae	*Aderus* sp.	M1-Ade	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Aderidae	*Syzeton* sp.	M2-Ade	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Coleoptera	Trogidae	*Omorgus* sp.	M1-Trog	Beetles of the World - Key Search (J. F. Lawerence, A. M. Hasting, A. Seago, and A. Slipinski, CSIRO Entomology)
Isopoda	Philosciidae	*Ischioscia variegata*	M5-Iso	Pérez-Schultheiss, J. (2010). Families of terrestrial isopods (Crustacea: Isopoda: Oniscidea) of Chile, with a practical identification key.
Isopoda	Philosciidae	NA	M1-Iso	Pérez-Schultheiss, J. (2010). Families of terrestrial isopods (Crustacea: Isopoda: Oniscidea) of Chile, with a practical identification key.
Isopoda	Philosciidae	NA	M2-Iso	Pérez-Schultheiss, J. (2010). Families of terrestrial isopods (Crustacea: Isopoda: Oniscidea) of Chile, with a practical identification key.
Isopoda	Philosciidae	NA	M3-Iso	Pérez-Schultheiss, J. (2010). Families of terrestrial isopods (Crustacea: Isopoda: Oniscidea) of Chile, with a practical identification key.
Isopoda	Philosciidae	NA	M13-Iso	Pérez-Schultheiss, J. (2010). Families of terrestrial isopods (Crustacea: Isopoda: Oniscidea) of Chile, with a practical identification key.
Isopoda	Scleropactidae	NA	M6-Iso	correspondence on iNaturalist
Isopoda	Trichoniscidae	NA	M10-Iso	correspondence on iNaturalist
Isopoda	Trachelipodidae	*Nagurus cristatus*	M11-Iso	The woodlice of Switzerland (Crustacea, Isopoda, Oniscidea), with 6 new records from heated greenhouses
Isopoda	Trachelipodidae	*Nagurus* cf. *cristatus*	M12-Iso	The woodlice of Switzerland (Crustacea, Isopoda, Oniscidea), with 6 new records from heated greenhouses
Zygentoma	Nicoletiidae	Atelurinae	M1-Zyge	Order Zygentoma – ENT 425 – General Entomology
Gastropoda	NA	NA	NA	not further identified

Olygochaeta	NA	NA	NA	not further identified
Onychophora	Peripatidae	*Oroperipatus* sp.	M1-Peri	A world checklist of Onychophora (velvet worms), with notes on nomenclature and status of names - PMC
Hymenoptera	Formicidae	*Nylanderia* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Wasmannia* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Solenopsis* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Pheidole* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Monomorium pharaonis*	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Octostruma amrishi*	M1-Octo	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Cyphomyrmex* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Prionopelta* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Pachycondyla harpax*	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Anochetus* cf. *inca*	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Hypoponera* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Pseudocolobopsis* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Formicidae	*Typhlomyrmex* sp.	NA	Key to subfamilies of the Neotropical region - AntWiki
Hymenoptera	Diapriidae	*Trichopria* sp.	M1-Myma	http://www.diapriid.org/public/site/diapriid/home
Schizomida	Hubbardiidae	*Surazomus palenque*	NA	DOI:10.1371/journal.pone.0147012
Araneae	Agelenidae	*Tegenaria domestica*	M2-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Zodariidae	NA	M3-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Zodariidae	NA	M14-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Theraphosidae	Theraphosinae	M7-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Theraphosidae	NA	M24-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Theraphosidae	NA	M46-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Salticidae	NA	M16-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf

Araneae	Salticidae	NA	M17-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Salticidae	NA	M18-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Salticidae	NA	M27-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Oonopidae	*Niarchos* sp.	M50-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Araneae	Oonopidae	NA	M23-Aranea	africamuseum.be/sites/default/files/media/docs/research/publications/rmca/online/zoology-documentation/spider-families_of_the_world.pdf
Opiliones	Zalmoxidae	NA	M1-Opi	correspondence on iNaturalist
Opiliones	Zalmoxidae	NA	M2-Opi	correspondence on iNaturalist
Opiliones	Zalmoxidae	NA	M3-Opi	correspondence on iNaturalist
Opiliones	Zalmoxidae	NA	M5-Opi	correspondence on iNaturalist
Symphyla	Scolopendrellidae	NA	M1-Sym	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Scolopendromorpha	NA	*Cryptops* sp.	M2-Scolo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Scolopendromorpha	NA	*Cryptops* sp.	M3-Scolo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Scolopendromorpha	NA	*Cryptops* sp.	M4-Scolo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Scolopendromorpha	NA	*Cryptops* sp.	M5-Scolo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Scolopendromorpha	NA	*Scolopocryptops* sp.	M7-Scolo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Diplopoda	Rhinocricidae	NA	M2-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Stemmiulidae	NA	M3-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Stemmiulidae	NA	M13-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Stemmiulidae	NA	M18-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Pyrgodesmidae	NA	M4-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Pyrgodesmidae	NA	M6-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Pyrgodesmidae	NA	M7-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Pyrgodesmidae	NA	M10-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Cyrtodesmidae	NA	M8-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Cyrtodesmidae	NA	M15-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf

Diplopoda	Trichopolydesmoidea	NA	M16-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Glomeridesmidae	NA	M9-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Glomeridesmidae	NA	M11-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Diplopoda	Glomeridesmidae	NA	M12-Dip	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Polyxenida	NA	NA	M1-Pol	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Polyxenida	NA	NA	M2-Pol	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Polyxenida	NA	NA	M3-Pol	datocms-assets.com/44232/1632764482-millipedekeyenglish.pdf
Geophilomorpha	Mecistocephalidae	NA	M1-Geo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Geophilomorpha	Schendylidae	Ballophilinae	M3-Geo	https://doi.org/10.1016/B978-0-12-809633-8.02259-7
Pseudoscorpiones	Chthoniidae	*Chthonia* sp.	M1-Pse	correspondence on iNaturalist
Pseudoscorpiones	Syarinidae	*Ideoblothrus* sp.	M2-Pse	10.5852/ejt.2022.821.1801
Diplura	Campoeidae	NA	M1-Diplu	https://doi.org/10.1016/B978-0-12-374144-8.00084-9
Diplura	Campoeidae	NA	M2-Diplu	https://doi.org/10.1016/B978-0-12-374144-8.00084-9
Diplura	Campoeidae	NA	M3-Diplu	https://doi.org/10.1016/B978-0-12-374144-8.00084-9
Diplura	Campoeidae	NA	M4-Diplu	https://doi.org/10.1016/B978-0-12-374144-8.00084-9
Diplura	Evalljapygidae	*Evalljapyx* sp.	M5-Diplu	https://doi.org/10.1016/B978-0-12-374144-8.00084-9
Blattodea	Blattidae	NA	M6-Blat	correspondence on iNaturalist
Blattodea	Blattidae	*Neostylopyga* sp.	M10-Blat	correspondence on iNaturalist
Blattodea	Blattidae	*Periplaneta* cf. *australasiae*	M13-Blat	correspondence on iNaturalist
Blattodea	Blaberidae	NA	M12-Blat	correspondence on iNaturalist
Dermaptera	Spongiphoridae	NA	M3-Derm	correspondence on iNaturalist
Dermaptera	Spongiphoridae	NA	M5-Derm	correspondence on iNaturalist
Dermaptera	Spongiphoridae	NA	M7-Derm	correspondence on iNaturalist
Lepidoptera	NA	NA	NA	not further identified
Hemiptera	Rhyparochromidae	*Paragonatas divergens*	M1-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Rhyparochromidae	NA	M4-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.

Hemiptera	Rhyparochromidae	NA	M5-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Rhyparochromidae	NA	M49-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Ceratocombidae	*Ceratocombus* sp.	M16-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Ceratocombidae	NA	M3-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Ceratocombidae	NA	M7-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Ceratocombidae	NA	M22-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Miridae	*Ceratocapsus* sp.	M20-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Schizopteridae	*Ceratocomboides* sp.	M24-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Schizopteridae	NA	M21-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Gelastocoridae	*Nerthra* sp.	M13-Hemi	Schuh, R. T., & Slater, J. A. (1995). True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell UNIVERSITY press.
Hemiptera	Cicadellidae	*Hortensia similis*	M23-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	*Ladoffa sannionis*	M50-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M12-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M14-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M15-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M19-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M27-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M28-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M29-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M34-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M35-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M36-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M37-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2

Hemiptera	Cicadellidae	NA	M42-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M44-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M45-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M46-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M52-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M53-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M54-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Cicadellidae	NA	M55-Hemi	https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
Hemiptera	Ortheziidae	NA	M33-Hemi	https://doi.org/10.3897/zookeys.431.7474
Hemiptera	Ortheziidae	NA	M34-Hemi	https://doi.org/10.3897/zookeys.431.7474
Trichoptera	NA	NA	NA	not further identified
Neuroptera	Myrmeleontidae	Haplogleniini	M1-Nopt	correspondence on iNaturalist
Psocodea	Liposcelididae	*Liposcelis entomophila*	M1-Pso	William H. Robinson (2005): Urban Insects and Arachnids: A Handbook of Urban Entomology
Psocodea	Liposcelididae	*Liposcelis entomophila*	M3-Pso	William H. Robinson (2005): Urban Insects and Arachnids: A Handbook of Urban Entomology
Psocodea	Lepidopsocidae	NA	M4-Pso	correspondence on iNaturalist
Thysanoptera	Phlaeothripidae	NA	M1-Thys	TH. Johnson, M. Shyam & R. Varatharajan (2022): A Manual on the Collection, Identification and Biology of Thrips (Insecta: Thysanoptera)
Thysanoptera	Phlaeothripidae	NA	M2-Thys	TH. Johnson, M. Shyam & R. Varatharajan (2022): A Manual on the Collection, Identification and Biology of Thrips (Insecta: Thysanoptera)
Thysanoptera	Phlaeothripidae	NA	M4-Thys	TH. Johnson, M. Shyam & R. Varatharajan (2022): A Manual on the Collection, Identification and Biology of Thrips (Insecta: Thysanoptera)
Thysanoptera	Phlaeothripidae	NA	M6-Thys	TH. Johnson, M. Shyam & R. Varatharajan (2022): A Manual on the Collection, Identification and Biology of Thrips (Insecta: Thysanoptera)
Thysanoptera	Phlaeothripidae	NA	M8-Thys	TH. Johnson, M. Shyam & R. Varatharajan (2022): A Manual on the Collection, Identification and Biology of Thrips (Insecta: Thysanoptera)
Thysanoptera	Phlaeothripidae	NA	M11-Thys	TH. Johnson, M. Shyam & R. Varatharajan (2022): A Manual on the Collection, Identification and Biology of Thrips (Insecta: Thysanoptera)