Environmental gradients and the evolution of successional habitat specialization: a test case with 14 Neotropical forest sites

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Summary

1. Successional gradients are ubiquitous in nature, yet few studies have systematically examined the evolutionary origins of taxa that specialize at different successional stages. Here we quantify successional habitat specialization in Neotropical forest trees and evaluate its evolutionary lability along a precipitation gradient. Theoretically, successional habitat specialization should be more evolutionarily conserved in wet forests than in dry forests due to more extreme microenvironmental differentiation between early and late-successional stages in wet forest.

2. We applied a robust multinomial classification model to samples of primary and secondary forest trees from 14 Neotropical lowland forest sites spanning a precipitation gradient from 788 to 4000 mm annual rainfall, identifying species that are old-growth specialists and secondary forest specialists in each site. We constructed phylogenies for the classified taxa at each site and for the entire set of classified taxa and tested whether successional habitat specialization is phylogenetically conserved. We further investigated differences in the functional traits of species specializing in secondary vs. old-growth forest along the precipitation gradient, expecting different trait associations with secondary forest specialists in wet vs. dry forests since water availability is more limiting in dry forests and light availability more limiting in wet forests.

3. Successional habitat specialization is non-randomly distributed in the angiosperm phylogeny, with a tendency towards phylogenetic conservatism overall and a trend towards stronger conservatism in wet forests than in dry forests. However, the specialists come from all the major branches of the angiosperm phylogeny, and very few functional traits showed any consistent relationships with successional habitat specialization in either wet or dry forests.

4. *Synthesis*. The niche conservatism evident in the habitat specialization of Neotropical trees suggests a role for radiation into different successional habitats in the evolution of species-rich genera, though the diversity of functional traits that lead to success in different successional habitats complicates analyses at the community scale. Examining the distribution of particular lineages with respect to successional gradients may provide more insight into the role of successional habitat specialization in the evolution of species-rich taxa.

Key-words: determinants of plant community diversity and structure, functional traits, life-history evolution, phylogeny, pioneer species, precipitation gradient, tropical dry forest, tropical wet forest

Introduction

Environmental gradients provide opportunities for understanding the evolution of habitat specialization (Grime 1977; Grubb 1977). Many of the gradients observed in ecosystems are associated with the process of succession, as communities reassemble after disturbances (Pickett 1976; Sousa 1984). Successional habitat specialization – the radiation of lineages to take advantage of particular points on this successional gradient – is

potentially a strong driver of plant evolution (van Steenis 1958; Gómez-Pompa 1971; Pickett 1976). Grubb (1977) reiterated the importance of the regeneration niche in community assembly, and many studies have explored the potential of disturbance for maintaining diversity (Sousa 1984; Ricklefs 1987; Tilman & Pacala 1993), yet relatively few studies have examined successional gradients as an evolutionary force.

Neotropical forests are a fascinating laboratory for studying plant evolution due to their floristic diversity and environmen-

tal heterogeneity (Gentry 1988). The specialization of tropical trees into successional habitats has long been recognized. Pioneer tree species – the species that establish and dominate early in succession – form an important component of the tropical forest flora, particularly in wet forests (van Steenis 1958; Gómez-Pompa 1971; Whitmore 1989). Gómez-Pompa (1971) proposed that the evolution of many tropical plant taxa could only be understood through the lens of secondary forest succession. He postulated that species richness and taxonomic diversification in the tropics could be explained, at least partially, by strong selection for growth and survival in early successional habitats following large-scale disturbances. Pioneer species evolved to take advantage of natural disturbances such as fires, floods, landslides, cyclones and volcanic eruptions, and they have proliferated in recent millennia with the expansion of anthropogenic disturbances (Whitmore 1989; Chazdon 2003, 2014). Yet the exact definition of pioneer species has remained somewhat ambiguous (Swaine & Whitmore 1988; Gitay & Noble 1997), and relatively few studies have examined the evolutionary origins of the taxa that dominate early successional forests vs. the taxa that are more abundant in undisturbed forest (Gentry 1988; Dalling, Hubbell & Silvera 1998).

The massive expansion of available molecular data in recent decades (Wikström, Savolainen & Chase 2001; Magallón & Castillo 2009; Stevens 2014) gives us unprecedented power to examine the distribution of traits on the angiosperm phylogeny and test hypotheses about their evolutionary origins. Like extinction risk (Fritz & Purvis 2010), successional habitat specialization is a complex emergent characteristic of a species, stemming from the interaction of many traits and the environment. Here, we develop a new conceptual model of how the strength of environmental gradients during succession affects the evolution of successional habitat specialization. We test the model by evaluating the phylogenetic conservatism of habitat specialization in tropical forest trees across a precipitation gradient.

Successional processes involve changes in resource availability and abiotic conditions (Fig. 1). The magnitude of these changes depends on the intensity of the disturbance that begins the succession (Sousa 1984) and also on the similarity between the starting point and the endpoint in succession (Pickett 1976). In ecosystems where the early successional and late-successional stages are structurally similar (e.g. grasslands, shrublands and open forests), these resource/condition gradients are less strong than in ecosystems where successional stages differ greatly in structure (e.g. tropical wet forests). Changes in conditions and resource availability during succession mediate the success of individuals that arrive at a site. When successional gradients are weak, the valley between adaptive peaks on the fitness landscape is shallow: being a specialist at one end of the successional gradient involves little reduction in fitness at the other end of the gradient (Fig. 1). When successional gradients are strong, though, being a specialist at one end of the gradient has a considerable fitness cost at the other end of the gradient. Thus, we expect to see fewer independent origins of successional habitat specialization where gradients are strong.

Instead, we expect to see conservatism of habitat specialization; specialist lineages consist of close relatives that radiated within that habitat rather than crossing the fitness barrier between habitats (Fig. 1).

Neotropical forest succession involves numerous environmental gradients. As succession proceeds, light availability decreases, temperatures (and diel temperature fluctuations) decrease, and relative humidity increases (Bazzaz & Pickett 1980; Swaine & Whitmore 1988; Finegan 1996; Guariguata & Ostertag 2001; Ruiz, Fandiño & Chazdon 2005). These environmental gradients are present in every forest during succession, but the relative strength of the gradients depends on the similarity in abiotic conditions between early successional and late-successional habitats, which in turn is a function of habitat structure. Precipitation is a major driver of structural differences among Neotropical forests. Tropical dry forests have lower stature and greater canopy openness than wet forests (Ewel 1977; Holbrook, Whitbeck & Mooney 1995). In dry forests, light conditions differ less strongly between early successional and late-successional habitats (Holbrook, Whitbeck & Mooney 1995; Lebrija-Trejos *et al.* 2011). In mature wet forests, generally 1–2% of the incident sunlight reaches the forest floor except in canopy gaps (Chazdon & Fetcher 1984). In dry forests, 5–10% of the incident sunlight reaches the forest floor in the wet season, with higher values during the dry season when many species are leafless (Coomes & Grubb 2000; Poorter 2009). Canopy closure in dry forests during succession is slower than in wet forests (Ewel 1977; Ruiz, Fandiño & Chazdon 2005; Letcher & Chazdon 2009; Lebrija-Trejos *et al.* 2010), potentially leaving a longer window of time for pioneer species to colonize in dry forests. The microclimatic stressors that plant seedlings face are markedly different between open areas and forest understorey in wet forests and less distinct in dry forests (Ewel 1977). The precipitation gradient in Neotropical forests therefore produces a gradient in the environmental dissimilarity of early successional and late-successional habitats.

The ability to thrive in particular successional habitats is a composite trait resulting from many physiological, anatomical and phenological adaptations (Poorter & Markesteijn 2008; Lebrija-Trejos *et al.* 2010), many of which are likely to be phylogenetically conserved (Prinzing 2001; Losos 2008). Based on our model of the evolution of successional habitat specialization (Fig. 1), we expect to observe different patterns of successional habitat specialization in wet and dry forests due to the depth of the 'valley' between adaptive peaks in the fitness landscape (Fig. 1). Specifically, we predict that there will be lower levels of successional habitat specialization in dry forest floras, with specialists in each group (SG and OG) originating from many lineages and not necessarily being closely related. In wet forests, by contrast, where the adaptive peaks are separated by a deeper 'valley', we predict that there will be fewer origins of the specialist strategies, but that the lineages that do evolve into specialists will undergo adaptive radiations. Thus, we predict that the successional habitat specialists in wet forest will be closely related and that habitat specialization is more likely to be a phylogenetically conserved trait in wetter forests.

Fig. 1. Resource availability and abiotic conditions change during succession. The species that are prevalent early in succession contend with different stressors and take advantage of different resources than later successional species. In successional systems where the endpoint is structurally similar to the starting point, these resource/condition gradients are weak, and where the endpoint is structurally distinct, the gradients are strong. Species that are adapted to take advantage of early successional environments (second-growth specialists, indicated here as 'SG specialist') are less successful in late-successional conditions, producing a 'valley' between adaptive peaks on the fitness landscape. This trade-off is particularly pronounced when successional gradients are strong. Thus, assuming that the traits underlying successional habitat specialization are conserved on the angiosperm phylogeny, we expect to see fewer origins and greater conservatism of SG specialization in successional systems with stronger environmental gradients. Old-growth specialization should follow a similar pattern.
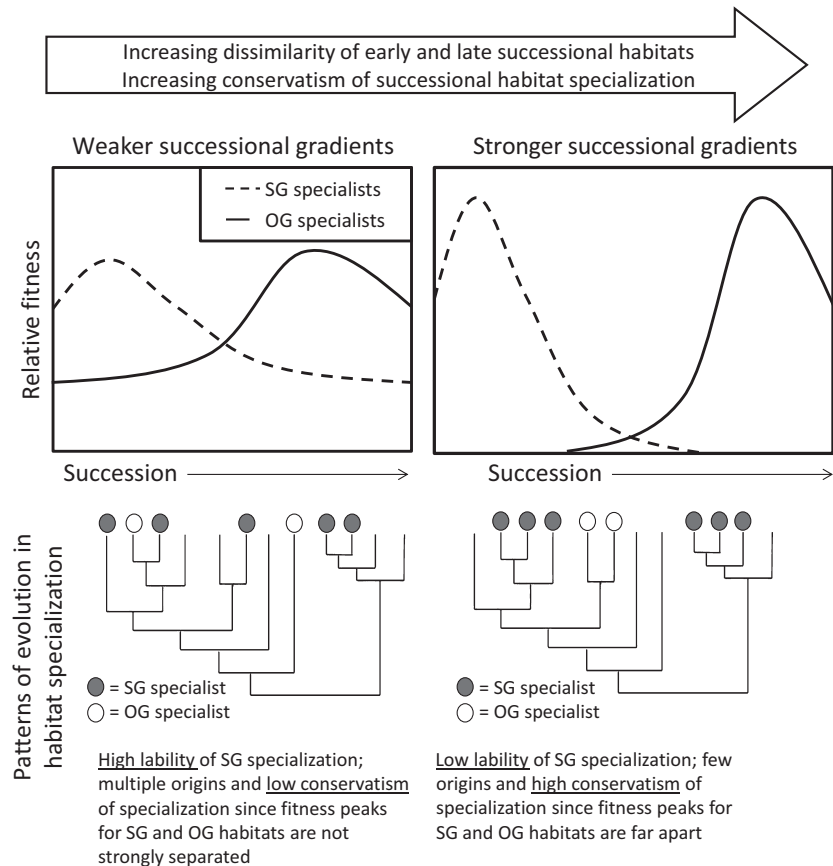
Because the mechanisms driving habitat specialization in wet and dry forests are likely to depend on plant functional traits rather than species phylogenetic relatedness per se, we predict that the functional traits characterizing the early successional specialist species will differ between wet and dry forests (Lohbeck *et al.* 2013). Early successional habitats in wet forests are presumed to favour tree species with traits associated with fast growth and cheap construction costs: rapid height growth rates, high rates of photosynthesis, high leaf nutrient concentration, thin leaves – high SLA, small easily dispersed seeds and low density wood (Bazzaz & Pickett 1980; Guariguata & Ostertag 2001; Poorter *et al.* 2004; Poorter & Rose 2005). In dry forests, the most important early successional traits are likely to be related to desiccation tolerance; thus, dry forest SG specialists should have lower growth rates and photosynthetic rates, lower SLA and higher wood density than wet forest SG specialists (Bazzaz & Pickett 1980; Poorter 2009; Lebrija-Trejos *et al.* 2010).

Analysis of functional trait variation among specialist groups will provide critical insights into the selective pressures that may have led to the evolution of successional specialization of trees in tropical forest regions. This synthesis paper is the first to test the hypothesis of phylogenetic conservatism of successional habitat affinities of plant lineages, with a robust comparison among fourteen regions spanning wet and seasonally dry forests in the tropical Americas. The data sets we analyse form an unprecedented base of information for understanding habitat specialization in relation to phylogeny and functional traits in Neotropical forests.

Materials and methods

Based on existing woody vegetation surveys in a range of wet and seasonally dry Neotropical lowland forests, we examined the phylogenetic distribution and functional traits of trees that are specialists in successional vs. mature forest. We tested whether patterns in successional habitat specialization and trait conservatism differ across forest regions along a rainfall gradient. We identified 14 sites across the Neotropics (Fig. 2), all in lowland forests (< 1000 m asl), representing a precipitation gradient from 788 to 4000 mm per year. We selected sites with extensive sampling of both old-growth and secondary forest with good species-level identification of at least 75% of stems. For 12 of the 14 sites, functional trait data are available for a large fraction of the species present (Table 1). Many of these sites include ongoing monitoring projects. When using data from monitored sites, we selected a single year of data to focus on, generally the most recent year of data available with full taxonomic resolution (Table 1). In 12 of the 14 sites, the samples are spread over a fairly small geographic range (Table S1), but larger regional sampling areas were necessary in the Atlantic forest sites (FES and FOD) due to the heavily fragmented nature of the remaining forest patches in that landscape (Rodrigues *et al.* 1989; Rodrigues 1999).

The data incorporated in this paper include columnar cacti, palms and woody trees; we omitted lianas, understorey shrubs and other growth forms. At all sites, trees were sampled using plot-based methods (see Table S1 and references cited in Table 1 for details), and

Fig. 2. The 14 sites span a wide range of locations in the Neotropical lowlands.

unknown individuals were collected for identification using local and international herbarium collections. Trees at each site that could be identified as belonging to a distinct genus but could not be matched to described species were given internally consistent morphospecies names at that site (e.g. *Dussia* sp. A_SAR). Individuals that were not identified below the family level were omitted from analysis. We also limited the taxonomic scope of our study to angiosperms, omitting tree ferns and gymnosperms, which contributed a negligible amount of biomass in these sites. At all sites, multiple-stemmed individuals were only counted once. For nine sites, we include all individuals ≥ 5 cm diameter at 1.3 m height (DBH), and for two sites (SAR and GUA), we include individuals ≥ 10 cm DBH. At FES and FOD, we include all individuals ≥ 4.8 cm DBH since this was the diameter threshold used in sampling. At 13 out of 14 sites, we were able to use the same size classes in old-growth and secondary forest, but at BRA, we include stems ≥ 5 cm DBH in secondary forests and stems ≥ 10 cm DBH in old-growth forests due to constraints of data availability. If anything, the size class sampling discrepancy at BRA will detect a greater abundance of old-growth-adapted species in the second-growth forest at that wet forest site, since the tree species that are characteristic of old growth are often present in small size classes in the undergrowth of older secondary forests (Chazdon 2008). Since the sites where we used different stem size class criteria span the precipitation gradient (Table 1), we can be fairly confident that any effect of size class sampling is not confounded with the effect of precipitation.

We compiled a species list from all 14 sites and checked synonymy using http://www.tropicos.org (Missouri Botanical Garden 2014). We applied the multinomial model of Chazdon *et al.* (2011) to classify the trees at each site according to their successional habitat affiliations. Given species abundances in two different habitats, the model classifies species into habitat 1 specialists, habitat 2 specialists, generalists or too rare to classify with confidence. One major advantage of this method over prior classification algorithms is the ability to make a statistical determination of whether a species is common enough to be classified with confidence (Chazdon *et al.* 2011). Another advantage of this classification algorithm is that it explicitly corrects for differences in sampling intensity across habitats, thus avoiding the bias inherent in other classification methods when incomplete samples are used (Chazdon *et al.* 2011; Parker 2013; Chao *et al.* 2015). Particularly in species-rich assemblages, the

observed relative abundance of species i in a given sample (p_i) is a biased estimator of its actual relative abundance, due to the contribution of undetected species to the denominator of the actual relative abundance (Chazdon *et al.* 2011; Chao *et al.* 2015). This bias is more severe for rare species than for common species (Chao *et al.* 2015). The multinomial classification algorithm of Chazdon *et al.* (2011) uses Turing-Good coverage estimation (Good 1953; Chazdon *et al.* 2011 Appendix B) to correct p_i for the contribution of undetected species to the assemblage.

In this study, we used secondary forest and nearby old-growth forest as the two types of habitats. Species in each region were divided into second-growth (SG) specialists, old-growth (OG) specialists, generalists and too rare to classify. We used the settings recommended for the model given the structure of our data set (Chazdon *et al.* 2011): a simple majority threshold ($K = 1/2$) since sample sizes of individuals at each site are large (Table 2) and $P = 0.005$ to correct for the family-wise error rate since each site had a large number of species to be classified. In all of our further analyses, we used only the species that were abundant enough to be classified with confidence in at least one site.

Phylogenies were constructed using the method of Letcher *et al.* (2012) with updated information on node ages. The species list was mapped onto a maximally resolved supertree of angiosperms (R20120829) using Phylomatic version 3 (http://phylodiversity.net/phylomatic/; Webb & Donoghue 2005). Branchlengths were assigned using the bladj algorithm in Phylocom 4.2.1 (Webb, Ackerly & Kembel 2008). Node ages were based on Wikström, Savolainen & Chase (2001), employing the corrections for node names in Phylomatic trees identified by Gastauer & Meira-Neto (2013) and updated node ages from Magallón & Castillo (2009) where available. We constructed one supertree of all classifiable taxa (SG specialists, OG specialists and generalists), applied the branchlength corrections and then used Phylomatic (Webb & Donoghue 2005) to take subsets of this tree for the taxa at each site.

We examined the phylogenetic signal in species' habitat specializations using the D statistic (Fritz & Purvis 2010), a metric of phylogenetic conservatism that is robust to differences in phylogenetic tree size and the prevalence of the trait being examined. D assesses the phylogenetic signal of a binary trait. It was first used to investigate the relative strength of phylogenetic signal in extinction risk caused by different types of environmental threats (Fritz & Purvis 2010). Like extinction risk, successional habitat specialization is a complex emergent trait that is related to many underlying characters. One feature that makes D particularly useful for our analysis is that it is specifically designed to investigate the relative strength of phylogenetic signal in a binary trait among different groups, with progressively lower values indicating a higher level of phylogenetic signal (Fritz & Purvis 2010). Values below zero indicate extreme clustering, zero indicates clustering (Brownian expectation), one indicates randomness, and values above one indicate overdispersion. The method gives two P values, one from a test whether the trait is distributed randomly on the phylogeny and one from a test whether the trait is clumped as would be expected from Brownian motion descent with modification (Fritz & Purvis 2010). Most measures of phylogenetic signal focus on assessing the significance, rather than the relative strength, of the phylogenetic signal in binary traits, but since D is comparable across data sets, it can be used to assess whether particular features of the groups examined – or particular environmental features – are linked to greater phylogenetic signal strength (Fritz & Purvis 2010). In our analysis, we test whether there is a relationship between average annual rainfall and the

Table 1. The 14 sites used in this study. 'OG' stands for old-growth forest. Sites are ordered by increasing annual rainfall; data contributors' names are listed alphabetically

Site	Abbreviation	Year sampled (secondary)	Year sampled (OG)	Median age of secondary forest (years)	Contributors	Average annual rainfall (mm)	Stem size class	Key references
Chamela, Mexico	CHM	2007	2007	7	Balvanera, Bhaskar, Mora, Paz, Pineda-García	788	≥ 5 cm	Balvanera et al. (2002), Mora et al. (2015), Bhaskar, Dawson & Balvanera (2014)
Nizanda, Mexico	NIZ	2005	2008	20	Bongers, Lebrija-Trejos, Meave, Muñoz, Pérez-García, Romero-Pérez	879	≥ 5 cm	Pérez-García et al. (2010), Lebrija-Trejos et al. (2010, 2011)
Chiquitania, Bolivia	CHI	1998	1994–1995	16	Kennard, Killeen	1100	≥ 5 cm	Kennard (2002), Killeen et al. (1998)
Kiuic, Mexico	KIU	2008–2009	2008–2009	8	J.L. Andrade, Dupuy, Hernández-Stefanoni, Sanaphre-Villanueva	1129	≥ 5 cm	Hernández-Stefanoni et al. (2011), Dupuy et al. (2012)
Guanacaste, Costa Rica	GUA	2007	2005	35	Becknell, González-Jiménez, Powers, Quesada-Monge	1667	≥ 10 cm	Powers et al. (2009)
Piracicaba, Brazil	FES	1989–2012	1999–2012	31	Brancalion, César, Rodrigues, Viani	1389	≥ 4.8 cm	Rodrigues (1999), R.R. Rodrigues, P.H.S. Brancalion, R.G. César, R.A.G. Viani, unpub. data
Carite, Puerto Rico	CAR	2007	2011	45	Muscarella, Swenson, Uriarte	1835	≥ 5 cm	Flynn et al. (2010)
Juquiá, Brazil	FOD	1989–2012	1999–2012	32.5	Brancalion, César, Rodrigues, Viani	1758	≥ 4.8 cm	Rodrigues et al. (1989), R.R. Rodrigues, P.H.S. Brancalion, R.G. César, R.A.G. Viani, unpub. data
BDFFP, Manaus, Brazil	BRA	2007	2007	20	A. Andrade, Bentos, Massoca, Mesquita, Laurance, Williamson	2200	≥ 5 cm in SG; ≥ 10 cm in OG	Mesquita et al. (2001), Laurance, Andrade & Laurance (2010)
Agua Salud and Barro Colorado Island, Panama	PAN	2011	2005	14	Craven, Hall, Harms, van Breugel, Wright	2600	≥ 5 cm	van Breugel et al. (2013), Leigh (1999)
Chajul, Mexico	CHJ	2008	2008	10	Bongers, Hietz, Lohbeck, Martínez-Ramos, Schüller, Tauro, van Breugel	3000	≥ 5 cm	van Breugel, Martínez-Ramos & Bongers (2006), van Breugel, Bongers & Martínez-Ramos (2007)
Luquillo, Puerto Rico	LUQ	2007	2011	40	Muscarella, Swenson, Uriarte	3502	≥ 5 cm	Thompson et al. (2002)
Sarapiquí, Costa Rica	SAR	2006–2011	1988, 2007–2011	19	Boukili, Chazdon, D.A. Clark, D.B. Clark, DeFrancesco, Finegan, Letcher, Wendt, Vargas-Ramírez	3900	≥ 10 cm	Letcher & Chazdon (2009), Chazdon et al. (2011), Wendt (2014)
Osa, Costa Rica	OSA	2010–2011	2010–2011	30	Chazdon, Sandor	4000	≥ 5 cm	Morales-Salazar et al. (2012), Sandor (2012)

strength of phylogenetic signal in successional habitat specialization. Based on the predictions in Fig. 1, we would expect to see lower values of *D* (i.e. greater phylogenetic signal strength) in sites with higher rainfall.

In order to examine the relative strength of the phylogenetic signal in our data, we analysed *D* for the whole data set using the tree of all classifiable taxa, and for each site using the site-specific phylogeny. Because *D* is only applicable to binary traits, we conducted two different tests in each case: one for SG specialists vs. [OG specialists + generalists] and one for OG specialists vs. [SG specialists + generalists]. We used the *phylo.d* function in the package *caper* (Orme *et al.* 2013) to calculate *D*, using R 2.13.1 (R Development Core Team 2013).

We examined a wide range of functional traits related to seeds, leaves, wood density and plant stature (Table 3). Not every trait was available for every species; for instance, we did not measure wood or leaf traits for cacti. The number of taxa included for each trait at each site is given in Table 3. For two sites (SAR and OSA), seed length was reported as categorical values (seed length: < 1, 1–6, 6–15, 15–30, 30–50, 50–100 and > 100 mm). Tree height at OSA was a categorical variable (canopy or subcanopy). All other traits were reported as continuous variables: seed dry mass (mg), seed length (mm), specific leaf area (SLA; $cm^2 g^{-1}$), leaf dry matter content (LDMC; $mg g^{-1}$), wood specific gravity (WSG; unitless) or wood density ($g cm^{-1}$), and maximum height (m). Leaf and seed traits were collected according to standard protocols (Cornelissen *et al.* 2003b). Wood density was reported at NIZ, CHM, FES and FOD, while WSG was reported at KIU, GUA, CAR, PAN, LUQ and SAR. Because of differences in measurement protocols including core diameter and length, drying temperature, and whether corrections were made for radial variation, WD and WSG measurements are not directly comparable among sites (Williamson & Wiemann 2010).

To examine the associations of particular functional traits with successional habitat specialization, we used functions developed by Purvis & Rambaut (1995) that calculate phylogenetically independent contrasts for a set of variables and then test for evolutionary relationships in the contrasts using linear models. We used the functions crunch (for continuous data) and brunch (for categorical data) in *caper* (Orme *et al.* 2013) to model the relationship between habitat specialization, coded as a binary variable and each of the functional traits measured. Again, we did two sets of tests for each site–trait combination, one using SG specialists vs. [OG specialists + generalists] and one using OG specialists vs. [SG specialists + generalists].

Results

Our 14 sites contained a total of 162 532 individuals and 2654 species, from 87 families and 28 orders (higher taxa following APG III, Stevens 2014). Three hundred and eleven of these species, accounting for 1306 individuals (0.8%), were morphospecies; the rest were identified at the species level and linked to a valid name. The number of species present at each site ranged from 62 in the dry forest at CAR to 743 in the moist forest at BRA (Table 2). Across the whole data set, 921 species (34.7%) were common enough to be classified with confidence using the multinomial model (Chazdon *et al.* 2011) in at least one site. Of these, 355 species were SG specialists, 52 of which were classified as SG specialists at multiple sites. A total of 443 species were classified as OG specialists, 56 at multiple sites. Only, 10 species had conflicting classifications at different sites. The algorithm classified between 12.5 and 72.5% of species at each site with confidence (Table 2). However, since the species that are classified with confidence are the common species (Chazdon *et al.* 2011), these relatively low percentages of species made up large percentages of the individuals at each site; > 60% in every site, with a median of 90.0% (Table 2).

Although the classification algorithm can be sensitive to the age of the secondary forests sampled (Chazdon *et al.* 2011), we did not find evidence of such sensitivity in this data set: there was no relationship between the median secondary forest age and the per cent of individuals classified as secondary forest specialists ($R^2 = 0.033$, $P = 0.56$). There was also no relationship between median secondary forest age and rainfall ($R^2 = 0.093$, P = 0.33; Table 1), suggesting that these variables are not confounded in our data set.

Table 2. The number of species and individuals at each site, and the per cent of species and individuals that were classified with confidence using the multinomial model of Chazdon *et al.* (2011). The remaining species at each site were classified as too rare for reliable estimates of habitat specialization

Site	No. spp.	No. individuals in secondary forest	No. individuals in old-growth forest	% of spp. classified with confidence	% of individuals classified with confidence	No. secondary forest specialist spp.	No. old-growth specialist spp.	No. generalist spp.
CHM	91	496	533	29.7	81.3	10	5	12
NIZ	110	629	892	30.9	87.2	9	21	4
KIU	137	8712	686	31.4	93.0	10	7	26
CHI	115	1269	7947	43.5	96.2	16	25	3
GUA	168	3587	1027	39.3	89.5	23	22	21
FES	350	15 817	1556	30.3	90.5	40	33	32
CAR	62	1043	720	46.8	95.3	11	8	9
FOD	378	12 766	835	28.8	84.3	31	61	16
BRA	743	2010	2272	12.5	63.0	28	51	10
PAN	349	12 849	47 814	72.5	99.3	93	129	31
CHJ	149	2403	257	16.1	75.3	11	11	2
LUQ	133	5383	8161	54.1	98.4	29	28	14
SAR	507	5921	7768	29.6	87.7	38	78	38
OSA	359	3420	7273	42.9	94.7	57	49	43

Table 3. Results from the brunch/crunch analysis (Purvis & Rambaut 1995) of the relationship between successional habitat specialization and functional traits. 'SG' stands for second-growth specialization; 'OG' is old-growth specialization (shaded rows). N is the number of species that were classifiable with the multinomial model (Chazdon *et al.* 2011) at each site and habitat category for which the trait was measured. For seed length and maximum height, a dagger (†) indicates that the trait was measured as categorical. For wood traits, a double dagger (††) indicates that wood density was measured instead of wood specific gravity. See text for details. Functional trait data were available for all sites except CHI and BRA. R is the brunch/crunch-corrected correlation coefficient between habitat specialization and trait values; for instance, the negative coefficient for seed length at CHM indicates that SG specialists had lower seed size than generalists/OG specialists at that site

Site	Forest age	Seed mass (mg)	Seed length (mm) († = categorical)	SLA	LDMC (mg g^{-1})	Max. height (m) († = categorical)	WSG (†† = WD)	No. species	No. valid contrasts
CHM	SG	$N = 24$ NS	$N = 22$ $R = -0.57$ $P = 0.008$	$N = 26$ NS	–	$N = 27$ $R = -0.44$ $P = 0.008$	††$N = 26$ NS	27	19
	OG	$N = 20$ NS	$N = 19$ NS	$N = 20$ NS	–	$N = 21$ NS	$N = 20$ $R = 0.316$ $P = 0.05$	21	19
NIZ	SG	–	–	$N = 20$ NS	–	$N = 20$ NS	††$N = 20$ NS	26	19
	OG	–	–	$N = 16$ NS	–	$N = 16$ NS	††$N = 16$ NS	29	19
KIU	SG	–	$N = 25$ $R = -0.41$ $P = 0.048$	$N = 31$ NS	$N = 31$ NS	–	$N = 35$ NS	43	22
	OG	–	$N = 24$ NS	$N = 30$ NS	$N = 30$ NS	–	$N = 35$ NS	42	22
GUA	SG	–	–	$N = 43$ NS	–	–	$N = 43$ NS	61	40
	OG	–	–	$N = 35$ NS	–	–	$N = 35$ NS	52	40
FES	SG	–	–	$N = 52$ NS	$N = 15$ NS	$N = 74$ NS	††$N = 100$ NS	117	54
	OG	–	–	$N = 62$ $R = -0.51$ $P = 0.012$	$N = 22$ NS	$N = 52$ $R = 0.35$ $P = 0.052$	††$N = 138$ NS	306	54
CAR	SG	$N = 22$ NS	–	$N = 23$ NS	–	$N = 22$ $R = -0.70$ $P = 0.001$	$N = 23$ NS	25	21
	OG	$N = 22$ NS	–	$N = 23$ NS	–	$N = 22$ NS	$N = 23$ NS	25	21
FOD	SG	–	–	$N = 24$ NS	–	$N = 52$ $R = -0.56$ $P = 0.03$	††$N = 93$ NS	128	35
	OG			$N = 14$ $R = -0.74$ $P = 0.01$	–	$N = 27$ NS	†† $N = 51$ $R = 0.40$ $P = 0.015$	324	35
PAN	SG	$N = 125$ NS	–	$N = 195$ NS	$N = 195$ NS	$N = 150$ $R = -0.25$ $P = 0.032$	$N = 191$ $R = -0.34$ $P = 0.003$	200	72
	OG	$N = 164$ NS	–	$N = 202$ NS	$N = 202$ NS	$N = 201$ NS	$N = 201$ NS	207	72
CHJ	SG	$N = 14$ NS	$N = 14$ NS	$N = 12$ NS	$N = 14$ NS	$N = 14$ NS	$N = 14$ $R = -0.62$ $P = 0.031$	17	11
	OG	$N = 12$ NS	$N = 12$ $R = 0.70$ $P = 0.011$	$N = 10$ NS	$N = 12$ NS	$N = 14$ $R = 0.58$ $P = 0.046$	$N = 12$ $R = 0.89$ $P < 0.0001$	17	11
LUQ	SG	$N = 49$ NS	–	$N = 50$ NS	–	$N = 50$ NS	$N = 50$ NS	63	41
	OG	$N = 48$ NS	–	$N = 48$ NS	–	$N = 47$ $R = -0.49$ $P < 0.0001$	$N = 48$ NS	60	41
SAR	SG	–	†$N = 125$ $R = -0.31$ $P = 0.0038$	$N = 125$ $R = -0.25$ $P = 0.028$	$N = 125$ $R = 0.28$ $P = 0.013$	$N = 125$ $R = -0.23$ $P = 0.048$	$N = 125$ NS	125	82

(continued)

Table 3. (continued)

Site	Forest age	Seed mass (mg)	Seed length (mm) († = categorical)	SLA	LDMC (mg g^{-1})	Max. height (m) († = categorical)	WSG (†† = WD)	No. species	No. valid contrasts
	OG	–	$N = 133$ NS	$N = 146$ NS	$N = 133$ NS	$N = 146$ NS	$N = 146$ $R = 0.32$ $P = 0.005$	146	84
OSA	SG	–	†$N = 129$ NS	–	–	†$N = 130$ NS	–	141	84
	OG	–	†$N = 107$ NS	–	–	†$N = 109$ NS	–	118	84

Successional habitat specialization in our data set was significantly non-random, with D values lower than 1, suggesting a tendency towards phylogenetic clustering (SG specialization: $D = 0.7641$, $P_{random} < 0.0001$, $P_{Brownian} < 0.0001$; OG specialization: $D = 0.7159$, $P_{random} < 0.0001$, $P_{Brownian} < 0.0001$). For SG specialization, values of D for individual sites fell between 0.158 (clustering) and 1.11 (slight overdispersion). There was a trend towards lower D values (i.e. stronger phylogenetic signal) in the wetter forest sites (Fig. 3a), although the correlation between D values and precipitation was weak and not significant ($R^2 = 0.212$, $P = 0.09$). For OG specialization, values ranged from −0.35 to 1.48. There was also a tendency towards lower D values in wetter forest sites (Fig. 3b) except for the dry forest at NIZ, which had the lowest value of all. The relationship here was not significant ($R^2 = 0.065$, $P = 0.37$). There were also suggestive trends in the proportion of stems that were specialists along the precipitation gradient: wetter sites had a higher proportion of individuals classified as specialists (Fig. 4), although again the correlations were weak and not significant ($R^2 = 0.243$, $P = 0.105$ for SG specialists, $R^2 = 0.095$, $P = 0.282$ for OG specialists).

Considering the relationship between functional traits and secondary habitat specialization, relatively few traits showed a strong relationship with habitat specialization when phylogenetically independent contrasts were taken into account (Table 3). Seed length (measured in five sites) showed significant relationships with SG specialization in three sites and OG specialization in one site. The slope of all the significant relationships was negative in SG and positive in OG, indicating that seed length tends to be shorter in SG specialists and longer in OG specialists (Table 3). However, seed mass (measured in five sites) showed no significant relationship with habitat specialization in any site (Table 3). Leaf traits (SLA and LDMC) also showed relatively few significant relationships with habitat specialization. SLA (measured in 11 sites) was negatively related to OG specialization at two sites and positively related to SG specialization in one site; LDMC (measured in five sites) was positively related to SG specialization in only one site. Maximum height (measured in 10 sites) had a significant negative relationship to SG specialization in three sites and a significant positive relationship with OG specialization in two sites, indicating that maximum height is lower in SG specialists, but there was also a significant negative relationship between OG specialization and

maximum height in one site (LUQ). Wood specific gravity/wood density (measured in 11 sites; see Table 3) had a significant negative relationship with SG specialization in four sites and a significant positive relationship with OG specialization in two sites, indicating denser wood in OG trees.

Examining the distribution of secondary forest specialist taxa across the angiosperm phylogeny (Fig. 5), clustering of successional habitat specialization is evident in some lineages. Certain families have a large representation of SG specialists, for example Melastomataceae and Myrtaceae (Fig. 5). Other families have a greater proportion of OG specialists, for example Sapotaceae and Primulaceae (Fig. 5). In some cases, closely related groups of taxa differed in the prevalence of SG vs. OG specialists; see, for instance, Salicaceae and Violaceae; Clusiaceae and Hypericaceae; Moraceae and Urticaceae; Burseraceae and Anacardiaceae (Fig. 5).

Despite overall conservatism of successional habitat specialization, there have been multiple origins of SG and OG specialists in a wide range of lineages. Successional habitat specialization occurs in every major clade of angiosperms (Table 4). The Rosid I and II clades contain a large number of SG specialists, but the flora of this region as a whole is Rosid-dominated (Gentry 1988; Chave *et al.* 2006; Fig. 5; Table 4). Many clades contain both generalist and specialist taxa without clear patterns of clustering; for instance, Fabaceae, Rubiaceae and the Magnoliids (Fig. 5).

Discussion

This is the first study, to our knowledge, to demonstrate that successional habitat specialization tends to be conserved among angiosperms, with significantly non-random patterns of successional habitat specialization evident in a broad sample of the angiosperm phylogeny from a diverse range of Neotropical forest sites. In a previous study of Neotropical trees, Norden *et al.* (2012) found that the SG specialists and OG specialists at SAR are both significantly clustered on the angiosperm phylogeny; here, we extended the scope of the study and confirmed that there is phylogenetic clustering of successional habitat specialists in numerous sites across a broad geographic area.

Our data also reveal a weak association between the degree of clustering in the secondary forest specialist habit and the amount of rainfall at a site (Fig. 3a). Although the trend is

Fig. 3. *D* (Fritz & Purvis 2010) for second-growth specialization (panel a) and old-growth specialization (panel b) plotted against annual rainfall at the 14 sites. *D* values approaching 0 indicate a more clumped distribution of the trait on the phylogeny. Three-letter codes correspond to the site names given in Table 1.
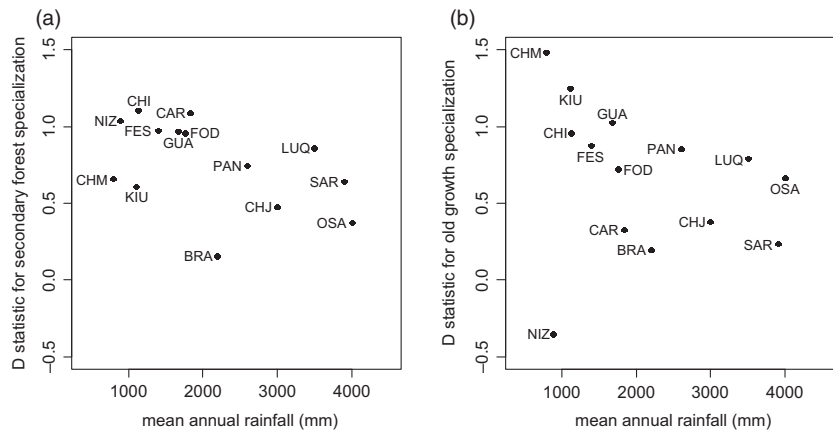
Fig. 4. The per cent of individuals in secondary forest classified as SG specialists (panel a), and the per cent of individuals in old-growth forest classified as OG specialists (panel b) for the 14 sites.
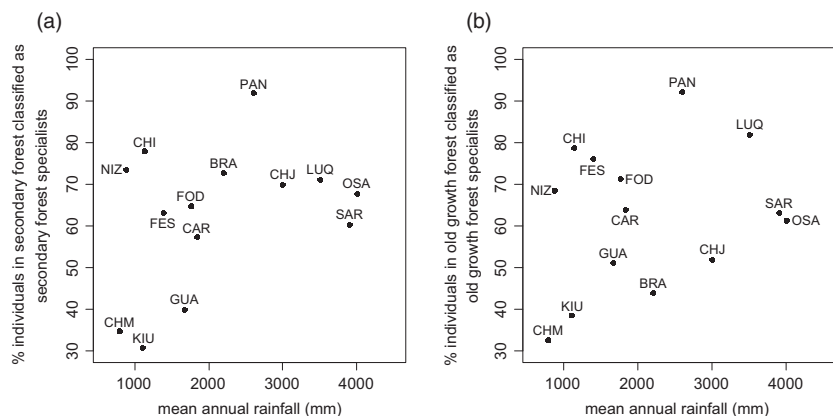
not significant, the direction of the pattern generally agrees with our predictions about the evolution of successional habitat specialization along a gradient of dissimilarity between early successional and late-successional habitats (Fig. 1). There is a trend towards greater conservatism of successional habitat specialization in wetter forests, suggesting that specialization may be less evolutionarily labile in these systems. In addition, when we consider the abundance of individuals, specialists tend to make up a larger fraction of the individuals in wet regions than in dry regions – more SG specialists in secondary forests and more OG specialists in old-growth forests (Fig. 4). These trends are much more evident in SG specialists than OG specialists, perhaps due to the strong constraints on the life-history strategies of pioneer species and the ephemeral nature of their habitat.

Based on the differences in the abiotic environment of wet and dry forests during succession, we predicted that functional trait profiles would differ between wet and dry forest SG specialists, with wet forest pioneers exhibiting traits for rapid growth and light gathering while dry forest pioneers should exhibit traits related to desiccation tolerance. Lohbeck *et al.* (2013) reported contrasting successional changes in the community-weighted means of functional traits in wet and dry forests in Mexico, with traits indicating the importance of light availability driving successional changes in wet forests and water availability driving changes in dry forests. In our broader data set, however, we identified relatively few traits that were strongly and consistently associated with successional habitat specialization (Table 3).

The lack of strong relationships that we observed between functional traits and successional habitat specialization is somewhat surprising, given the directional changes in plant functional traits that are generally observed during tropical forest succession (Bazzaz & Pickett 1980; Finegan 1996; Guariguata & Ostertag 2001; Chazdon *et al.* 2003; Lebrija-Trejos *et al.* 2010; Dupuy *et al.* 2012; Lohbeck *et al.* 2013; Chazdon 2014; Bhaskar, Dawson & Balvanera 2014). One potential explanation is the methodological differences between our study and previous work. Studies that use community-weighted means are strongly influenced by the most abundant species in a community. The community-weighted mean approach is useful for understanding the synecology of co-occurring species (*sensu* Odum & Odum 1959), but less useful for understanding the autoecology of each species. The brunch/crunch algorithms treat each species as a data point, rather than each individual (Purvis & Rambaut 1995). These algorithms also explicitly correct for the lack of phylogenetic independence among data points. For highly phylogenetically conserved traits, comparisons that do not take phylogenetic non-independence into account may overestimate the magnitude and significance of differences among groups (Felsenstein 1985).
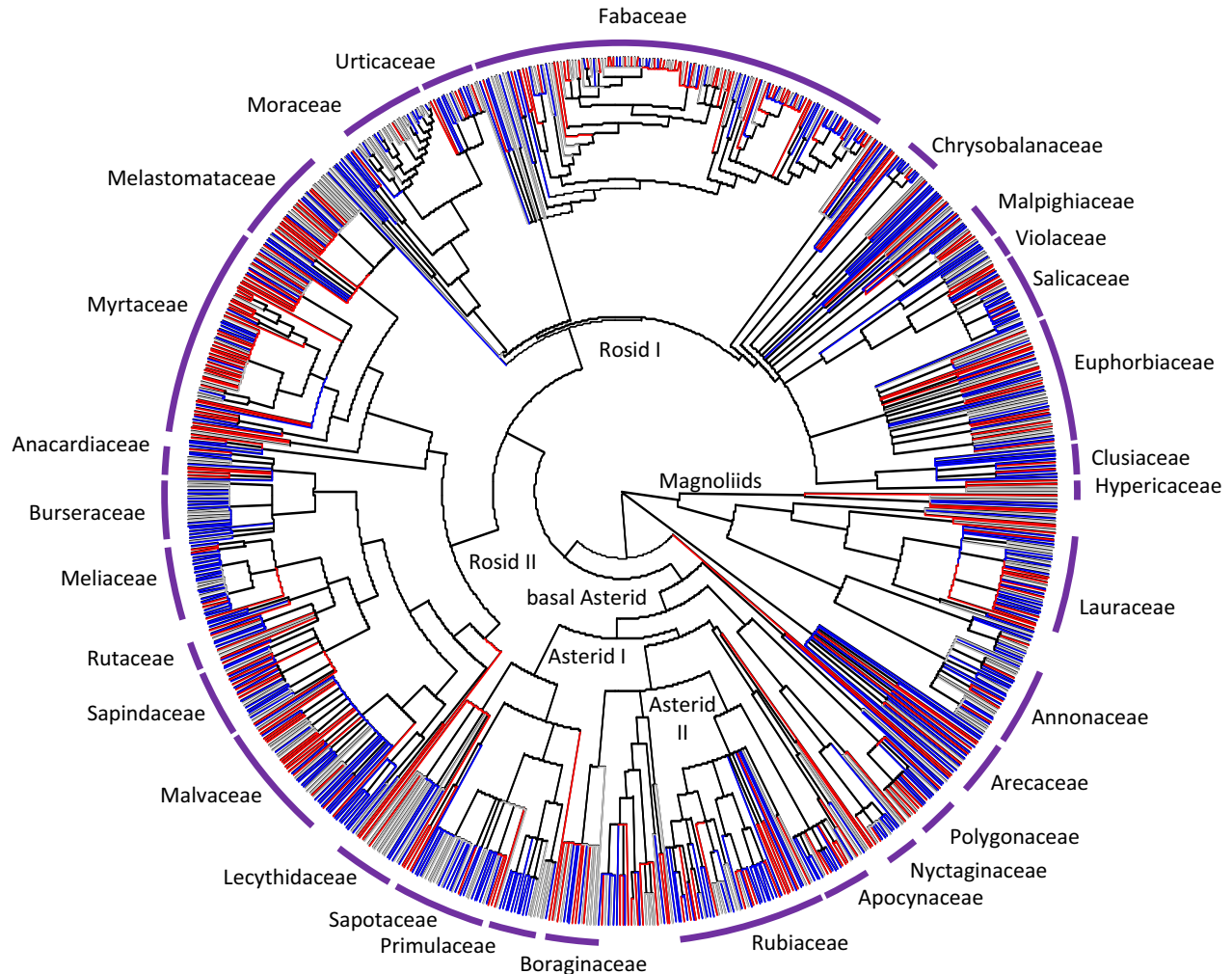
Fig. 5. The phylogeny for the 921 species that were common enough to be classified with confidence. Branch colours indicate second-growth specialists (red), old-growth specialists (blue) and generalists (grey). The labels of smaller families are omitted for clarity.

Table 4. The number of species in each major angiosperm clade that was classified with confidence using the multinomial model of Chazdon *et al.* (2011) at each of the 14 sites. The numbers in parentheses indicate the number of species in that clade classified as secondary forest specialists and old-growth forest specialists, respectively; for example, 8 (0, 3) indicates that eight species were classified with confidence, zero as secondary forest specialists, three as old-growth specialists and the rest as generalists

	Asterid I	Asterid II	Basal Asterid	Eudicot	Magnoliid	Monocot	Rosid I	Rosid II
CHM	2 (0, 0)	0	6 (2, 2)	0	1 (1, 0)	0	13 (6, 2)	5 (1, 1)
NIZ	2 (0, 2)	0	6 (2, 2)	0	1 (0, 1)	0	19 (7, 10)	6 (0, 6)
KIU	6 (0, 1)	0	11 (2, 2)	0	0	0	16 (5, 4)	10 (3, 0)
CHI	4 (1, 3)	0	7 (3, 4)	0	0	0	20 (7, 12)	13 (5, 6)
GUA	9 (3, 3)	0	9 (3, 3)	0	3 (1, 0)	0	26 (11, 6)	19 (5, 10)
FES	5 (1, 3)	2 (1, 0)	9 (4, 1)	0	7 (3, 2)	2 (0, 2)	38 (14, 12)	42 (17, 13)
CAR	4 (2, 1)	1 (0, 0)	2 (0, 1)	0	1 (0, 0)	1 (0, 1)	10 (3, 3)	9 (6, 2)
FOD	13 (3, 10)	2 (1, 1)	15 (5, 5)	0	14 (5, 5)	3 (1, 2)	27 (9, 14)	34 (7, 24)
BRA	0	0	21 (2, 19)	0	9 (4, 3)	2 (0, 1)	37 (12, 19)	20 (10, 9)
PAN	27 (9, 14)	3 (2, 0)	21 (7, 12)	1 (1, 0)	24 (3, 17)	5 (0, 5)	97 (38, 46)	75 (33, 35)
CHJ	0	0	2 (1, 1)	0	1 (1, 0)	0	11 (4, 5)	10 (5, 5)
LUQ	10 (5, 2)	3 (2, 0)	7 (2, 5)	0	3 (1, 1)	2 (1, 1)	26 (8, 12)	20 (10, 7)
SAR	16 (2, 13)	2 (0, 1)	16 (4, 10)	0	20 (5, 7)	5 (1, 4)	60 (14, 25)	35 (12, 18)
OSA	12 (7, 1)	1 (0, 0)	11 (2, 6)	0	21 (6, 7)	4 (0, 2)	58 (22, 20)	42 (20, 13)

Another explanation for the lack of strong trait-successional habitat association that we observed is the importance of intraspecific variation in plant traits, and particularly the onto-

genetic shifts that occur between seedlings and adults (Clark & Clark 1992; Poorter & Rozendaal 2008). We measured wood and leaf traits of adults, following standard protocols,

but the seedling may be the most relevant life stage for understanding how traits mediate community assembly during succession (Poorter & Markesteijn 2008; Lu *et al.* 2014), and seedling traits are not always directly related to adult traits (Cornelissen *et al.* 2003a; Poorter 2007).

Although few of the traits that we studied showed strong associations with successional habitat specialization, the significant trait relationships that we identified generally did conform to expectations based on the physiological ecology of plants during succession. For seed size, our data supported the widespread finding that secondary forest trees have smaller seeds (Swaine & Whitmore 1988; Chazdon *et al.* 2003). In three of the five sites where we had seed length data, we found that SG specialists tended to be smaller seeded than OG specialists in both wet and dry forests. Small-seeded taxa like *Cecropia* and *Miconia* are important pioneers in both wet and dry forest (Dalling *et al.* 2002). The absence of large-seeded taxa in early successional forests may be a product of dispersal limitation; small seeds are more easily transported, and the large animals that disperse large-seeded taxa may not venture into secondary forest habitats (Guariguata & Ostertag 2001; Dalling *et al.* 2002; Chazdon *et al.* 2003). Germination of smaller seeds also tends to be sensitive to either light or diel temperature fluctuations (Vázquez-Yanes *et al.* 1990; Pearson *et al.* 2002), which could contribute to the high abundance of small-seeded taxa in secondary forests.

For leaf traits, very few of the traits that we investigated showed a consistent relationship with successional habitat specialization. Recent work on leaf traits in tropical forest species has demonstrated that leaf traits have high intraspecific variation in moist forest (Rozendaal, Hurtado & Poorter 2006) and dry forest (Markesteijn, Poorter & Bongers 2007). The plasticity of traits, rather than the magnitude of interspecific trait variation, may be a key factor in understanding how leaf traits mediate plant success in different light environments (Markesteijn, Poorter & Bongers 2007). Ontogenetic shifts may be a particularly important factor complicating our ability to generalize about leaf traits that mediate success in different environments (Clark & Clark 1992; Chazdon *et al.* 2010). Seedling leaf traits may be more informative than adult leaf traits for understanding community assembly (Rozendaal, Hurtado & Poorter 2006; Poorter 2007), and the relationship between seedling and adult leaf traits is not necessarily straightforward (Cornelissen *et al.* 2003a).

Maximum height was one of the traits that showed the strongest relationships with successional habitat specialization (Table 3). According to our data, SG specialization is negatively related to maximum height (i.e. SG specialists tend to be shorter statured) and OG specialization is positively related to maximum height, especially in dry forests. The only site where we found a negative association between OG specialization and maximum height was in the wet forest at LUQ (Table 3). In wet and moist forests, the shorter statured trees are often long-lived, slow-growing understorey species that persist in low light (Bazzaz & Pickett 1980; Poorter, Bongers & Bongers 2006; Kitajima & Poorter 2008). Since dry forest trees have slower growth rates (Ewel 1977; Ruiz, Fandiño &

Chazdon 2005), light-demanding short-statured species can persist longer before being overtopped. A light-demanding short-statured strategy would not be advantageous in wet forests, where canopy closure occurs rapidly (van der Meer & Bongers 1996) and where canopies are generally higher (Ewel 1977; Bazzaz & Pickett 1980).

Wood density is an important functional trait related to growth rate, structural stability and longevity of trees (Chave *et al.* 2006). Tropical secondary forest trees tend to have lower wood density, faster growth and shorter life spans (Woodcock 2000; Guariguata & Ostertag 2001; Wiemann & Williamson 2002). In our data set, we found significant relationships between successional habitat specialization and wood traits in only half the sites studied. However, the studies that have found stronger and more consistent relationships between successional stage and wood density, with low wood density in early successional tree species (Woodcock 2000; Wiemann & Williamson 2002), did not correct for phylogenetic relatedness. Since wood density is a highly conserved trait in most tropical tree lineages (Chave *et al.* 2006), analysis of wood traits may be particularly susceptible to overinflation of significance due to phylogenetically non-independent data points (Felsenstein 1985).

The great diversity of lineages that have produced SG specialists and OG specialists (Fig. 5) complicates our ability to generalize about the life-history traits and functional traits of the species that specialize at the ends of the successional habitat gradients in Neotropical forests. Trade-offs along multiple axes govern the way that species partition resources during succession; different lineages have different physiological and anatomical strategies for confronting the range of stresses that occur along successional gradients (Harms *et al.* 2001; Poorter & Markesteijn 2008; Baraloto *et al.* 2010; Lebrija-Trejos *et al.* 2010; Pineda-García, Paz & Tinoco-Ojanguren 2011; Lu *et al.* 2014). The great diversity of functional traits found in tropical tree seedlings in forests across a precipitation gradient (Markesteijn & Poorter 2009; Pineda-García, Paz & Tinoco-Ojanguren 2011; Lu *et al.* 2014) and the relatively low number of strong correlations between functional traits and successional habitat specialization (Table 3) both suggest that there are many ways of being a successful pioneer.

In this analysis, we have considered only the endpoints of the successional gradient. Studies of resource partitioning generally find species that specialize all along the gradient, not just at the endpoints (Grime 1977; Ricklefs 1987; Tilman & Pacala 1993). Our conceptual model of trade-offs along a successional gradient (Fig. 1) is necessarily an oversimplification, and when more extensive data are available, it may be possible to identify taxa that specialize at multiple points along the gradient rather than focusing on the endpoints. In addition, examining multiple successional stages may provide a more nuanced understanding of the evolution of plant strategies. At present, we have few large-scale data sets with sufficient replication at enough forest ages that would allow us to assess this finer-scale partitioning of the successional habitat gradient in Neotropical trees. Several previous studies do suggest the possibility. Letcher (2010) studied five stages of succession in

Costa Rican wet forests and identified clades of angiosperms that were more abundant than the null model expectation in every stage of succession. Extending this work to three wet forest sites (Brazil (BRA), Mexico (CHJ), and an expanded set of sites in Costa Rica (SAR)), Letcher *et al.* (2012) found significantly under- and overrepresented clades for each stage of succession examined.

The scale at which phylogenetic conservatism is measured can have a strong impact on the detection of conservatism; traits can be overdispersed within clades yet conserved across the phylogeny as a whole or vice versa (Cooper, Jetz & Freckleton 2010; Fritz & Purvis 2010). Focusing on particular lineages, instead of the angiosperm phylogeny as a whole, may provide more insight into the evolution of successional habitat specialization (Richardson *et al.* 2004). A tantalizing finding of Letcher (2010) was that some genera contained species that were overrepresented in several distinct age categories; for instance, one *Miconia* species (Melastomataceae) was significantly associated with old-growth forest, and two others were significantly associated with young forest. One *Protium* species (Burseraceae) was significantly associated with old-growth forest, while another was indicative of older secondary forest. This pattern suggests that taxa can radiate into specialists at particular stages in the successional gradient, as first envisioned by Gómez-Pompa (1971) for genera such as *Piper* and *Acalypha* over four decades ago. The new availability of phylogenetic data provides opportunities to study these patterns.

Incorporating phylogenetic relatedness into the study of succession has revealed new insights about community assembly (Letcher 2010; Letcher *et al.* 2012; Norden *et al.* 2012). Incorporating the study of succession into biogeography and evolutionary biology could provide new insights as well. When exploring the biogeography and evolution of species-rich taxa, it may be illuminating to include an investigation of successional habitat specialization as well as climate and dispersal history (Chanderbali, van der Werff & Renner 2001; Richardson *et al.* 2004).

In sum, our results show that successional habitat specialization is a conserved trait for Neotropical trees; though, there are many different pioneer lineages and a concomitant diversity of functional traits associated with successional habitat specialization. Our data further suggest that successional habitat specialization may be more evolutionarily labile in dry forests than in wet forests, potentially due to the lower dissimilarity of early successional and late-successional habitats in dry forests. Future studies will test the strength and generality of this pattern and reveal the extent to which radiation into successional niches has shaped plant evolution.

Data accessibility

Except where otherwise noted, the phylogenetic tree used in this study and data on plot locations, species abundances and functional traits are archived at doi:10.5061/dryad.d87v7.

Species abundance data for:
GUA: DOI:10.1016/j.foreco.2008.10.036,
CAR and LUQ: http://luq.lternet.edu/research/luquillo-forest-dynamics-plot-lfdp,
PAN: old-growth data at http://ctfs.arnarb.harvard.edu/webatlas/datasets/bci/; secondary forest data at http://ctfs.arnarb.harvard.edu/Public/plotdataaccess/.
KIU: DOI 10.1111/j.1744-7429.2011.00783.x and DOI 10.1007/s10980-010-9561-3.

Functional trait data for:
GUA: doi: 10.1111/j.1365-2435.2010.01701.x,
PAN: doi: 10.1890/09-2335.1, doi: 10.1007/s00442-015-3339-x.
CAR/LUQ: uploaded to TRY on 5/26/15 as 'CTFS Luquillo Forest Dynamics Plot – Swenson'; it will be available in the next data base update.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Detailed information on the study sites, including plot dimensions and ages. For specific methodological details, see the references cited in Table 1 for each site.