Variation in successional niche turnover of multiple taxa in a recovering tropical rainforest

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Abstract

Understanding the niche turnover of ecological communities is fundamental for advancing successional theory and effective restoration. However, since niche preferences are known for a few taxa, ecosystem succession is only partially understood. To fill this gap, using a null model approach, we determined the niche optimal within eighteen ecological communities (bacteria, animals, and plants) across a tropical rainforest chronosequence to assess niche successional turnover. The approach was reliable, as niche determinations aligned with known habitat preferences of well-studied taxa (birds, trees, mammals). We found that niche turnover was pronounced, with one-third classified as early (pioneers), mid (intermediate), or late-successional (climax). Such turnover was continuous, with low species overlap and the highest species richness in old-growth forests, rejecting the intermediate disturbance hypothesis, which predicts a peak in mid-successional forests. Our results highlight the importance of old growth and the necessity of addressing the distinct needs of various ecological communities for restoration.

Keywords: tropical forest, secondary succession, niche turnover, intermediate disturbance hypothesis, multiple taxa.

Main

In recent decades, the growing loss of habitat and the expansion of secondary forests, especially in tropical regions[1] has intensified interest in understanding secondary succession due to its key role in forest restoration [2–4]. Secondary succession, defined as the process in which a disturbed but not completely lifeless area undergoes natural recovery[2] has proven to be complex and remains a major topic in community ecology[5]. Research has provided valuable insights into the recovery of species diversity(e.g.,6), species interactions(e.g.,7) and the importance of species traits (e.g.,8). However, a less explored topic is how ecological communities with varying traits differ in niche successional turnover, as studies examining multiple ecological communities are relatively scarce.

The successional theory assumes that after a perturbation, initial colonisation by early successional species is followed by species replacement and establishment, driven by environmental conditions that favour species adapted to the newly created environment until a "climax" community is reached[9–11]. Based on their establishment sequence, species are classified as pioneer species or climax species [12]. Pioneers are, for example, light-tolerant species with good dispersal capabilities, resource generalisation, and the ability to thrive in open environments, while climax species reach their optimum under the "climax" environment, (e.g., shade [5]). Some authors also recognise "intermediate" species groups that reach their optimum in intermediate successional stages, namely, early successional and late successional species[13]. Additionally, some species may be consistently present throughout the entire successional trajectory, with no preference for a specific stage of recovery (neutral theory of biodiversity [14]) but also contributing to the successional process [15].

At the community level, those individual niche preferences determine the niche turnover, ultimately contributing to the overall recovery trend. In this regard, the intermediate disturbance hypothesis (IDH [16]), a notable yet controversial framework, proposes that intermediate disturbances promote species coexistence by preventing competitive dominance and maintaining a non-equilibrium state. A key prediction is that succession after disturbance leads to peak species diversity at mid-succession due to the overlap of early- and late-successional species rather than a continuous increase in diversity (e.g., niche partitioning hypothesis [17]). Despite criticisms, IDH remains actively studied [18–20] with evidence in pro and con: on Barro Colorado Island, recruitment limitation outweighed successional effects [21], whereas in French Guiana, peak tree diversity aligned with IDH predictions [22]. Such discrepancies, though, may stem from methodologies [23] or to the nature of the disturbance, which can influence diversity patterns by resetting succession and increasing mortality [18].

Moreover, a main limitation of hypotheses on secondary succession is that they have primarily been developed based on plant communities, particularly trees[5]. Effects of drivers of successional changes - such as biotic factors, biological factors, human-induced factors and stochasticity [4,24] – vary depending on the life history and traits of species such as mobility, trophic niche, generation time [3,25,26]. As a result, non-plant taxa are expected to follow different successional trajectories according to their ecological traits [27, TM], leading to differences across communities. That said, few studies have compared the successional trends among multiple taxa or communities in tropical forests, with most relying on metanalyses (e.g., [28–30]), literature reviews (e.g., [31]), or small-scale comparisons of ecological communities (eg.,[32,33]). While these studies show that species diversity recovers in most communities, none have compared niche species turnover across ecological communities within the same ecosystem. This gap limits our understanding of successional dynamics in tropical forests and hinders the development of effective restoration and conservation practices beyond plant communities.

In this study, we compared the successional niche turnover of 44,718 species (611 plants, 347 vertebrates, 6950 arthropods, and 36,810 bacteria) across eighteen ecological communities spanning different trophic levels (decomposers, producers, herbivores—including pollinators—and predators) in a well-replicated rainforest chronosequence in the Lowland Chocó Forest, Ecuador [34]. Specifically, we (a) assessed the contribution of early-, mid-, and late-successional niches (pioneer, intermediate and climax species) to each and overall community and (b) tested whether species richness peaks at mid-succession, as predicted by the intermediate disturbance hypothesis. To do this, we first identified the successional niche optima of each species within each ecological community. Due to limited information for most species, we defined successional niche optima as the successional stage where a species is significantly more abundant relative to other stages, based on a null model assuming no stage preference [35]. We tested this approach by comparing the niche optima of our model with information from literature on habitat preference for birds and mammals and growth types for trees. We expected these traits to align with successional niche optima, for example, fast-growing trees should mostly correspond to pioneer species.

Results

Our null model's niche successional classifications largely aligned with the literature for birds, mammals, and trees. (Fig. 1). All species our model identified as climax corresponded to old-growth forest preferring birds and mammals, while pioneer species were mainly those of scrubland, human-modified habitats, and woodlands, habitats with similar conditions to those of early successional stages [36] (e.g., humidity and vegetation structure). Likewise, the model did not identify a niche optimum for any habitat generalist mammals documented in the literature. For trees, concordance was less clear, as half of fast- and slow-growing species were categorised as neutral (consistent abundance and presence across the chronosequence). However, aside from the generalist species, fast-growing species were mainly classified as pioneers and slow-growing species (mainly found in climax communities[5]), were determined as climax species, indicating that our approach provides a good approximation of successional niche optima. The results of this comparison are reported in Supplementary Information Table 1.

The main successional niche preference varies across ecological communities.

Communities varied in their successional stage preferences, with some communities showing a higher abundance of pioneer species while others had higher numbers of climax species (Fig. 2). Across the communities, climax species ranged from 0–36%, pioneers from 0–42%, intermediates from 0–11%, and generalists from 35–90% (Fig. 2). Among ecological communities, litter frogs had the highest proportion of climax species (36%), followed by non-frugivorous birds (28%), while saproxylic beetles, termites, and seedlings had none. However, only a fraction of seedling species could be classified due to a limited number of observations. Meanwhile, dung beetles had the highest proportion of pioneers (41.2%), followed by non-frugivorous birds (33%). Intermediate species were most common in bats (11%) and litter arthropods (9%), while none were found in litter frogs, ground seed dispersers, ground mammals, or saproxylic beetles. Finally, at least 90% of bacteria (at 10 and 50 cm soil depths), saproxylic beetles, ground mammals, and seedlings showed no niche optima. (see supplementary information Table 2 for the complete information for all ecological communities).

Most species are generalist with around one-third of species exhibiting a successional niche optima.

When comparing the overall community (the eighteen communities together standardized by species richness), fewer than 35% of species showed a clear preference for a specific successional stage (Fig. 3). On average, the pooled community consisted of 13.7% pioneer species, 5.5% intermediate species, and 14% climax species, with most species (about 40%) showing no niche preference (generalists). The remaining species were too rare to classify (23.7%).

As expected, the trend of each successional niche varied across the chronosequence, while generalists remained equally prevalent across all successional stages, old secondary forests—after 38 years of abandonment (the oldest age in our plots)—marked a significant turning point in the recovery process. Here, we observed the greatest increase in climax and rare species coupled with a decline in pioneer species. From agricultural plots to old-growth forests, pioneer species decreased by 18.2%, climax species increased by 11.2%, and rare species by 6.32%. Meanwhile, intermediate species peaked in the late-regeneration secondary forest, where their proportion was 3-4% higher than in agricultural plots and old-growth forests (see Supplementary information Table 3).

Most ecological communities do not support the intermediate disturbance hypothesis.

Most ecological communities did not exhibit a peak in species richness at mid-successional stages; instead, they showed a linear increase toward the higher end of the gradient. Only in the frugivorous birds community the AIC values showed a better fit for the polynomial model over the linear model. We also observed some support in dung beetles but the AIC difference was less than 7 (difference = 4). Both communities showed a peak in species richness at mid-succession, followed by a decline. However, they displayed substantial variation in species richness along the gradient (Fig. 4). In contrast, moths showed a dip in species richness at mid-succession followed by an increase at the end of the successional gradient. Interestingly, some groups, like bacterial communities at 10 cm and 50 cm depths, showed no significant change along the chronosequence. The summary of the models results are reported in the Table 4a-c in supplementary information.

Discussion

Overall, all results show that a) successional niche preferences vary across ecological communities, with different groups showing distinct proportions of pioneer, intermediate, climax, and generalist species, while many exhibit no clear successional niche optima (generalist), b) generalists species highly contribute to the composition of the communities being the most dominant; and c) most ecological communities do not support IDH as they show a continuous increase in species richness along the successional gradient, with only a few exceptions, such as frugivorous birds and marginally dung beetles, which peak at mid-succession.

The observed variations in successional niche optima across ecological communities reflect differences in resource requirements and the availability of these resources along the chronosequence. For instance, litter frogs, which rely heavily on humidity and temperature, [37], factors that are more stable in late regeneration stages and old-growth forests [EVG,SE,DD,ME,JE,KP,MS,JM,NB], exhibited the highest proportion of climax species. In contrast, communities with high mobility and broader feeding niches, such as non-frugivorous birds and dung beetles that can potentially utilise resources available or derived from agricultural activities (e.g., dung from farm animals[38]), showed the highest proportion of pioneer species among the groups studied. These differences in niche optima highlight the importance of implementing diverse management practices in tropical forests to ensure the conservation and restoration of their full biodiversity.

Generalist species also play a role in the successional process.

Successional dynamics are often discussed in terms of differing colonisation processes among species, including a turning point from fast colonisation of pioneers to competitive advantages of late-successional species [5]. Less attention has been paid to the role of species that can thrive equally well at all stages of succession (i.e., with no niche optima or generalists). Our observations revealed that generalist species dominate overall communities without affecting the recovery trend, as shown by the significant increase in species richness with recovery, making them a significant component of secondary successional forests. Nonetheless, the underlying causes and consequences of this generalism require careful analysis to avoid assuming that a species lacking a defined niche optima is unaffected by deforestation. For instance, in mammals, the prevalence of generalists may be linked to their high mobility and large habitat area requirements (e.g., [39]). For this community, their generalism depends heavily on the structure and connectivity of the remaining forest matrix [40]. Similarly, high generalisation in groups such as bacteria and saproxylic beetles does not necessarily equate to greater resilience to deforestation. TM and collaborators found that these groups exhibit low resilience, with the species composition turnover becoming "stuck" after a certain period, leading to a static community, (arrested succession[41]). Moreover, while a dominance of generalist species exists, the successional niches identified in other species suggest that the successional process is not entirely random, as expected under the neutral niche hypothesis [21,24]. Nevertheless, given the proportion of species with limited data in our sample (rare), we do not rule out that the percentage of generalist species may decrease with long-term data collection. However, this potential decrease does not alter our conclusion that generalist species represent a substantial portion of ecological communities.

Challenging the intermediate disturbance hypothesis

One reason for the unresolved controversy of IDH may be the limited taxonomic scope of each case study, failing to generalise the hypothesis and capture the dynamics of entire ecosystems (see[19,20,42]). This limitation is especially important given species' intrinsic ecological differences. For the context of secondary succession in a tropical rainforest, our results across multiple taxa did not support the unimodal curve of species diversity predicted by the IDH. Frugivorous birds and dung beetles were the only groups exhibiting a hump-shaped species richness trajectory. However, while in these groups, the number of pioneer species was slightly higher in the intermediate successional stages compared to old-growth forests for these groups, intermediate species did not peak in the middle of the successional gradient, suggesting that the convergence of the other successional groups including generalists and rare are shaping the pattern instead of specialisation of some species to an intermediate state. Although intermediate species played a role, they did not contribute to a non-linear trajectory of the total number of species. Instead, species richness was often greatest in late regeneration and old-growth forests. Our findings of a strong species turnover but no intermediate peak in diversity suggest that rejecting the IDH does not imply a neutral or random neutral species response to habitat changes as proposed by the neutral hypothesis [21]. Instead, our findings highlight a prevailing monotonous recovery trend and gradual community re-assembly towards the old growth level, shaping the successional dynamics [29,33,TM].

Studying multiple ecological communities provides valuable insights into secondary succession in tropical rainforests. However, a limitation for comparisons is the lack of information on ecological traits for many taxonomic groups. In this regard, null-based approaches provide a valuable alternative to overcome this limitation. While they do not replace the need for ecological data, they offer useful approximations necessary for the advancement of ecological knowledge, especially in the urgent context of forest restoration. Our findings show that successional niche preferences vary across ecological communities depending on their species' ability to exploit resources in regenerating forests, with generalists being the most dominant. They also show that across most ecological communities there is a gradual recovery of species richness toward the old-growth forest characterised by high niche turnover, which contradicts the IDH prediction of peak species richness at mid-regeneration stages. Our results emphasise the need to consider the specific habitat requirements of different ecological communities with different ecological traits when developing forest restoration strategies rather than relying on a one-size-fits-all approach. Finally, while secondary forests are important and vast reservoirs of biodiversity [2], preserving old-growth forests is crucial for restoring ecological communities and protecting species-rich climax communities (eg., frogs[43]).

Methods

Study site

Our study is part of the *Reassembly* project in the Chocó lowland tropical forest of North-West Ecuador (0.52°n, 79.2°W), where only 2% of the original forest remains intact [1]. The project aims to understand the recovery of species communities, species interactions and associated ecological processes by studying a successional chronosequence. The chronosequence represents the secondary succession of the lowland Ecuadorian forest well-replicated in spatially independent plots. It consists of 62 plots: twelve plots under agricultural use (six low-intensity pastures and six cacao plantations), 33 recovery forests (from one to 38 years, mean = 19.23 years of abandonment ± 11.22 SD), and seventeen old-growth forests (see [34] for details).

Data

We studied eighteen ecological communities sampled between 2022 and 2023 in 30 to 64 plots of the chronosequence. The ecological communities studied are: soil bacteria at 10 cm depth (hereafter Bacteria 10 cm), soil bacteria at 50 cm depth (hereafter Bacteria 50 cm), seedlings, trees, litter arthropods, ants, termites, saproxylic beetles, dung beetles, litter frogs, ground seed dispersers (mammals and birds), ground mammals, frugivorous birds, non-frugivorous (all birds recorded except frugivorous), moths, bees, nocturnal insects and bats. The sampling methods for each ecological community are detailed in the supplementary information.

Determining the successional niche optima of the species

To ensure a standardised methodology across groups, we estimated the successional niche optima following the niche optimum and breadth definition along environmental gradients proposed by Chisté et al. [35]. This method employs a randomisation framework based on a null model that assumes species have an equal likelihood of occurring at any point along the chronosequence. Values derived from the species’ observed occurrence and abundance are then compared against this neutral expectation. Specifically, we used the mean successional gradient weighted by species' relative abundance (RAWM) to account for their niche optima, assuming that species are more abundant in their preferred niches than others. Moreover, the abundance-weighted standard deviation (RAWSD) defines the niche breadth. We defined the successional gradient as a rank order variable instead of using the regeneration age itself, as old-growth forests do not have a specified age of regeneration. The rank-transformed regeneration age yields the lowest rank (1) for agricultural plots and the highest rank (20) for old-growth forests.

In each iteration, the null model randomly assigned successional gradient ranks to plots for each species, with the same total number of plots in which the species occurred. A total of 10,000 null models were performed per species. As with any randomization-based model, the proportion of RAWMs from the 10,000 null models that were higher or lower than the observed RAWM was used to compute the significance (one-tailed P-value). Species with a higher observed RAWM than 95% of the null models ($P < 0.05$) were classified as climax (or late-successional) species, and those with significantly lower observed RAWM than null models ($P < 0.05$) as pioneer (or early-successional) species. For species that could not be classified as either climax or pioneer (i.e., $P > 0.05$ on both ends), we tested whether they were 'intermediate', i.e. specialists on intermediate succession stages. Null models defined this category as having a significantly narrower niche breadth (RAWSD) than expected. We thus compared the observed and expected RAWSD based on the 10,000 null models. Species that were neither significant climax, pioneer, nor intermediates were classified as "generalist" referring to niche generalism or no preference for a successional niche.

Since our statistical approach to successional niches considers only the species' distribution along the chronosequence and not the species' ecological traits, we compared our results with information in the literature for well-known groups. Information on habitat preference (e.g., forest, human-modified habitat) for birds and mammals and growth type (i.e., slow growth or fast growth) for trees [44–46]. We verified our model's accuracy by assessing whether species' habitats or traits aligned with their assigned successional niche optima. For example, slow-growing trees should primarily correspond to intermediate or climax species. In contrast, habitat-generalist mammals should align with niche-optima generalists, and birds from human-modified habitats should correspond to pioneer species.

To minimize misclassification due to limited observations, we classified species as pioneer, intermediate, or climax only if they occurred in at least three plots and five plots for generalist. This classification was based on simulated communities with a log-normal abundance distribution, predefined successional preferences, and literature comparisons (see supplementary information for details). Species with fewer observations, as defined above, were classified as "rare."

Contribution of successional niches to community composition.

After determining the successional niche optima of species across ecological communities, we analysed the community composition at two levels: a) community-specific composition, focused on the individual ecological communities showing the proportion of each successional niche optima group (e.g., pioneer, climax, etc.) within each community, for this level we did not include the species determined as "rare" since this category does not represent a successional niche optima; and b) among all eighteen communities to show its general community composition and change across the chronosequence. In this approach, we estimated the abundance and species richness of each successional group and "rare" species within each of the four main successional stages in our chronosequence: active agriculture, early-regeneration forest (< 10 years), late-regeneration forest (> 10 years), and old-growth forest. To this end, we standardised the species abundance and richness across all communities to ensure that each community contributed equally to the total composition, summing to 100%. This approach prevents the disproportionate influence of highly abundant or diverse groups (e.g., bacteria or insects), which could otherwise skew the results. Specifically, we normalised each community's log-transformed observed species and abundance values by the total for all communities recorded within each successional stage. Subsequently, we adjusted the number of species in each community by multiplying it by a scaling factor (equal to the total number of communities), ensuring that each community accounted for 1/18 of the total percentage.

Testing the intermediate disturbance hypothesis IDH

Under the IDH, species richness is expected to follow an unimodal (bell-shaped) curve, reflecting higher species richness in intermediate successional stages rather than a linear trend [16]. Therefore, we fitted both linear and polynomial regression models (with the polynomial model including both linear and quadratic terms) to assess the effect of the successional gradient on species richness for each community separately. Model selection was based on Akaike Information Criterion (AIC) values, with a model being considered better supported if the AIC difference follows the general thumb rule that a difference greater than seven indicates the model has considerably more support [47]. To meet the assumptions of normality and homoscedasticity, we applied log(x+1) or square transformations to the species richness data. We also checked the residuals for normality using the Shapiro-Wilk test and visually. For bats, where transformation did not resolve normality violations, we applied a generalised additive model (GAM) with a Poisson distribution to better account for the data. We used the package *mgcv* to perform the GAM analysis [48] in the base package in the R programming environment version 4.3.3 [49].

Data Availability Section

Data and code will be uploaded with the manuscript for review (via Figshare) and will be made publicly available in Figshare upon acceptance of this work with an embargo of one year after publication.

Figures and Figure Legends

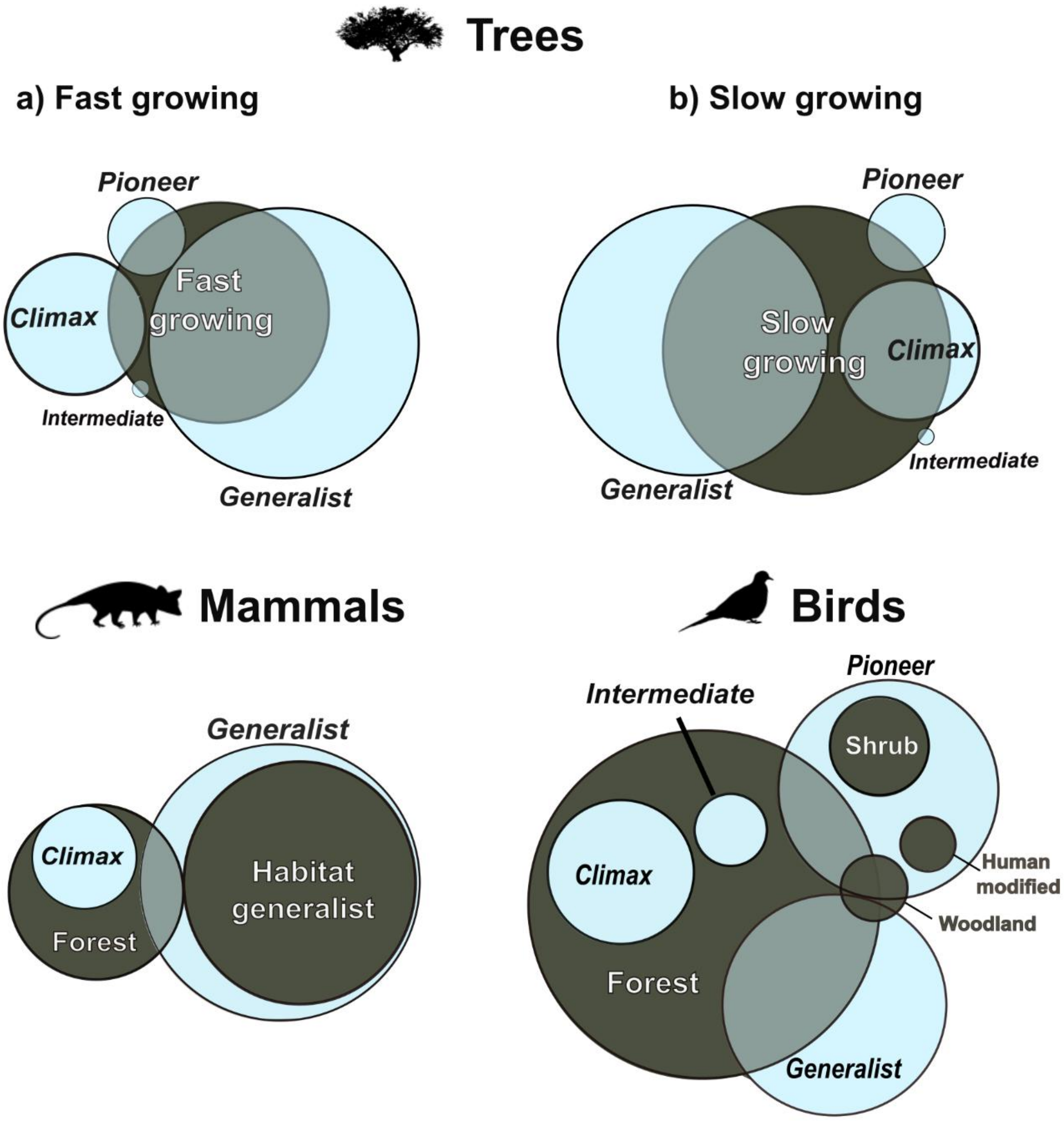

Figure 1. *Comparison of niche optima from the null modes with literature.* The figure illustrates the overlap between the successional niches defined by the null models and the species characteristics from the literature for three well-studied communities: Trees, Mammals, and Birds. The niches defined by the null models (climax, intermediate, pioneer and generalist [no niche preference]) are shown in light blue, and the categories from the literature are in dark grey. For trees, we compared with their growth type: (a) fast-growing and (b) slow-growing. For mammals and birds, we compared their habitat preference. "Forest" refers to species that typically inhabit non-forest habitats, such as agricultural plots, while "Habitat generalists" refers to species without a strong preference for any particular habitat type. The size of the circles is proportional to the number of species within each group.

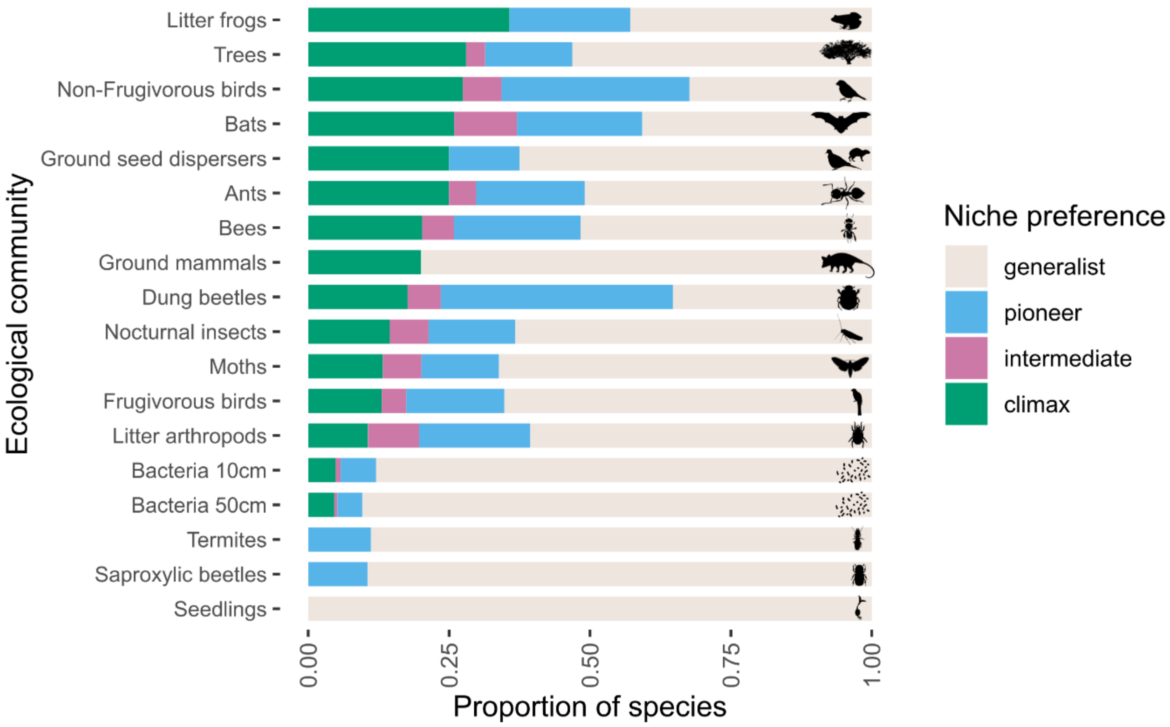

Figure 2. *Species composition within each ecological community.* The figure shows the proportion of pioneer (blue), climax (green), intermediate (pink), and those with no niche preference (generalist (grey)) species relative to the total number of species (excluding rare species) for each ecological community. The communities are arranged in descending order based on the proportion of climax species.

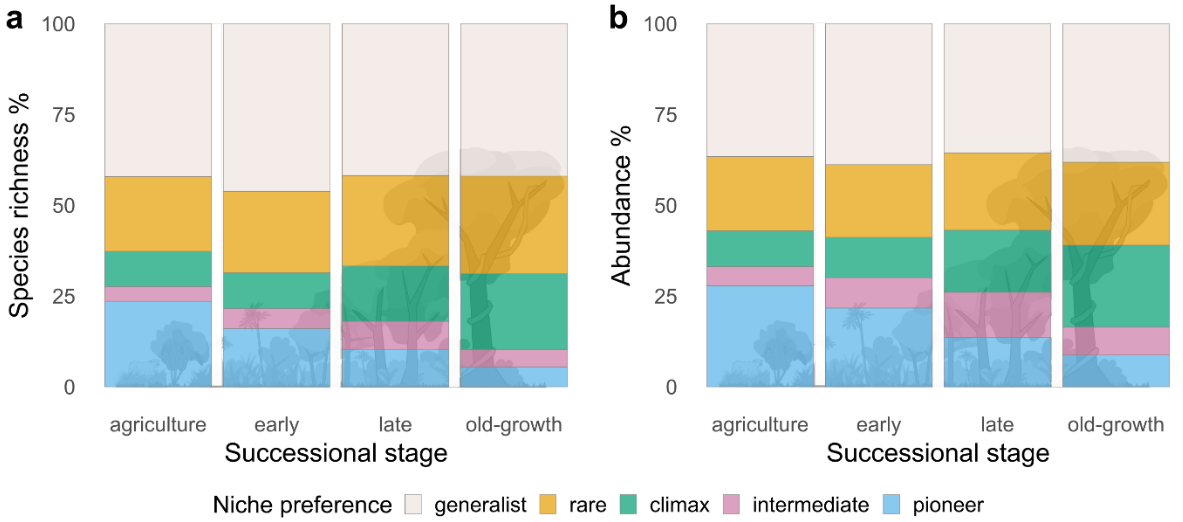

Figure. 3 *Overall trend in species composition among all ecological communities*. Changes in percentage of a) species richness and b) abundance across the four main successional stages in the chronosequence: active agriculture plots (agricultural), early successional forest (early <10 years of recovery), late successional forest (late, > 10 years of recovery) and old-growth forest (old-growth). The values of each community were standardised to contribute 1/18 to the overall trend. The trend of each group's species according to their successional niche preference is indicated in green for climax, pink for intermediate, blue for pioneer and grey species with no niche preference (generalist). Species occurring in less than 10% of plots were regarded as rare and indicated in yellow in the figure.

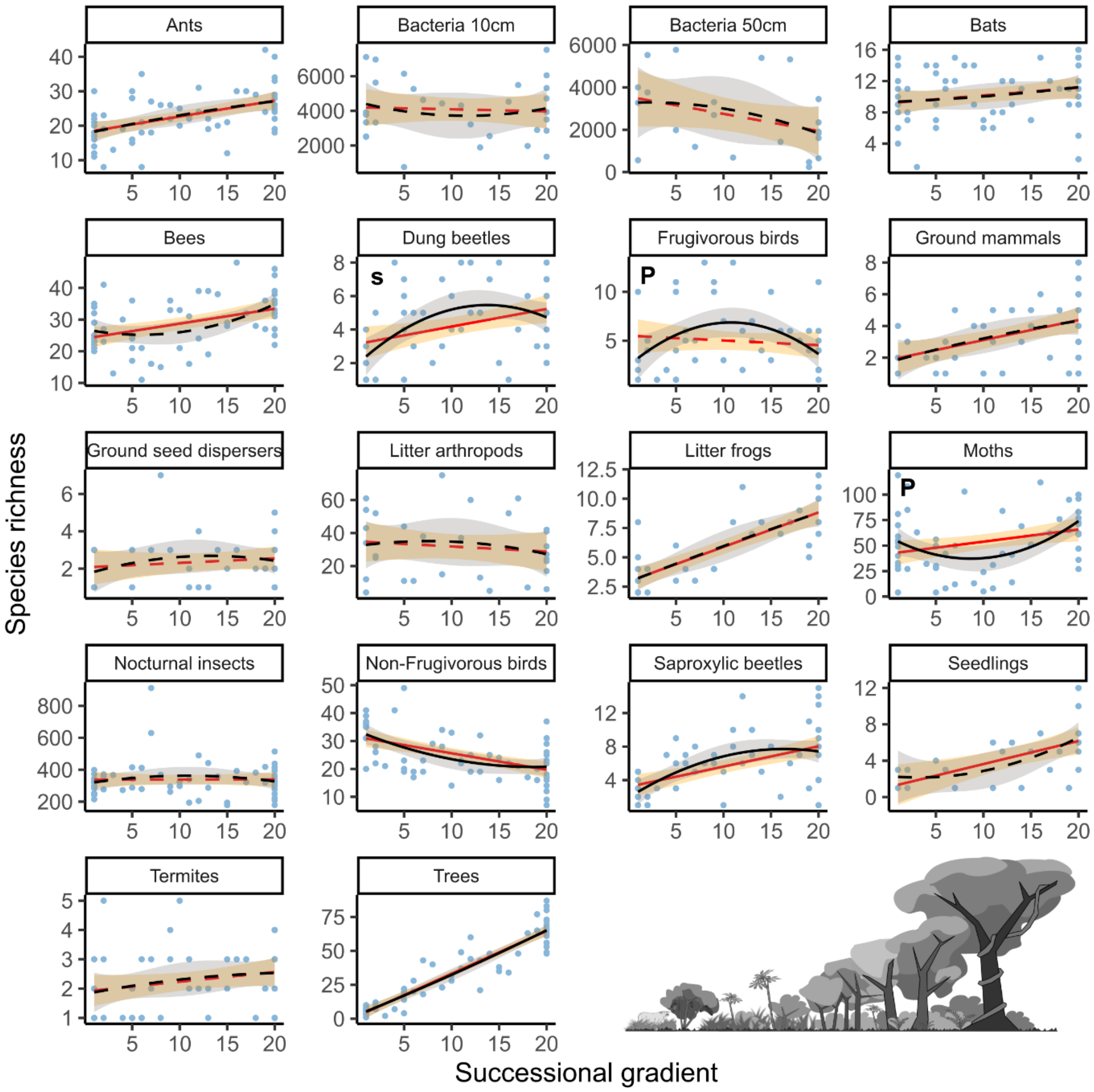

Figure 4. *Response of species richness to the successional gradient for each ecological community.* The figure shows the effect of the successional gradient (x-axis) on species richness (y-axis) for each ecological community, as indicated at the top of each graph. For the linear regression model, the regression line is shown in black, and the standard error is in grey. For the polynomial regression (x^2), the regression curve is in red, and the standard error is in orange. Solid lines indicate significant effect of the successional gradient ($P< 0.05$) and dashed lines no significant effect.

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Supplementary Methods

Survey methods for each taxon

Bacteria: Soil samples were collected with the help of a soil penetrometer at 10 cm and 50 cm depth at 32 plots. At each plot, four samples were taken for both depths. Upon collection, the respective samples were stored in 2mL microcentrifuge tubes containing 1mL of DNA Shield Buffer (Zymo Research) and were stored in the fridge at 4°C until further processing. The DNA extraction was conducted with the ZymoBIOMICS™ 96 DNA Kit and followed the manufacturer's protocol with these modifications: 400 µl of the sample and 400 µl of DNA shield were added to ZR BashingBead™ Lysis Tubes. Mechanical lysis was performed via bead beating in a vortexer at 2000 rpm for three 15-minute intervals, with 2-minute breaks between each. 16S amplicon sequencing was performed according to the protocol of Kozich et al. (2013)[1], including PCR amplification, normalization using SequalPrep Normalization Plates (Invitrogen), and cleanup with AmPure XP (Beckman Coulter). Libraries were quality checked using a Quibit fluorometer and dsDNA HS kit (Thermo Fisher) and Bioanalyzer High Sensitivity DNA Chip (Agilent Technologies). Sequencing was performed on an in-house Illumina MiSeq using 2x250 cyc v2 chips. Bioinformatic cleanup, processing including denoising and ASV generation, and taxonomic classification were performed according to the https://github.com/chiras/metabarcoding_pipeline workflow utilizing VSEARCH as a main tool. Further cleanup steps and transformation to relative read abundances per sample were performed with phyloseq in R also according to the script above. Samples with less than 15,000 quality-controlled reads were removed from the analyses. If multiple samples for both investigated samples were available after quality control, the sample with the highest throughput was selected for further analysis

Leaf-litter arthropods: In spring 2022 we sampled 30 study plots, covering five forest types (8 old-growth forest plots, 3 active cacao plantations, 3 active pastures, 8 secondary forests recovering from use as cacao plantations, and 8 secondary forests recovering from use as pastures). The sampling consisted of taking 1 m² of leaf litter in each study site and then sieving it with a 1 cm mesh to upconcentrate the arthropods. The resulting subsample was then brought to the lab and Berlese-extracted for 60 hours. The arthropods were collected and stored in 96% EtOH until identification. The arthropods were sorted first into orders and then into morpho-species. Diptera larvae and Formicidae were removed from this dataset, which comprises a total of 4067 individuals classified into 377 morpho-species.

Saproxylic beetles: All 62 study plots were sampled. To assess the potential specialization of saproxylic insects towards specific host trees, we quantified dead wood × insect networks using logs from five phylogenetically distinct local tree species in a standardized way along a forest recovery gradient. Logs (approximately 6-12 cm in diameter and 50 cm in length) were cut from branches or stems of young healthy trees with no visible signs of insect or fungal activity. Specifically, Trema micrantha (Sapanillo) and Theobroma cacao (Cacao) were selected as fast-decomposing species; Inga spp. (Guaba) as a medium-decomposing species; and Triplaris cumingiana (Fernán Sánchez) and Hieronyma chocoensis (Mascarey) as slow-decomposing species based on local knowledge. The logs were placed on the ground in each plot for six months, following a similar protocol to a global experiment[2]. We exposed a total of 310 logs in the plots. When removing the logs from the field, we first collected surface-active ants and termites using the logs as nesting space. Before placing the logs in the emergence chambers, a wooden disc was cut from each end of the log for subsequent characterization of fungal communities using metabarcoding. The emergence chambers consisted of net tubes made from mesh cloth used for insect nets. All emerging insects were collected in tubes hanging at the lower end of the emergence chambers. Beetle species were initially identified as morphospecies within the subfamily, and one individual per sample and morphospecies was selected for subsequent barcoding.

Dung beetles: We sampled all 62 study plots. The first round of sampling was conducted from September to November 2021, and the second round from March to May 2022. Within each 50 m x 50 m study site, four pitfall traps were set 50 m apart to avoid trap interference. The traps were one-quarter filled with 70% Ethanol, and two leaves were placed over the top as rain protection. Each trap had a different bait: cow dung, rotten cow muscle, rotten millipede, or fermented fruit (banana). The traps were collected after 48 hours, emptied into small containers, and transported back to the lab. The dung beetles were separated from the other arthropods in the lab and stored in pure Ethanol. A taxonomic expert (Diego Marin-Armijos) identified the beetles as precisely as possible. We captured 844 dung beetles in the six months of fieldwork. Two of the 23 species are undescribed and remain morphospecies.

Nocturnal insects (metabarcodes): We sampled nocturnal insects with an autonomous light trap for one night per plot. These traps were equipped with an LED light optimized for insect sampling powered by a Power bank (LepiLED Mini, Brehm, Jena, Germany[3]). For 8 hours after dusk, insects were collected in a jar mounted under a funnel and killed by chloroform. We removed large-bodied Lepidoptera from the Saturnidae and Sphingidae families (moths) for taxonomic identification. The remaining insect bulk was frozen and transferred to 96% alcohol. The samples were then passed through an 8-mm sieve, thereby separating larger and smaller insects, opening the avenue for using read numbers for abundance estimates. This was done to increase the likelihood of detecting small-bodied and rare species in samples, as individuals with larger biomass provide disproportionate amounts of DNA and can therefore be over-represented when metabarcoding bulk samples. The CO1-5P (mitochondrial cytochrome oxidase 1) target region was sequenced for collected bulk samples. These COI sequences were used to attribute Barcode Index Numbers (BINs), which are clusters of barcode sequences that can be used as a proxy taxonomic unit. The BIN clusters match the actual taxonomically identified species at different levels (90–99% COI genetic similarity), depending on the taxa, thus allowing comparisons with studies based on morphological determination. The reference library was restricted to countries from Central and Southern America (for more details see Müller et al. 2023[4]). Sequencing errors were removed according to Chiu et al. (2016)[5].

Moths: The two focal groups of moths (Sphingidae and Erebidae: Arctiinae) were collected at the 62 plots belonging to the unit. Thirty-two plots were sampled between March and May 2022, and the remaining 30 between October and December 2022. A similar proportion of plot types (actively used cacao plots, actively used pasture plots, secondary forest plots with a legacy of cacao use, secondary forest plots with a legacy of pasture use, and old-growth forest plots) were sampled in the two seasons. Moths were captured with a white vane trap equipped with a LepiLED Maxi Switch light[6] set to emit a mixed light (UV and visible white light). The vanes were connected to a collection and killing chamber, where chloroform fumes were used as a dry and fast-killing agent. The trap was protected from rain by a wide plastic roof. At all plots, we set one trap at the understory (ca. 1.5 m above ground), and at older plots (secondary forest plots with legacy of cacao use, secondary forest plots with legacy of pasture use with more than 15 years of regeneration and that had a clear vertical structure and at least one tree taller than 15 m, and all old-growth forest plots), we also set an additional canopy trap ranging from 15 – 35 m above ground using a pulley system set with the aid of a bow (N = 27). Using a digital timer, the lights were set to turn on at 1800 and remained working for 12 hours. Lights were connected to a power bank. The following morning, moths were collected and filtered according to our focal groups. Individuals were identified to the (morpho)-species level based on a personal catalog curated by a moth expert (Dr. Gunnar Brehm, Phyletisches Museum Jena, Germany). We recorded a total of 11,902, from which 11,271 could be identified to (morpho)-species level (279 species recorded).

Bees: Bees were collected using a variety of methods. Between March and May 2022 and between October and December 2022, diurnal bees were collected using a modified vane trap similar to commercially available models[7], adapted with a yellow and a blue vane attached transversally to attract a wider range of bees. The collection and killing chamber, roof, canopy setting, and number of plots sampled per season were the same as described above for moths. Traps were always set in the morning and emptied 24 hours later. Additionally, in 2022, nocturnal Megalopta (Halictidae) and Ptiloglossa (Colletidae) bees were often collected by the moth traps described above. In 2023, vane traps were set again similarly to 2022 and in the same plot setting, this time with added honey baits at the bottom of the vanes to increase capture rates. Additionally, fragrance traps, targeted at male orchid bees (Apidae: Euglossini), were set simultaneously to the vane traps. These traps were modified 2L PET bottles with two entrance holes guided by plastic funnels. We used four traps per plot (and per stratum when the canopy was sampled, see “Moths” section above), each with one of the following scents known to attract different species of orchid bees[8]: 1,8-cineole, Eugenol, Methyl Salicylate, and Skatol. A piece of cotton imbibed in common household insecticide was used as a fast-killing agent. Lastly, sessions of hand-netting were carried out in the plots after traps were set. Four hours of free walking were carried out within the 50x50 m area of each plot, in which all bees were captured on sight and stored individually for sorting and identification. Bees were identified through specialized keys for each group (e.g refs [9–11]).

Ants: Ants were collected on all 62 plots in February-April 2022 by hand sampling of the ground and trees and with the use of Winkler traps as described by Hoenle et al. (2022)[12]. In the same sampling period, five naturally occurring dead wood pieces per plot were opened and insects nesting in the dead wood were collected. Additionally, ants were collected in an experimental approach on 62 plots with wood from five different tree species. In August-September 2022, one piece of wood with a diameter of 7-10 cm and a length of 50 cm originating from the tree species Trema micrantha (Sapanillo), Theobroma cacao (Cacao), Inga sp. (Guaba), Triplaris cumingiana (Fernán Sánchez), and Hieronyma chocoensis (Mascarey) was placed on each plot. After 6 months in February-April 2023, the wood was retrieved from the plot and reared in emergence chambers. These emergence chambers consisted of mesh tubes made of fabric used for insect nets and a falcon tube filled with ethanol. Insects emerging from the wood and falling into the ethanol were collected for the following three months. Ant species were identified with a genetic approach using the COI barcoding gene in combination with the examination of morphological traits.

Frogs: We sampled 38 plots. Each plot was visited six times over three rounds, with each round including both day and night sampling sessions. The first round took place from March to June 2022, the second from July to October 2022, and the third from March to June 2023. In each plot, we performed systematic searches for two person-hours, visually scanning for frogs from the leaf/litter up to vegetation approximately 1.2 meters in height. While our focus was on leaf-litter frogs, we recorded all frog species encountered. Each frog was caught and temporarily placed in an individual plastic bag until the end of the sampling. Frogs were then identified using BioWeb[13]. To minimize temporal effects on the results, plots from different habitat types were sampled alternately.

Ground seed dispersers and Frugivorous birds: Frugivorous birds and mammals on the forest floor and in the canopy (frugivorous birds) were recorded across the 62 study plots using camera traps. In each plot, fruits of fruiting plant species growing at the plot were deployed in front of the camera traps and continuously recorded for six days. Cameras were positioned at each of the four corners of each plot. Sampling was carried out from 2022 to 2023 during both rainy (March-June) and dry (September-December) seasons. We recorded all events where ground-dwelling frugivores consumed fruits. Birds were identified following Freile & Restall (2018)[14] and mammals following Tirira (2017)[15]. The total interaction frequency was used as a proxy for animal abundance. In total, we recorded 13 bird species interacting 70 times and 9 mammal species interacting 137 times with fruits on the forest floor across all plots. All observed interactions, including those involving cultivated plants, are included in this study.

Ground mammals: mammals were captured by camera traps as described in Grella et al. 2025[16]. In short, sampling took place in the dry season from October-November in the years 2021 and 2022. One camera (Reconyx Hyperfire) was installed on each plot over the course of three weeks and retrieved in the same order, resulting in three weeks of operating time for each camera. Cameras were installed on trees at 30-80 cm height, facing open areas or animal trails. 65 plots (3 plots were part of an older study design) were sampled, but due to malfunctions of some cameras or vegetation blocking the vision, 8 plots were excluded, resulting in 57 successfully sampled plots. Cameras were deployed to take three images per trigger event with a 1-second delay between triggers. Species were identified using the management software TRAPPER[17] and literature about local mammal and bird fauna[18–20]. For assessing the number of species occurrences, individual birds and mammals were counted. As individuals of most species cannot be distinguished, we counted individuals of the same species as a new occurrence after a minimum of 5 minutes from the last image or sequence of images[21,22].

Non-Frugivorous birds (sound data): We deployed one Bioacoustic Recorder (BAR-LT, Frontier Labs, Meanjin, Australia) with one omnidirectional microphone facing down at a height of ca. 1.70 meters above ground, at each plot during November for several weeks. The recorders were programmed to record 2 minutes every 15 minutes throughout the day for two weeks (Julian day 299-314 in 2021) concurrently, with a sampling rate of 44.1 kHz. Two experts identified all birds from 2-minute files recorded at 06:00h, 06:15h, 06:30h, 06:45h, 07:00h, 07:15h, 12:00h, 12:15h, 16:00h, 16:15h, 17:00h, 17:15h, 18:00h, and 18:15h from two days without heavy rain, covering the high activity phases of birds around dusk and dawn, as well as a few minutes during the day to cover flock activities. For more details, see Müller et al. 2023[4], Falconi et al. 2024[23].

Frugivorous birds: Frugivorous birds were recorded across all 62 study plots through direct observations of the upper forest layers (midstory and canopy) using binoculars. Each plot was observed for 5 hours starting at sunrise over three consecutive days, resulting in 15 hours of observations per plot. Sampling was carried out from 2022 to 2023, during both rainy (March-June) and dry (September-December) seasons. Bird species were identified following Freile & Restall (2018)[14]. We recorded all events where birds consumed fruits. The total interaction frequency of each bird species was used as a proxy for bird abundance. In total, we recorded 68 bird species interacting 1597 times with fruits across all plots. This study contains all bird-plant interactions, including those involving cultivated plants.

Bats: Bat sampling was conducted at all 62 sites in four field campaigns, from March 2022 to December 2023, during the dry and rainy seasons. Mist nets have proven to be an effective method for capturing phyllostomid bats[24], which are our study group. At each site, six mist nets (6m x 2.5m) were set at ground level and captures were made on three consecutive nights, for 186 sampling nights. They were open from 18:30 to 24:00 (5.5 hours) and were checked approximately every 30 minutes. The total sampling effort was 6138 hours/net. Guidelines such as Sikes et al. (2016)[25] and Erazo et al. (2022)[26] were followed for handling and manipulating bats. For the registration of the captured individuals, general morphometric measurements were taken, as well as data on sex, age, and reproductive status. Identification and taxonomic classification were carried out using guides, keys, and updated species lists (e.g., [15,20,27,28]). To identify recaptures, a temporary mark was applied to each individual, with numbered punches placed in tweezers to make small holes in the membrane of the extended right-wing[25,29,30]. As a reference collection, 67 individuals were deposited in the Mammal Collection of the Zoology Museum of the Pontificia Universidad Católica del Ecuador (QCAZ-M), registered under the Contrato Marco MAAE-DBI-CM-2021-0165, issued by the Ministry of Environment of Ecuador.

Seedlings: We monitored tree seedling recruitment on four 1-m² subplots on 39 plots. We defined seedlings as all young plants (including palm trees), which grow from a seed or resprout from a fallen branch and have a root-collar diameter (RCD) between 2 mm and 10 mm. All tree seedlings were tagged and identified to the lowest taxonomic level possible (species or morpho-species level). For every seedling, we measured its height, RCD, and number of leaves, as well as monitored its survival over 31 months with repeated measurements every four months. For this study, we used the data of the seedling communities gathered in the fourth monitoring (March to May 2023) to calculate taxonomic diversity and composition per plot.

Trees: In each of the 62 study plots, all trees (N = 6426), palms (N = 1108), and lianas (N = 8) with ≥ 25 cm of circumference at 1.3 m above the ground (≥ 7.95 cm diameter at breast height, DBH) were labeled and identified in the 50 x 50 m plot area. Within active plots, which were not fenced, we tried to cover the same area as in the 50 x 50 plots (250 m²) and also tried to include remnant wild trees if these were not too far away from the center of the plot. The tree survey was conducted from February 2022 to July 2023. A botanical collection and silica samples for further genetic and chemical analyses were obtained from each tree species. Tree identification was performed at the Herbario Nacional del Ecuador–INABIO using the collections deposited there as references. From a total of 7968 stems of 7542 cultivated and non-cultivated tree individuals (some with several stems), we identified a total of 539 tree species and morphospecies. In total, 7408 tree individuals were identified to species and morphospecies level, which is more than 98% of the 7542 trees surveyed. Only 134 tree individuals have not been identified because they did not present leaves during the survey or additional identification work at the herbarium is required. For this study, we use all trees, including cultivated ones (798 stems of 678 cultivated trees of 11 species, including cacao, coffee, coconut, and lemon trees common in the area). An alternative meaningful subset, focusing on wild trees and excluding cultivated ones, is reported and analyzed elsewhere (see Escobar et al. 2024)[31].

Determining the minimum plots needed to minimize error in estimating niche successional optima

We estimated the successional niche optima using the niche optimum and breadth definitions along environmental gradients, as proposed by Chisté et al. (2016)[32]. This method relies on a null model approach, as described in the main text. It can estimate both niche optimum and niche breadth using either occurrence data alone or a combination of occurrence and abundance data. We opted for the latter, as it provides a more comprehensive representation of species distribution. However, we first conducted all preliminary analysis, such as determining the minimum sample size for accuracy and comparing results with the literature to check for significant differences. Overall, we found that both methods yielded similar results. Nevertheless, the method can misclassify species in two main ways:

1. **False Generalists** – Species with a distinct niche successional optimum (e.g., climax species) being incorrectly classified as generalists.
2. **False Positives** – Generalist species being incorrectly assigned a niche successional optimum.

To determine the minimum number of plots needed to reduce false generalists, we simulated communities based on an experimental design mirroring our empirical data: 62 plots, including 12 under agricultural use (six low-intensity pastures and six cacao plantations) and 33 recovery forests (ranging from one to 38 years since abandonment, with a mean of 19.23 years ± 11.22 SD). As in the empirical dataset, we transformed regeneration years into a gradient to incorporate old-growth forests, which lack a regeneration time.

We created a simulated community of 100 species assigned to specific successional stages: only present in early regeneration plots, in intermediate stages, and exclusively in old-growth forests, representing pioneers, intermediate species, and climax species, respectively. This base community was then subdivided into smaller subsets by randomly removing one plot at a time until no plots remained.

For each subset, we estimated niche successional niche. We then analysed the relationship between the number of plots in which a species occurred and the probability of weighted mean and standard deviation estimated by the null model. The threshold was set at the point where the mean successional weighted by species´ relative abundance was closest to zero and the probability of the standard deviation was the lowest, which occurred at three plots for the three cases (Fig. 1).

Estimating the minimum number of plots to avoid false positives was more challenging since random classification inherently introduces variability. To address this, we compared our null model results with existing literature for well-documented taxonomic groups (trees, birds, and mammals). We assessed the proportion of species misclassified as generalists relative to the number of plots in which they occurred. The minimum number of plots required was determined as the threshold where the proportion of misclassified species fell below 5% (0.05) (Figu. 2). For this analysis, we omitted all the species that are classified as neutral by the literature.

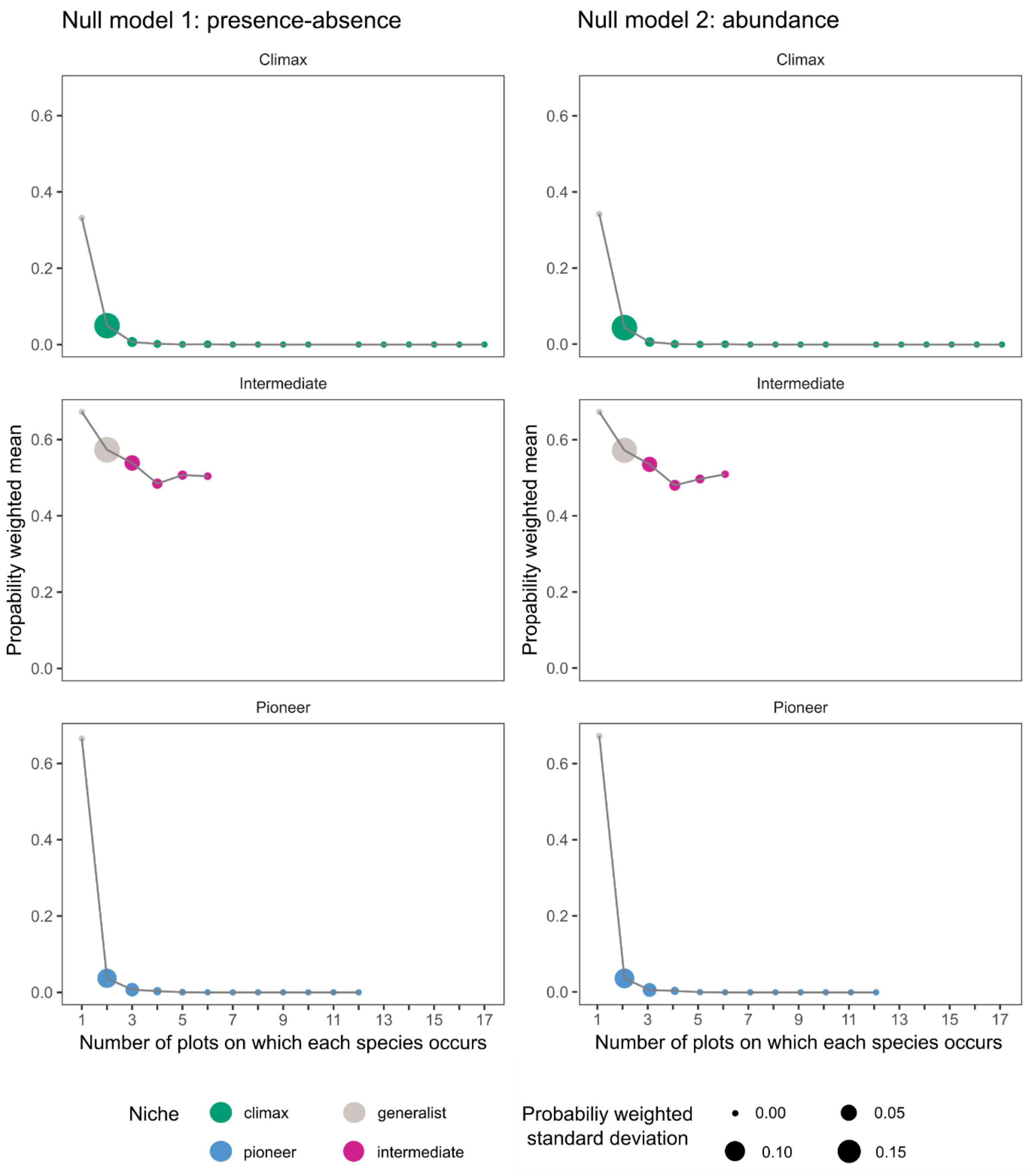

Figure 1. The probability of the weighted mean of abundance of the null model vs the number of plots the species occurs. On the left, the results for Null Model 1 are displayed, which are based on species occurrence or presence-absence data. On the right, the results for Null Model 2 are shown, incorporating species abundance. The niche successional groups are color-coded: green for climax species, blue for pioneer species, pink for intermediate species, and grey for generalists or those without a distinct niche optimum. The size of the circles represents the probability of the weighted standard deviation, with larger circles indicating a higher probability. The x-axis represents the number of plots in which a species occurs. The y-axis shows the probability of the weighted mean of abundance from the null model

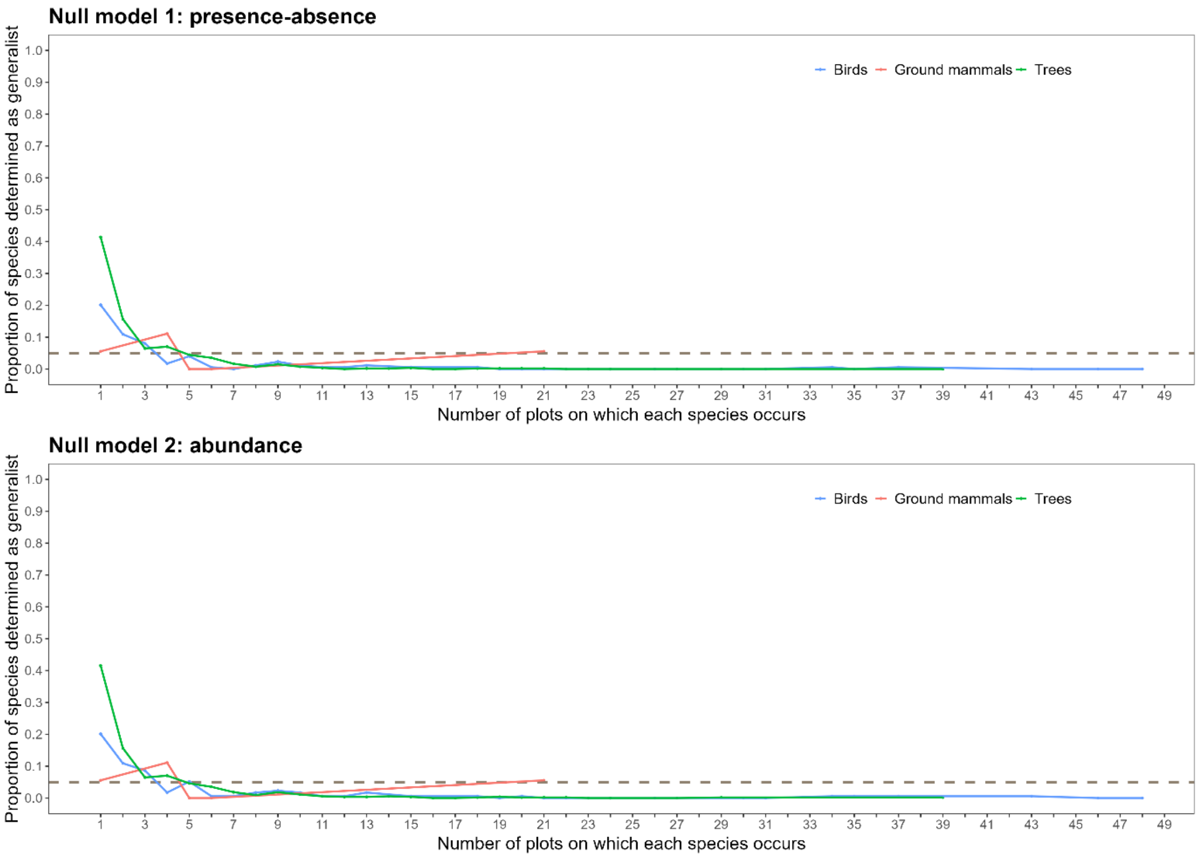

Figure. 2 Proportion of misclassified generalist (no successional optima) species based on literature. We compared the results of the model with information on literature for birds, (blue), ground mammals (red) and trees (green). The x-axis represents the number of plots in which a species occurs. The y-axis shows the proportion of species determined as generalist by the null model approach. On top the results of Null model1 and on the bottom the results for the null model 2. The dashed line indicates the proportion values equal to 0.05.

Literature vs null model approach

We compared the information on literature for three well studied taxonomic groups birds, mammals and trees with the results from the null models. We made the comparison after removing those species for which there was not enough information according to the criteria explained in the section determining the minimum plots needed to minimize error in estimating niche successional optima.

Table 1 Comparison of information on literature with the results of our null model approach. The number of species in each habitat (for birds and mammals) or growth type (trait; trees) classified as pioneer, intermediate, climax, or generalist (no niche successional optima) based on the null model approach.

Taxon	Habitat/trait	pioneer	intermediate	climax	generalist
Null model 1: occurrence (presence-absence)					
Birds	Forest	21	9	30	23
	Human Modified	4	0	0	0
	Shrubland	13	0	0	0
	Woodland	2	0	0	1
Mammals	Forest	0	0	2	1
	Neutral	2	1	0	5
Trees	Fast-growing	25	5	16	44
	Slow-growing	14	5	47	51
Null model 2: Abundance					
Birds	Forest	15	7	28	32
	Human Modified	4	0	0	0
	Shrubland	13	0	0	0
	Woodland	2	0	0	1
Mammals	Forest	0	0	2	1
	Neutral	0	0	0	7
Trees	Fast-growing	20	5	15	50
	Slow-growing	12	2	43	60

Supplementary results

Niche successional optima across and among all the ecological communities

Table 2. Proportion of species in each successional niche for each ecological community. As noted in the main text, rare species were excluded from the proportion calculations as they do not represent a successional niche. The table includes both the number of species excluding rare species and the total number of species.

Ecological community	Spp.	Number spp witout rare	Proportion climax	Proportion intermediate	Proportion pioneer	Proportion generalist
Ants	299	104	0.25	0.048	0.192	0.51
Bacteria 10cm	20467	9205	0.049	0.009	0.063	0.88
Bacteria 50cm	16343	4018	0.046	0.005	0.044	0.904
Bats	42	27	0.259	0.111	0.222	0.407
Bees	178	89	0.202	0.056	0.225	0.517
Dung beetles	23	17	0.176	0.059	0.412	0.353
Frugivorous birds	63	23	0.13	0.043	0.174	0.652
Ground mammals	18	10	0.2	0	0	0.8
Ground seed dispersers	25	8	0.25	0	0.125	0.625
Litter arthropods	354	66	0.106	0.091	0.197	0.606
Litter frogs	25	14	0.357	0	0.214	0.429
Moths	400	204	0.132	0.069	0.137	0.662
Nocturnal insects	5591	1341	0.145	0.069	0.154	0.633
Non-Frugivorous birds	174	102	0.275	0.069	0.333	0.324
Saproxylic beetles	76	19	0	0	0.105	0.895
Seedlings	73	4	0	0	0	1
Termites	29	9	0	0	0.111	0.889
Trees	538	207	0.28	0.034	0.155	0.531

Table 3. Percentage of species of each niche successional optima and rare species in each of the successional stages in the chronosequence. Agriculture (plots in active agriculture plots) (< 10 regeneration years), late regeneration (> 10 regeneration years) and old-growth forest. Rare species refers with no enough information to be determined the niche optima.

Successional stage	Climax %	Intermediate %	Pioneer %	Generalist %	Rare %
Abundance					
Agriculture	9.9	5.25	27.84	36.56	20.46
Regeneration early	11.14	8.37	21.68	38.8	20.02
Regeneration late	17.11	12.43	13.6	35.58	21.28
Old-growth forest	22.57	7.67	8.76	38.16	22.84
Species richness					
Agriculture	9.74	4	23.58	42.1	20.58
Regeneration early	9.87	5.49	16.04	46.13	22.46
Regeneration late	15.22	7.87	10.17	41.82	24.93
Old-growth forest	20.94	4.8	5.4	41.97	26.9

Testing the intermediate disturbance hypothesis

To test the intermediate disturbance hypothesis, we fitted both linear and polynomial regression models (with the polynomial model including both linear and quadratic terms) to assess the effect of the successional gradient on species richness for each community separately. To meet the assumptions of these models, we applied logarithmic or square transformations to species richness where necessary. The type of transformation is specified in the first table, but the same transformation was applied consistently across all models. The results are summarized in the following tables. For bats, where transformations did not adequately resolve normality violations, we used a generalized additive model (GAM) with a Poisson distribution to better account for the data, and we report these results separately.

Results of the generalized additive model for bats

The model explained 2.3% of the variance in species richness, as indicated by an R-squared value of 0.029. The smooth term for the successional gradient was non-significant (p = 0.0673), and its effective degrees of freedom (edf) was 1. This suggests a linear relationship between the successional gradient and species richness, as an edf of 1 indicates no non-linearity although the effect was no significant.

Table 4a. Results of the Models Without Predictors. Transf. refers to the transformation of species richness to meet the assumption of normality.

		No predictors (y=0+ε)			
Community	*Transf.*	*Estimate ± SE*	*t value*	*P value*	*AIC*
Ants	square	4.7241 ± 0.0947	49.903	<0.001*	145.76
Bacteria 10cm	square	62.3324 ± 2.6026	23.9497	<0.001*	247.55
Bacteria 50cm	log	7.563 ± 0.1909	39.6274	<0.001*	60.54
Bees	log	3.3207 ± 0.041	81.0396	<0.001*	37.11
Dung beetles	square	2.0027 ± 0.0759	26.3959	<0.001*	101.23
Frugivorous birds	square	2.1016 ± 0.0996	21.0954	<0.001*	116.17
Ground mammals	square	1.763 ± 0.0805	21.9118	<0.001*	72.6
Ground seed dispersers	log	0.7182 ± 0.0939	7.6463	<0.001*	63.86
Litter arthropods	square	5.3209 ± 0.3435	15.4914	<0.001*	126.04
Litter frogs	log	1.8143 ± 0.0763	23.7778	<0.001*	51.19
Moths	square	7.0449 ± 0.2907	24.2343	<0.001*	270.67
Nocturnal insects	log	5.7819 ± 0.038	152.1552	<0.001*	26.5
Non-Frugivorous birds	log	3.2043 ± 0.0453	70.8014	<0.001*	49.23
Saproxylic beetles	square	2.2879 ± 0.0988	23.1672	<0.001*	144.42
Seedlings	square	1.9797 ± 0.1467	13.4955	<0.001*	68.26
Termites	square	1.4617 ± 0.0516	28.331	<0.001*	51.49
Trees	square	5.4603 ± 0.307	17.785	<0.001*	288.4

Table 4b. Results of the lineal model. The asterisk (*) indicates the values P< 0.05

	Lineal model ($y = x + \varepsilon$)			
Community	*Estimate x ± SE*	*t value*	*P value*	*AIC*
Ants	0.0497 ± 0.0112	4.4328	<0.001*	130
Bacteria 10cm	-0.0874 ± 0.342	-0.2556	0.8001	249.48
Bacteria 50cm	-0.0385 ± 0.0247	-1.5586	0.1348	60.02
Bees	0.0172 ± 0.0051	3.4012	0.0012*	28.18
Dung beetles	0.03 ± 0.0095	3.1411	0.0027*	93.83
Frugivorous birds	-0.0069 ± 0.0143	-0.4808	0.6328	117.93
Ground mammals	0.0337 ± 0.0102	3.297	0.002*	64.47
Ground seed dispersers	0.016 ± 0.0129	1.2341	0.2256	64.28
Litter arthropods	-0.0253 ± 0.0458	-0.5513	0.5858	127.71
Litter frogs	0.0464 ± 0.0059	7.8525	<0.001*	15.6
Moths	0.0931 ± 0.0369	2.5229	0.0144*	266.42
Nocturnal insects	2e-04 ± 0.0051	0.0452	0.9641	28.5
Non-Frugivorous birds	-0.0241 ± 0.0052	-4.6432	<0.001*	32.23
Saproxylic beetles	0.0515 ± 0.0114	4.5212	<0.001*	128.28
Seedlings	0.0602 ± 0.0186	3.2291	0.0034*	60.81
Termites	0.0117 ± 0.0068	1.7061	0.094	50.55
Trees	0.2987 ± 0.0145	20.5577	<0.001*	161.13

Table 4c. Results of the Linear Polynomial Model for Each Ecological Community. An asterisk (*) indicates values with P < 0.05, or the best model based on the lowest AIC (difference greater or equal to 7).

	Polynomial model ($y=x+x^2+\varepsilon$)						
Community	*Estimate x*	*t value*	*P value*	*Estimate x^2 ± SE*	*t value*	*P value*	*AIC*
Ants	-9e-04 ± 0.0023	-0.4075	0.6851	0.0701 ± 0.0513	1.3663	0.1769	130.17
Bacteria 10cm	0.0479 ± 0.0777	0.6164	0.5428	-1.1038 ± 1.6848	-0.6551	0.5179	251.06
Bacteria 50cm	-0.002 ± 0.0056	-0.3686	0.7165	0.0064 ± 0.1243	0.0511	0.9597	61.86
Bees	0.0022 ± 0.001	2.1663	0.0344*	-0.03 ± 0.0223	-1.3443	0.1841	25.44
Dung beetles	-0.005 ± 0.0019	-2.7196	0.0088*	0.1407 ± 0.0417	3.374	0.0014*	88.51
Frugivorous birds	-0.0086 ± 0.0028	-3.0958	0.0032*	0.1886 ± 0.0645	2.9236	0.0052*	110.64*
Ground mammals	-9e-04 ± 0.002	-0.4286	0.6705	0.0532 ± 0.0468	1.1378	0.2618	66.27
Ground seed dispersers	-0.0021 ± 0.0026	-0.819	0.4187	0.0629 ± 0.0588	1.07	0.2924	65.56
Litter arthropods	-0.0027 ± 0.0099	-0.274	0.7861	0.0321 ± 0.2143	0.1496	0.8822	129.63
Litter frogs	-0.001 ± 0.0014	-0.6995	0.489	0.0663 ± 0.029	2.2852	0.0287*	17.07
Moths	0.0232 ± 0.0072	3.2192	0.0021*	-0.4055 ± 0.1586	-2.556	0.0133*	258.4*
Nocturnal insects	-6e-04 ± 0.0011	-0.5932	0.5554	0.0137 ± 0.0233	0.5886	0.5584	30.13
Non-Frugivorous birds	0.001 ± 0.0011	0.8873	0.3786	-0.0447 ± 0.0238	-1.8755	0.0658	33.41
Saproxylic beetles	-0.0057 ± 0.0023	-2.4998	0.0153*	0.1737 ± 0.0501	3.4673	0.001*	124.03
Seedlings	0.0032 ± 0.0038	0.8321	0.4132	-0.0114 ± 0.088	-0.1295	0.898	62.05
Termites	-6e-04 ± 0.0015	-0.4034	0.6884	0.0248 ± 0.0333	0.7455	0.4594	52.38
Trees	-0.0073 ± 0.0029	-2.5289	0.0141*	0.4569 ± 0.0641	7.1283	<0.001*	156.75

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