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Seed-rain–successional feedbacks in wet tropical forests

Nohemi Huanca Nuñez,[1,4] Robin L. Chazdon,[2] and Sabrina E. Russo[1,3]

[1]*School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588-0118 USA*
[2]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043 USA*
[3]*Center for Plant Science Innovation, University of Nebraska, Lincoln, Nebraska 68588-0660 USA*

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Abstract. Tropical forest regeneration after abandonment of former agricultural land depends critically on the input of tree seeds, yet seed dispersal is increasingly disrupted in contemporary human-modified landscapes. Here, we introduce the concept of seed-rain–successional feedbacks as a deterministic process in which seed rain is shaped by successional dynamics internal to a forest site and that acts to reinforce priority effects. We used a combination of time series and chronosequence approaches to investigate how the quantity and taxonomic and functional composition of seed rain change during succession and to evaluate the strength of seed-rain–successional feedbacks, relative to other deterministic and stochastic mechanisms, in secondary wet forests of Costa Rica. We found that both successional niches and seed-rain–successional feedbacks shaped successional trajectories in the seed rain. Determinism due to successional niche assembly was supported by the increasing convergence of community structure to that of a mature forest, in terms of both functional and taxonomic composition. With successional age, the proportions of large-seeded, shade-tolerant species in the seed rain increased, whereas the proportion of animal-dispersed species did not change significantly. Seed-rain–successional feedbacks increased in strength with successional age, as the proportion of immigrant seeds (species not locally represented in the site) decreased with successional age, and the composition of the seed rain became more similar to that of the adult trees at the forest site. The deterministic assembly generated by seed-rain–successional feedback likely contributed to the increasing divergence of secondary forest sites from each other during succession. To the extent that human modification of tropical forest landscapes reduces connectivity via factors such as forest cover loss, our results suggest that seed-rain–successional feedbacks are likely to increasingly shape regeneration trajectories in and amplify floristic heterogeneity among tropical secondary forests.

Key words: community assembly; Costa Rica; forest succession; secondary forest; seed rain; seed-rain–successional feedbacks; wet tropical forest.

Introduction

Most of the original global extent of tropical forests (about 69%) has been lost to deforestation (FAO 2018) caused by many processes, such as fires, hurricanes, and conversion to agricultural use (Brown and Lugo 1990, Chazdon et al. 2007, Philpott et al. 2008). Despite the growing land area occupied by secondary successional forests, the dynamics, drivers, and outcomes of successional processes in tropical forests remain poorly known (van Breugel et al. 2013, Chazdon 2014). Given the key role forests play in moderating local climate and ecosystem function (Hoffmann et al. 2003, Alkama and Cescatti 2016), as well as global carbon and water cycles (Ellison et al. 2017), understanding how secondary forests regenerate is of critical importance.

Among the many ecological processes involved in forest regeneration (Pickett et al. 1987, Foster and Tilman 2000, Guariguata and Ostertag 2001), seed input into deforested areas, particularly during early successional stages, can strongly influence successional trajectories (Svenning and Wright 2005). Seed dispersal is a key process in forest regeneration because it determines colonization of deforested areas (Howe and Smallwood 1982, Levin et al. 2003, Muscarella and Fleming 2007), establishes the initial spatial template for tree recruitment (Schupp et al. 2002, Russo and Augspurger 2004), and can affect the recovery and the maintenance of species diversity (Hubbell 2001, Wright 2002, Terborgh et al. 2017). We define seed rain as the outcome of seed dispersal when seeds arrive into an area due to active dispersal by frugivores or passive dispersal (e.g., gravity, wind). Although early studies of tropical forest succession focused more on the dynamics of post-dispersal processes (Guariguata et al. 1997, Chazdon et al. 2007, Dent et al. 2013, van Breugel et al. 2013, Poorter et al. 2016), the successional dynamics of seed rain is gaining

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[4] E-mail: nohemihuanca@huskers.unl.edu

increasing attention (Castillo and Ríos 2008, Costa et al. 2012, Reid et al. 2015, San-José et al. 2020).

While succession in plant communities is shaped by both stochastic and deterministic processes (Chazdon 2008, Purves and Turnbull 2010), long-standing disagreements persist as to which processes predominate (Terborgh et al. 1996, Hubbell 2001, Chazdon 2008). Successional determinism produces predictable, directional, and orderly changes in species abundance and composition through time at a location with convergence toward a climax community, given a pool of potential colonizing species and a particular environmental setting (Clements 1916, Peet 1992). Recent studies have viewed determinism principally as a function of successional niches, defined in tropical forests as a replacement series from early successional, well-dispersed, light-demanding species to later successional, more dispersal limited, shade-tolerant species (Rees et al. 2001, Lebrija-Trejos et al. 2010, Dent et al. 2013, Cequinel et al. 2018, Poorter et al. 2019). Stochasticity is viewed as arising from non-deterministic outcomes of ecological processes controlling the arrival and survival of species (Schupp et al. 1989, Levin et al. 2003, Kreyling et al. 2011). Combined with priority effects (Fukami 2010, Dickie et al. 2012), stochastic assembly can lead to idiosyncratic successional trajectories (Gleason 1926, Aide and Cavelier 1994, Schröder et al. 2005, Norden et al. 2015). Moreover, community divergence can be amplified as landscapes become increasingly human-modified and heterogenous (Laurance et al. 2007, Arroyo-Rodriguez et al. 2017).

While seed dispersal is often viewed as highly stochastic (Webb et al. 2006, Lowe and McPeek 2014), the composition and abundance of seed rain into forest sites undergoing succession, is expected to change due to several deterministic and stochastic processes. Seed rain into secondary forests is influenced by many processes, including the proximity to and species composition of seed sources, the availability and diversity of seed dispersers, and the landscape context influencing movements of seed dispersers (Cubiña and Aide 2001, Ricketts 2001, Castillo and Ríos 2008, Culot et al. 2010, San-José et al. 2019, 2020). However, seed rain into secondary forests is also affected by the successional trajectory of the forest vegetation itself, creating seed-rain–successional feedbacks that operate in addition to assembly trajectories defined by successional niches.

We define seed-rain–successional feedback as a deterministic assembly process in which seedling regeneration and seed rain are more strongly shaped by successional vegetation dynamics within the local site, than by external input of seeds. Seed-rain–successional feedbacks are different from successional niches because successional niches arise due to changes in the local environmental conditions, such as understory light availability, caused by succession in tropical forests. For example, the understories of older successional forests have lower light availability, which increasingly favors establishment of more shade-tolerant species as succession proceeds. In the case of seed-rain–successional feedbacks, the feedback is driven by the particular species present in the overstory, not simply the changing environmental conditions, and so priority effects are magnified by limited seed dispersal in human-modified landscapes. Thus, seed-rain–successional feedback operates in envelopes constrained by successional niches, but represents a process distinct from successional niche assembly.

Forest succession in human-modified landscapes is influenced by many factors that operate at a range of scales (Arroyo-Rodríguez et al. 2017, San-José et al. 2019), including deforestation and resulting forest fragmentation and isolation, hunting of frugivorous animals, and reduced permeability to seed movement of matrix habitats surrounding the forest sites (Peres et al. 2010, Lewis et al. 2015, Curtis et al. 2018). Depending upon the dominant mode of human modification and its severity, seed-rain–successional feedbacks will vary in strength, but they are likely to be more influential in more highly modified, compared to less modified, secondary forest landscapes (Fig. 1). For animal-dispersed species, to the extent that secondary forest sites are inaccessible due to matrix impermeability to animal movement, do not provide suitable food or roosting habitat attractive to frugivorous animals, or have been emptied of frugivorous animal populations, then reduced diversity and quantity of animal-dispersed seeds into such sites from external sources is expected. For non-animal-dispersed species, matrix permeability is generally less important of a factor than for animal-dispersed species, although forest edges may reduce movement of wind-dispersed seeds (San-José et al 2020). Still, deforestation eliminates sources of seeds of non-animal and animal-dispersed species alike, limiting external seed input into regenerating forests. As a result, much of the seed rain would be generated by trees within the site, producing a seed-rain–successional feedback. In contrast, in landscapes with abundant intact and connected forests that have ample disperser populations, as was historically the case in tropical regions, seed-rain–successional feedback is likely to be weaker, and successional trajectories in - different secondary forest sites would be more similar to each other. This is because, while seed dispersal is nearly always spatially limited (Howe and Smallwood 1982, Turnbull et al. 2000, Clark et al. 2007), it is less limited in landscapes with abundant intact and connected forest, which has high forest cover, and so there is more opportunity for assembly of the seed rain to be shaped by the surrounding forest composition (Myers and Harms 2009). However, ecological connectedness no longer describes many contemporary tropical forest landscapes, which are substantially affected by human modification that exacerbates dispersal limitation (Peres et al. 2010, Lewis et al. 2015). In these scenarios, seed-rain–successional feedbacks within sites is expected to create a landscape mosaic of forest sites characterized by idiosyncratic assembly trajectories that strongly reflect

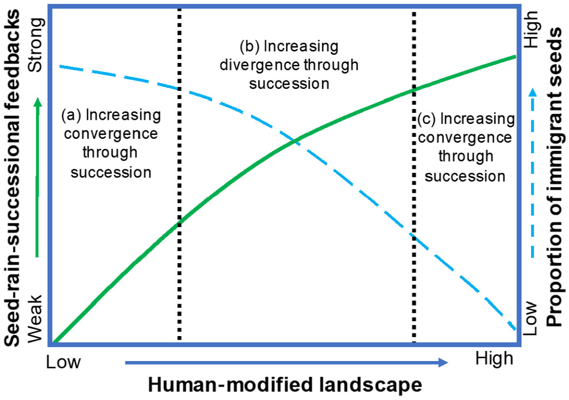

Fig. 1. The strength of seed-rain–successional feedbacks should increase with forest successional age and as human modification of the landscape increases (solid green curve). Human modification of the landscape involves many processes, including deforestation and reduction in matrix permeability, that can affect the movement of seeds across the landscape. Increasing strength of seed-rain–successional feedbacks will be driven by the declining proportion of immigrant seeds in the seed rain with successional age and with increasing human modification of the landscape (dashed green curve). These processes have consequences for spatial heterogeneity in plant species composition among regenerating forest sites. (a) In less human-modified landscapes, deforested sites should recover faster and receive ample seed rain from a larger proportion of the regional species pool, because more seed sources are nearer, and dispersal agents can move more freely between forested and regenerating areas. As a result, regenerating forests are expected to converge more strongly to each other and to the mature vegetation surrounding the sites as succession proceeds. (b) When landscapes are more human modified, many seed sources may be out of reach of a deforested site, and so regeneration becomes more strongly influenced by priority effects followed by local, within-site seed rain as succession proceeds. As a result, seed-rain-successional feedbacks will create greater spatial heterogeneity and divergence in plant community composition among secondary forest sites. (c) In the case of the most severe human modification of the landscape, seed-rain-successional feedbacks should promote convergence between successional sites in seed rain because the composition of the adult tree community will be strongly constrained to represent the most well-dispersed, generalist species from the regional pool (Laurance et al. 2007, Arroyo-Rodriguez et al. 2017).

priority effects (Chase 2003, Körner et al. 2008, Fukami 2010), thereby producing deterministic successional dynamics through time in which the seed rain is shaped by regeneration processes internal to the forest site. Thus, seed-rain–successional feedback can drive variation in assembly trajectories among secondary forests, which may ultimately increase the spatial heterogeneity of forest community composition in highly human-modified landscapes by generating forests in stable states with dissimilar composition. (Fig. 1, Appendix S1: Fig. S2).

In this study, we evaluated the strength of seed-rain–successional feedbacks, relative to other deterministic and stochastic mechanisms, in secondary forests undergoing post-agricultural regeneration in the wet rain forest biome of northeastern Costa Rica, as a first step to evaluating the premise of our seed-rain–successional feedback conceptual model (Fig. 1). We combined both time series and chronosequence approaches and used four years of data on seed rain of woody species collected during two time periods over an 18–20 yr time interval in four forest sites representing a range of successional ages in order to estimate how the quantity of and the taxonomic and functional composition of seed rain changed during succession. We also collected seed rain data in a mature forest site as a reference point of comparison representing a late successional community, rather than an exemplar of a “climax” community. First, we evaluated whether the seed rain in successional forests was more shaped by stochasticity or determinism, and how the balance between these factors changed with successional age. Second, we investigated how the strength of two deterministic mechanisms, successional niches and seed-rain–successional feedback, changed during succession. If the seed rain is structured by successional niches, then the taxonomic composition of the seed rain in secondary successional forest sites with similar environments should become more similar to the one in a mature forest as succession progresses. Likewise, the functional composition of the seed rain should also become more similar to that of a mature forest, such that the proportion of seeds and species with large, animal-dispersed seeds and shade-tolerant seedlings should increase with successional age. If the seed rain is structured by seed-rain–successional feedbacks, then as succession progresses, the taxonomic composition of the seed rain into a forest site should become more similar to the composition of the forest site’s reproductive trees, and the proportion of the seed rain comprised of immigrant species (species not locally represented in the site) should decline. As a consequence, due to the combined influence of priority effects and dispersal limitation, the taxonomic composition of the seed rain should diverge among forest sites with increasing successional age. Tracing changes in seed rain through time across forests differing initially in successional age provides a robust approach to parsing assembly processes shaping regeneration in these forest communities. Moreover, the use of time series data within the context of a chronosequence study is a powerful tool for disentangling the time-for-space assumption underlying most chronosequence studies.

METHODS

Study site

This study was conducted in tropical, premontane, wet forest (Holdridge and Grenke 1971) at La Selva Biological Station (hereafter, La Selva) and in surrounding areas in the Sarapiqui province of northeastern Costa Rica (Appendix S1: Fig. S1). La Selva hosts a diversity of more than 1,850 plant species, with 350 species of trees. The dominant plants families are Orchidaceae, Araceae, Rubiaceae, Melastomataceae, Fabaceae, and Piperaceae, with *Welfia regia* (Arecaceae), *Socratea exorrhiza* (Arecaceae), and *Pentaclethra macroloba* (Fabaceae) being the most abundant canopy tree species (Hartshorn and Himmel 1994). Mean annual rainfall and temperature is about ~4,000 mm and 26.5°C, respectively (Frankie et al. 1974). The areas surrounding La Selva once contained tropical forests with a certain degree of similar tree species composition, given the shared, regional, tree-species pool, but have experienced significant deforestation during the past 50 yr. Five 1-ha forest sites (50 × 200 m) (Table 1; Appendix S1: Fig. S1) were established in 1997 (four in secondary successional forest) and 2005 (one in mature forest) and have been censused annually for seedlings and trees (Chazdon et al. 2010). Extensive data have been collected at these sites for trees, seedlings, saplings, and seed banks (e.g., Dupuy and Chazdon 1998, Guariguata, et al. 1997, Boukili and Chazdon 2017, Norden et al. 2017) and our study of seed rain fills an important gap in understanding successional vegetation dynamics. These sites are located within a matrix of secondary and mature forest patches, agricultural areas, and human settlements (Norden et al. 2012). The four secondary successional forest sites were used as cattle pastures after initial cutting of the mature forest and range in successional age (i.e., time since the abandonment of pasturing) from 12 to 25 yr old at the time of site establishment (32 to 45 yr old in 2017).

The initial selections of secondary forests sites were based on advanced status as close-canopy secondary forests rather than old field. So even the youngest site had an established tree canopy. The mature forest site has not been cleared or used for agriculture during modern times. Three sites are located inside La Selva, and two are approximately 6 km west of La Selva in privately owned farms. Site names used in this study are alphabetically ordered by increasing successional age (A1 to D1) in time period 1 (1997–1999) and (A2 to D2) in time period 2 (2015–2017) and M for mature forest.

Tree community and seed rain monitoring

All free-standing woody stems (trees, shrubs, and palms) in each forest site with a diameter (DBH) $\geq$ 5 cm at breast height (1.3 m) have been tagged, mapped, and monitored for survival and growth annually since site establishment in 1997 for secondary forest and 2005 for the mature forest (Chazdon et al. 2005). The diameter of all living stems was measured to the nearest 0.1 mm, and new recruits (untagged trees $\geq$5 DBH cm) were recorded at each forest site.

Seed rain was quantified using the same methods for a total of 48 months over two time periods (24 months per time period) in the eight successional forests sites and for 24 months in the mature forest site during the second time period. Seed rain data from the mature forest site were used as a reference point for selected analyses. Comparison with the mature forest site is informative because it enables us to quantify successional niche assembly processes without implying that this mature forest site represents the regional “climax” community. In each site, 10 1-m^2 seed traps (made from 1-

TABLE 1. Stand characteristics of five 1-ha forest sites in successional and mature forest in Sarapiqui, Costa Rica.

	Site abbreviation (1997, 2017)				
Characteristic	A1, A2	B1, B2	C1, C2	D1, D2	M
Successional age in 1997 (yr)	12	15	20	25	mature forest
Successional age in 2017 (yr)	32	35	40	45	mature forest
Site name	Lindero Sur	Tirimbina	El Peje secondario	Cuatro Rios	El Peje primario
Tree density, 1997 (no. trees/ha)	1,132	1,071	1,265	1,140	n.a
Tree density, 2015 (no. trees/ha)	925	1,020	1,301	1,256	1,114
No. woody species, 1997	64	100	110	136	n.a
No. woody species, 2015	71	130	98	125	155
Location	LS	Tirimbina	LS	Cuatro Rios	LS
Latitude, longitude	10.41° N, 84.03° W	10.40° N, 84.11° W	10.43° N, 84.03° W	10.39° N, 84.13° W	10.42° N, 84.04° W
Surrounding landscape	mature and secondary forest	pasture, plantations, and secondary forest	mature and secondary forest	pasture, secondary and mature forest	mature forest

Notes: Site names are those used in previous publications (Chazdon et al. 2010). Tree density is for stems $\geq$5 cm in diameter at breast height. LS indicates La Selva Biological Station. Sites names are alphabetically ordered by increasing successional age (A1–D1) in 1997–1999 and A2–D2 in 2015–2017 and M for mature forests. The abbreviation “n.a” stands for not applicable.

mm fabric mesh suspended by a frame 1 m above the ground) were placed in a line down the middle of each site every 20 and 24.5 m from the site edges. Traps were monitored monthly for 24 months at two time points: from 1997 to 1999 in the four successional sites and from 2015 to 2017 for the same four successional sites plus the mature forest site. All contents of the traps were collected, and plant reproductive parts were separated from litter, sorted, counted, and identified to the species level, or in limited cases to genera or morpho-species (15%). Taxonomic names were standardized using the package Taxonstand (Cayuela et al. 2017), and species were assigned codes for analyses (Appendix S1: Table S1). Species with seeds ≤1.5 mm were excluded because seeds of this size could pass through the mesh and could not be reliably trapped. The length and width of a sample of seeds for each species were also measured (three to five seeds per species). As seed size categories are a great way to deal with intraspecific variation (Tabarelli and Peres 2002), seed length was aggregated into a categorical variable: small (≤6 mm) and large (>6 mm) seeds (Frankie et al. 1974, Tabarelli and Peres 2002). Based on literature and natural history (Comita et al. 2010, Sandor 2012, Wendt 2014), species in the seed rain were classified into two dispersal modes (animal-dispersed and non-animal dispersed) and two shade tolerance categories (light-demanding and shade tolerant). While species exist on a gradient of shade tolerance (Valladares and Niinemets 2008), we chose to categorize species into two groups, as is commonly done (Whitmore 1989), as our categories were based on natural history information.

Statistical analysis

All analyses were performed in R statistical software (R Core Development Team 2019). We constructed community matrices of the seed rain data for all site × time point combinations and used these matrices for all analyses. Construction of the community matrices is described in the supplementary methods section (Appendix S1). We quantified whether, through succession, the number of seeds increased. Using a negative binomial generalized linear model, we fit a linear model of the number of seeds as our dependent variable vs. the age of the successional forest site and the forest site itself. Using only successional sites at each time period (1997–1999 and 2015–2017), we determined the species present during the 12 consecutive months at each time period as well as the number of seeds by month. To explore variation in seed rain, we calculated multivariate distances in taxonomic composition between each of the sites × time period (1997–1999, 2015–2017) combinations, using multivariate homogeneity of groups' dispersions (variances) and nonmetric multidimensional scaling (NMDS; Legendre and Legendre 1998). Dispersion on abundance-weighted data using betadisper function in the VEGAN package (v. 2.5-3; Oksanen et al. 2018) was implemented, distance values for each seed trap to the forest site centroid in a multivariate dispersion were obtained. Differences in the distance between groups were analyzed with ANOVA. Then based on both presence/absence and abundance-weighted analyses, NMDS was implemented using the function metaMDS in the vegan package with the Chao-Jaccard dissimilarity estimator (Chao et al. 2004) and two dimensions. Results using other dissimilarity estimators were similar, so we only report those obtained with the Chao-Jaccard estimator. Multivariate distances in NMDS are represented metrically, and we so visualized multivariate differences in the seed rain using biplots of NMDS components with 95% confidence ellipses based on the standard error. To test the statistical significance of differences in species composition, we used permutational multivariate analysis of variance (Anderson 2001), as implemented in the adonis function in the vegan package, with site × time period combinations as factors.

To assess whether the taxonomic composition of the seed rain was more shaped by stochasticity or determinism, and how this balance changed with successional age of the forest, we assembled null seed rain communities using a modified version of the approach proposed by Chase et al. (2011). This method employs a modified Raup-Crick index of dissimilarity (Raup and Crick 1979), taking into account species abundances (Stegen et al. 2013, Alberti et al. 2017) using the abundance-weighted Chao dissimilarity estimator, which has the advantage of correcting for unseen species using a probabilistic approach. This index indicates whether the seed rain is more strongly structured by stochastic vs. deterministic processes, and whether determinism is more convergent (seed rain is significantly more similar) or divergent (seed rain is significantly dissimilar), relative to what is expected based on random assembly. We conducted this null model analysis at two levels. First, to evaluate how the balance of stochasticity and determinism changed with forest successional age, the Raup-Crick index was calculated within each of the eight site × time point combinations for all pairs of the 10 traps in a forest (e.g., trap 1 and trap 2 within forest A1), producing 45 comparisons for each site × time point combination. Second, to evaluate whether the seed rain of each site was changing deterministically (converging or diverging) or stochastically through time, the Raup-Crick index between time points for seed rain into the same trap for each site (e.g., trap 1 at A1 forest and trap 1 A2 forests; trap 1 at B1 forest and trap 1 B2 forests), producing 10 comparisons for each site. Specifically, the null seed rain community for each case was generated 9,999 times, and at each iteration, the abundance-weighted Chao dissimilarity index between the two traps was calculated using function vegdist. The resulting metric was the proportion of iterations in which the calculated Chao index was smaller or equal than the observed index. This metric compares the measured β-diversity against the β-diversity that would be obtained under the assumption of stochastic community assembly. The index was scaled to range from −1 to 1 (Chase et al. 2011, Stegen et al. 2013). Hereafter, we will refer to this metric as RC_{ab} (abundance-based Raup-Crick), which indicates whether a pair of traps is less similar (approaching 1), as similar (approaching 0), or more similar (approaching −1), than expected by chance. Therefore, values not different from zero indicate stochastic assembly of the seed rain, whereas values approaching 1 or −1 indicate the predominance of processes causing divergence or convergence in seed rain composition, respectively. We regressed the mean RC_{ab} index of each pair of traps against successional age using a linear mixed model in the lme4 package with site (in the first case) or trap (in the second case) as random effect. For the first case, we also assigned each trap comparison to a category based on the distance ranges from each other, far (>130 m), mid (>50 < 130 m) and near (<50 m) and found no visual evidence of strong spatial structuring (see Fig. 2a). We calculated 95% confidence intervals on mean RC_{ab} values for forests of each successional age assuming a Student's *t* distribution.

We investigated how the strength of mechanisms of determinism (successional niches and successional feedback) changed during succession. To evaluate whether successional forests are converging or diverging in taxonomic composition from each other and from the mature forest, we used two sets of comparisons of similarity indices. First, for each successional forest site, we compared how its similarity to the mature forest changed between the first and second time points and across the chronosequence. Second, for all pairs of successional forest sites, we compared how their similarity changed between the first and second time points and across the chronosequence. Similarity indices were calculated using the SimilarityMult function in the SpadeR package (Chao et al. 2016), using a bootstrap approach of 200 simulations and Hill numbers $q = 0$, 1, and 2. We used Sorensen incidence-based (presence/absence) index, which weighs all species equally ($q = 0$). Then used abundance data to calculate Horn index ($q = 1$), which weighs all individuals equally and thus weighs each species according to its abundance assessing if compositional change is driven by abundance (Gotelli and Chao 2013), and Morisita-Horn index ($q = 2$), which is very sensitive to dominant species (Chao et al. 2016). Whether similarity indices increased or decreased with successional age between the two time points was tested using a Student's *t* test and across the chronosequence using linear regression with successional age and site as fixed effects. We expect that if deterministic processes related to successional niches are important drivers of successional trajectories in the seed rain taxonomic composition of the seed rain in each secondary forest should become more similar to each other and to that of an exemplar mature forest with time. However, the increase in similarity may vary depending on how strongly the index is weighted by abundance. For example, incidence-based ($q = 0$) similarity between two secondary forests may increase more slowly with time than abundance-based ($q = 1$, $q = 2$) similarity, which could imply that successional niches or seed-rain–successional feedbacks are operating to elevate the abundance of locally common species in the seed rain.

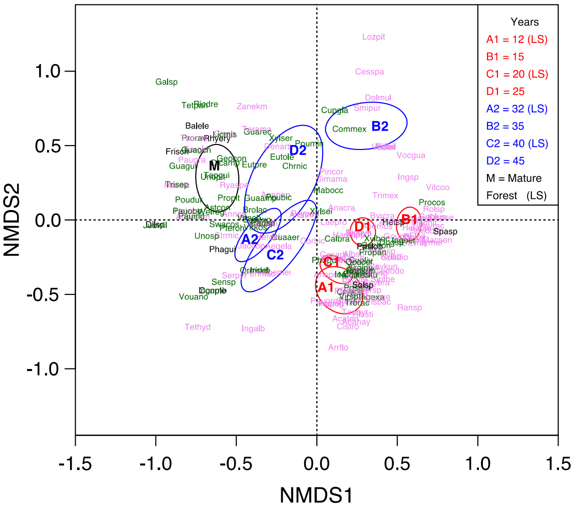

FIG. 2. Variation in species composition of the seed rain across seed traps in four secondary and mature forest sites over two time periods in Sarapiquí, Costa Rica. Secondary forest sites were sampled in 1997–1999 (A1–D1 in red) and 2015–2017 (A2–D2 in blue), and the reference mature forest (M in black) only in 2015–2017. Species abbreviations correspond to the first three letters of the genus and species, given in Appendix S1: Table S1, with green font indicating shade-tolerant species and purple font indicating light-demanding species. Ellipses are 95% confidence ellipses based on standard errors. Sites A, C, and M are located inside La Selva Biological Station (LS).

To determine which species contributed most to changes in the abundance-based similarity between sites, we first determined and group the species shared in a pair of sites for each time period. For each group of shared species, we then calculated the species' relative abundance. We selected, as contributing species of increased similarity in a pair of sites, the 15 upper percentile of all species in each group, which relative abundance increased through time or that were shared only the late time period.

To quantify whether the changes in functional composition were consistent with what is expected based on determinism mediated by successional niches, we compared species richness of functional groups based on seed size, shade tolerance, and dispersal mode represented in the seed rain across forests of different successional ages using rarefaction. Rarefaction curves were estimated using the iNEXT package in R (Hsieh et al. 2016) with 200 bootstrap replications. For each forest site, we then extracted the rarefaction values (Hill number $q = 0$) by functional group and categories (e.g., seed size: large and small) and summed both categories to 100% to calculate the percentage of species by category, functional group, and forest sites. Using these values, across the chronosequence, we fit a linear model of the percentage of species in a specific functional group category as a function of forest successional age and site as fixed effects. To compare the two time points we used a Student's t test. We expected the number of seeds and richness of large, animal-dispersed seeds, and shade-tolerant species to increase with successional age.

We assessed determinism structured by seed-rain–successional feedbacks using two analyses. First, for all species together, and then separately for animal- and non-animal-dispersed species, we quantified whether, during succession, the seed rain into a site became increasingly dominated by the tree species present in the site, indicating a seed-rain–succession feedback involving a transition from seed rain sources outside the site to sources inside the site. Using ordinary least squares regression, we fit a linear model of the species abundances in the seed rain as our dependent variable vs. the tree community as our independent variable, using the tree community data for 1997–1998 and 2014–2015. Species not represented in the seed rain but present in the tree community, or vice versa, were assigned abundance of zero. We excluded seeds from lianas in this analysis because they were not included in tree censuses. We log-transformed the number of trees and number of seeds for values >0, and zero abundances were left as zeroes. The slope of the relationship between the number of seeds of each species in the seed rain vs. the number of adult individuals of each woody species was estimated for each site by time period. Second, we classified seeds with zero tree abundance as immigrant species, and the percentage of immigrants was regressed against forest successional age and site in a general linear model. If determinism generated by seed-rain–successional feedbacks is present, we expected that the correlation between species abundance in the seed rain and mature woody species in the forest should increase as succession proceeds and that the proportion of the seed rain that is comprised of immigrant species should decline with succession.

RESULTS

Variation in seed rain during succession

Across all sites and time periods, a total of 53,552 seeds of 178 species (including 26 morpho-species), representing 51 angiosperm families, were captured in traps (Appendix S1: Table S1). The quantity of seed rain did not increase with forest successional age across the chronosequence or over time (Appendix S1: Fig. S3a). Across all secondary forest sites and time periods, the two most abundant species in the seed rain were *Casearia arborea* and *Alchorneopsis floribunda*, which were present from April to October and more intermittent throughout the year, respectively. Among secondary forest sites, seed rain did not vary strongly among months in both 1997–1999 and 2015–2017 (Appendix S1: Fig. S3b). In the secondary forest sites, four species were present in every month's seed rain during the 12 months of 1997–1999 (*Aristolochia sprucei*, *Cordia bicolor*, *Pinzona coriacea*, and *Zanthoxylum* sp.1) and of 2015–2017 (*Euterpe precatoria*, *Goethalsia meiantha*, *Laetia procera*, and *Welfia regia*; Appendix S1: Fig. S4).

Taxonomic composition of the seed rain differed across forests of different successional ages across both time periods and between secondary and mature forest sites (Fig. 2). Based on both presence/absence and abundance-weighted analyses of all nine site × time period combinations, the taxonomic composition varied significantly ($F_{8,81} = 8.3$, $P = 0.001$ and $F_{8,81} = 3.7$, $P = 0.001$, respectively). Based on visual inspection of the community ordination, seed rain into secondary forests sampled in 1997–1999 (A1–D1 in red) clustered together in a distinct region of the ordination space, compared to the same forests sampled in 2015–2017 (A2–D2 in blue), which were mostly closer in ordination space to the mature forest (M in black). Shade-tolerant species (species codes in green font) were present in the seed rain in both 1997–1999 and 2015–2017, but were more prevalent in secondary forests in 2015–2017, whereas light-demanding species (purple font) were abundant across both 1997–1999 and 2015–2017, but were more prevalent in the secondary forests in 1997–1999. The taxonomic dispersion of the seed rain also increased significantly within each successional forest from 1997–1999 to 2015–2017 for three of the four sites (B: $F = 16.06$, $P < 0.001$; C: $F = 29.95$, $P < 0.001$; D: $F = 9.90$, $P < 0.001$).

Temporal changes in determinism vs. stochasticity of the seed rain

Within sites, assembly processes structuring the seed rain shifted from convergent to divergent with forest successional age, as indicated by a positive, statistically significant relationship between the abundance-based Raup-Crick dissimilarity index (RC_{ab}), measuring within-site spatial variation in taxonomic structure of the seed rain ($R^2 = 0.33$, $P < 0.01$; Fig. 3a). The RC_{ab} for the seed rain of the 12-yr-old forest site was significantly less than zero, indicating a more similar community structure of the seed rain than expected by chance (i.e., deterministically convergent seed rain composition across traps within each forest). The RC_{ab} values in the 20, 25, 33, and 36-yr-old forest sites did not differ from zero, consistent with stochastic assembly, but by 42 and 46 yr of successional age, the RC_{ab} values became greater than zero, indicating a significantly less similar community structure of the seed rain than expected by chance (i.e., deterministically divergent seed rain composition across traps within each forest). Comparing each site after 20 yr of succession, there was no relationship among the RC_{ab} measuring between time periods for the same site turnover and forest successional age (Fig. 3b).

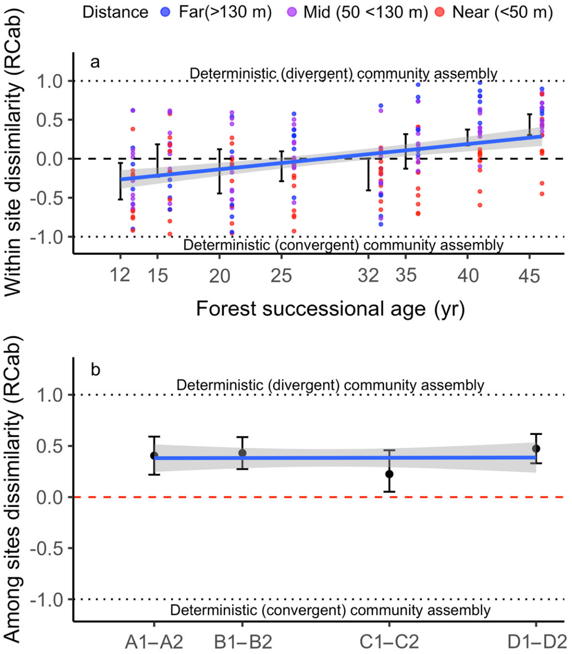

FIG. 3. Changes in determinism and stochasticity of seed-rain assembly processes during succession, based on the abundance-weighted Raup-Crick dissimilarity index (RC_{ab}). RC_{ab} values range from −1 to 1, indicating whether (a) community structure within sites across all successional ages or (b) between time periods for the same site (turnover), 1997–1999 and 2015–2017, are more dissimilar (approaching 1), as dissimilar (approaching 0), or more similar (approaching −1), than expected by chance. The red horizontal line at RC_{ab} of zero denotes purely stochastic community assembly, whereas RC_{ab} of 1 or −1 indicates assembly processes producing divergent or convergent community structure, respectively. Points are mean trap RC_{ab} values, error bars indicate 95% confidence intervals. Between traps distances ranges were classified as far (>130 m), mid (>50 < 130 m) and near (<50 m).

However, all RC_{ab} indices measuring the turnover were greater than zero, indicating that taxonomic composition within sites diverged over time more than expected by chance.

Effects of successional niche and successional feedback assembly processes on the seed rain

We used the mature forest site as a reference point for seed rain composition in a late successional forest representative for this region of Costa Rica. Regardless of the similarity index used, taxonomic composition of the seed rain in each secondary forest site became more similar to that of the reference mature forest over time (Fig. 4a), consistent with the influence of successional niche assembly processes. Averaging across all secondary forest sites, similarity to the reference mature forest increased significantly, although sometimes marginally so, from 1997–1999 to 2015–2017, using indices calculated based on species' presence/absence (t = 2.89, P = 0.04; Fig. 4a), weighted by abundance (t = 3.24, P = 0.04; Fig. 4b), and weighed by the more dominant species (t = 2.98, P = 0.05; Fig. 4c). Successional forest sites located inside La Selva (A and C) converged towards the mature forest site within La Selva in composition more so than did those outside La Selva (B and D), based on a presence/absence-weighted (Sorenson's) index. This is likely due to the closer proximity of these sites to the representative mature forest site inside La Selva, reducing dispersal limitation, relative to other successional forest sites, which are located outside of La Selva. Successional forest site A, the youngest, showed the smallest increase in similarity to the mature forest when species' abundances were taken into account (Fig. 4b, c). This is likely because, while late successional species abundant in the mature forest slowly accumulate during succession, they are still far less abundant in young forests than earlier successional species. Integrating time series and chronosequence approaches, we found similar patterns, in that similarity to the mature forest increased with successional age for all indices (presence/absence R^2 = 0.82, slope = 0.011, P = 0.01; abundance-weighted R^2 = 0.72, slope = 0.013, P = 0.04; weighted by dominant species R^2 = 0.63, slope = 0.022, P = 0.05; Appendix S1: Fig. S5).

The proportion of immigrant seeds declined significantly with successional age (R^2 = 0.84, P < 0.01; Fig. 5), consistent with increasing strength of seed-rain–successional feedbacks. Moreover, the similarity of seed rain composition between all pairs of successional forest sites decreased over time, based on species presence/absence (t = 5.38, P = 0.003; Fig. 4d). Even for the oldest successional forest (45 yr old), 25% of the total number of seeds were still of species not present in that site's adult tree community. However, based on similarity indices weighted by species abundance and by dominant species, not all pairs of successional forest sites became less similar to each other through time (Fig. 4e, f). Similarity increased for site pair B and C and pair C and D through time, whereas for all other pairs, it decreased. The contrasting behavior of these two pairs of sites is due to large increases through time in the relative abundance of seeds of several species in these four sites, including *Pinzona coriacea*, *Cordia bicolor*, *Casearia arborea*, *Vourana anomala*, and *Euterpe precatoria*. Of these species, the latter four are trees and were censused in the tree community in 1997–1999, consistent with seed-rain–successional feedbacks influencing seed rain composition. Similarity between dominant species for site pair A and B was low and decreased through time from 3% to 1%, possibly because even though these sites were close in age, A is located inside, whereas B is outside, of La Selva.

For all species, the taxonomic composition of the seed rain into each forest site was correlated with that site's tree abundance, and the strength of this correlation

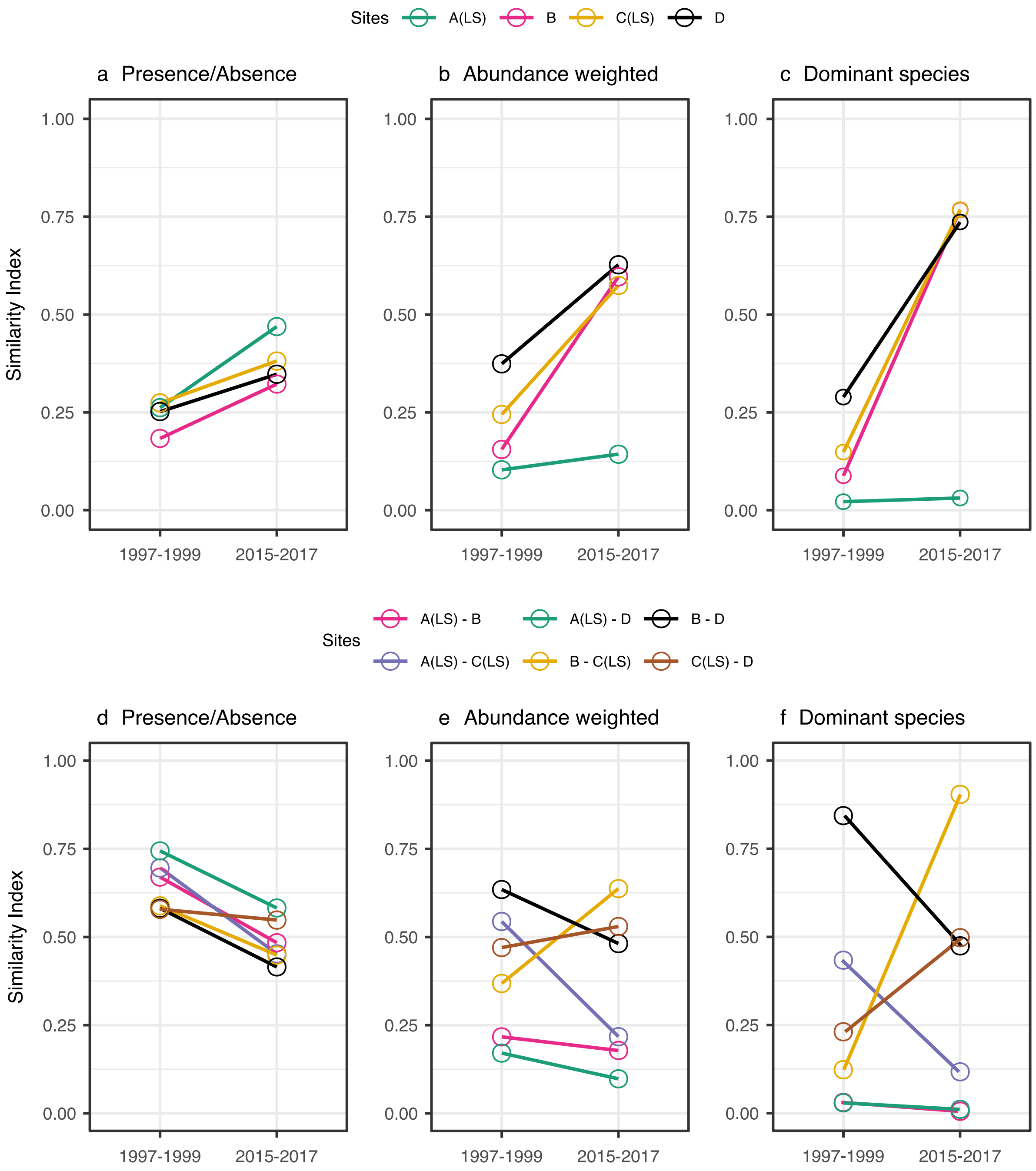

FIG. 4. Variation in similarity indices in species composition of the seed rain across four secondary and mature forest sites over two time periods in Sarapiquí, Costa Rica. Sites names are alphabetically ordered by increasing successional age (A–D), and M for mature, forests. The mature forest was used as a reference point representing a late successional community composition for this region of Costa Rica. Sites A, C, and M are located inside La Selva Biological Station (LS). (a–c) Indices comparing the similarity of each secondary forest with the mature forest based on (a) Sorensen incidence-based, (b) Horn abundance-based, and (c) Morisita-Horn dominance-based indices. (d–f) Indices comparing the similarity of each pair of secondary forests in 1997–1999 vs. 2015–2017 based on (d) Sorensen incidence-based, (e) Horn abundance-based, and (f) Morisita-Horn dominance-based indices. See Appendix S1: Fig. S5 for comparisons across all successional ages.

generally increased with successional age, consistent with increasing importance of seed-rain–successional feedbacks (Fig. 6). In 1997–1999, species abundances in the seed rain were not significantly related to those in the tree community for any successional forest (Fig. 5a–d). However, after 20 yr of succession, species abundance in the tree community became more strongly related to species abundance in the seed rain and more similar to that

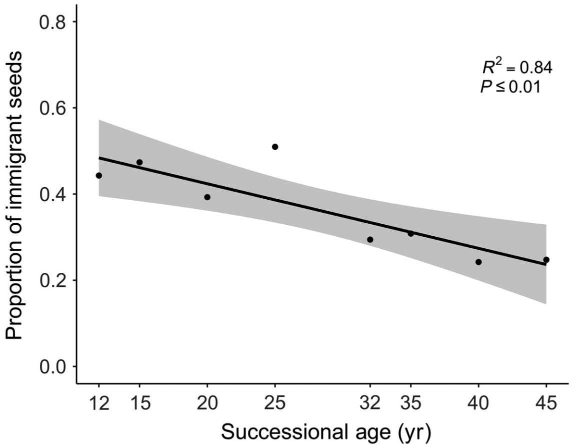

FIG. 5. Decreasing proportion of immigrant seeds (species not locally represented in the tree community of the site) in secondary forests of increasing successional age in Sarapiquí, Costa Rica. The black line is the expected relationship based on a linear model (forest successional age and site as fixed effects) and the gray shading indicates the 95% confidence interval on the fit.

in the reference mature forest. Estimates of the slope of this relationship were significantly positive for all successional forests in 2015–2017, with the exception of forest B (Fig. 6, panel f). Animal-dispersed species followed patterns similar to the all-species case in that the slope of the seed-adult abundance relationship increased across the two time points, whereas the slopes for non-animal-dispersed species did not exhibit as dramatic increases (Fig. 6 caption). Moreover, for non-animal-dispersed species, some early successional forests exhibited significant correlations (Fig. 6 caption). Functional composition of the seed rain varied with successional age, consistent with successional niche assembly processes (Fig. 7). Integrating time series and chronosequence scales, the percentage of species in the seed rain of large and shade-tolerant species increased with successional age, with corresponding decreases in the percentages of small and light-demanding species, although for shade tolerance, the change was only marginally significant ($R^2 = 0.99$, slope = 0.02, $P = 0.0003$ and $R^2 = 0.78$, slope = 0.01, $P = 0.09$, respectively; Fig. 6a, b). However, the percent of animal-dispersed species in the seed rain did not increase significantly.

DISCUSSION

Landscapes modified by humans, associated with habitat fragmentation and defaunation, are becoming ever more prevalent in tropical forest landscapes (Peres et al. 2006, Chazdon et al. 2009, Chazdon 2014, Dirzo et al. 2014, Benítez-López et al. 2017), with the potential to disrupt the essential seed dispersal processes (Graham 2001, Herrera and García 2010, San-José et al. 2019, 2020) that are the first step in forest regeneration (Wunderle 1997, Arroyo-Rodríguez et al. 2017). By combining time series and chronosequence approaches in these secondary tropical forests of Costa Rica, we found evidence that successional trajectories of seed rain are not only shaped by successional niches, as expected, but also by seed-rain–successional feedback. We defined seed-rain–successional feedback as a local, deterministic assembly process operating in addition to successional niches that causes seed rain to be more strongly structured by priority effects combined with successional dynamics internal to a forest site, due to comparatively lower external input of seeds. Seed-rain–successional feedbacks increased in strength with successional age, especially for animal-dispersed species, producing deterministically divergent seed rain patterns across these secondary forests.

If the imprint of seed-rain–successional feedback persists to the seedling and later life stages, then secondary forests in human-modified landscapes should continue to diverge as succession progresses, creating a historically contingent landscape of forest sites in compositionally dissimilar stable states (Appendix S1: Figs. S1, S2). Dynamic land-use change has historically characterized many forested regions, including many in Costa Rica, creating a mosaic of forests in various stages of succession (Foster 1992, Zahawi et al. 2015). While reforestation has increased in recent decades in much of Costa Rica (Sloan and Sayer 2015), many secondary forests are not in protected areas and are often deforested again while they are still young (Schwartz et al. 2017, Reid et al. 2019). As animal populations continue to decline, regenerating empty forests (Peres et.al. 2006, Benítez-López et al. 2017) may be unable to support the diversity of seed dispersal processes and range of seed dispersal distances characteristic of less human-modified landscapes (Kurten 2013). Although our statistical power was lower for non-animal-dispersed species, our analyses suggest that seed-rain–successional feedbacks may be stronger for animal-dispersed species, which may reflect the facts that seed dispersal by animals may be more impeded in human-modified landscapes. Thus, there should be variation in the extent to which seed-rain–successional feedbacks effect divergence in composition of regenerating secondary forest patches in the landscape. To the extent that forest connectivity continues to decline, we expect such divergence to become more prevalent.

Shift from convergence to divergence in seed rain composition during succession

Assembly of forest communities is governed by both stochastic and deterministic processes (Chazdon 2008, Purves and Turnbull 2010). While we also found evidence that both types of processes were operating, we observed a shift in the spatial community structure of the seed rain with successional age, from convergent in the youngest, to divergent in the oldest, successional

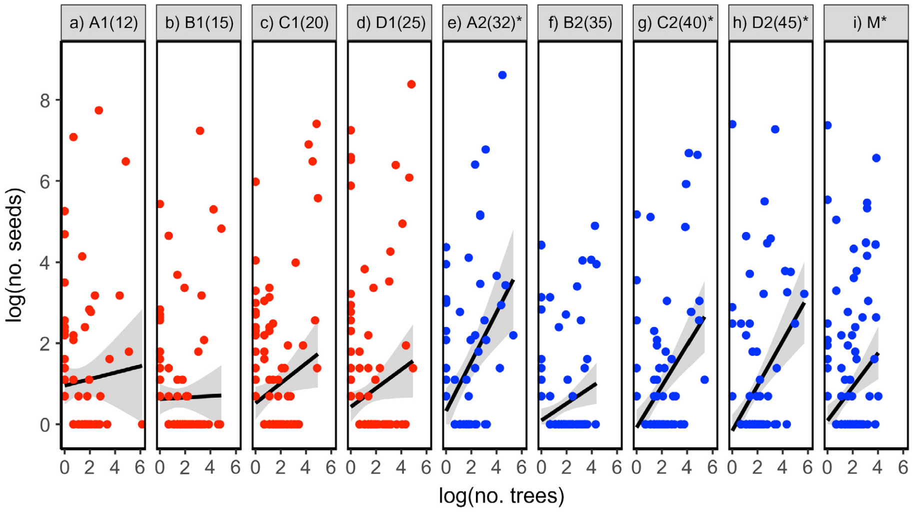

FIG. 6. Positive seed-rain–succession feedback increasing with successional age of the forest, as indicated by the relationship between the number of stems and the number of seeds of each woody species, with all species (n = 331) included in the analysis. Different panels correspond to forests of different successional ages (parentheses after the abbreviation, except for the mature forest, M). Non-zero values were log-transformed, and value of 0 is equivalent to absence of that species in either the seed rain or tree community. The asterisk indicates that the slope parameter was significantly different from zero (1997–1999; A1, $P > 0.10$, slope = 0.07; B1, $P > 0.10$, slope = 0.02; C1, $P > 0.05$, slope = 0.25; D1, $P > 0.05$, slope = 0.23; 2015–2017; A2, $P < 0.01$, slope = 0.61; B2, $P = 0.05$, slope = 0.21; C2, $P < 0.01$, slope = 0.51; D2, $P < 0.01$, slope = 0.55; E, $P < 0.01$, slope = 0.42). Analyses for animal-dispersed species alone (n = 250) mirrored the all-species relationships (1997–1999; A1, $P > 0.10$, slope = 0.19; B1, $P > 0.10$, slope = 0.09; C1, $P > 0.10$, slope = 0.21; D1, $P > 0.10$, slope = 0.20; 2015–2017; A2, $P < 0.01$, slope = 0.46; B2, $P = 0.04$, slope = 0.20; C2, $P < 0.01$, slope = 0.55; D2, $P < 0.01$, slope = 0.63; E, $P < 0.01$, slope = 0.47). In analyses for non-animal-dispersed species (n = 27), some early successional forest showed significantly positive slope, although steeper slopes were also found in late successional forests (1997–1999; A1, $P = 0.04$, slope 0 = 0.82; B1, $P > 0.10$, slope = 0.63; C1, $P > 0.10$, slope = 0.60; D1, $P < 0.01$, slope = 0.38 and 2015–2017; A2, $P = 0.04$, slope = 0.92, B2, $P = 0.05$, slope = 0.72; C2, $P > 0.05$, slope = 0.61; D2, $P = 0.04$, slope = 0.40; E, $P > 0.10$, slope = 0.18).

forests. These results are consistent with a less spatially aggregated seed community in late successional forests (Costa et al. 2012), even though the number of species in the seed rain within each secondary forest site in the 2015–2017 was not higher than in 1997–1999. As in studies of trees in successional forests (van Breugel et al. 2013), our results also showed that seed rain was taxonomically more similar earlier, than later, in succession. This combined with our findings that the seed rain earlier in succession consisted of a higher proportion of immigrants, as well as of smaller-seeded and light-demanding species, compared to later in succession, suggests that regionally abundant, well-dispersed early successional species that are effective colonists in a human-modified landscape may be agents of convergence (Martínez-Garza et al. 2009, Norden et al. 2009, Costa et al. 2012, Norden et al. 2017).

Our finding of divergence among sites in seed rain as succession progressed is predicted by our conceptual model of seed-rain–successional feedbacks. Our model predicts that the seed rain into forest sites should become increasingly dominated by internal regeneration processes, amplifying priority effects. Increasing dissimilarity in the seed rain during succession was also found in a chronosequence study of Atlantic rainforest sites in Brazil (Costa et al. 2012). Our time series approach allows for a strong test for divergence in the seed rain at a site through time, which we also found, providing concrete evidence that these sites are still undergoing successional changes in species composition consistent with successional niche assembly processes. Compared to taxon-based analyses, stronger evidence has been found of functional convergence to mature forests during tropical forest succession (Chazdon 2008, Liebsch et al. 2008, Norden et al. 2012, Dent et al. 2013, but see Boukili and Chazdon 2017). Our results are consistent with these findings and with the influence of successional niche assembly in that we found the representation in the seed rain of both large-seeded and, to some extent, shade-tolerant species increased with successional age, consistent with other studies (Tabarelli and Peres 2002, Castillo and Ríos 2008, Reid et al. 2015). All these results reflect successional niches in tropical forest, as shorter-lived, light-demanding tree species are replaced by longer-lived, shade-tolerant species (Bazzaz and Pickett 1980, Wright et al. 2010, Poorter et al. 2019). Functional convergence in terms of dispersal modes represented in the seed rain was less distinct, consistent with the facts that, even in mature forests, there are also non-animal-dispersed species (Howe and Smallwood 1982). In our study sites, animal-dispersed species in secondary forests varied from 70% to 90%, did not change with

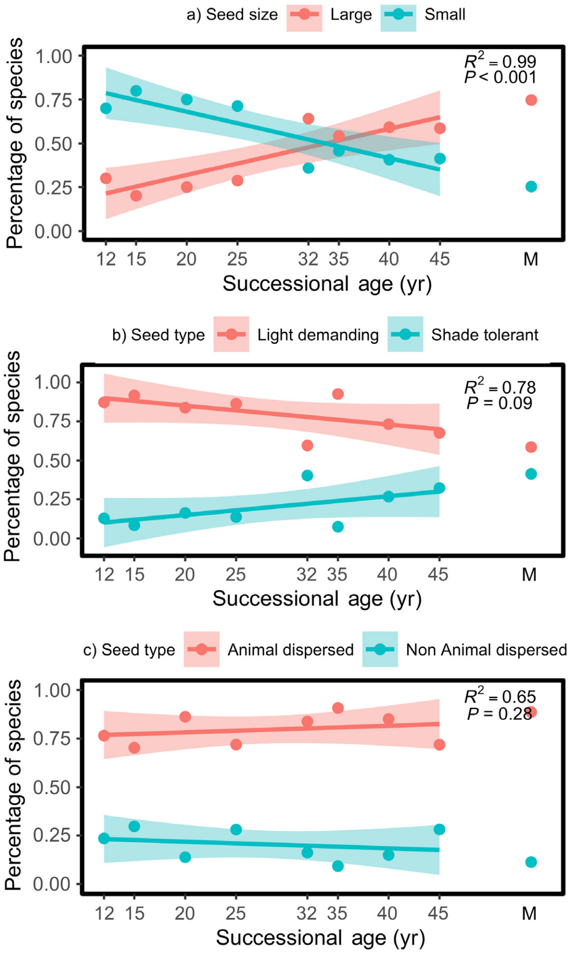

FIG. 7. Changes in the functional composition of the seed rain in secondary forests of increasing successional age in Sarapiquí, Costa Rica. Shifts in the percentages of (a) species with small (≤6 mm) and large seeds (>6 mm), (b) shade-tolerant and light-demanding species, and (c) animal-dispersed and non-animal-dispersed species represented in the seed rain. The percentage of species by category is based on calculated asymptotic Chao diversity estimates from rarefactions, converted to percentages. Since there are only two categories, the correlation was conducted for the category that was increasing.

successional age, and was similar to the 89% found in the mature forest site. Our findings integrating time series and chronosequence approaches, are consistent with those from a chronosequence study of Brazilian secondary forests, in which animal-dispersed species represented 67–75% of species in the seed rain, regardless of successional age (Costa et al. 2012). However, another chronosequence study found increases in vertebrate dispersed seeds in the seed rain with successional age (Tabarelli and Peres 2002). Many animal seed dispersers are known to visit successional forests, and principle among these are bats. Phyllostomid bats are thought to make important contributions to seed rain in early successional forests because many are abundant even in human-modified forests (Gorresen and Willig 2004), consume fruits and disperse seeds of early successional species (Bernard and Fenton 2003), and fly across even large openings in the forest (Muscarella and Fleming 2007). Small, tent-roosting bats, such as *Artibeus watsoni*, promote dispersal of larger seeded species abundant mostly in late successional forest (Melo et al. 2009). Thus, due to variable specialization of some animal species to successional vs. mature forests, functional composition of the seed rain in terms of dispersal mode may not converge reliably to that of mature forest. Moreover, our findings also indicate the presence of functional redundancy across succession, which is important for maintaining stability of the forests.

Within a site, our conceptual model predicts that seed-rain–successional feedbacks should produce increasing self-similarity through time. We found evidence for this prediction in that the seed rain composition became more correlated with the reproductive tree community at each site in 2015–2017, compared to 1999–1997, and that the proportion of immigrants in the seed rain declined with successional age. These results are consistent with the interpretation that mature forest specialists are dispersal limited (Norden et al. 2017). Since the woody stems (DBH ≥ 5 cm) themselves are also becoming more similar in composition to the mature forest (Letcher and Chazdon 2009*b*), our results are indicative of seed-rain–successional feedback. The seed rain of most pairs of successional forests diverged from each other through time, but in contrast to predictions of our conceptual model, some became more similar when species abundances, particularly of dominant species, were taken into account. The species responsible for these contrasting results may demonstrate exceptions that prove the rule. One of the species causing convergence in the seed rain is a dominant, regionally abundant, bird-dispersed species, *Pinzona coriacea,* a liana that has been found to be one of the largest in the mature forest of our study site (Letcher and Chazdon 2009*a*). Likewise, *Cordia bicolor*, *Casearia arborea*, *Vourana anomala*, and *Euterpe precatoria* also contribute to the convergence in the seed rain of some sites during succession, as these species were present as fruiting adults in 1997–1999, thereby contributing to the seed rain. Thus, seed-rain–successional feedbacks have the potential to promote convergence between successional sites in seed rain when the composition of the adult tree community is strongly constrained by similar ecological filtering of species from the regional pool. However, seed-rain–successional feedbacks may also promote divergence between sites when ecological filtering is weak, and the adult tree community is shaped primarily by seed input, opening the door to strong priority effects. Here, we found evidence of both outcomes. In addition to seed-rain–successional feedbacks, divergence in the successional trajectories of forests may arise from site-specific differences in landscape context, such as proximity to seed sources, the species composition of seed sources, visitation by dispersal agents, and the surrounding landscape (Ricketts 2001). Some of the successional differences that we found could be traced to whether sites were located inside (sites A and C) or outside of (sites B and D) La Selva. Sites in La Selva are surrounded by a higher proportion of old-growth forest than the sites outside of La Selva (Fagan et al. 2013), which highlights the influence of the landscape context. Seed rain in successional forests shared at most 47% of the species in the mature forest, highlighting that seed rain is spatially variable and that these secondary forests still require substantial time to reach a mature state, as found in post-dispersal stages (Finegan 1996). While we used the single mature forest site in our study only as a reference for comparison, not as an exemplar of a climax to which all successional forests were headed, this is one important limitation of our study, since there is substantial variation in the composition of mature forests, even at the spatial scale of our study (e.g., Clark et al. 1999, Norden et al. 2009, Sesnie et al. 2009).

Conclusions

Seed dispersal is a process that is often considered to be highly stochastic. However, combined data from a chronosequence and time series revealed significant determinism in seed rain that increased as succession progressed in these Costa Rican secondary forests. Successional changes in the structure of the seed rain were influenced by processes simultaneously generating both convergence and divergence. While successional niches largely promoted convergence in the community structure of the seed rain in regenerating forests, seed-rain–successional feedbacks largely promoted divergence, but also had the potential to promote convergence. We hypothesize that seed-rain–successional feedbacks may become ever more influential in increasingly human-modified tropical forest landscapes characterized by reduced forest connectivity, smaller and more isolated forest sites, and smaller frugivore populations. Since in most tropical forests, the regional species pool of late successional woody species is large, isolated secondary forest sites may be likely to mature into dissimilar stable states that each consist of a stochastic subset of the pool of possible mature forest species, creating a landscape defined by historical contingency. Future studies should parse the effects of specific local and landscape scale processes to examine how seed-rain–successional feedbacks vary with the severity of different drivers of human modification, which will be important predicting the future of successional tropical forests.

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Supporting Information

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Open Research

Code (Huanca Nuñez 2021) is available on Zenodo: https://doi.org/10.5281/zenodo.4543772.