


LETTER

Opposing mechanisms affect taxonomic convergence between tree assemblages during tropical forest succession

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Abstract

Whether successional forests converge towards an equilibrium in species composition remains an elusive question, hampered by high idiosyncrasy in successional dynamics. Based on long-term tree monitoring in second-growth (SG) and old-growth (OG) forests in Costa Rica, we show that patterns of convergence between pairs of forest stands depend upon the relative abundance of species exhibiting distinct responses to the successional gradient. For instance, forest generalists contributed to convergence between SG and OG forests, whereas rare species and old-growth specialists were a source of divergence. Overall, opposing trends in taxonomic similarity among different subsets of species nullified each other, producing a net outcome of stasis over time. Our results offer an explanation for the limited convergence observed between pairwise communities and suggest that rare species and old-growth specialists may be prone to dispersal limitation, while the dynamics of generalists and second-growth specialists are more predictable, enhancing resilience in tropical secondary forests.

Keywords

Determinism, life-history strategies, stochasticity, succession, taxonomic similarity, tropical second-growth forests.

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INTRODUCTION

Forecasting biological responses of transformed landscapes has become an urgent task, as most tropical forests are in some stage of recovery from past human disturbances. A century since Clements (1916) and Gleason's (1926) seminal work on forest succession, the relative roles of determinism and stochasticity in determining plant community reassembly as succession unfolds are still widely debated (Vandermeer *et al.* 2004; Chazdon 2008; Norden *et al.* 2015). Successional theory has been mostly built upon the foundation of niche differentiation theory, where forests regrowing following disturbance gradually recover to their original state (Finegan 1996; Rees *et al.* 2001). Empirical evidence, however, challenges this perspective, suggesting that successional trajectories are idiosyncratic (Vandermeer *et al.* 2004; Norden *et al.* 2015) and do not always lead to a single equilibrium state (Connell & Slatyer 1977). These unpredictable outcomes suggest the existence of multiple basins of attraction, which has been usually approached from a stochastic perspective (Hubbell 2001; Vandermeer *et al.* 2004). When it comes to evaluating successional trajectories in species composition in tropical forests, results are mixed. Several studies have shown high levels of forest resilience after disturbance (Dent & Wright 2009; Letcher & Chazdon 2009; Norden *et al.* 2009) – supporting a

niche-based view of community reassembly, while others have shown that secondary stands diverge floristically over time, suggesting that non-equilibrium processes are at play (Vandermeer *et al.* 2004; Longworth *et al.* 2014; Norden *et al.* 2015). Nevertheless, failure to detect convergence among stands may result from overlooking species-specific responses to the successional gradient.

Indeed, a major issue that has hampered attempts to resolve these conflicting patterns is that most approaches have considered communities as a unit, without acknowledging the fact that species vary widely in the strength of their responses to niche-based processes. Most of the work on succession relies on the paradigm that successional dynamics are driven by the differential ability of light-demanding and shade-tolerant species to thrive in distinct successional stages (Finegan 1996; Rees *et al.* 2001). These life-history strategies, however, represent two extremes of the growth-mortality trade-off. In reality, species responses to environmental conditions vary along a continuum (Wright *et al.* 2010), and it is not always clear how species relate to the local environment. For instance, generalist species perform well across a wide variety of habitats and can represent a significant portion of the individuals in secondary stands (Norden *et al.* 2009; Chazdon *et al.* 2011).

Also, considering species abundance is critical for explaining the different results found across studies. In particular, the

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role of rare species has been overlooked, despite the fact that they prevail in tropical forests (ter Steege *et al.* 2013). Small population sizes and restricted geographical ranges may limit rare species dispersal ability and accentuate their local extinction risk, enhancing compositional divergence among communities (Hubbell 2001). In parallel, dominant species may magnify patterns of taxonomic similarity among assemblages, depending on whether they show a local or widespread spatial distribution, which may promote divergence (Dent *et al.* 2013) or convergence (Norden *et al.* 2009), respectively.

Addressing these issues is essential as species populations may be subject to different strengths of determinism and stochasticity, depending on their responses to biotic and abiotic variables, their population size and the extent of dispersal limitation (Li *et al.* 2016). For instance, the dynamics of light-demanding and shade-tolerant species are likely to be driven by niche-based processes (Finegan 1996), whereas rare species may be more prone to demographic drift (Chase *et al.* 2005) and dispersal limitation (Muller-Landau *et al.* 2002), regardless of their functional response to light availability. If deterministic and stochastic processes operate simultaneously for different subsets of species, patterns of pairwise taxonomic similarity between communities will be the net outcome of these opposing forces, limiting our ability to detect their respective strength.

Here, we evaluate the contribution of different subsets of species to patterns of taxonomic similarity between second-growth (SG) and old-growth (OG) stands, and between pairs of SG stands. We hypothesise that the magnitude of convergence between pairwise communities depends upon the relative abundance of species exhibiting different responses to the successional gradient (Li *et al.* 2016). If niche-based processes drive community dynamics over succession, we predict SG and OG specialists to determine temporal changes in taxonomic similarity among forest patches. Specifically, OG specialists are expected to contribute to convergence between SG and OG, whereas SG specialists are more likely to increase similarity between pairs of SG stands, but to decrease it between SG and OG stands (Fig. 1). Generalists are expected to enhance overall resilience as they typically occur in both SG and OG stands (Norden *et al.* 2009). Conversely, if stochasticity is the major driver of community dynamics, most likely resulting from dispersal-based processes, rare species as well as locally rare OG and SG specialists are expected to be an important source of floristic variation among stands.

We test these scenarios using a unique, long-term data set on tree dynamics in SG and OG stands in Costa Rica. First, we assess whether SG stands converge towards a similar community composition as succession unfolds, and whether the observed patterns are different from those expected by chance. Second, we evaluate which species contribute the most to the observed patterns of similarity between stands. More specifically, we assess whether the strength in convergence (or divergence) in pairwise successional trajectories varies among groups of species with different successional strategies or relative abundances (Fig. 1). Finally, as secondary forests have the potential to recruit many of the species occurring in mature forests, floristic recovery in SG with respect to OG stands is likely to be more conspicuous when considering

earlier life stages (Guariguata *et al.* 1997; Norden *et al.* 2009). Thus, we examine the first two questions by comparing the patterns observed for large and small trees, as these two size classes may reflect past recruitment legacies vs. recent recruitment patterns, respectively.

METHODS

Site description

This study was conducted in and around La Selva Biological Station, northeastern Costa Rica. This region is classified as tropical lowland rainforest, with an average annual temperature of 26.5 °C, and 3900 mm of rainfall (McDade & Hartsorn 1994). We conducted this study in eight 1-ha plots, where the species composition and diameter at breast height (DBH) of all stems ≥ 5 cm DBH have been monitored annually for 10–18 years (Chazdon *et al.* 2007). The eight plots include two OG forest plots and six SG forest plots, which had been regenerating naturally for 10–42 years following pasture abandonment. The elevation of the plots ranges from 40 to 200 m above sea level. In total, our data set included 372 species, of which 359 were woody trees and 13 were palms.

Analyses

Taxonomic similarity

We evaluated temporal trends of taxonomic similarity between plot-pairs using incidence- and abundance-based similarity metrics based on Hill numbers, also called the effective number of species. The effective number of species within an assemblage refers to the number of equally abundant species that are needed to obtain the same value of a diversity measure (Chao *et al.* 2014). When comparing pairs of assemblages, Hill numbers of the pooled assemblages (gamma diversity) can be decomposed into independent alpha and beta components of diversity. The latter can be monotonically transformed into similarity measures (Chao *et al.* 2014), which are more appropriate than other commonly used metrics because Hill numbers obey the replication principle (Jost *et al.* 2011). These similarity measures differ among themselves by a parameter q that determines their sensitivity to species relative abundance. Setting $q = 0$ yields the incidence-based Sørensen index, which weighs all species equally. Setting $q = 1$ yields the abundance-based Horn index, which weighs all individuals equally and thus weighs each species according to its abundance. Setting $q = 2$ yields the abundance-based Morisita-Horn index, which is very sensitive to dominant species, and rare species have little effect on its value (Chao *et al.* 2014).

We calculated these three similarity metrics for all pairwise comparisons between SG and OG forest plots and between SG plots. For each possible plot-pair between SG and OG plots, we calculated similarity between the assemblage recorded in each annual census in SG plots and the first year of data in OG plots ($N = 12$ plot-pairs). We only used the first census data in OG plots, instead of the entire set of annual census data, to avoid the confounding effect of census year in the pairwise comparisons. As OG stands underwent little compositional change over time, similar results were

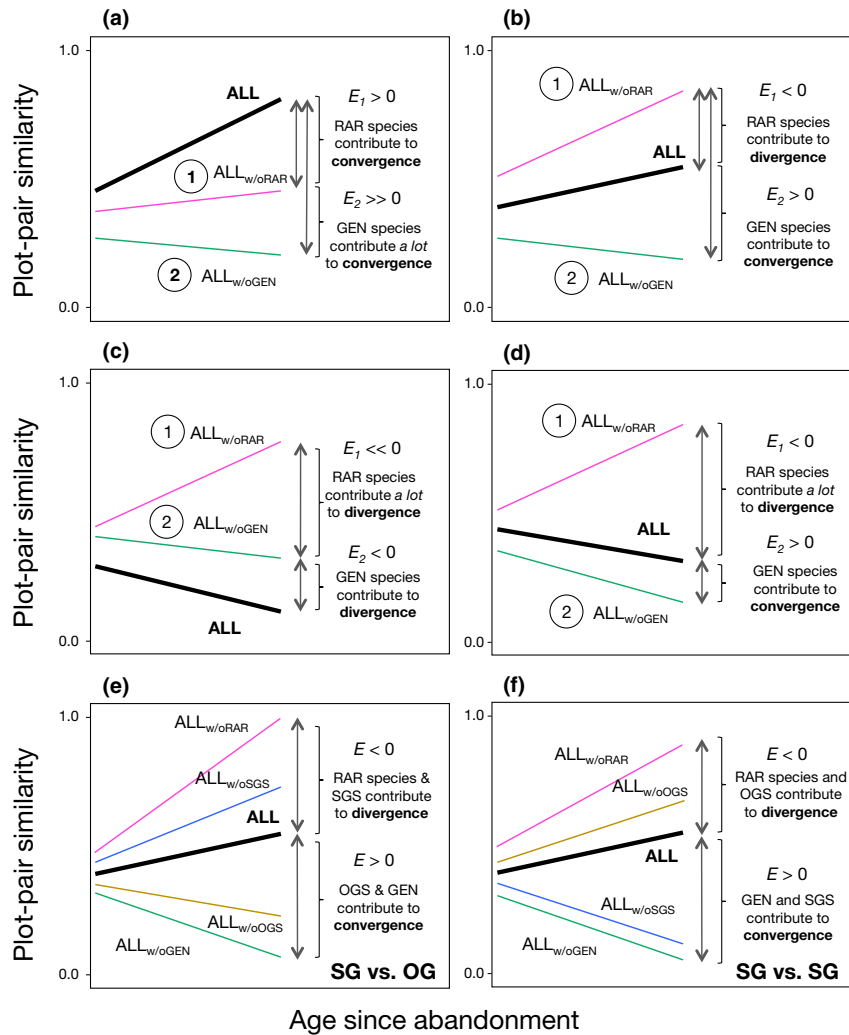


Figure 1 Conceptual model illustrating the potential contribution of generalists (GEN), rare (RAR), second-growth specialists (SGS) and old-growth specialists (OGS) to temporal patterns of taxonomic similarity between plot-pairs. E is the distance between the trajectory that includes all species and each of the four trajectories obtained from the sensitivity analysis (ALL vs. ALL_{w/oSGS}, ALL vs. ALL_{w/oOGS}, ALL vs. ALL_{w/oGEN}, and ALL vs. ALL_{w/oRAR}). (a–d) If $E > 0$, the removal of a group of species decreases taxonomic similarity in a pairwise trajectory over time; in other words, this group contributes to *convergence*. If $E < 0$, the removal of a group of species has the opposite effect, and thus, it contributes to *divergence*. For the sake of clarity, we illustrate the cases of generalist and rare species only. (e, f) Summarised predictions of the expected contribution of GEN, RAR, SGS and OGS to patterns of taxonomic similarity in SG vs. OG (e) and SG vs. SG (f) plot-pair comparisons.

obtained when using data from any other year or the dynamic data from OG plots. For the SG-OG plot comparisons, we therefore obtained pairwise trajectories for the length of the monitoring period of each of the SG plots. For the SG-SG plot comparisons, we selected all the possible pairs of plots where ages since abandonment overlapped for at least five consecutive years, to obtain a trajectory of at least four time intervals. Although we are not accounting for the year effect, which might affect tree mortality (Chazdon *et al.* 2005), controlling for the effect of age rather than year is a more conservative way to address temporal changes of taxonomic similarity along succession. Finally, we calculated the three similarity metrics between the two OG plots for each census year (2005–2014) to have a point of reference. To compare patterns of plot-pair similarity between tree-size classes, all the analyses were performed separately for trees ≥ 10 cm DBH (henceforth large trees) and for trees between 5 and

10 cm DBH (henceforth small trees). These tree-size thresholds are likely to capture differences in life stage, with most trees between 5 and 10 cm DBH representing a transition between young and adult individuals (Norden *et al.* 2009).

To evaluate whether SG assemblages were converging towards a single equilibrium state, similar to that of OG stands, we used linear mixed-effect models to assess the effect of stand age since abandonment (fixed effect) on plot-pair taxonomic similarity, separately for each similarity metric (dependent variable). Each model contained a random effect term (intercept and/or slope) for plot identity, which accounted for the repeated censuses in each plot across years. The random plot effect is interpreted as a proxy for residual variance due to idiosyncratic local site factors. We did not include distance as a factor affecting plot-pair taxonomic similarity, as it did not have a significant effect on the extent of convergence (or divergence) in pairwise trajectories (Table S1).

Because the P -values of linear mixed-effects models are not reliable (Pinheiro & Bates 2000), we assessed the influence of the fixed effect (age since abandonment) on the dependent variables (similarity metrics) by comparing a simple intercept model to a model that included the fixed effect using the small sample size corrected Akaike information criterion (AIC_c). For each of the best-fit mixed-effects models, we calculated the marginal correlation metric, R^2_m , which measures the variance explained by fixed effects only, and the conditional correlation metric, R^2_c , which expresses the variance explained by both fixed and random factors (Nakagawa & Schielzeth 2013).

Then, we evaluated whether taxonomic similarity between plot-pairs deviated from a random expectation based on a null model analysis. During each of 999 iterations, we used a swap algorithm where we randomly shuffled the species names in the species by census matrix for each plot separately, and recalculated taxonomic similarity between plot-pairs. This way, species names are not shuffled at each census, thereby keeping consistency in species abundance over time for each plot (Fig. S1). We considered two different species pools: one comprising all the species that occurred at any point during the study interval in the six SG plots, and another comprising all the species that occurred at any point during the study interval in the two OG plots. We used the SG species pool for SG plots and the OG species pool for the OG plots. We evaluated whether our observed values were more or less extreme than expected by chance for each plot-pair by calculating the standardised effect size (SES) as the difference between the observed and mean expected (null) similarity, divided by the standard deviation of the expected values from the 999 iterations of the null model. Using a P -value of 0.05, SES values higher than 1.96 or lower than -1.96 indicate significantly higher, or lower, taxonomic similarity than expected by chance, respectively. To assess the effect of age since abandonment on SES plot-pair taxonomic similarity, we repeated the series of linear mixed-effect model analyses.

Species contribution to plot-pair taxonomic similarity

To understand which species drive patterns of taxonomic similarity between plot-pairs, we first classified all the species occurring in the plots according to their successional niche, using the multinomial model developed by Chazdon *et al.* (2011). Based on species relative abundances in SG or OG forests, the model classifies species as second-growth specialists (SGS), old-growth specialists (OGS), generalists (GEN) and too rare to classify with confidence (RAR). For further details on this method, please see Chazdon *et al.* (2011). We used the settings recommended for the model given the structure of our data set: a simple majority threshold ($K = 1/2$) and $P = 0.005$ (Letcher *et al.* 2015). We used data on the abundance of trees ≥ 10 cm DBH sampled in 11.3 ha of tropical SG forests of various ages and land-use history and in 18.3 ha of OG forests with no recorded history of recent major human disturbance. Although the eight study plots were included in this data set, species classification relied on a much larger sample, thereby providing an adequate approximation of species successional niche, based on a robust statistical method. Overall, we classified 72 species as OGS, 38 as SGS, 40 as GEN and 222 as RAR (Table S2).

We evaluated the contribution of each of these groups of species to the overall patterns of taxonomic similarity between plot-pairs by performing a sensitivity analysis. To do so, we compared the observed temporal trends of taxonomic similarity (ALL) to those obtained by removing the subset of species belonging to each of four classification groups: (1) second-growth specialists (ALL_{w/oSGS}), (2) old-growth specialists (ALL_{w/oOGS}), (3) generalist (ALL_{w/oGEN}) or (4) rare (ALL_{w/oRAR}). We henceforth refer to each of these cases as a sensitivity scenario. After recalculating the Sørensen, Horn and Morisita-Horn indices for each pairwise trajectory j for the four sensitivity scenarios, we calculated E , the distance between the trajectory that included all species and each of the four trajectories obtained from the sensitivity analysis (i.e. ALL vs. ALL_{w/oSGS}, ALL vs. ALL_{w/oOGS}, ALL vs. ALL_{w/oGEN}, and ALL vs. ALL_{w/oRAR}). This approach allowed comparing the strength in the effect of each subset of species on temporal changes in taxonomic similarity across classification groups.

For each of the three similarity metrics, E was calculated as:

$$E_{jk} = \sum_{i=1}^N \frac{S_{ij} - S_{ijk}}{N - 1}$$

where S_{ij} is the observed taxonomic similarity between plot-pair (pairwise trajectory) j at time i based on all species, S_{ijk} is the observed taxonomic similarity between plot-pair j at time i for the sensitivity scenario k , and $N - 1$ is the number of time intervals of each pairwise trajectory j . If $E > 0$, the removal of a group of species decreases taxonomic similarity in a pairwise trajectory over time; in other words, this group contributes to *convergence*. If $E < 0$, the removal of a group of species has the opposite effect and thus contributes to *divergence* (Fig. 1). To compare E across the four sensitivity scenarios, across pairwise trajectories and across similarity indices (Sørensen, Horn and Morisita-Horn), we normalised E as follows:

$$E_{nor,k} = \frac{E_{jk}}{\max(|E_{jk}|)}$$

where E_{jk} is the distance between the pairwise trajectory j that includes all the species and the pairwise trajectory j obtained from the sensitive scenario k , and $\max(|E_{jk}|)$ is the maximum of the absolute value of E_{jk} . These calculations were performed for each of the three similarity indices separately. $E_{nor,k}$ varies between -1 and 1 .

To evaluate the contribution of each of the four groups of species (SGS, OGS, GEN, RAR) to patterns of taxonomic similarity over time, we tested for significant differences in E_{nor} among the different k sensitivity scenarios using a Dunn's test, a nonparametric pairwise multiple comparison test based on rank sums that is often used as a post hoc procedure following rejection of a Kruskal–Wallis test.

All statistical analyses were performed in the R statistical program, version 3.3.0 (R Core Team 2016). Linear mixed-effects models were performed using the 'lme4' package (Bates *et al.* 2015). Marginal and conditional R^2 values were calculated using the 'piecewiseSEM' package (Lefcheck 2016). The Dunn's test was performed using the 'dunn.test' package (Dinno 2016).

RESULTS

Taxonomic similarity

Overall, taxonomic similarity was higher for SG vs. SG plot-pair comparisons than for SG vs. OG comparisons (Figs 2 and 3). Based on all three similarity metrics, SG and OG

stands showed significant yet slow floristic convergence over time for both large (DBH > 10 cm) and small trees (DBH 5–10 cm), gradually approaching the observed similarity between the pair of OG stands (Fig. 2). In contrast, temporal changes in floristic similarity among SG stands showed different patterns depending upon size class and the similarity metric used (Fig. 3). For large trees, similarity between plot-pairs was

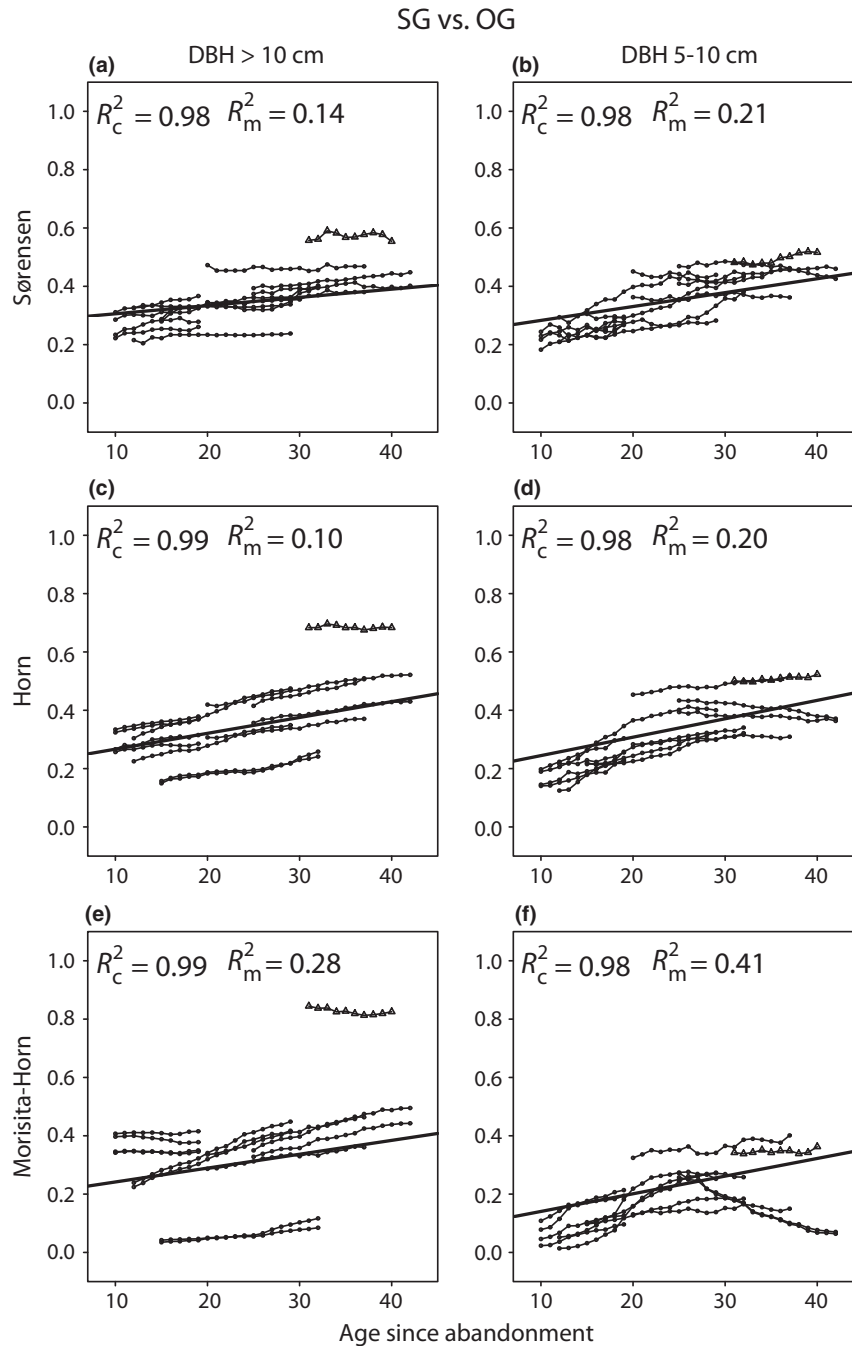


Figure 2 (a-f) Trajectories of taxonomic plot-pair similarity over time based on Sørensen, Horn and Morisita-Horn indices for 12 plot-pairs comparing second-growth (SG) and old-growth (OG) stands for large (DBH > 10 cm) and small (DBH 5–10 cm) trees assemblages. We included the trajectory for the plot-pair comparing OG stands as a point of reference (open triangles). Note that the age of this trajectory does not correspond to the age of the plots, which we estimate is over 400 years since the last disturbance. Solid black lines display predicted values from the best-fit linear mixed-effects model for which the fixed effect was found to be significant. On all panels, the R_c^2 incorporates the variation explained by both fixed and random effects, whereas R_m^2 considers the fit based on fixed effects only.

stable over time, except when accounting for dominant species (Morisita-Horn), for which similarity increased slightly over time (Fig. 3e). For small trees, plot-pair taxonomic similarity between SG stands based on species incidence (Sørensen) increased slightly over time (Fig. 3b), whereas taxonomic similarity decreased over time when accounting for species relative abundance and species dominance (Horn and Morisita-Horn, respectively; Fig. 3d and f). Overall, in most of these models, stand age (fixed effect) explained < 30% of the variation in

taxonomic similarity, while differences among plot-pairs (random effect) explained the rest of the variance (Figs 2 and 3).

SES taxonomic similarity between plot-pairs based on Sørensen, Horn and Morisita-Horn indices was significantly higher than expected by chance for most of the pairwise trajectories (Figs S2 and S3). Overall, the outcome of the null model analysis (SES taxonomic similarity) was highly consistent with the observed temporal trends in taxonomic similarity between plot-pairs (Figs 2 and 3, S2, S3).

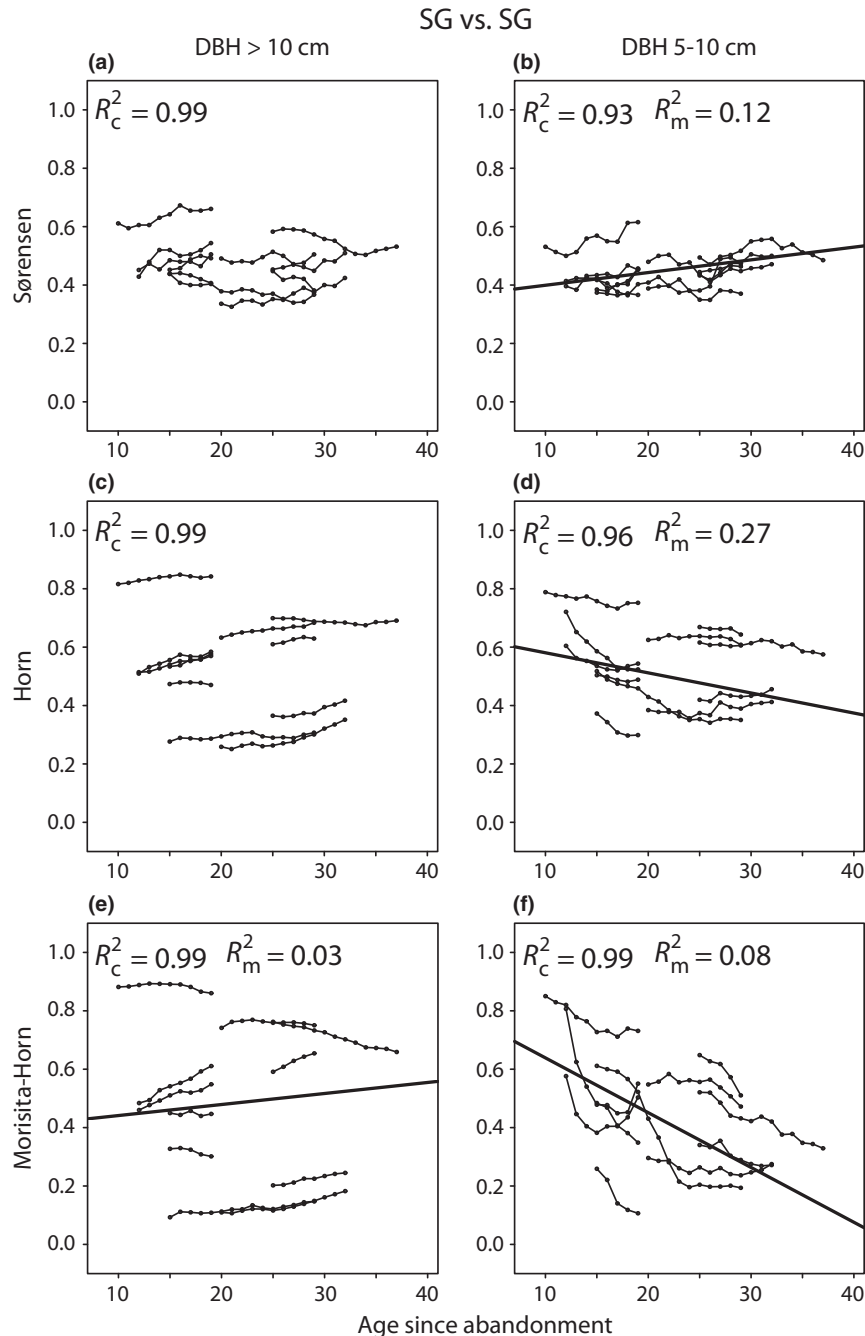


Figure 3 (a-f) Trajectories of taxonomic plot-pair similarity over time based on the Sørensen, Horn and Morisita-Horn indices for 11 plot-pairs comparing second-growth (SG) stands of the same age since abandonment in large (DBH > 10 cm) and small (DBH 5–10 cm) tree assemblages. Solid black lines display predicted values from the best-fit linear mixed-effects model for which the fixed effect was found to be significant. On all panels, the R_c^2 incorporates the variation explained by both fixed and random effects, whereas R_m^2 considers the fit based on fixed effects only.

Species contribution to plot-pair taxonomic similarity

The sensitivity analysis showed that the contribution of the species belonging to the different classification groups (GEN, RAR, SGS, OGS) to overall taxonomic convergence varied depending upon the similarity metric and the size class evaluated. When evaluating taxonomic similarity in large trees between SG and OG stands based on species incidence (Sørensen), generalists and SGS showed positive values of E_{nor} , thereby contributing to floristic convergence, whereas rare species showed negative values of E_{nor} , thereby contributing to divergence (Fig. 4a). When accounting for species relative abundance (Horn) and species dominance (Morisita-Horn),

OGS was the group that contributed the most to divergence between SG and OG stands, especially when considering dominant species (Morisita-Horn). The group of generalists was markedly differentiated from the others, showing a high contribution to convergence (Fig. 4c and e).

Small trees showed some concordance with the patterns observed for large trees. Rare and generalist species also contributed to taxonomic divergence and convergence, respectively, for all similarity metrics (Fig. 4b, d and f). Similar to large trees, when considering dominant species (Morisita-Horn), only generalists contributed to convergence (Fig. 4f). The effect of OGS on taxonomic similarity between small tree assemblages shifted from convergence to divergence as the

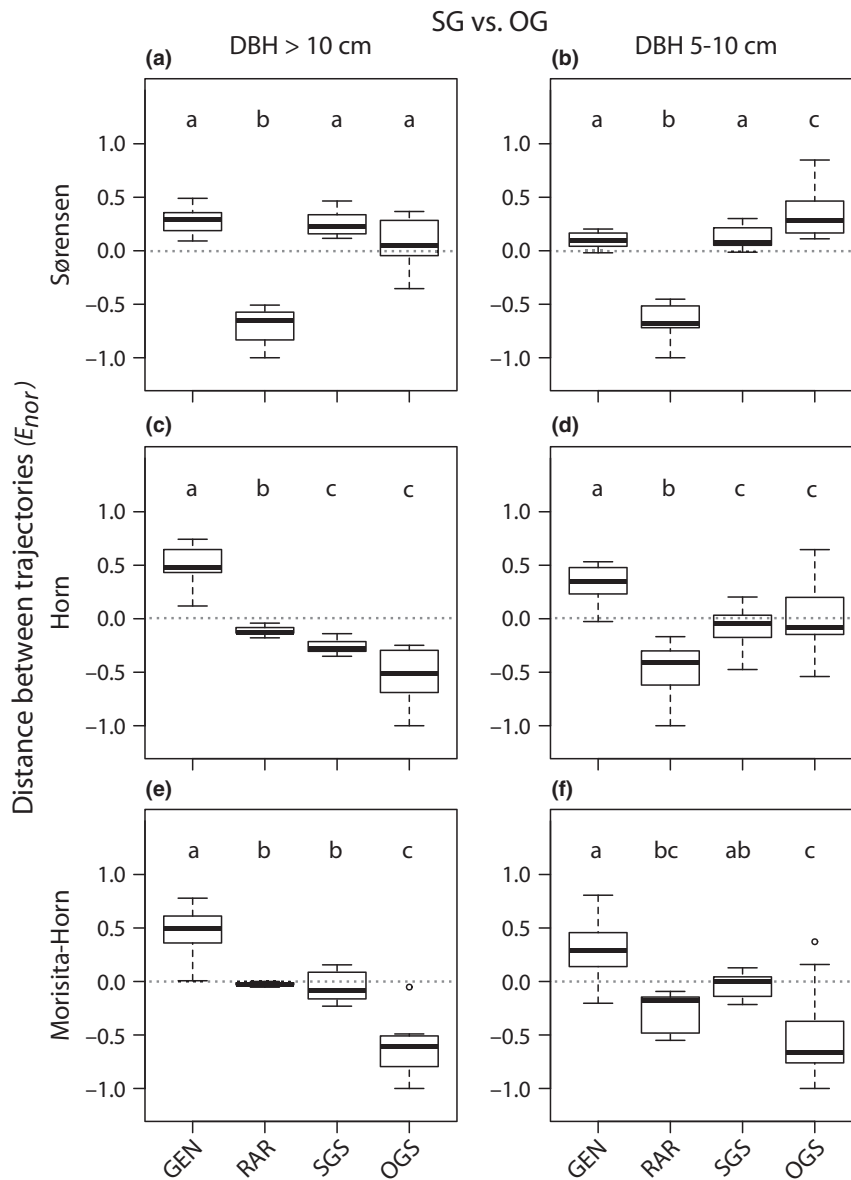


Figure 4 (a-f) Boxplot illustrating differences in the distance, E_{nor} , between the trajectory that included all species and each of the four trajectories obtained from the sensitivity analysis (i.e. ALL vs. ALL_{w/o}SGS, ALL vs. ALL_{w/o}OGS, ALL vs. ALL_{w/o}GEN, and ALL vs. ALL_{w/o}RAR) for second-growth (SG) vs. old-growth (OG) stands. If $E_{nor} > 0$, the group of species contributes to convergence, whereas if $E_{nor} < 0$, it contributes to divergence. Letters indicate significant differences among mean values of E_{nor} based on the Dunn's test. Boxplots show median (thick horizontal line), first and third quartiles (lower and upper fences, respectively). The lower and upper whiskers represent minimum and maximum values, respectively, that do not exceed 1.5 times the interquartile range, and open circles represent outliers. Abbreviations: GEN = generalists, RAR = rare, SGS = second-growth specialists, and OGS = old-growth specialists.

similarity metric became more sensitive to dominant species, yet this pattern was more conspicuous in small than in large tree assemblages (Fig. 4b, d and f).

When evaluating taxonomic similarity among SG stands, rare species contributed to divergence for both large and small trees based on species incidence (Sørensen), and SGS was the group that contributed the most to convergence (Fig. 5a and b). However, based on species relative abundance (Horn) and species dominance (Morisita-Horn), the classification groups showed little effect on the overall trend observed across trajectories (Fig. 5c–f). Generalists and SGS in small trees contributed slightly to convergence based on species relative

abundance (Horn), and rare and OGS contributed slightly to divergence (Fig. 5d).

DISCUSSION

By examining tree dynamics in successional stands for over a decade, we evaluated whether regrowing tropical forests are converging towards an equilibrium state in species composition, and identified which groups of species were responsible for the observed patterns of taxonomic similarity among stands. Our results provide deeper insights into the process of forest resilience in human-impacted tropical regions, a central

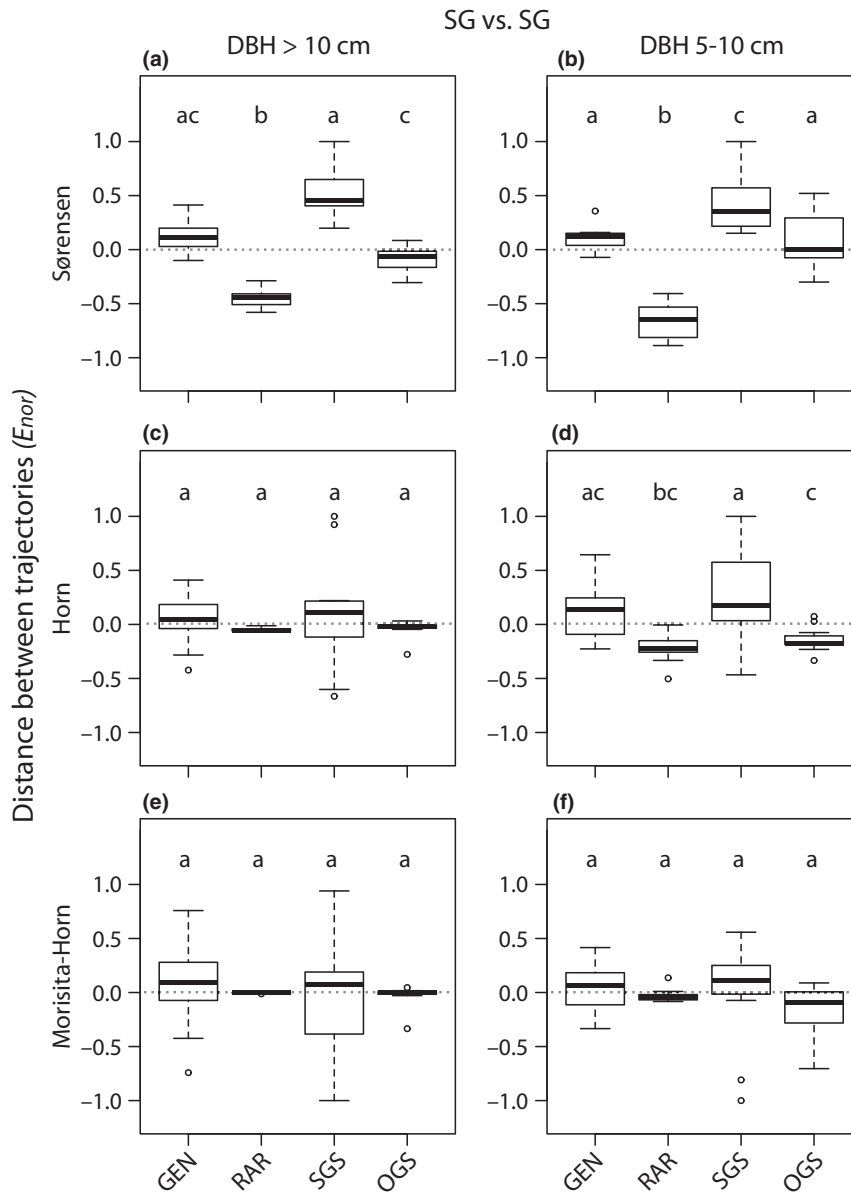


Figure 5 (a–f) Boxplot illustrating differences in the distance, E_{nor} , between the trajectory that included all species and each of the four trajectories obtained from the sensitivity analysis (i.e. ALL vs. ALL_{w/o}SGS, ALL vs. ALL_{w/o}OGS, ALL vs. ALL_{w/o}GEN, and ALL vs. ALL_{w/o}RAR) for pairs of second-growth (SG) stands of the same age since abandonment. If $E_{nor} > 0$, the group of species contributes to convergence, whereas if $E_{nor} < 0$, it contributes to divergence. Letters indicate significant differences among mean values of E_{nor} based on the Dunn's test. Boxplots show median (thick horizontal line), first and third quartiles (lower and upper fences, respectively). The lower and upper whiskers represent minimum and maximum values, respectively, that do not exceed 1.5 times the interquartile range, and open circles represent outliers. Abbreviations: GEN = generalists, RAR = rare, SGS = second-growth specialists, and OGS = old-growth specialists.

issue as landscape transformation is jeopardising the world's forests biodiversity and function (Chazdon 2014). Below, we discuss the key implications of these findings for the current debate about the future of tropical forests (Melo *et al.* 2013; Arroyo-Rodríguez *et al.* 2017).

Convergence and divergence at different time scales

Although taxonomic similarity between SG and OG stands was higher than expected by chance, convergence between these two types of forest was weak within the time frame assessed. These patterns were consistent across similarity metrics and tree-size classes, indicating that similarity between these two types of forests was not strongly driven by species relative abundance or recruitment cohort. Convergence between secondary and mature forests in NE Costa Rica is therefore likely to occur over decades and even centuries. These results support previous chronosequence-based studies from the same study area, showing evidence of recovery in tree species composition through the successful establishment of mature forest tree seedlings in the understory of secondary stands (Letcher & Chazdon 2009; Norden *et al.* 2009). High levels of resilience in SG forests have been usually associated with a deterministic view of succession (Terborgh *et al.* 1996), whereby niche-based processes explain the sequential replacement of species over time until reaching a steady stable state (Clements 1916).

Under this scenario, patterns of taxonomic similarity between SG stands over time are somewhat unexpected, as directionality and strength in convergence varied depending upon similarity metric and tree-size class. Taxonomic similarity between pairwise assemblages of large trees in SG stands was stable over time, except when accounting for dominant species, where convergence was significant yet limited. SG assemblages of small trees showed a weak convergence based on species incidence but, remarkably, showed strong divergence when accounting for species relative abundance and species dominance, suggesting that locally abundant species are a source of taxonomic divergence between SG plot-pairs.

Overall, the seemingly contradictory results between SG vs. OG and SG vs. SG stands likely reflect ecological processes occurring at different time scales. When evaluating convergence between SG and OG stands, we are comparing species composition between assemblages of very distinct ages since the last stand-removing disturbance (at least *c.* 400 years). Taxonomic similarity between these two types of forest is therefore lower than between plot-pairs of the same age since abandonment, and the modest convergence observed between SG and OG forests reflects the slow recruitment of mature forest species into SG stands (Finegan 1996). In contrast, when evaluating taxonomic similarity between SG stands by controlling for age differences, we are evaluating processes occurring during a 14-year time window across assemblages that typically show higher dynamism than mature forests (Finegan 1996; van Breugel *et al.* 2007). Our findings therefore do not exclude the possibility that SG stands are taking different successional pathways due to idiosyncratic recruitment and mortality events, and yet finally reach a relatively stable state, with similar species composition to that of OG forests. High spatial variation in species composition among

secondary forests of similar age may thus reflect short-term stochasticity and local site factors (Norden *et al.* 2015), whereas convergence between SG and OG stands underlies long-term ecological processes driven by the niche-based replacement of species showing wide differences in their life history (Finegan 1996; Rees *et al.* 2001).

Species contribution to temporal changes in taxonomic similarity

Limited or lack of convergence between pairwise forest stands may be the result of one of two processes. The first is that temporal changes in taxonomic similarity are limited by very slow species turnover over succession. A large body of successional literature, however, supports the view that secondary stands are highly dynamic (e.g. van Breugel *et al.* 2007; Lasky *et al.* 2014; Norden *et al.* 2015). Shifts in species composition resulting from differential recruitment and mortality rates among species are therefore expected to drive either convergence or divergence between stands (Dent *et al.* 2013; Longworth *et al.* 2014). The second possibility is that opposing trends in changes of taxonomic similarity among different subsets of species nullify each other, resulting in a net outcome of stasis over time. Our results support the latter, as second-growth specialists, old-growth specialists, generalists and rare species contributed in very distinct ways to temporal changes in taxonomic similarity.

For instance, while generalists consistently contributed to convergence between SG and OG forests, rare species showed the opposite trend. The importance of generalists to convergence is not surprising as these species were classified as such because of their co-occurrence in both SG and OG stands. Our findings further show that regardless of their relative abundance, generalists occur across the landscape, enhancing secondary forest resilience in both small and large tree assemblages (Norden *et al.* 2009). Species such as *Euterpe precatoria*, *Iriartea deltoidea*, *Pentaclethra maculosa* and *Socratea exorrhiza* dominate the study area (Norden *et al.* 2009). Except for *P. maculosa*, these species have also been reported as 'oligarchs' in Amazonian forests (Pitman *et al.* 2001). This marked pattern of dominance along the north-south axis of Latin America may enhance resilience in regrowing forests across human-impacted Neotropical landscapes.

Rare species, in contrast, were major drivers of divergence over time in most of the plot-pair comparisons performed. This pattern was more marked when analyses were based on species incidence, which is not surprising since abundance-based similarity metrics attenuate the role of rare species in overall similarity. The fact that distinct rare species occurred in different forest patches reflects, to some extent, the prevalence of stochastic colonisation and recruitment events (Chase *et al.* 2005). Low tree abundance promotes seed limitation, thereby reducing species ability to disperse (Muller-Landau *et al.* 2002), and causing further spatial aggregation (Seidler & Plotkin 2006). Moreover, because of their low abundance, rare species may be prone to local extinction in small forest patches, thereby increasing the importance of spatial processes in explaining species relative abundance across the landscape (Leibold & Loeuille 2015). Indeed, previous research has shown that dispersal limitation may be particularly important in fragmented landscapes

(Arroyo-Rodríguez *et al.* 2013), amplifying the effect of rare species on floristic variation among stands.

The contribution of old-growth specialists (OGS) to taxonomic similarity showed contrasting patterns depending upon the type of pairwise comparison performed (SG-OG vs. SG-SG, small vs. large tree assemblages, similarity metric). When accounting for species incidence, OGS contributed to either convergence or divergence in small and large tree assemblages, respectively. This finding suggests that OGS typically occurring in mature forests are absent from SG stands, yet they are successfully recruiting as small trees in some secondary stands, although not in high abundance (Norden *et al.* 2009). The contribution of OGS to divergence between SG and OG stands strengthened when accounting for species dominance both in small and large tree assemblages, indicating that locally abundant OGS in OG stands were rare or absent in SG stands. Overall, these findings are in agreement with Dent *et al.* (2013), who showed that, although shade tolerance increased over succession, taxonomic similarity between SG and OG stands remained idiosyncratic. Our results provide deeper insights into which species are responsible for the weak (or lack of) directionality in the successional trajectories in species composition.

Second-growth specialists (SGS) were the group of species that contributed most to convergence among SG stands, yet only when accounting for species incidence. As SGS were defined as species occurring preferentially in SG stands, it is not surprising that successional plots share the same species, but we expected them to play a stronger role in convergence. Although SGS play an important role during the first phases of succession (1–40 years), they slowly decline in abundance as succession unfolds (Finegan 1996; Rozendaal & Chazdon 2015). For instance, SGS accounted for 47–72% of the individuals (mean = 57%) in SG large tree assemblages, while this value dropped to 7–55% of the individuals (mean = 35%) in SG small tree assemblages. As SGS show a wide array of functional strategies (Letcher *et al.* 2015), differential changes in the relative abundance of large and small tree species within and across SG plots likely explain the broad variation in the effect of SGS in taxonomic similarity across pairwise trajectories, resulting in a neutral median effect. Landscape and local site factors, which are difficult to quantify, have been shown to have a considerable effect on the successional pathways observed in the study area (Norden *et al.* 2015; Boukili & Chazdon 2017). Long-term dynamic data are therefore critical to better understand whether secondary stands are converging to a stable state in species composition over time.

CONCLUSIONS

Our findings provide critical insights into the processes underlying successional dynamics and species turnover in secondary forests. Overall, temporal patterns of taxonomic similarity between plot-pairs resulted from conflicting forces, where some groups of species contributed to convergence while others contributed to divergence. Stochastic processes may be important drivers of successional trajectories for rare species and OGS. In turn, SGS and generalists provided support for the traditional niche-based model of succession. Our results, however, depend on the regional context where SG forests are embedded. In a scenario where OG forest cover is high, OGS

may contribute to convergence rather than divergence, assuming low dispersal limitation (Arroyo-Rodríguez *et al.* 2017). In contrast, in strongly degraded and fragmented landscapes, the loss of OGS and rare species, as well as the prevalence of SGS and generalists, may lead to floristic homogenisation among SG stands (Arroyo-Rodríguez *et al.* 2013). Given the overriding effect of historical contingencies during succession, we urgently need to integrate the effect of local and landscape variables in successional studies, as well as other facets of biodiversity (e.g. functional and phylogenetic), to strengthen theories of forest dynamics in secondary stands, which are critical for predicting the future of tropical ecosystems.

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STATEMENT OF AUTHORSHIP

RLC designed and performed field research; NN conceived the study together with RLC, VB and SGL. NN analysed the data, with the help of AC and KHM. NN wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

Tree dynamics data set can be found from https://figshare.com/articles/Supplement_1_Data_on_tree_dynamics_during_secondary_succession_and_wood_specific_gravity_in_northeastern_Costa_Rica_/3520553 (Rozendaal & Chazdon, 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Appendix

Figure S1.

Schematic representation of the swap algorithm, where species names are shuffled in the species by census matrix for each plot separately, keeping consistency in species abundance over time for each plot. This permutation maintains observed occupancy rates, plot abundance distributions, and plot species richness for each plot at each census.

Randomizing the identity of the living stems at each census would have inflated temporal turnover in the null model. When randomizing a second-growth (SG) plot, the species pool comprised all the species that occurred at any point during the study interval in the six SG plots. When randomizing an old-growth (OG) plot, the species pool comprised all the species that occurred at any point during the study interval in the two OG plots. For each of 999 iterations, taxonomic similarity between plot-pairs was recalculated.

Figure S2. Trajectories of taxonomic plot-pair similarity over time based on the SES Sørensen, Horn and Morisita-Horn indices for 12 plot-pairs comparing second-growth (SG) and old-growth (OG) stands for large (DBH > 10 cm) and small (DBH 5-10 cm) tree assemblages. Dashed grey lines indicate significance levels; points higher than 1.96 or lower than -1.96 demonstrate significantly higher or lower taxonomic similarity, respectively, than expected based on the null expectation. Solid black lines display predicted values from the best-fit linear mixed-effects model for which the fixed effect was found to be significant. On all panels, the R^2_c incorporates the variation explained by both fixed and random effects, whereas R^2_m considers the fit based on fixed effects only.

Figure S3. Trajectories of taxonomic plot-pair similarity over time based on SES Sørensen, Horn and Morisita-Horn indices for 11 plot-pairs comparing second-growth (SG) forests of the same age since abandonment in large (DBH > 10 cm) and small (DBH 5-10 cm) tree assemblages. Dashed grey lines indicate significance levels; points higher than 1.96 or lower than -1.96 demonstrate significantly higher or lower taxonomic similarity, respectively, than expected based on the null expectation. Solid black lines display predicted values from the best-fit linear mixed-effects model for which the fixed effect was found to be significant. On all panels, the R^2_c incorporates the variation explained by both fixed and random effects, whereas R^2_m considers the fit based on fixed effects only.

Figure S1

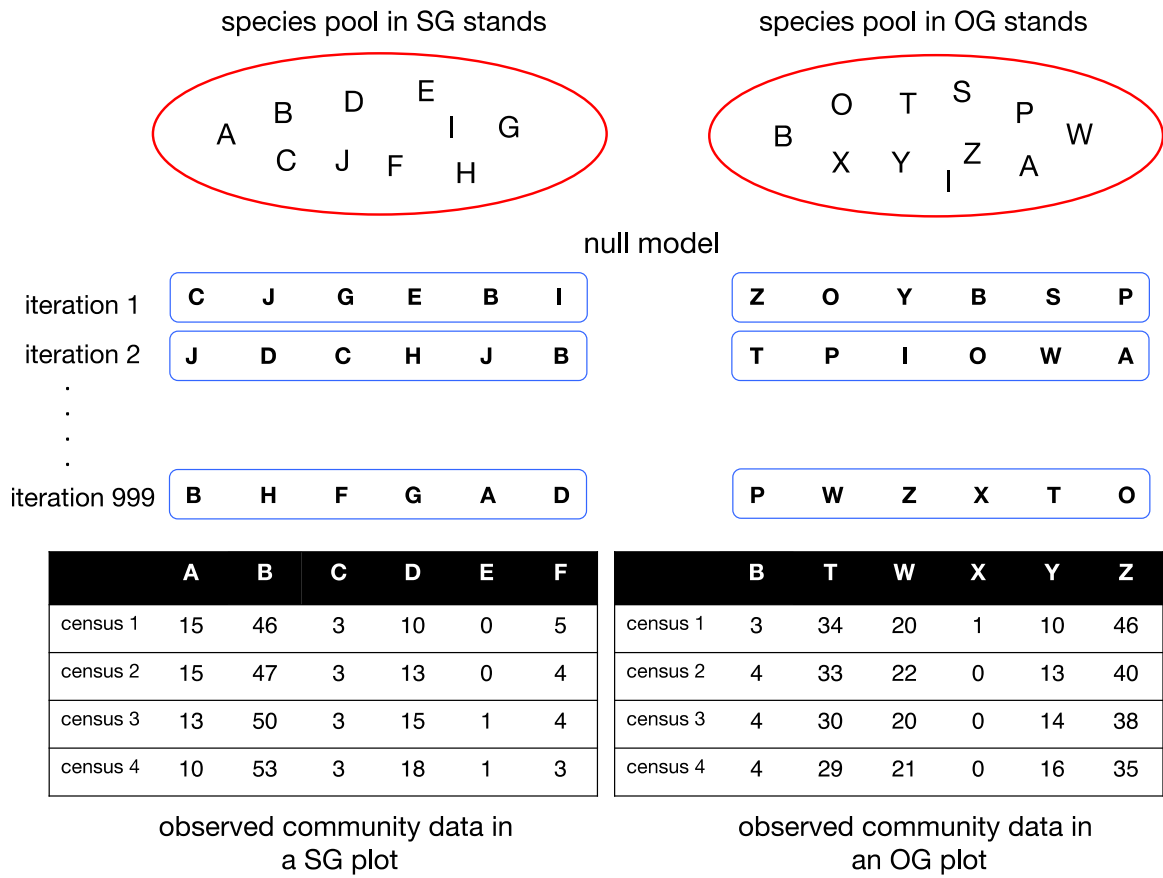


Figure S2.

SG vs. OG

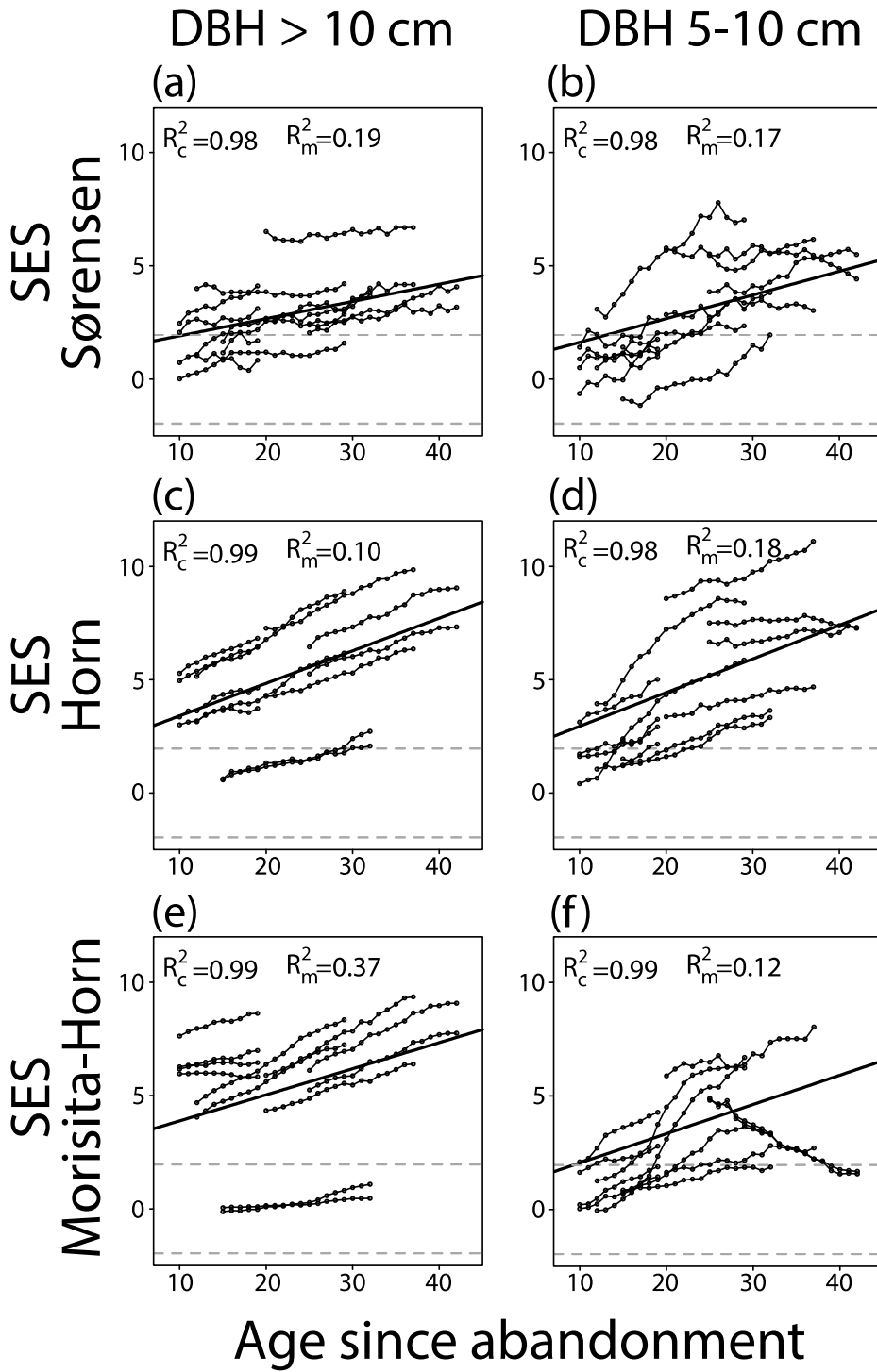


Figure S3.

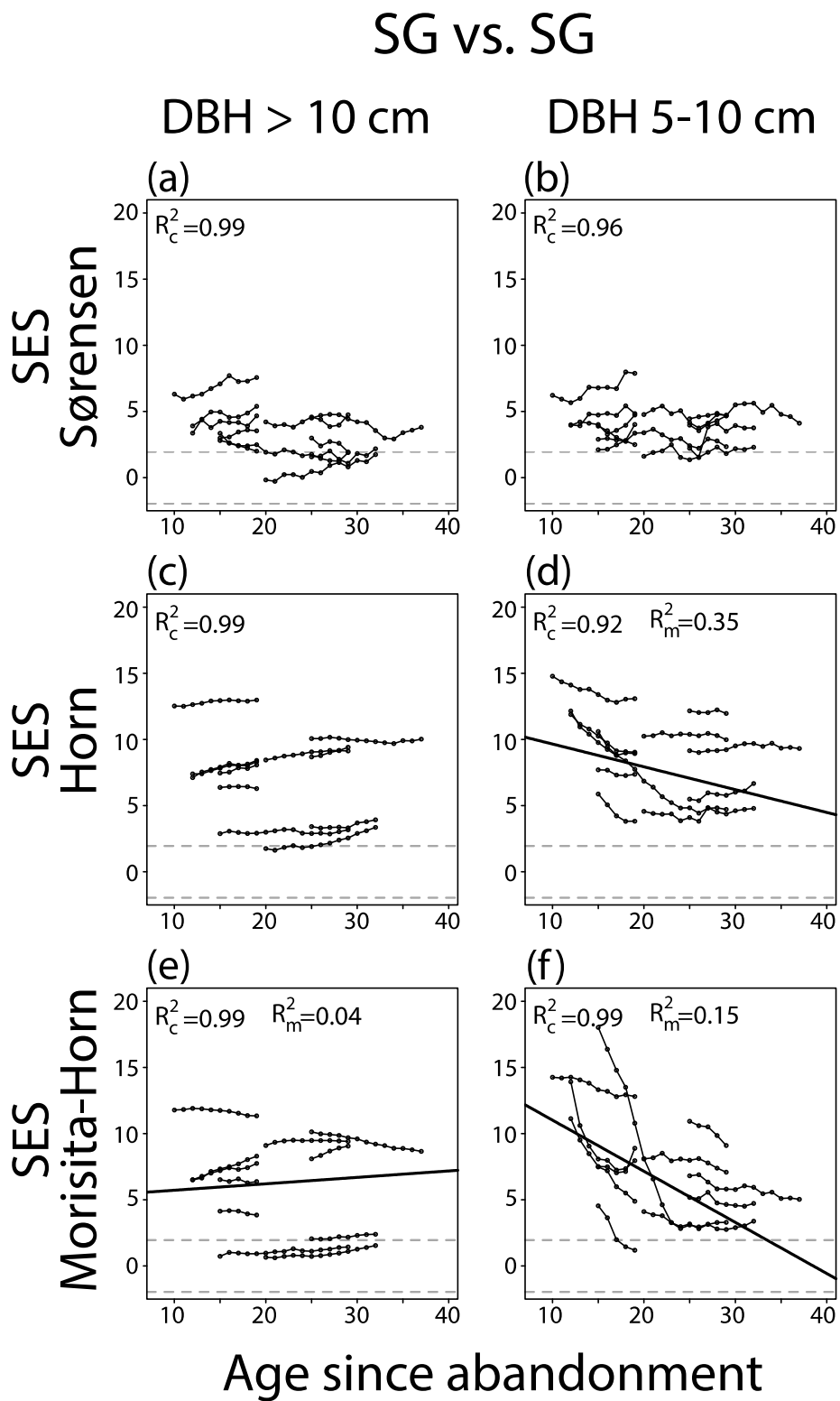


Table S1. Effect of distance between plot-pairs on temporal changes in taxonomic similarity. Reported are the parameter estimates of the linear model predicting the slope of a pairwise trajectory as a function of geographical distance between plot-pair. None of the parameter estimates were significant.

| | SG. vs OG (N=12) | | SG. vs SG (N=11) | |
|---------------|------------------------|------------------------|------------------------|------------------------|
| | large trees | small trees | large trees | small trees |
| Sørensen | $+2.3 \bullet 10^{-4}$ | $-5.8 \bullet 10^{-6}$ | $-1.2 \bullet 10^{-3}$ | $-1.1 \bullet 10^{-4}$ |
| Horn | $-1.6 \bullet 10^{-4}$ | $-7.2 \bullet 10^{-4}$ | $-2.2 \bullet 10^{-4}$ | $-3.5 \bullet 10^{-4}$ |
| Morisita-Horn | $-3.2 \bullet 10^{-5}$ | $-1.3 \bullet 10^{-3}$ | $+1.0 \bullet 10^{-4}$ | $-1.4 \bullet 10^{-3}$ |

Table S2. Number of species in each of the four classification groups defined (SGS, OGS, GEN, RAR), and, in parenthesis, percentage of individuals belonging to each group in small and large tree assemblages within each 1-ha study plot. Strictly speaking, species classified as RAR correspond to those for which abundances were too low to detect significance in the multinomial analyses. Although in our dataset other species classified as OGS or SGS may have shown similar abundances to those classified as RAR, their abundance across the landscape was higher (Chazdon *et al.* 2011). Although part of our analyses included trees ≥ 5 cm DBH, we used the outcome of the multinomial model based on trees ≥ 10 cm DBH for all the analyses because this is a more conservative classification, as habitat preferences have been shown to develop as trees grow (Comita *et al.* 2007).

Abbreviations: SG = second-growth, OG = old-growth.

| Plot | Tree size class | SGS | OGS | GEN | RAR | Total number of species |
|-----------|-----------------|-----------|-----------|-----------|-----------|-------------------------|
| JE (SG) | large trees | 32 (64.4) | 7 (2.5) | 14 (29.5) | 16 (3.4) | 69 |
| | small trees | 31 (55.5) | 14 (6.3) | 14 (24.8) | 33 (13.4) | 94 |
| BEJ (SG) | large trees | 25 (51.6) | 13 (6.2) | 9 (37.6) | 17 (4.6) | 64 |
| | small trees | 23 (53.6) | 16 (10.8) | 12 (29.7) | 25 (5.9) | 76 |
| LSUR (SG) | large trees | 18 (56.7) | 12 (12.5) | 12 (28.5) | 9 (2.3) | 51 |
| | small trees | 19 (43.2) | 23 (20.3) | 12 (28.9) | 23 (7.6) | 77 |
| LEP (SG) | large trees | 16 (46.0) | 24 (24.1) | 25 (28.7) | 11 (1.2) | 76 |
| | small trees | 15 (18.9) | 34 (47.8) | 22 (22.7) | 37 (10.6) | 108 |
| TIR (SG) | large trees | 24 (70.5) | 17 (8.8) | 17 (12.4) | 27 (8.1) | 85 |

| | | | | | | |
|-----------|-------------|-----------|-----------|-----------|-----------|-----|
| | small trees | 27 (40.8) | 36 (20.5) | 23 (14.6) | 63 (24.1) | 149 |
| CR (SG) | large trees | 22 (46.5) | 27 (22.5) | 24 (25.7) | 29 (5.2) | 102 |
| | small trees | 18 (8.2) | 38 (64.1) | 20 (16.3) | 46 (11.4) | 122 |
| LEPP (OG) | large trees | 9 (5.2) | 49 (69.1) | 17 (18.5) | 25 (7.2) | 100 |
| | small trees | 9 (4.5) | 48 (55.7) | 10 (8.1) | 50 (31.7) | 117 |
| SV (OG) | large trees | 16 (4.6) | 46 (62.6) | 14 (17.4) | 50 (15.4) | 126 |
| | small trees | 5 (2.4) | 42 (62.2) | 19 (10.3) | 62 (25.1) | 128 |

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