Recovery of phylogenetic diversity and phylogenetic structure in trees and animals along a chronosequence of tropical forest regeneration

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Abstract

Tropical forests are highly threatened habitats with the capacity to recover after disturbance. Integrating phylogenies in the study of forest recovery provides key information on the evolutionary relationships of communities through succession, and also serves as a proxy of their functional trait diversity and resilience capacity. We used phylogenetic and community data for trees and animal groups to study the recovery of phylogenetic diversity (PD) and phylogenetic structure along a chronosequence of forest regeneration in the Ecuadorian Chocó. Phylogenetic diversity recovered with regeneration time, and it occurred after species richness for five out of eight studied groups. Only two groups showed increasing phylogenetic overdispersion, while three groups tended to clustering, and three more showed random structure. Phylogenetic clustering potentially occurred mainly because of environmental filtering during early and late regeneration, while phylogenetic overdispersion occurred because of biotic factors potentially related to competition and dispersal capacity. Our results show the complex nature of succession in tropical forests, making it difficult to raise generalizations about the trajectory of PD and phylogenetic structure after disturbance. However, they also show that PD can recover relatively rapidly under natural forest regeneration, suggesting that the studied communities are resilient to disturbance from an evolutionary perspective.

1. Introduction

Tropical forests are experiencing a pervasive and rapid modification due to human activities promoting extensive land use changes (1,2). However, they also have the capacity to recover after disturbance when pastures and agricultural fields are abandoned for regeneration (3,4). Secondary regenerating forests play a fundamental role in the regeneration and maintenance of the different aspects of biodiversity and ecosystem functioning because they can harbor species from old-growth forests that would disappear otherwise (5,6). It has been estimated that around 28% of forest cover in the Neotropics corresponds to secondary forests recovering from previous disturbance (7), highlighting their importance in the region. There is growing evidence that secondary regenerating forests can recover from disturbance reaching similar

diversity levels as old-growth forests at relatively fast rates (4,8–13). Some works have made even more progress in understanding the evolutionary mechanisms and processes involved in forest regeneration by incorporating phylogenies (14–19). However, these studies have focused on single taxonomic groups, impeding a comprehensive understanding of biodiversity regeneration and the entailing forest functions. Such an endeavor would require the simultaneous analysis of multiple taxa. Therefore, we perform here an exhaustive analysis of the phylogenetic dynamics during forest regeneration by studying various plant and animal communities to offer robust insights into the evolutionary mechanisms driving succession.

The use of phylogenetic diversity in the study of forest regeneration may offer complementary insights on community assembly and biodiversity recovery. By incorporating the evolutionary history of coexisting species, one can gain insights into how closely related the species in a local assemblage are and whether ecological similarity is determined by common ancestry. For instance, phylogenetic diversity (PD) measures the total amount of phylogenetic distance among species within a community based on the branch lengths of a reference phylogenetic tree (20), and it is usually correlated with species richness (SR) (21). Furthermore, PD can be used as a surrogate of functional trait diversity because, as PD increases within a local assemblage, more disparate evolutionary histories are incorporated and therefore more functionally complementary traits are included in the local community (21–24). Nevertheless, this surrogacy can be problematic and the correlation between PD and functional diversity can also be weak and depend on the traits analyzed (25,26). Because PD may work as a proxy for functional diversity, it could inform how species respond to disturbance since higher PD values would mean a higher number of different traits and mechanisms to face environmental changes and vice versa. For instance, the recovery of PD after disturbance is key for communities because it is associated with an increase in their productivity, stability, and resistance to invasions (5,15,23,27–29). Hence, studying the recovery of PD after disturbance provides inferences on the resilience capacity and functioning of communities, besides just the recovery of taxonomic diversity.

The speed of PD recovery compared to that of SR may depend on how closely or distantly related the species occupying a local assemblage are during succession. Closely related species usually colonize newly formed habitats after forest disturbance

because they tend to share similar niches and display similar phenotypes because of their evolutionary proximity, allowing their survival under harsh environmental conditions (30–32). For example, environmental filters commonly present during early forest regeneration, such as high solar radiation, high temperature, or low humidity can be tolerated only by species adapted to such harsh conditions. This functional similarity (e.g., fast growth in trees, skin thickness in frogs, daily activity in birds) allows closely related species to colonize and establish in recently disturbed habitats (33,34). On the contrary, distantly related species tend to occupy habitats during late regeneration because these habitats provide a variety of resources and niches that can be used by phylogenetically distant species that usually display divergent traits (32,35), reducing competition for these resources (34,36–38). Given that closely related species are connected by short phylogenetic branches, their contribution to PD is lower compared to distantly related species, which are connected by longer branches (17,39). Thus, SR would be expected to increase and recover faster than PD during forest regeneration because closely related species would start accumulating in the community shortly after disturbance whereas a later arrival of distantly related species would be needed for an increase in PD.

Understanding the patterns and processes that determine community structure during succession has been a recurrent but elusive question since the early era of ecology (40). Theory suggests that the assembly of communities is the result of the interplay of abiotic and biotic filters which promote phylogenetic clustering or phylogenetic overdispersion (22,41,42). Phylogenetic clustering usually occurs at early stages of forest regeneration (22,43,44) while phylogenetic overdispersion usually occurs at late stages of forest regeneration (45,46). This pattern of decreasing clustering or increasing overdispersion through succession has been widely observed in herbaceous plants and trees (15,36,37,47–50), and in ants (51,52). Nevertheless, decreasing overdispersion has been also observed in subtropical herbaceous plant and tree communities (49,53). Communities can also be randomly structured meaning that closely and distantly related species are equally likely to coexist at local scales and different mechanisms may interact simultaneously to promote such a pattern (34,37), as it has been observed in bats (54) and in tropical ants (11).

Here, we aim to test expected phylogenetic patterns during forest succession for one plant and seven animal groups along a chronosequence of tropical rainforest regeneration (4) in order to raise generalizations on phylogenetic recovery. This approach provides a unique opportunity to study the recovery of multiple communities simultaneously allowing a better comprehension of forest regeneration and community assembly from different taxonomic perspectives. Although previous research on phylogenetic dynamics has been done for individual taxonomic groups, this study represents the first synthesis across multiple taxa including trees, flying and ground-dwelling vertebrates, and insects. Our goal is to determine phylogenetic patterns during succession across taxa with different life histories and strategies which could influence how these communities respond to disturbance. We first hypothesize that SR recovers faster than PD because closely related species are expected to colonize habitats during early regeneration as they are potentially able to survive the harsh environmental conditions of these habitats (30–32). We therefore also test if phylogenetic overdispersion increases with regeneration time because distantly related species would be expected to colonize habitats during late regeneration where they can share multiple forest resources (32,34,35,38). Lastly, we test whether phylogenetic structure correlates with abiotic and biotic variables during early and late regeneration to disentangle the role of environmental filtering and biotic factors in promoting phylogenetic clustering and overdispersion along the chronosequence. With this synthesis paper we aim to increase our understanding on the recovery dynamics of communities and how they assemble from a phylogenetic perspective, contributing to bridge the gap between community ecology, evolutionary history, and conservation.

2. Material and methods

(a) Study site

This study was performed at the chronosequence of forest regeneration of the Reassembly Research Unit (www.reassembly.de) located in the lowland rainforest of the Ecuadorian Chocó which is considered one of the most threatened ecosystems worldwide (55,56). The chronosequence consists of 62 plots (50 x 50 m) including active cacao plantations and pastures (no regeneration), former cacao plantations and

pastures during early (1–15 years of regeneration) and late natural regeneration (16–38 years of regeneration), and old-growth forests (unknown time since last possible human disturbance). In this study, we consider active plots as the earliest stage of regeneration and old-growth forests as the latest because they represent the status that regenerating habitats should reach. The climate is typical for a lowland rainforest with high precipitation (5000 mm per year), high humidity (90–100%), and in-situ loggers recorded mean temperatures of 21–25° C within the plots. Plot elevation ranges between 130–540 masl and it is not significantly correlated with regeneration time. A more detailed description of the study site and the chronosequence design can be found in Escobar et al. (4).

(b) Sampling

We surveyed angiosperm trees, understory frogs, frugivorous and vocalizing birds, bats, ants, dung beetles, and bees between 2021–2023 in 62 plots (50 x 50 m) of a chronosequence of forest regeneration in the Ecuadorian Chocó (4). Trees, frugivorous birds, bats, ants, and bees were sampled in all 62 plots while frogs were sampled in 38 plots, vocalizing birds in 61 plots, and dung beetles in 57 plots. More detailed information on the specific sampling protocol for each group can be found in Supplementary Material and in (4,57,58). We acknowledge that many of our datasets may not reflect abundance properly and therefore it was not used during analysis.

(c) Phylogenies reconstruction

For all groups, we first pruned previously published mega-phylogenies using our community data matrices to obtain community phylogenies. For trees, we pruned the mega-phylogeny for seed plants *GBOTB.extended.TPL.tre* stored in the R package V.PHYLOMAKER2 (59) to obtain a tree community phylogeny. For all animal groups, we pruned the mega-phylogenies using the package APE (60). We used the mega-phylogenies from Portik et al. (61) for frogs, Jin & Qian (62) for birds, Shi & Rabosky (63) for bats, Economo et al. (64) for ants, Tarasov & Dimitrov (65) for beetles, and Henríquez-Piskulich et al. (66) for bees. More detailed information on the

reconstruction of phylogenies for trees and animals can be found in Supplementary Material.

(d) Phylogenetic and taxonomic diversity

We calculated rarefied phylogenetic diversity (Faith PD) and rarefied species richness (SR) for each plot with the package iNEXT3D (67). We estimated the coverage level of each plot and then averaged these values for each group in order to perform the rarefaction/extrapolation approach. Only for dung beetles, we calculated PD and SR without rarefaction/extrapolation using PICANTE because iNEXT3D was not able to compute PD for this dataset. This may have occurred because many genera in the beetle phylogeny consisted of polytomies, which probably impeded the package to perform these calculations.

We performed Pearson correlations to test whether PD and SR increase with (square-root transformed) regeneration time. We square-root transformed regeneration time because it linearizes the slope of relationships, a basic assumption for linear models. We did not include old-growth forests in the models because of their unknown time of regeneration (if any). We then estimated the time for total recovery of PD and SR diversity using the modified linear model $T_{full} = (OG_{median} – a) / b)$ where 'a' is the intercept at time 0 and 'b' is the slope of (square-root transformed) regeneration time. The median value of phylogenetic and taxonomic diversity in old-growth forests (OG_{median}) were used as a reference to estimate the recovery time of these variables. Then, we back-transformed the time for total recovery since square-root transformed regeneration time was used in the models.

(e) Phylogenetic community structure

We obtained two indices of community phylogenetic structure using the package PICANTE (68). We calculated the standardized effect size of the mean pairwise distance between all species at each plot (ses.MPD). This index describes phylogenetic community structure at deep nodes of the phylogeny and is equivalent to -1 times the Nearest Relative Index (NRI). We also calculated the standardized effect size of the

mean nearest taxon distance (ses.MNTD), which is the mean distance between species and their closest relatives at each plot. This second index reports structure at shallow nodes (i.e. the tips of a phylogeny) and it is equivalent to -1 times the Nearest Taxon Index (NTI). Therefore, ses.MNTD is more indicative for competition than ses.MPD. We used the option *independent swap* to create a null model for comparison, along with 1000 runs and 1000 iterations. This null model randomizes the data matrix while maintaining the frequency of species occurrence and sample species richness (Gotelli et al., 2000), simulating a scenario where all species have the same probability of colonizing and establishing at any site. Plots with values of ses.MPD and ses.MNTD below 0 (null model) and that are statistically significant are phylogenetically clustered while those with significant values over 0 are phylogenetically overdispersed. We did not use abundance-weighted analyses because community data were obtained in different ways and not all of them included 'true abundance' such as the bird or ant datasets.

We performed Pearson correlations to test whether ses.MPD and ses.MNTD of each plot change with (square-root transformed) regeneration time under the assumption that phylogenetic overdispersion increases with regeneration time. We did not include old-growth forest plots because of their unknown regeneration time. However, to further explore the tendency of phylogenetic structure with succession, particularly in old-growth forests, we grouped the plots in four categories: active plots, early regeneration (1–15 years), late regeneration (16–38 years), and old-growth forests. Two-tailed Wilcoxon tests were performed to check if the mean values of ses.MPD and ses.MNTD in each category were different from zero (null model).

We then used linear models to test the influence of abiotic and biotic variables on the recovery of ses.MPD and ses.MNTD during early (active and early regeneration plots) and late stages of forest regeneration (late regeneration and old-growth forest plots). We then analyzed the resulting models using ANOVA tests which provide information on type II errors. All the variables used in the models were obtained from Escobar et al. (2025) where they were used to test the recovery of tree attributes. The abiotic variables included in the linear models were elevation, climate, soil composition at 10 cm depth, and soil texture at 10 cm depth, which could promote phylogenetic clustering through environmental filtering. Climate and soil composition were obtained

by performing two independent principal component analyses (PCAs) with the package FactoMineR (69). The climate PCA was done using plot data on precipitation, humidity, temperature, and solar annual radiation. The soil PCA was obtained using pH and common soil elements (C, N, Ca, Fe, K, Na, Mg, Mn, P) at 10 cm depth. Since bees showed a strong pattern of phylogenetic clustering during late regeneration but it was not correlated with any environmental variable (see Results), we also included temperature in the model for late regeneration in addition to the climate PCA values to further explore their drivers of phylogenetic structure. As a biotic variable that could promote phylogenetic overdispersion through competition or dispersal limitation, we included the distance from the plots to the nearest old-growth forest. Distance to the nearest forest was included because community assembly and phylogenetic structure would depend on how close plots are to the nearest old-growth forest border as it could influence species dispersal capacity, resource availability, and protection from predators. Plots within old-growth forests were assigned a distance of 0 m to the nearest forest. The models were validated by: 1) testing the lack of variance homogeneity through a Pearson correlation between fitted and residual values of the models and 2) through a Barlett test; 3) determining the lack of spatial autocorrelation of the model residuals with a Moran's I test using the package APE.

3. Results

(a) Tree and animal communities

Our sampling resulted in an angiosperm tree community of 514 species and morphospecies distributed in 60 out of 62 plots along the chronosequence of Reassembly. We did not record any wild tree in one of the active cacao plots and we also excluded a second plot with two wild species from the analysis because their branch disposition (polytomy) in the plot phylogeny impeded running the rarefied phylogenetic diversity (PD) analysis. We found 22 species and morphospecies of understory frogs in 37 out of 38 plots. For frugivorous birds, 80 species were recorded eating fruits in 52 out of 62 plots. A total of 323 vocalizing bird species were identified in 61 out of 61 plots sampled. The phyllostomid bat community dataset was composed of 42 species observed in 62 plots. For ants, our sampling resulted in 289 species and

morphospecies from 62 plots too. The dung beetle community included 23 species and morphospecies recorded in 57 out of 57 plots. Finally, we analyzed 166 species and morphospecies of bees from 62 plots. Plots where no species were recorded were automatically removed during analysis.

(b) Phylogenetic and taxonomic diversity

Phylogenetic diversity (PD) increased with species richness (SR) for all groups (all Pearson's $r = 0.64–0.99$, $p < 0.001$). For trees, frugivorous birds, vocalizing birds, ants, and dung beetles, PD increased with regeneration time, whereas for vocalizing birds and bees, PD decreased with regeneration time ($p < 0.01$; Table 1; Figure S1). In turn, SR increased with regeneration time for trees, frogs, ants, and dung beetles, and it again decreased with regeneration time for vocalizing birds and bees ($p < 0.01$; Table 1; Figure S1). The recovery of PD was fastest for both groups of birds and ants, it was intermediate for dung beetles and bees, while for trees, frogs, and bats it took the longest. The recovery of SR was fastest for both groups of birds and ants, intermediate for frogs, dung beetles, and bees, and took the longest for bats and trees. Our model estimated that the recovery of PD occurs after the recovery of SR in frogs, frugivorous birds, bats, ants, and dung beetles, whereas PD recovered before SR for trees, vocalizing birds, and bees (Figure 1).

(c) Phylogenetic community structure

Phylogenetic structure at deep (ses.MPD) and shallow (ses.MNTD) phylogenetic nodes increased with regeneration time for frugivorous birds, indicating phylogenetic clustering at early stages of regeneration and phylogenetic overdispersion at late stages ($p < 0.05$; Table 2; Figure 2). Although bats did not show significant changes for ses.MPD and ses.MNTD with regeneration time ($p > 0.05$; Table 2; Figure 2), they showed a tendency to phylogenetic overdispersion at shallow nodes because ses.MNTD was significantly different from the null model in old-growth forests ($p < 0.05$; Figure S2) while ses.MPD was close to statistical significance ($p < 0.1$; Figure S2). On the other side, ses.MPD and ses.MNTD decreased with regeneration time for frogs and bees, showing phylogenetic overdispersion during early regeneration and phylogenetic

clustering during late regeneration ($p < 0.05$; Table 2; Figure 2). Phylogenetic structure for trees did not change through the chronosequence ($p > 0.05$; Table 2; Figure 2), but it showed a tendency to phylogenetic clustering for ses.MNTD ($p < 0.05$; Figure S2). Vocalizing birds, ants, and dung beetles showed random phylogenetic structure ($p > 0.05$; Table 2; Figure 2; Figure S2).

During early regeneration, tree phylogenetic structure is potentially shaped by climate because ses.MPD and ses.MNTD was significantly correlated with climate in the linear models ($p < 0.05$; Table S1). For frugivorous birds, in turn, ses.MPD and ses.MNTD correlated with elevation ($p < 0.05$; Table S1). Regarding ants, ses.MNTD changed significantly with soil composition ($p < 0.05$; Table S1). The phylogenetic structure of any other taxonomic group was not significantly correlated with any other variable during early regeneration ($p > 0.05$; Table S1). During late regeneration, frogs' ses.MPD was correlated with elevation, soil texture, and distance to the nearest forest while ses.MNTD was correlated with climate ($p < 0.05$; Table S2). Both ses.MPD and ses.MNTD were correlated with distance to the nearest forest for frugivorous birds ($p < 0.05$; Table S2). For bees, ses.MPD correlated with elevation and temperature ($p < 0.05$; Table S2) but ses.MNTD was not influenced by any variable. No other variable was correlated with phylogenetic structure in any other taxonomic group during late regeneration ($p > 0.05$; Table S2). The assumptions for all models during early (Table S3) and late regeneration (Table S4) were met, except the Barlett test for frogs during early regeneration ($p < 0.05$; Table S3).

4. Discussion

This synthesis paper contributes to understanding the recovery patterns of phylogenetic diversity (PD) and phylogenetic structure through a chronosequence of natural forest regeneration using a multi-taxa approach. Although interesting results arose for individual tree and animal groups, phylogenetic recovery patterns cannot be generalized for all the studied groups. Among our main results, we found that: 1) PD and species richness (SR) have the capacity to recover with time, albeit at different speed between groups; 2) Although PD and SR are strongly correlated, SR recovers faster than PD in more than half of the studied groups; 3) Plant and animal groups showed contrasting

patterns of phylogenetic structure. Phylogenetic overdispersion does not necessarily increase with succession because only two of the eight studied groups followed this pattern. Instead, three groups showed decreasing phylogenetic overdispersion or increasing clustering, while three more groups showed random phylogenetic structure; 4) Phylogenetic clustering is apparently shaped by environmental filtering during early and late regeneration. Regarding phylogenetic overdispersion, it can be shaped by biotic factors related to competition or dispersal capacity; however, the development of this phylogenetic pattern is more difficult to elucidate. The addition of other biotic variables that are more specific to each taxonomic group could help to elucidate the drivers of phylogenetic overdispersion observed here. Our findings show that expected phylogenetic patterns through succession can be detected for some taxonomic groups, but each group responds differently at an evolutionary level to post-disturbance succession.

(a) Recovery of phylogenetic diversity

Phylogenetic diversity (PD) and species richness (SR) increase or decrease along the chronosequence in most of the groups studied here, reaching similar levels as old-growth forests after some time. This shows that phylogenetic and taxonomic diversity has the capacity to recover after disturbance in tree and animal communities under natural regeneration at different time spans and is mainly influenced by regeneration time. The recovery of PD is key for communities because besides correlating with SR, PD also usually correlates with functional trait diversity (21,22,24,26). This would mean that the functional diversity of communities could also recover with time, potentially increasing their resilience capacity (70) and ecological stability (71). It has been observed that community productivity and stability increase with an increase in PD (5,15,23,29). Hence, PD could represent a useful measure of restoration success (14) and its recovery can potentially contribute to the long-term persistence of plant and animal communities. Our study contributes to the growing body of evidence that shows that biodiversity can recover in the studied chronosequence after enough time under natural regeneration (4,11–13,57,72,73). Based on the observed change in PD with succession, we could state that the taxonomic groups analyzed in this study have the

potential to be resilient to disturbance after enough time without further disturbance occurring.

Predicting the recovery speed of PD compared to SR is not an easy task when predictions are based only on phylogenetic structure patterns through succession. More than half of the studied groups followed our hypothesis that PD recovers after SR, including frogs, frugivorous birds, bats, ants, and dung beetles. This is interesting because this hypothesis was based on the assumption that closely related species, which would contribute lower PD than distantly related species, colonize habitats during early regeneration (30–32) while distantly related species colonize habitats during later stages of regeneration (32,35). This pattern was only observed for frugivorous birds and partially for bats. Contrary, frogs showed a pattern of decreasing overdispersion while ants and dung beetles showed random phylogenetic structure, but nonetheless, their PD recovered after their SR. On the other hand, PD recovered before SR for trees, vocalizing birds, and bees. This could be expected under a pattern of decreasing overdispersion, which was actually observed for bees and partially for trees while vocalizing birds showed random structure. Our results suggest that a faster recovery of PD compared to SR can be associated with increasing phylogenetic overdispersion and that a slower recovery of PD could occur because of decreasing phylogenetic overdispersion. Nevertheless, particular cases such as frogs or those with random phylogenetic structure suggest that other factors are involved in the recovery of PD and SR besides phylogenetic branch lengths, and could include the slope and direction of the recovery trend, the diversity levels of old-growth forests, and other intrinsic aspects of each taxonomic group. It seems like making generalizations about the recovery of PD considering phylogenetic structure patterns only is difficult as several factors including idiosyncratic patterns of diversification, dispersal, and the relative importance of local-scale abiotic and biotic filters for each group may influence the time at which PD and SR recover towards the levels of old-growth forests. Our predictions are however a first attempt to relate PD recovery patterns with phylogenetic structure during forest succession.

(b) Patterns of phylogenetic structure

Only frugivorous birds strictly follow the expectation of phylogenetic clustering at early stages of forest regeneration and phylogenetic overdispersion at late stages. We determined that phylogenetic clustering in frugivorous birds was driven by elevation during early regeneration and by distance to the nearest forest during late regeneration. Because elevation is inherently related to topographic variation and forest structural complexity changes, we argue that environmental filtering promotes the coexistence of closely related species of frugivorous birds shortly after disturbance (22,31). Elevation is associated with changes in abiotic factors such as temperature and precipitation, and with biotic ones such as vegetation structure or competition (74,75). However, these changes are usually the result of stronger altitudinal gradients than the ones we report here. Thus, it is interesting that microclimatic variation can promote phylogenetic clustering at the spatial scale of our study. Elevation can influence taxonomic diversity patterns for tropical frugivorous birds (76), and apparently it can also promote phylogenetic clustering during early regeneration. Phylogenetic overdispersion during late regeneration is potentially shaped by biotic factors evidenced by the increase of overdispersion with decreasing distance to the nearest forest, meaning that plots harboring distantly related species tend to be within or close to old-growth forests. It is therefore possible that competition for the obtention of resources, which are expected to be higher within old-growth forests, has allowed the coexistence of distantly related species with disparate functional traits during late regeneration. This also suggests that these forests work as a refuge from which species and individuals can colonize suitable habitats and compete with established species, which would depend on their dispersal capacity (77). Assuming that PD can be used as a surrogate of functional trait diversity (22,24), we suggest that low functional trait diversity could be expected during early regeneration because of low PD and phylogenetic clustering while an increase in trait diversity would occur during late regeneration for this group because of increased PD and phylogenetic overdispersion. The analyzed frugivorous bird species assemble as expected under the ecological theory of succession, following a pattern of increasing phylogenetic overdispersion shaped by environmental filtering during early regeneration and by biotic variables during late regeneration.

In this study, bats partially followed a similar pattern as birds because we detected a tendency to overdispersion during late succession at shallow phylogenetic

scales (i.e. the tips of the phylogeny). Since phylogenetic clustering was not detected for bats during early regeneration, environmental filtering was not expected to shape their phylogenetic structure, as it was observed. Nevertheless, phylogenetic overdispersion detected during late regeneration was not either shaped by distance to the nearest forest although phylogenetic overdispersion has been generally attributed to competitive exclusion and the extinction of closely related and functionally similar species (22,45,78). Thus, other biotic factors related to dispersal capacity may have promoted phylogenetic overdispersion for bats because colonization of distant relatives, rather than extinction of close relatives, drives phylogenetic and functional overdispersion over succession (79). Random phylogenetic structure in tropical bats has also been observed irrespective of the forest disturbance status (54,80). However, contrary to our results, phylogenetic clustering has been detected for tropical bats in disturbed habitats (80–82). Taken together, these results suggest that tropical bat communities can present idiosyncratic phylogenetic structure patterns depending on intrinsic factors from each site. Bats and frugivorous birds share similar patterns of phylogenetic overdispersion during late regeneration which could be promoted, but not limited, by their dispersal capacity.

Understory frogs showed the opposite pattern than frugivorous birds, with phylogenetic overdispersion during early regeneration and phylogenetic clustering during late regeneration. This pattern may have arisen because of the high richness of frogs from the genus *Pristimantis*, particularly in old-growth forests, as it is known that the Chocó region and the tropical Andes are diversification hotspots for this genus (83). In contrast, early regenerating habitats allow the presence of species from distant lineages to *Pristimantis*, such as those from the genus *Leptodactylus*, which are more tolerant to habitat disturbance. Although environmental conditions after disturbance can promote phylogenetic clustering (33,34), this promoted phylogenetic overdispersion for frogs instead of phylogenetic clustering as it would be expected (31,32). This suggests that frog skin features that allow them to survive low humidity or high temperatures may have appeared multiple times during the evolution of the amphibian species recorded during our study, making possible the coexistence of distantly related species at early regeneration stages. Therefore, variables related to competition for the obtention of resources could be promoting phylogenetic overdispersion for frogs during early

regeneration. During late regeneration, phylogenetic clustering is shaped by different environmental and biotic factors, particularly at deep phylogenetic scales. As with frugivorous birds, environmental filtering shapes phylogenetic clustering as expected (22,31), although during late regeneration. However, biotic factors may be also involved in generating this pattern because phylogenetic clustering decreased with distance to the nearest forest. Given that climatic conditions are harsher for frogs outside forests because of lower humidity and higher temperatures, distantly related species would be able to tolerate the harsh environmental conditions of disturbed habitats. This supports our hypothesis that traits allowing these frogs to survive in disturbed habitats may have appeared through convergent evolution. Our findings for frogs are interesting because they show that the role of environmental filtering promoting phylogenetic clustering is not limited to early regenerating stages as it can also occur during late regeneration.

Bees, similar to frogs, also display a pattern of phylogenetic overdispersion during early regeneration and phylogenetic clustering during late regeneration. This pattern may be the result of increasing diversity of meliponines as forest regenerates; however, it is not shaped by any of the variables tested here. Phylogenetic overdispersion and high PD during early regeneration suggests that high functional diversity would be expected during this stage if PD is assumed as a surrogate of functional trait diversity (22,24). On the other hand, phylogenetic clustering and lower PD during late regeneration suggests that functional trait diversity decreases for bees with succession. Phylogenetic overdispersion during early regeneration is probably shaped by ground-nesting opportunities and diverse floral resources, which would allow the presence of species with high trait diversity that can use the available resources. During late regeneration, higher elevation and lower temperature promote a strong pattern of phylogenetic clustering at deep phylogenetic scales. Elevation and temperature are apparently strong predictors of bee diversity as it has also been observed that increasing elevation and decreasing temperature promote a decrease in bee taxonomic diversity (84,85). In line with our results, bumble bees' communities show phylogenetic and trait clustering at local and regional scales suggesting that this pattern of structure may be common for members of the Apidae family (86). Our results for bees add evidence on the role of environmental filtering in promoting phylogenetic clustering not only during early regeneration but also during late regenerating stages.

Angiosperm trees show random phylogenetic structure during early regeneration but also a tendency to phylogenetic clustering during late succession at the tips of their phylogeny. Although climate correlates with phylogenetic structure during early regeneration, it is not strong enough to promote phylogenetic clustering at this stage as it would be expected (22). On the other hand, phylogenetic clustering detected during late regeneration is not shaped by environmental filtering but it could be explained by recent and even potential ongoing diversification in the Chocó (87). Although migration without subsequent in-situ speciation is the most common pattern of plant diversification in the Chocó, its high species endemism but low genera endemism suggests low morphological differences among diversifying lineages (87). Therefore, we suggest that closely related tree species surveyed here are able to coexist through functional redundancy as they potentially share similar traits (31). Closely related tree species, such as sister species or those within the same genus, can inhabit habitats at late stages of regeneration such as old-growth forests (49). Consequently, many genera are represented by at least two species within a single old-growth forest plot studied here. We observed, among other examples, up to six species of the genus *Guarea* or up to four species of the genera *Eschweilera*, *Miconia*, and *Inga* within a single plot. Interestingly, all these genera belong to different families such as Meliaceae, Lecythidaceae, Melastomataceae, or Fabaceae, among others, explaining the lack of phylogenetic clustering at deep nodes. The pattern of increasing clustering observed agree with few studies in subtropical regions (49,53), but contrast to many others in tropical and temperate forests where overdispersion occurs during late regeneration (15,36,37,45,47–50). These contrasting patterns of phylogenetic structure show that increasing overdispersion is not a mandatory pattern for trees as most of previous evidence suggested. Our results also show that phylogenetic clustering is not always shaped by environmental conditions, contrary to what was observed here for frugivorous birds, frogs, and bees.

Vocalizing birds, ants, and dung beetles show random phylogenetic structure, with some plots harboring clustered and overdispersed groups of species distributed at different regeneration stages. Random phylogenetic structure in vocalizing birds is not shaped by any of the variables tested here, which contrasts to what was observed for frugivorous birds. This pattern may have appeared because this group includes all birds

555 performing sounds, which are not necessarily interacting or competing for resources as
556 frugivorous birds do. Regarding ants, random phylogenetic structure was detected even
557 though soil composition has some influence at shallow phylogenetic scales during early
558 regeneration; however, it is not strong enough to promote any pattern of structure. This
559 random pattern may have appeared because tropical ant species tend to be habitat and
560 resource generalists (88) and therefore they may be able to develop in any habitat
561 irrespective of its regeneration status. We found similar results as Hoenle et al. (11) who
562 detected random phylogenetic structure for ants sampled in many of the plots analyzed
563 here. Furthermore, our results for ants do not agree with previous research where
564 phylogenetic clustering and overdispersion were observed at habitats with different
565 degrees of disturbance and elevations (51,52,89) showing that ant communities can be
566 phylogenetically structured. The lack of phylogenetic structure for dung beetles may
567 occur because they also tend to be habitat and resource generalists (90,91). For instance,
568 20 out of the 23 species and morphospecies identified here are considered generalists.
569 Our results on dung beetles do not agree either with previous research because
570 phylogenetic clustering and overdispersion were also detected under different degrees of
571 disturbance and elevations (92–94). The phylogenetic patterns observed for vocalizing
572 birds, ants, and dung beetles analyzed in this paper suggest that generalist groups
573 develop random phylogenetic structure as they do not face the pressures that habitat
574 disturbance or resource availability can imprint in their evolutionary dynamics.

575

576 **(d) Conclusions**

577 In this study, we determined that proposing generalizations on phylogenetic patterns
578 with respect to how tree and animal groups respond to forest disturbance is not an easy
579 task because each group responded differentially to eco-evolutionary dynamics. For
580 instance, we detected partial congruence with our hypothesis that SR recovers before
581 PD during forest succession potentially because it was based on the assumption that
582 phylogenetic overdispersion increases with succession (45,46). Consequently, we
583 rejected this assumption as a common phylogenetic pattern through forest succession
584 because we detected it in only two of the eight taxonomic groups analyzed here. In
585 addition, our results did not always agree with others obtained for similar groups in
586 other regions. This strengthens the idea that phylogenetic patterns cannot be generalized

because they also depend on intrinsic factors to each group, besides biotic and abiotic ones (22). In spite of this, we were able to determine that the studied communities are resilient to forest disturbance from an evolutionary perspective because their PD can recover after some time under natural regeneration. This in turn assures the long-time permanence and functioning of the studied communities in the future.

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Data accessibility. Open Research statement: Data and code will be provided as private-for-peer review.

Competing interests. We have no competing interests.

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Tables

Table 1. Results of Pearson correlations between phylogenetic diversity and species richness with (square-root transformed) regeneration time. Old-growth forest plots are not included in the correlations because of their unknown time of regeneration. Values in bold represent statistical significance ($p < 0.05$).

	Phylogenetic diversity		**Species richness**	
	Pearson's *r*	***p***	**Pearson's *r***	***p***
Trees	0.76	**<0.001**	0.72	**<0.001**
Frogs	0.34	0.07	0.43	**0.02**
Frugivorous birds	0.58	**<0.001**	0.19	0.29
Vocalizing birds	-0.35	**0.02**	-0.36	**0.02**
Bats	0.24	0.11	0.17	0.26
Ants	0.36	**0.02**	0.45	**<0.01**
Dung beetles	0.4	**0.01**	0.42	**<0.01**
Bees	-0.53	**<0.001**	-0.31	**0.04**

Table 2. Results of the Pearson correlations between ses.MPD and ses.MNTD with (square-root transformed) regeneration time. Old-growth forest plots are not included in the correlations because of their unknown time of regeneration. Values in bold represent statistical significance ($p < 0.05$).

	ses.MPD		**ses.MNTD**	
	Pearson's *r*	***p***	**Pearson's *r***	***p***
Trees	-0.05	0.73	-0.15	0.35
Frogs	-0.72	**<0.001**	-0.67	**<0.001**
Frugivorous birds	0.64	**<0.001**	0.57	**<0.001**
Vocalizing birds	0.27	0.07	0.01	0.94
Bats	0.26	0.09	0.2	0.2
Ants	-0.2	0.18	-0.3	0.05
Dung beetles	-0.33	0.07	-0.28	0.12
Bees	-0.63	**<0.001**	-0.63	**<0.001**

Figures

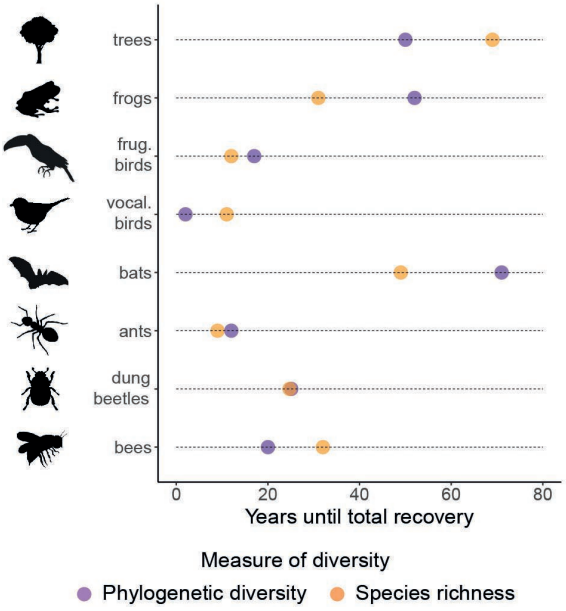
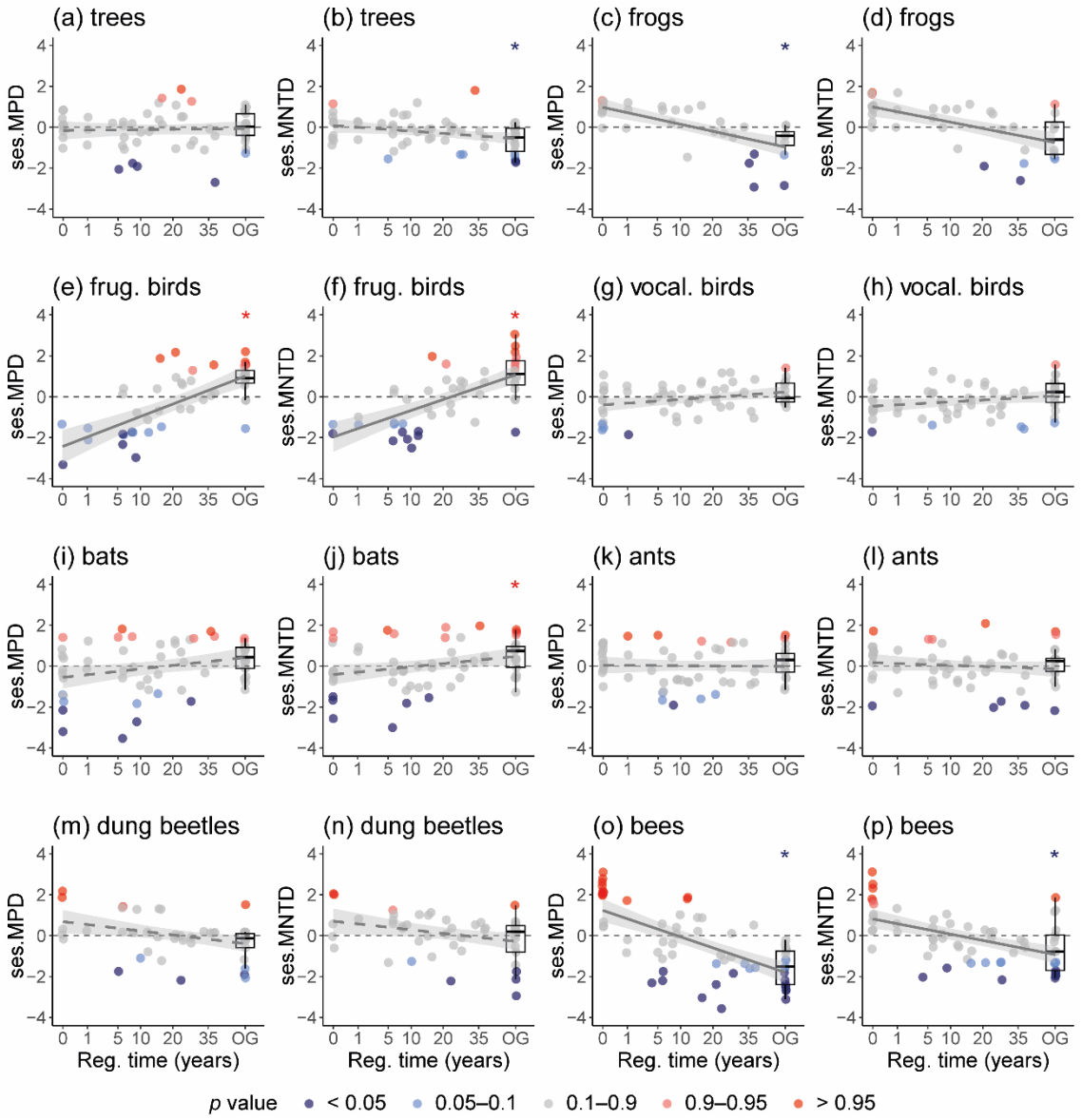


Figure 1. Estimated recovery time of phylogenetic diversity and species richness in trees and animals based on linear models..



911

912 Figure 2. Changes in the phylogenetic structure measures ses.MPD (a, c, e, g, i, k, m,o)
913 and ses.MNTD (b, d, f, h, j, l, n,p) along the chronosequence in trees and animals. Solid
914 trend lines represent statistical significance ($p < 0.05$) in the Pearson correlations
915 between ses.MPD and ses.MNTD with (square-root transformed) regeneration time.
916 Old-growth (OG) forest plots are not included in the correlations because of their
917 unknown time of regeneration. A blue asterisk (*) means that OG forest plots as a
918 category are phylogenetically clustered while a red asterisk means that OG forest plots
919 as a category are phylogenetically overdispersed based on two-tailed Wilcoxon tests.

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SUPPLEMENTARY MATERIAL

Recovery of phylogenetic diversity and phylogenetic structure in trees and animals along a chronosequence of tropical forest regeneration

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1. Supplementary Material and methods

(a) Sampling

The tree survey occurred from February 2022 to July 2023 and comprised wild tree species identification and labeling of all individuals ≥ 25 cm of circumference at 1.3 m above the ground (≥ 7.95 cm diameter at breast height, DBH), including palms and lianas (see Escobar et al., 2025). Since we are only working with wild angiosperm trees for this study, ferns were not included in the dataset despite having a circumference ≥ 25 cm. Tree identification was performed at the Herbario Nacional del Ecuador–INABIO using the collections deposited there as references. In total, 7542 cultivated and non-cultivated trees were surveyed.

For understory frogs, three surveys were conducted. The first round occurred between March–June 2022, the second between July–October 2022, and the third between March–June 2023. We conducted visual searches over two person-hours, scanning from the leaf-litter to approximately 1.2 meters in height. Understory frogs were captured and identified using the BioWeb online service (https://bioweb.bio/faunaweb/amphibiaweb). To minimize potential time effects on the results, sampling was alternated across different habitat types. Each plot was sampled six times: three times during the day and three times at night, across three rounds.

For the frugivorous bird survey, we recorded plant-frugivore interactions using two different methods twice a year, during March–June (wet season) and September–December (dry season) in 2021 and 2022. In the upper forest layers including the canopy, we conducted direct observations of seed dispersal interactions using binoculars. At each plot, observations were conducted for 5 hours starting at sunrise over three consecutive days. On the forest floor or understory, interactions were recorded by deploying available fruits in front of four camera traps that continuously recorded for six days. The cameras were distributed across the four corners of each plot.

Vocalizing birds were identified by expert ornithologists using audio files recorded in each plot (see Müller et al., 2023; Falconí-López et al., 2024). One recorder with an omnidirectional microphone was set facing down at 1.7 m above ground at the center of each of the plots in October 2021. Recorders were programmed to record two minutes every 15 minutes during two weeks. Each recording was digitized and species

were identified by two ornithologists independently by listening to two-minutes recordings at 06:00 h, 06:15 h, 06:30 h, 06:45 h, 07:00 h, 07:15 h, 12:00 h, 12:15 h, 16:00 h, 16:15 h, 17:00 h, 17:15 h, 18:00 h and 18:15 h on days without heavy rain. These schedules cover high activity phases of birds around dusk and dawn and also flock activities during the day.

Bat sampling was conducted in four field campaigns from March 2022 to December 2023, during the dry and rainy seasons. In each plot, six mist nets of 6 x 2.5 m were set at ground level from 18h30 to 24h00 (5.5 hours) during three consecutive nights. Mist nets were checked approximately every 30 minutes and captured individuals were manipulated based on Sikes et al. (2016) and Erazo et al. (2022). General morphometric measurements were taken from captured individuals, as well as data on sex, age and reproductive status. Identification and taxonomic classification were carried out using updated guides, keys, and species lists (e.g., Díaz et al., 2021; Tirira et al., 2024; Simmons and Cirranello 2024). 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 (Sikes et al., 2016).

Ants were collected using three different methods. First, we collected ants during February–April 2022 (wet season) using winkler traps and by hand from the ground and trees as described by Hoenle et al. (2022). Additionally, ants were collected in an experimental approach with wood from five different species during August–September 2022 (dry season). One piece of wood with a diameter of 7–10 cm and a length of 50 cm originating from *Trema micrantha* (‘sapanillo’), *Theobroma cacao* (‘cacao’), *Inga* sp. (‘guaba’), *Triplaris cumingiana* (‘Fernán Sánchez’) and *Hieronyma chocoensis* (‘macarey’) trees were placed on each plot. After 6 months, the wood was retrieved and reared in emergence chambers which consisted of mesh tubes made of fabric used for insect nets and a falcon tube filled with ethanol. Ants emerging from the wood and falling into the ethanol were collected during 3 months.

For dung beetle collection, four pitfall traps were set 50 m apart within each plot to avoid trap interference. The traps were one-quarter filled with 70% ethanol, and two large 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. The traps were

collected after 48 hours, emptied into containers, and transported back to the lab. Dung beetles were separated from other arthropods in the lab and stored in pure ethanol.

For bees, three distinct collection methods were employed. In each plot, we set: (i) one adapted vane trap with transversal yellow and blue vanes (Rentería and Brehm, 2025), which targeted mainly stingless bees (Apidae: Meliponini). These were set at ground level (1.5 m) and consisted of the pair of vanes connected to a funnel which intercepted bees to a collection bucket. Chloroform fumes were used as dry fast killing agents. Traps remained active for 24h on the plot. We set one vane trap per plot in 2022 (32 plots in between March-May, 30 plots between October-December) and one trap per plot in 2023 (same plot distribution). Additionally, we set (ii) four fragrance traps per plot, each with a different fragrances (Cineole, Methyl Salicylate, Skatole and Eugenol) targeted at male orchid bees (Apidae: Euglossini). The traps were adaptations of (Ferreira et al., 2013). Fragrance traps were set in 2023 only and followed the same pattern of vane traps. Finally, we employed 4 hours of active netting per plot, during which the entire area of the plot was walked and all flying bees were captured. Bees were identified with specialized keys (e.g., Bonilla-Gómez & Nates-Parra, 1992; Roubik, 1992; Michener, 2007).

(b) Phylogenies reconstruction

We pruned the mega-phylogeny for seed plants *GBOTB.extended.TPL.tre* stored in the R package V.PHYLOMAKER2 (Jin & Qian, 2022) to obtain a tree community phylogeny. This package adds species that are not included in the mega-phylogeny as polytomies at the base or node of their respective genera. Although this approach reduces the resolution of phylogenetic trees, species-level phylogenies resolved at genus level with polytomies have proved useful for exploring phylogenetic structure in ecological communities along ecological gradients (Qian & Jin, 2021) such as forest regeneration. We used the option *build.nodes.1* and the *S3* scenario to build the phylogeny as this scenario is the most commonly used (Jin & Qian, 2022). To build the phylogenies for animals, we pruned mega-phylogenies using the package APE (Paradis & Schliep et al., 2019). We then attached species or morphospecies manually as polytomies to the base of their genera if these were not included in the mega-phylogenies using the package

PHANGORN (Schliep, 2011). For this purpose, we used our own taxonomic knowledge or consulted smaller published phylogenies of specific groups. If needed, we left in the mega-phylogenies one or two distantly related species from the same genus that were not originally included in the community data to attach species to that genus manually, and then removed the species used only for the placement of others. For frogs, we pruned the time-calibrated mega-phylogeny available at Portik et al. (2023) using our community data. We attached three species and morphospecies manually to the community phylogeny and removed one species that was left for the attachment of one of the three attached species. Regarding birds, we pruned a time-calibrated mega-phylogeny of all birds (Jin & Qian, 2023) and only added one species and one morphospecies to the community phylogeny for frugivorous birds and none for vocalizing birds. For bats, we pruned the time-calibrated mega-phylogeny from Shi & Rabosky (2015), attached four species and morphospecies manually, and removed two species. For ants, we also used a time-calibrated mega-phylogeny (Economo et al. 2018) to which we attached 160 species and morphospecies and then removed 40 species. For dung beetles we used a maximum-likelihood unroot mega-phylogeny (Tarasov & Dimitrov 2016) which we rooted using the outgroup of the study before attaching 18 species and morphospecies and then removing 22 species and morphospecies. Finally, for bees we used a dated phylogeny (Henríquez-Piskulich et al., 2024) to which we attached 93 species and morphospecies, posteriorly removing 41 species.

Supplementary Tables

Table S1. Results of linear models on the influence of abiotic and biotic factors on phylogenetic structure (ses.MPD and ses.MNTD) during early forest regeneration (plots 0–15 years of regeneration). Values in bold represent statistical significance ($p < 0.05$).

	trees - ses.MPD				**trees - ses.MNTD**			
	Sum Sq	**df**	***F***	***p***	**Sum Sq**	**df**	***F***	***p***
Elevation	0.98	1	1.6	0.22	0.79	1	1.87	0.19
Climate PCA	2.86	1	4.6	**0**	1.96	1	4.65	**0.04**
Soil PCA	0.01	1	0	0.92	0.55	1	1.29	0.27
Soil texture	0.62	3	0.3	0.8	1.45	3	1.15	0.35
Dist. to forest	0.27	1	0.4	0.52	0.07	1	0.17	0.69
Residuals	12.37	20			8.45	20		
	frogs - ses.MPD				**frogs - ses.MNTD**			
Elevation	0.09	1	0.2	0.7	0.42	1	0.7	0.42
Climate PCA	0.01	1	0	0.88	0.05	1	0.08	0.78
Soil PCA	0.09	1	0.2	0.69	0.65	1	1.08	0.32
Soil texture	0.79	3	0.5	0.69	1.64	3	0.91	0.47
Dist. to forest	0.92	1	1.7	0.21	0.56	1	0.94	0.35
Residuals	5.83	11			6.57	11		
	frugivorous birds - ses.MPD				**frugivorous birds - ses.MNTD**			
Elevation	8.41	1	7.3	**0**	8.04	1	16.24	**< 0.01**
Climate PCA	0.06	1	0.1	0.83	0.02	1	0.03	0.86
Soil PCA	0.78	1	0.7	0.43	0.0005	1	0.001	0.98
Soil texture	2.66	3	0.8	0.54	1.16	3	0.78	0.53
Dist. to forest	1.14	1	1	0.34	0.27	1	0.54	0.48
Residuals	11.55	10			4.95	10		
	vocalizing birds - ses.MPD				**vocalizing birds - ses.MNTD**			
Elevation	1.44	1	2.5	0.13	0.22	1	0.44	0.51
Climate PCA	0.6	1	1.1	0.31	0.003	1	0.01	0.94
Soil PCA	0.67	1	1.2	0.29	0.02	1	0.05	0.83
Soil texture	1.98	3	1.2	0.35	0.47	3	0.31	0.82
Dist. to forest	0.13	1	0.2	0.64	1.72	1	3.4	0.08
Residuals	12.47	22			11.1	22		
	bats - ses.MPD				**bats - ses.MNTD**			
Elevation	0.03	1	0	0.9	0	1	2E-04	0.99
Climate PCA	8.01	1	3.9	0.06	4.67	1	2.82	0.11
Soil PCA	0.01	1	0	0.94	0.28	1	0.17	0.69
Soil texture	4.09	3	0.7	0.59	3.42	3	0.69	0.57
Dist. to forest	0.12	1	0.1	0.81	0.31	1	0.19	0.67
Residuals	45.55	22			36.36	22		

	ants - ses.MPD				**ants - ses.MNTD**			
Elevation	0.29	1	0.4	0.56	0.44	1	0.82	0.38
Climate PCA	3.37	1	4.2	0.05	0.52	1	0.96	0.34
Soil PCA	1.6	1	2	0.17	3.32	1	6.18	**0.02**
Soil texture	3.22	3	1.3	0.29	1.08	3	0.67	0.58
Dist. to forest	1.08	1	1.3	0.26	1.52	1	2.82	0.11
Residuals	18.52	23			12.35	23		
	dung beetles - ses.MPD				**dung beetles - ses.MNTD**			
Elevation	0.52	1	0.5	0.5	1.64	1	2.04	0.18
Climate PCA	0.01	1	0	0.92	0.13	1	0.17	0.69
Soil PCA	0.55	1	0.5	0.49	0.001	1	0.002	0.97
Soil texture	5.16	3	1.6	0.25	4.96	3	2.06	0.16
Dist. to forest	3.78	1	3.5	0.09	2.91	1	3.62	0.08
Residuals	12.03	11			8.84	11		
	bees - ses.MPD				**bees - ses.MNTD**			
Elevation	0.01	1	0	0.94	0.08	1	0.05	0.83
Climate PCA	3.43	1	1.5	0.24	3.2	1	1.97	0.17
Soil PCA	1.89	1	0.8	0.38	2.29	1	1.41	0.25
Soil texture	13	3	1.8	0.17	5.26	3	1.08	0.38
Dist. to forest	3.51	1	1.5	0.24	0.38	1	0.23	0.64
Residuals	54.43	23			37.3	23		

Table S2. Results of linear models on the influence of abiotic and biotic factors on phylogenetic structure (ses.MPD and ses.MNTD) during late forest regeneration (plots 16–38 years of regeneration). Values in bold represent statistical significance ($p < 0.05$).

	trees - ses.MPD				**trees - ses.MNTD**			
	Sum Sq	**df**	***F***	***p***	**Sum Sq**	**df**	***F***	***p***
Elevation	0.7	1	0.62	0.44	0	1	0	0.95
Climate PCA	0.84	1	0.74	0.4	0.17	1	0.3	0.59
Soil PCA	0.01	1	0.01	0.92	0.65	1	1.2	0.29
Soil texture	1.27	6	0.19	0.98	3.41	6	1.05	0.43
Dist. to forest	1.68	1	1.49	0.24	0.4	1	0.73	0.4
Residuals	22.52	20			10.86	20		
	frogs - ses.MPD				**frogs - ses.MNTD**			
Elevation	4.53	1	28.7	**< 0.001**	1.78	1	4.49	0.06
Climate PCA	0.22	1	1.4	0.27	7.11	1	17.9	**< 0.01**
Soil PCA	0.14	1	0.9	0.37	0.23	1	0.58	0.47
Soil texture	3.02	4	4.78	**0.02**	5.08	4	3.2	0.07
Dist. to forest	1.9	1	12.1	**0.01**	0.9	1	2.27	0.17
Residuals	1.42	9			3.57	9		
	frugivorous birds - ses.MPD				**frugivorous birds - ses.MNTD**			
Elevation	0.1	1	0.09	0.76	0.02	1	0.01	0.92
Climate PCA	0.01	1	0.01	0.93	0.15	1	0.1	0.75
Soil PCA	0.02	1	0.02	0.89	0.13	1	0.09	0.77
Soil texture	4.78	6	0.77	0.61	4.09	6	0.45	0.83
Dist. to forest	6.11	1	5.89	**0.03**	7.35	1	4.9	**0.04**
Residuals	19.73	19			28.53	19		
	vocalizing birds - ses.MPD				**vocalizing birds - ses.MNTD**			
Elevation	0.04	1	0.07	0.79	1.12	1	2.04	0.17
Climate PCA	0.01	1	0.01	0.91	0.04	1	0.06	0.8
Soil PCA	0.3	1	0.59	0.45	0.42	1	0.77	0.39
Soil texture	1.03	6	0.34	0.91	5.11	6	1.56	0.21
Dist. to forest	0.12	1	0.24	0.63	1	1	1.82	0.19
Residuals	10.06	20			10.95	20		
	bats - ses.MPD				**bats - ses.MNTD**			
Elevation	3.34	1	4.26	0.05	1.94	1	2.33	0.14
Climate PCA	0.08	1	0.11	0.75	0.21	1	0.25	0.62
Soil PCA	1.08	1	1.39	0.25	0.23	1	0.27	0.61
Soil texture	3.88	6	0.83	0.56	1.66	6	0.33	0.91
Dist. to forest	0.004	1	0.01	0.94	0.16	1	0.19	0.67
Residuals	15.64	20			16.66	20		
	ants - ses.MPD				**ants - ses.MNTD**			
Elevation	0.33	1	0.57	0.46	0.57	1	0.52	0.48
Climate PCA	2.85	1	4.99	0.04	3.27	1	2.95	0.1

Soil PCA	0.97	1	1.69	0.21	3.87	1	3.5	0.08
Soil texture	8.56	6	2.5	0.06	5.36	6	0.81	0.58
Dist. to forest	1.57	1	2.76	0.11	0.29	1	0.27	0.61
Residuals	11.43	20			22.14	20		
	dung beetles - ses.MPD				**dung beetles - ses.MNTD**			
Elevation	0.06	1	0.08	0.78	0.73	1	0.67	0.42
Climate PCA	1.48	1	1.97	0.18	3.29	1	3.02	0.1
Soil PCA	0.81	1	1.08	0.31	0.98	1	0.9	0.36
Soil texture	3.22	6	0.72	0.64	3.83	6	0.59	0.74
Dist. to forest	0.01	1	0.01	0.93	0.1	1	0.09	0.76
Residuals	14.22	19			20.7	19		
	bees - ses.MPD				**bees - ses.MNTD**			
Elevation	5.42	1	5.09	**0.04**	0.01	1	0.01	0.94
Climate PCA	0.69	1	0.64	0.43	0.12	1	0.09	0.77
Temperature	8.9	1	8.35	**< 0.01**	0.25	1	0.18	0.67
Soil PCA	0.05	1	0.05	0.83	0.001	1	0	0.95
Soil texture	9.07	6	1.42	0.25	5.93	6	0.74	0.62
Dist. to forest	0.94	1	0.64	0.74	0.1	1	0.07	0.79
Residuals	20.24	19			25.39	19		

Table S3. Assumptions of the linear models on the influence of abiotic and biotic factors on phylogenetic structure (ses.MPD and ses.MNTD) during early forest regeneration (plots 0–15 years of regeneration). Assumptions include: 1) Pearson correlations between fitted and residual values of the models for testing the lack of variance homogeneity; 2) Barlett tests also for testing the lack of variance homogeneity; 3) Moran's I tests for determining the lack of spatial autocorrelation of the model residuals. Values in bold represent statistical significance ($p < 0.05$).

	ses.MPD		**ses.MNTD**	
	Pearson's *r*	***p***	**Pearson's *r***	***p***
Trees	-9.95E-17	1	-2.40E-16	1
Frogs	-1.60E-16	1	-5.92E-17	1
Frugivorous birds	5.82E-18	1	-5.62E-17	1
Vocalizing birds	-2.23E-17	1	6.85E-17	1
Bats	-6.18E-17	1	7.22E-17	1
Ants	5.98E-18	1	-2.82E-18	1
Dung beetles	1.74E-16	1	8.94E-18	1
Bees	2.89E-17	1	-5.77E-17	1
	Barlett K-Sq	***p***	**Barlett K-Sq**	***p***
Trees	0.02	0.88	0.16	0.69
Frogs	4.06	**0.04**	0.97	0.33
Frugivorous birds	0.16	0.69	0.27	0.61
Vocalizing birds	0.49	0.48	2.4	0.12
Bats	0.01	0.92	0.02	0.88
Ants	0.04	0.84	1.87	0.17
Dung beetles	0.35	0.55	0.01	0.93
Bees	0.46	0.5	0.33	0.56
	Moran's *I*obs	***p***	**Moran's *I*obs**	***p***
Trees	-0.03	0.88	-0.06	0.74
Frogs	-0.18	0.2	-0.12	0.58
Frugivorous birds	-0.16	0.4	-0.18	0.32
Vocalizing birds	-0.03	0.92	-0.04	0.95
Bats	0.05	0.27	0.08	0.15
Ants	0.01	0.61	0.05	0.25
Dung beetles	0.01	0.42	0.03	0.35
Bees	0.03	0.44	-0.03	0.95

Table S4. Assumptions of the linear models on the influence of abiotic and biotic factors on phylogenetic structure (ses.MPD and ses.MNTD) during late forest regeneration (plots 16–38 years of regeneration). Assumptions include: 1) Pearson correlations between fitted and residual values of the models for testing the lack of variance homogeneity; 2) Barlett tests also for testing the lack of variance homogeneity; 3) Moran's I tests for determining the lack of spatial autocorrelation of the model residuals. Values in bold represent statistical significance ($p < 0.05$).

	ses.MPD		**ses.MNTD**	
	Pearson's *r*	***p***	**Pearson's *r***	***p***
Trees	4.91E-17	1	1.49E-16	1
Frogs	1.91E-16	1	-1.30E-16	1
Frugivorous birds	2.68E-18	1	-1.17E-16	1
Vocalizing birds	1.07E-16	1	-8.47E-17	1
Bats	-2.81E-16	1	-1.45E-16	1
Ants	8.67E-17	1	1.81E-17	1
Dung beetles	-6.80E-17	1	-1.20E-16	1
Bees	7.94E-18	1	-1.79E-17	1
	Barlett K-Sq	***p***	**Barlett K-Sq**	***p***
Trees	6.03	0.05	1.75	0.42
Frogs	2.6	0.27	1.07	0.59
Frugivorous birds	1.62	0.45	0.7	0.7
Vocalizing birds	1.66	0.44	0.02	0.99
Bats	1.57	0.46	0.03	0.99
Ants	1.34	0.51	2.88	0.24
Dung beetles	0.07	0.97	1.29	0.53
Bees	2.63	0.27	3.74	0.15
	Moran's *I*obs	***p***	**Moran's *I*obs**	***p***
Trees	-0.03	0.36	-0.06	0.63
Frogs	-0.12	0.52	0.01	0.43
Frugivorous birds	-0.1	0.26	-0.7	0.57
Vocalizing birds	-0.07	0.61	-0.14	0.07
Bats	-0.09	0.37	-0.03	0.96
Ants	0.004	0.53	0.1	0.03
Dung beetles	-0.1	0.26	-0.1	0.32
Bees	-0.06	0.66	-0.05	0.76

Supplementary Figures

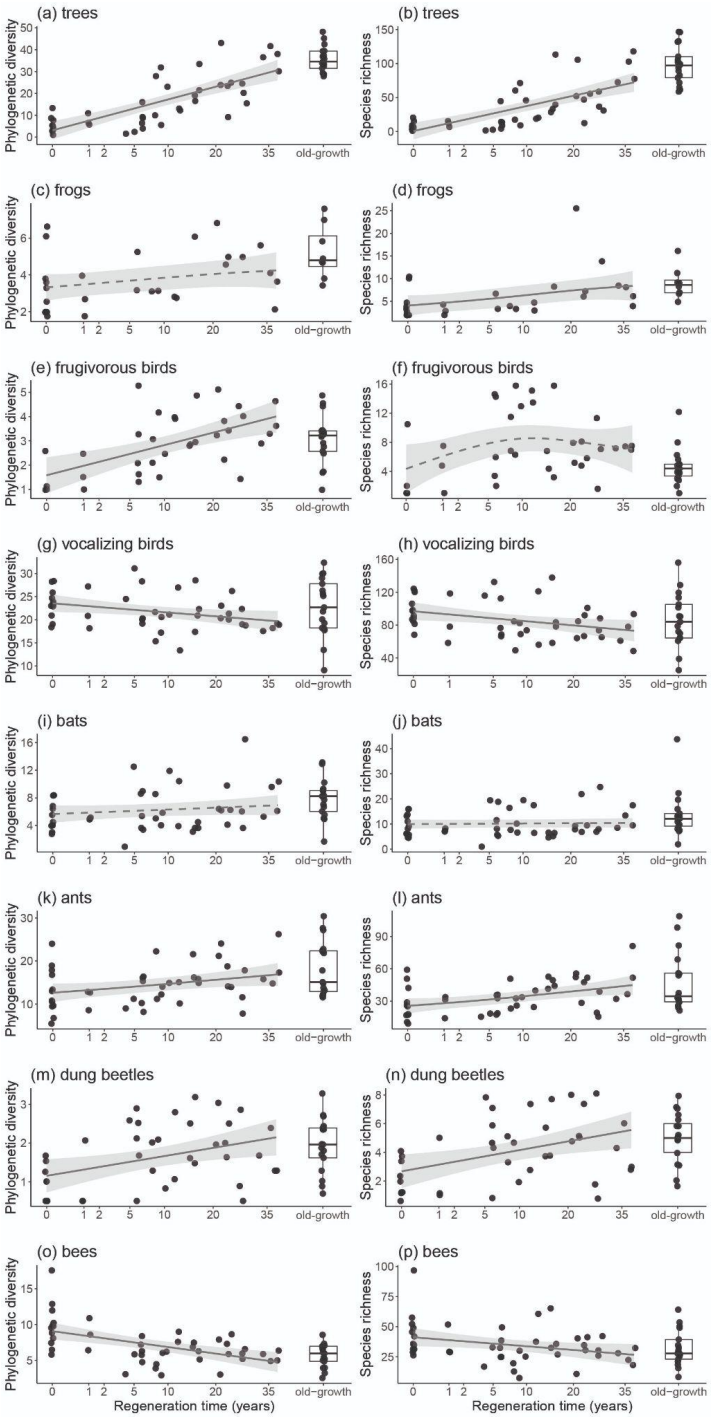

Figure S1. Recovery of phylogenetic diversity and species richness along the chronosequence in trees and animals. Solid trend lines represent statistical significance ($p < 0.05$) in the linear models.

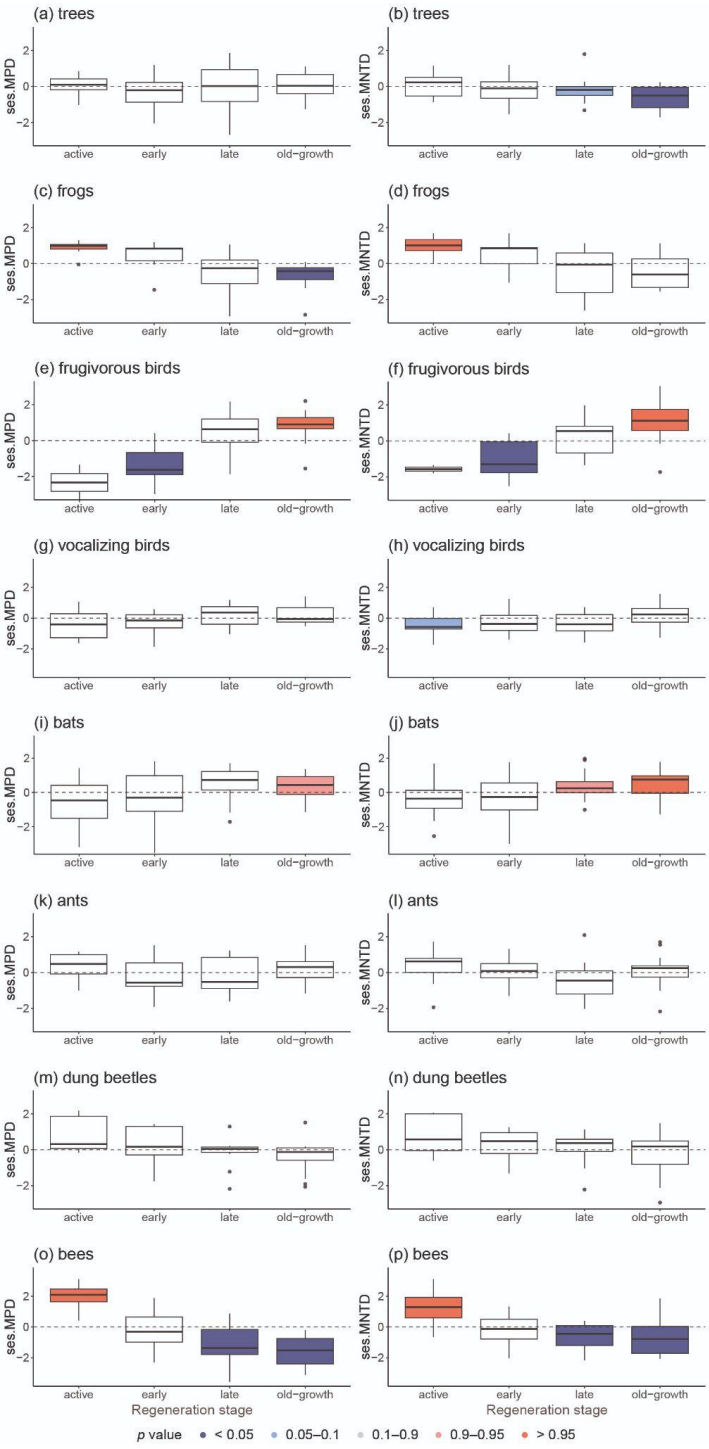

Figure S2. Changes in the phylogenetic structure measures ses.MPD (a, c, e, g, i, k, m) and ses.MNTD (b, d, f, h, j, l, n) between regenerating categories in trees and animals. Significant values below zero indicate phylogenetic clustering (blue) while those over zero indicate overdispersion (red) based on two-tailed Wilcoxon tests. Early regenerating plots range 1–15 years in regeneration, while late regenerating plots range 16–38 years in regeneration.

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