

Deconstructing the signal: phylogenetic structure, elevation change, and the implications for species co-existence

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ABSTRACT

Question: Is there evidence of temporal niche dynamics in the response of phylogenetic structure to environmental change?

Data studied: We evaluated change in species composition of tree communities along a 600 m elevation gradient in the tropical deciduous forest of southwestern Mexico, censusing 43 transects of 100 individuals each, with transects conforming to strict criteria of similarity. Along this gradient, maximum annual rainfall increases threefold from low to high elevation, and temperature decreases by 3°C.

Methods: (1) Within the regional-level phylogenetic tree, we located the source of the observed change in phylogenetic structure along the gradient. We did this by ‘deconstructing’ or splitting the full phylogenetic tree into two taxonomically distinct subtrees, and then conducting stepwise removal of taxonomic resolution and weighting (number of subtending taxa) for all three trees (full tree plus subtrees) starting at the tips. We then correlated all values of phylogenetic structure with elevation over the samples at each level of deconstruction. (2) We determined change in species composition with changing environmental conditions expected from an analytical model of temporal niche process, after which we correlated this change [mean and standard deviation of species-to-genus ratio (S/G)] with elevation and with the metric of changing phylogenetic structure. (3) We identified the genera most responsible for changing S/G and standard deviation of S/G.

Conclusions: (1) Community phylogenetic structure responds significantly to the elevation gradient, with signal located at the genus level and below. The latter result suggests that species interactions are primarily responsible for the patterns observed. (2) The observed relationship between elevation and both S/G and standard deviation of S/G accounts for all or most of the variation in phylogenetic structure and is consistent with the action of temporal niche dynamics – a pattern well illustrated by four influential, multi-species genera that collectively contain more than 20% of the individuals included in the study.

Keywords: environmental gradient, Mexico, nearest taxon index, net relatedness index, phylogenetic clustering, species-to-genus ratio, temporal niche dynamics, tropical dry forest.

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INTRODUCTION

During the past decade, there has been considerable interest in inferring ecological assembly rules from the structure of community-level phylogenetic trees (Webb *et al.*, 2002; Emerson and Gillespie, 2008; Cavender-Bares *et al.*, 2009). A recent review concluded that in over half of 39 studies examined, phylogenetic clustering – the selection of species from a phylogenetically restricted subset of a wider species pool – was a significant pattern in ecological communities (Vamosi *et al.*, 2009). It is postulated that phylogenetic clustering is caused by the action of strong environmental filters, i.e. abiotic conditions that select for specific traits or combinations of traits conserved within taxa (Weiher and Keddy, 1995; Webb *et al.*, 2002; Ackerly, 2003). Although it is acknowledged that phylogenetic pattern can result from other mechanisms, such as convergent evolution (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006), many studies have been quick to accept the generalization that clustering indicates environmental filtering and that the opposite pattern – phylogenetic overdispersion – results from competition.

However, closely related or otherwise highly similar species may co-exist for reasons other than environmental filtering, such as through the stable competitive interactions of temporal niche dynamics (*sensu* Chesson and Warner, 1981; Chesson, 2000b). In ecosystems where inter-annual variation in climatic conditions is common, species that share adult resource requirements may co-exist through distinct recruitment strategies that depend on different year climate types (Schwinning and Kelly, 2013). Under such a temporal dynamics model, stable co-existence of two closely related species occurs via differential recruitment over time, where the less common species is more sensitive to environmental fluctuations and only shows strong recruitment in favourable years. Meanwhile, the more common species is more resistant to environmental variation and has more consistent levels of recruitment during most years and across a range of environmental conditions (Kelly and Bowler, 2002, 2005; Kelly *et al.*, 2013). This competitive dynamic is played out at the level of seeds, seedlings or juveniles rather than adults, and the proximity of adults to one another for the dynamic to be effective is only as much as that required for overlapping seed dispersal.

Examples of temporal dynamics in tree species can be found in spatially inter-digitated populations of congeners in the tropical deciduous forest of Mexico. In addition to the differential response of seedlings to water availability noted above, Kelly and colleagues have demonstrated population- and community-level patterns consistent with successful temporal processes during recruitment (Kelly and Bowler, 2002, 2005; Kelly *et al.*, 2013). One particular result addressed congeneric species forming terminal dichotomies in the community-level phylogenetic tree. These species pairs were more similar in population size than that expected by a random draw, either from the entire community or from the subset of congeners. In contrast, the distribution of pairs forming terminal dichotomies above the level of congeners (i.e. at the family level) was not significantly different from the appropriate null model (Kelly *et al.*, 2008). Fitting the observed patterns to differing models of species interactions demonstrated that the temporal dynamics model best accounted for the data, with neither competitive exclusion nor neutrality able to explain the pattern observed (Leibold, 2008; Kelly and Bowler, 2009). Parallel findings of pair-wise abundances indicating the same temporal lottery dynamic have also been shown for tree species in the tropical moist forest of Barro Colorado Island, Panama (Kelly *et al.*, 2010).

Thus, although competitive interaction may occur at any level of phylogenetic relatedness (e.g. Connell, 1983; Schoener, 1983; Mayfield and Levine, 2010), the results of Kelly and colleagues imply that relatedness has no predictable connection to competitive interaction at the community scale

above the level of species within genera. Here we investigate how such community-level processes of stable competition may translate into larger-scale phylogenetic pattern by structuring analyses in the context of a strong environmental gradient at the landscape level. In this context, we seek to establish whether there is significant change in phylogenetic structure from one tree community to the next across an elevation gradient, and whether some or all of that change occurs at the level of species within genera.

We also address the question of whether changes in phylogenetic structure across the gradient are consistent with the action of the community-level temporal dynamics summarized in Kelly *et al.* (2013). In the study area, temperature and precipitation are strongly correlated with elevation (negatively and positively, respectively), such that increasing elevation is accompanied by decreasing water stress (i.e. greater rainfall), evident at the forest level by a significant, regular increase in average tree size with elevation (Williams, 2008). We apply the extension of the community-level model to the landscape level as it is presented in Kelly *et al.* (2013) and described in Appendix A (evolutionary-ecology.com/data/2794Appendix.pdf) to generate an expectation of pattern. We hypothesize that the relative advantage of the more competitive/responsive species will increase with what it experiences as more benign conditions, thereby lowering the probability of observing congeneric co-existence with increasing elevation. We thus predict that if a temporal dynamic is operating in genera in this region, it will carry with it at the landscape level a decrease in the number of species per genus (S/G) with increasing elevation. (*Note:* We do not expect that this process will necessarily be active in all genera, or that even in those genera in which it occurs it will engender the same level of response for all taxa involved, but we do expect it to be detectable at the community level.) There is no such inherent expectation of pattern in the qualitative model of congener co-existence through environmental filtering, the stochastic demography of neutral dynamics, or in the workings of competitive exclusion outside of the storage processes of temporal niche dynamics (Chesson, 1986, 2000a; Weiher and Keddy, 1995; Hubbell, 2001; Weiher *et al.*, 2011).

The ~600 m elevation span of the study area encompasses an increase of 3°C in mean daily temperature and a decrease from more than 3 m to less than 1 m in maximum annual rainfall with decreasing elevation. The effect of this environmental change on the phylogenetic structure of sample tree communities is evaluated here in a series of systematic operations on the highly resolved phylogenetic tree of the region. These operations successively eliminate the effects of resolution and differential distribution (weighting) of subtaxa within higher-level groupings to identify how tree topology changes with the gradient. We further separate the parent phylogenetic tree into two constituent subtrees to determine whether the regionally dominant, monophyletic plant family Fabaceae (Lott and Atkinson, 2006) exerts a significant effect on our findings.

METHODS

Study area and data collection

To determine change in phylogenetic structure over elevation, belt transects were established along an elevation gradient between 24 and 578 m above sea level in a forested coastal region near the city of Huatulco in the Mexican state of Oaxaca (15.77°N, 96.14°W; Fig. 1). The forest in the area is well conserved and classified as seasonally dry tropical forest (TDF), with a climatic profile typical of such a designation (Trejo and Dirzo, 2002). Local rainfall

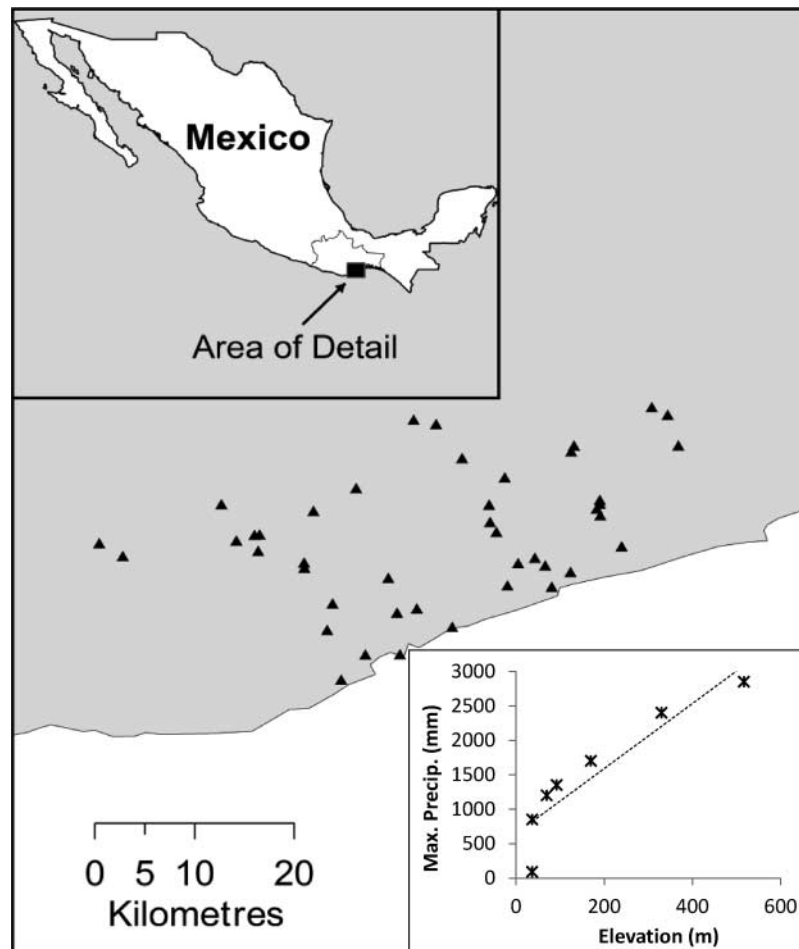


Fig. 1. Study site, showing location of the tropical deciduous forest in Oaxaca, Mexico (upper inset). Triangles depict transect sites relative to coastline (white border). Perpendicular distance from coastline generally corresponds to an increase in elevation and maximum annual rainfall, as shown in weather station data from the region (lower inset; raw data obtained from: www.worldclim.org/stations).

and elevation are tightly correlated within the study area ($P < 0.005$; $r^2 = 0.84$; Fig. 1). The lapse-rate for temperature determined for the region (Pacific coastal TDF) is 0.57°C per 100 m elevation, calculated from maximum cumulative high temperature over a range of 434 m falling within the altitudinal limits of the study. Raw data for rainfall and lapse-rate determinations came from www.worldclim.org (Hijmans *et al.*, 2005). Per transect average basal area provided a biological criterion of the effect of changing conditions (phytometer), showing a significant positive correlation with elevation [$r^2 = 0.23$, $P = 0.001$ (Williams, 2008)].

Criteria for transect selection were closed-canopy primary forest, no obvious signs of human influence (e.g. introduced species, grazing, or species extraction), and a minimum of 500 m distance between transects. Each transect consisted of a 2 m wide strip along a contour line (i.e. constant elevation, perpendicular to the slope) whose length was

determined by the distance necessary to include the first 100 trees or woody vines (lianas) encountered (mean distance = 150 m, s.d. = 35 m). Tree and liana identity were recorded from all transects. Trees were defined as woody individuals ≥ 2 m tall and ≥ 2.5 cm diameter at breast height (DBH = 1.3 m), and single stemmed or unbranched below that height. Lianas were included only if they broke ground within the 2 m wide transect and were ≥ 2.5 cm diameter above the root node. GPS coordinates were recorded for each transect. In total, data were collected for 4297 trees in 43 transects, totalling 1.26 ha dispersed over an area of roughly 60×30 km.

Individuals were identified to species based on vegetative and phenological characteristics, species lists (Salas-Morales *et al.*, 2003, 2007), and voucher specimens collected when fruit or flowers were present and when identity in the field was uncertain. Collected specimens were taken to the national herbarium (MEXU) in Mexico City or the National Polytechnic Institute herbarium in Oaxaca for identification, and were then donated to the respective permanent collections. Unidentified species were classified to the nearest taxon, but only individuals positively identified to genus and species or morpho-species were included in the analysis ($n = 4172$ or 97.1% of all individuals encountered, representing 273 species). Previous analyses showed no significant relationship between elevation and number of species, genus, or family (Williams, 2008; Williams *et al.*, 2010) (see also figures in Appendix C, [2794Appendix.pdf](#)).

Phylogenetic tree structure and analyses

Using Mesquite (Maddison and Maddison, 2008), we assembled a parent phylogenetic tree (Appendix D, [2794Appendix.pdf](#)) of all species found in all transects by first constructing a backbone tree with the structure adopted from Stevens (2010) and updated by Soltis *et al.* (2011). We resolved this tree to species according to authorities on individual families or clades. Where full resolution was not possible, nodes were left as polytomies, achieving a final resolution of 94.5%. Mabberley (2008) was useful for providing synonyms and access to alternative systems of classification.

Major lineages with differing evolutionary histories and physical characters may respond similarly to different environmental factors, or differently to the same factor (Schluter, 2000; Givnish, 2010; Rabosky, 2010; Droissart *et al.*, 2011; Pavoine *et al.*, 2011). Almost 30% of the species encountered belonged to one monophyletic family, the Fabaceae. Because of this, we partitioned the parent phylogenetic tree into two subtrees – the Fabaceae and non-Fabaceae – to examine how membership in these respective lineages might affect community structure. Thus, in a Fabaceae-only analysis, a sample consisted of only the members of that family found in a transect, and the dispersion of that sample was relative only to the Fabaceae clade of the parent tree. Analyses on the non-Fabaceae were conducted in a similar manner. We performed all analyses on the two subtrees separately, as well as on the full parent tree.

We used Phylocom (Webb *et al.*, 2009) to calculate phylogenetic dispersion in our sample communities (transects) relative to the parent phylogeny using the net relatedness index (NRI) and the nearest taxon index (NTI). The NRI gives an estimate of phylogenetic clustering or dispersion based on the mean phylogenetic distance between all species pairs within the sample relative to the null expectation of a sample of the same size taken from the parent tree. The NTI estimates mean phylogenetic distance between a sample taxon and its nearest co-occurring relative compared with the null expectation for a similar sample size taken from the parent tree.

Branch length algorithm

Branch length algorithms convert the distance between taxa in a phylogenetic tree into a number. Although there is little contention that closely related species are likely to be similar to one another and more distantly related species less so, there are different ways to calculate the number that represents the distance between taxa. One such measure used is evolutionary time, which approximates the real time separating the genesis of taxa. However, the calculation of evolutionary time intentionally excludes ecologically induced change, through the assessment of base-pair substitutions in neutral genome segments (segments *not* under selection during the period separating the target species). In fact, ecological change is irregular and multidimensional as a result not just of selection, but also epistasis, pleiotropy, innovation, and loss as well as gain of traits (Bolnick and Fitzpatrick, 2007; Krug *et al.*, 2008; Cooper *et al.*, 2010; Givnish, 2010; Venditti *et al.*, 2010; Schnitzler *et al.*, 2011). It should thus not be surprising that ecological change follows evolutionary time only in a loosely additive manner, rather than in a simple, linear fashion (Harmon *et al.*, 2003; Losos *et al.*, 2003; Davies and Savolainen, 2006; Burns and Strauss, 2011; Losos, 2011), as is assumed in a number of recent articles (e.g. Kress *et al.*, 2009; Burns and Strauss, 2011).

Branch or node counting is another way to assess the phylogenetic distance between taxa and consists of adding up the number of nodes or branches that separate species in the phylogenetic tree. Its use was more common prior to the increasing availability of calibrated clades within the angiosperm phylogeny (e.g. Wikstrom *et al.*, 2001). Recently, node counting has been viewed as a default option to use when information on evolutionary time is unavailable. Nonetheless, a number of notable studies have established significant patterns using node/branch counting rather than evolutionary time (e.g. Webb, 2000; Gerhold *et al.*, 2008; Schweiger *et al.*, 2008), and we suspect that there are more conceptual issues involved in this choice of algorithm.

Conceptual issues aside, we suggest that rather than search for one ‘right’ algorithm for all questions, it is of greater use to recognize and exploit the differences in information that can come from different algorithms (Fig. 2). In Phylocom, branch lengths among taxa are specified by the tool BLADJ. This tool applies those branch lengths available from fossil evidence or from neutral gene change assays and uses an ultrametric constraint to calculate branch lengths where such information is not readily applicable. An ultrametric assumption is based on the argument that extant species are equidistant in time from their common ancestors. With either of these evolution-based algorithms of difference between species, gain or loss of species at higher levels can weight more heavily than gain or loss at lower levels, even if both changes only involve a single species (e.g. loss of a mono-specific family or order versus the loss of a species from a large genus). This effect will be exacerbated by phylogenetic tree asymmetries (see Fig. 2), which are in turn likely to interact with degree of resolution. In contrast, node or branch counting weights the degree of difference between species equally, regardless of whether they are members of sparse or speciose clades, and so is more sensitive to lower-level change.

We therefore applied both algorithms to our data. For the evolutionary time method, we supplied BLADJ with branch length data from Wikstrom *et al.* (2001) for the basal nodes and from individual published phylogenies for the distal internode distances where available (Appendix D, [2794Appendix.pdf](#)). For the equal branch length algorithm, NRI and NTI were calculated using the *comstruct* function, setting the null model type to ‘1’. Randomizations were set to 10,000 for both algorithms.

Deconstruction

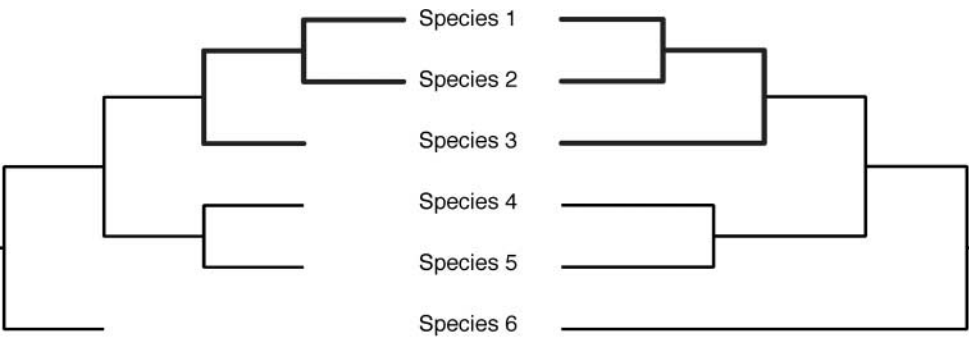
We conducted a series of structural modifications (Fig. 3) to the parent phylogeny to examine the effect of taxonomic level, resolution, and within-taxon diversity on phylogenetic signal as measured across the elevation gradient. Our premise is that by systematically removing (a) taxonomic resolution (e.g. a resolved multispecies genus becomes a polytomy), (b) weighting (a taxonomic level is consolidated, such that, for example, the species within a genus are dissolved, and the branch terminates at the genus rather than species level), or (c) both, one can identify the phylogenetic and taxonomic level(s) where taxa are interacting (i.e. through clustering or overdispersion) in response to changes across the elevation gradient. We note that this deconstruction method differs from pattern-searching tools, which test individual nodes within a phylogenetic tree for clumping or overdispersion relative to a random draw (e.g. NODESIG in Phylocom). By contrast, our approach tests specific clades or levels of the phylogenetic tree (i.e. *not* nodes) for changes in NRI or NTI due to loss of resolution or weighting.

Model analyses

We used generalized linear models (GLMs) to identify potentially relevant ecological variables contributing to the statistical relationship between our metrics of phylogenetic structure and elevation. A GLM is comparable to a step-wise analysis of variance (ANOVA) in terms of building hypotheses through the sequential addition of variables. However, the two differ in that with each additional variable, a stepwise ANOVA reapportions the variance among all variables, whereas in a GLM, once the variance is assigned to a given variable or variables, any sum of squares determined subsequently is calculated only relative to the remaining variance (Grafen and Hails, 2002). By comparing the effects on the sums of squares of different algorithms of variable entry, GLMs can show whether or not the effect of a pair of independent variables is due to the same source of variation in the dependent variable. To apply GLMs for this purpose, the sums of squares are calculated first sequentially, with the variance partitioned among the variables according to order of entry; corresponding individual sums of squares are then determined for each variable only after *all* other variables have been entered into the ANOVA. We compared the difference between the sequential and adjusted sums of squares for a number of factors to assess the degree to which they may be a result of the same or different variation in the relationship between elevation and changing phylogenetic structure.

The mechanism by which temporal dynamics facilitates co-existence of congeners leads us to expect that under the conditions of the Mexican tropical deciduous forest, the more responsive (and less robust) member of a species pair will become more dominant, and the more tolerant species less common with increasing elevation. Because evidence of this pattern should be visible as lower species-to-genus ratios (S/G) and standard deviation (SD) of S/G with increasing elevation, we calculated both values for the two phylogenetic subtrees and the full tree for each sample community. The S/G can be calculated as a simple ratio for each transect, but in order to also generate a per transect standard error/deviation for species number among genera, SD was determined from full information on number of species for each individual genus in each transect; all other subtaxon/taxon values were treated similarly.

As a subcategory/category ratio, S/G forms a non-linear relationship with increasing slope (convex) with increasing species number, and S/G can increase with sample size for



Triplet	Node Count	Ultra	Phyl Div NC	Phyl Div Ultra
1,2,3	4	5	-2.757	-2.180
1,2,4	6	7	0.000	-1.062
1,2,5	6	7	0.000	-1.062
1,2,6	6	9	0.000	0.056
1,3,4	6	8	0.000	-0.503
1,3,5	6	8	0.000	-0.503
1,3,6	6	10	0.000	0.615
1,4,5	6	7.5	0.000	-0.783
1,4,6	7	11	1.378	1.174
1,5,6	7	11	1.378	1.174
2,3,4	6	8	0.000	-0.503
2,3,5	6	8	0.000	-0.503
2,3,6	6	10	0.000	0.615
2,4,5	6	7.5	0.000	-0.783
2,4,6	7	11	1.378	1.174
2,5,6	7	11	1.378	1.174
3,4,5	5	7.5	-1.378	-0.783
3,4,6	6	11	0.000	1.174
3,5,6	6	11	0.000	1.174
4,5,6	5	9.5	-1.378	0.335

$\bar{x} =$	6	8.9
$SE =$	0.725	1.789

that reason alone (Järvinen, 1982; Gotelli and Colwell, 2001). We therefore applied a null model to frame the subtaxon/taxon values for each transect in terms of numbers of standard deviations from the null value for the sample size within the transect. To construct null values of S/G and the SD of S/G for each sample, species were drawn without replacement from the species list of the parent tree S number of times (where S is the number of species in a transect), from which G (the number of genera represented by S) was then determined. This routine was repeated 10,000 times for each transect to produce mean values of S/G and SD of S/G. The null S/G and SD of S/G values were subtracted from the observed values and the results were divided by the standard error of these null values to produce a corrected estimate of the variables that was independent of sample size and framed as number of standard deviations from the null value. We then used these corrected values to assess changes in the distribution of species among genera with elevation. Similar treatment was given to the species-to-family (S/F) and genus-to-family (G/F) ratios, in order to determine their possible contribution to changes in phylogenetic structure with changing environmental conditions.

The expected effect on phylogenetic structure of species within genera could be distributed among a number of taxa acting in parallel (Droissart *et al.*, 2011), or localized in a single, very large taxon. To characterize more specifically the effects of species within genera, the gradient was split into two elevation bands of equal breadth (277 m), high and low, and the average number of species per sample was compared for each genus of ≥ 3 species. Those genera showing significant differences between the upper and lower bands were further examined for linear correlations between elevation and number of species per sample along the full elevation gradient. As a further independent test of the distribution of

Fig. 2. Differing effects of two branch length algorithms. Here we use a hypothetical six-species phylogenetic tree to compare the effect of two different branch length algorithms – branch/node counting and ultrametric evolutionary clock calibration – on phylogenetic structure. For ease of visualization, we assess each three-species sample (column 1) as a minimum spanning subtree (MSST) (Kelly, 1999; Symons and Beccaloni, 1999), the subtree described by those branches that include the sample only; the MSST formed by the triplet of species 1, 2, and 3 is highlighted. The MSST value for the branch-counting algorithm (ecological divergences) is given in column 2 and that of an ultrametric algorithm as used by BLADJ (real time) in column 3. Because of the small size of the parent phylogenetic tree, we are able to determine MSST values for all possible three-species subtrees, and it is not necessary to simulate this distribution through random sampling. The values at the bottom of columns 2 and 3 are the means and standard errors of these distributions. From them, we calculated $[-1 * (MSST_{observed} - MSST_{\bar{x}}) / MSST_{SE}]$. This procedure determines the number of standard errors by which the MSST of a subtree deviates from the mean MSST for all subtrees with the same number of species; the result is numerically equivalent to the NRI index of Phylcom.

The two algorithms follow the same general pattern: in both, the triplet 1, 2, 3 gives the most positive value; the most negative values occur in triplets with one member from each of the three lineages (species 1 or 2, 3 or 4, 6). However, branch-counting produces a greater range of values than the ultrametric tree, so that pattern at the tips may be easier to detect. For example, the decrease in the degree of clustering (1, 2, 3 $\rightarrow$ 1, 2, 4) has greater relative impact in the branch count tree than in the ultrametric BLADJ-type tree. We attribute this at least in part to the difference in total branch length between the two. Also, in the ultrametric tree, any triplet containing species 6 gives a signal of dispersion (negative value), even when the other two species are the two most closely related species in the tree (e.g. triplet 1, 2, 6). In the branch-counting tree, no triplets incorporating a terminal dichotomy show a value less than 0.

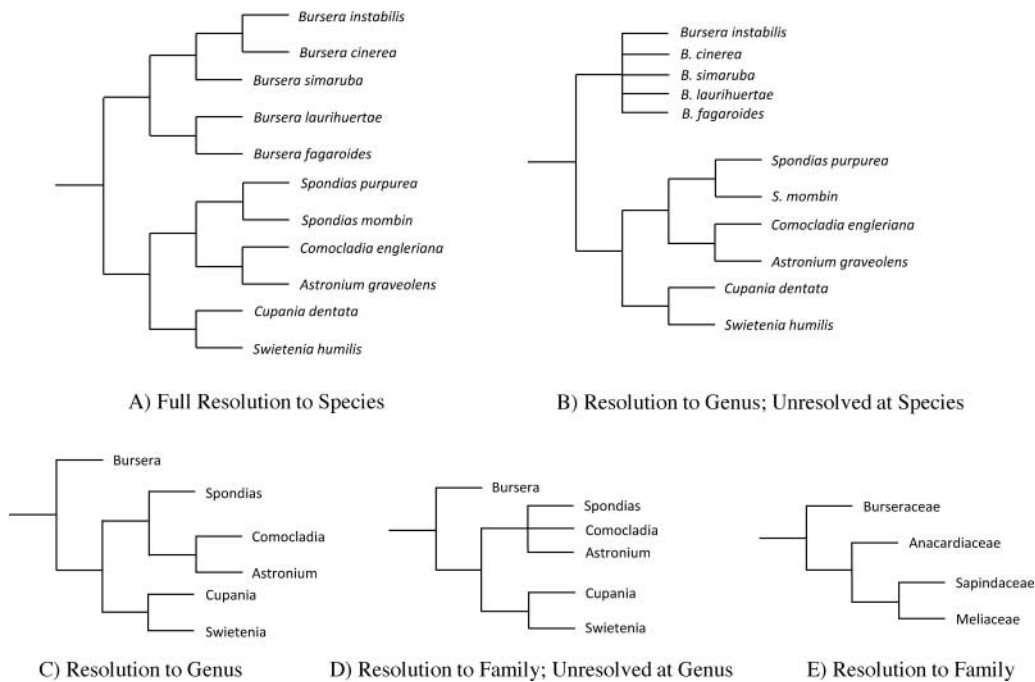


Fig. 3. Weighting and resolution manipulations of phylogenetic tree. The graphic shows an example partial phylogeny of how phylogenetic trees were manipulated by removing the weighting of subtaxa (C, E), the resolution of subtaxa within basal taxa (B), or both (D). The manipulations were performed to identify the taxonomic levels at which phylogenetic structure was evident (see text).

species among genera in determining NRI values, those genera in which species distributions were determined to have a significant correlation with elevation (preceding section) were eliminated individually and collectively from the dataset, after which NRI was recalculated. This procedure was also performed for the calculation of correlation between elevation and S/G.

RESULTS

Multi-species genera are a large part of the Mexican tropical dry forest. Overall, 53% of the species in the dataset had congeners in the parent phylogeny. Broken down by major clade, 72% of Fabaceae species and 46% of non-Fabaceae species occur in genera represented by two or more species. We found no significant correlation between elevation and either species, genus or family number (Appendix C, [2794Appendix.pdf](#)). However, we did find the weighting, resolution, and ratios of subtaxa within parent taxa to play an important part in the changing phylogenetic structure across the environmental gradient examined.

Consistent with the lack of correlation between elevation and taxon number, the null model corrections of S/G, the SD of S/G, G/F or S/F had little impact on the relationships between any of these values and elevation or NRI; the corrected variables were used in order to minimize error from the taxon/subtaxa relationship. Both S/G and the SD of S/G showed a significant negative correlation with elevation (Fig. 4). Neither S/G nor the SD of

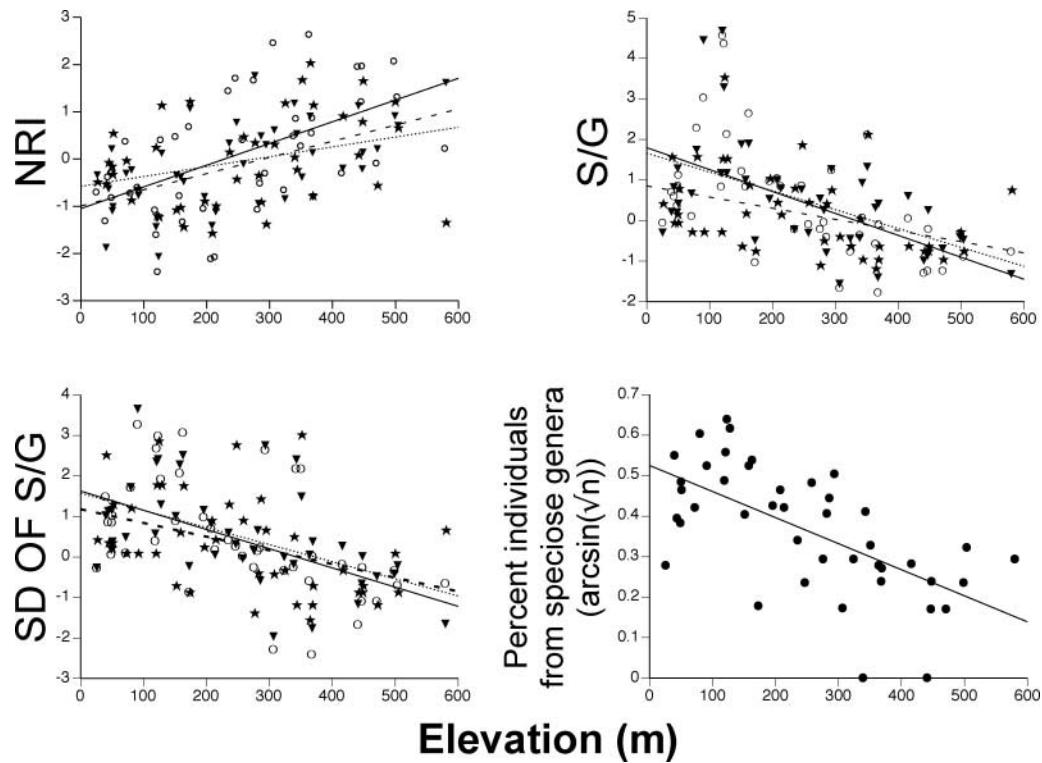


Fig. 4. Correlates of elevation. Elevation accounts for significant variation in NRI, the species-to-genus ratio (S/G), and the standard deviation (SD) of the S/G for all trees. In all panels, solid circles and solid lines represent the full phylogenetic tree (FT), open circles and dashed lines represent the non-Fabaceae subtree (NF), and open diamonds and dotted lines the Fabaceae subtree (Fa). Note that the values reported in panels (b) and (c) are derived from the null model procedure, and represent S/G and the SD of S/G as standard deviations of the observed value from the null value. Data for panel (d) were subjected to arcsine (square root) transformation prior to analysis, and the transformations are shown.

S/G deviated significantly from a normal distribution across elevation (S/G: Anderson-Darling = 0.639, $P = 0.09$; SD of S/G: Anderson-Darling = 0.353, $P = 0.45$), and although S/G and the SD of S/G are mathematically independent, they varied together in response to changing elevation, signifying an increasing concentration of species within a subset of genera as environmental conditions become hotter and drier. We tested for evidence of curvilinearity in any of these relationships, but found none (see Fig. 4).

Application of the NRI metric showed differences between the full phylogenetic tree and the two subtrees and suggested possible ecological causes behind those differences, but only when distance between taxa was calculated by node-counting; assessment of phylogenetic structure using branch lengths calculated with BLADJ revealed no pattern in the data (Table 1). With node-counting, the fully resolved parent tree and subtrees showed significant change in NRI across the elevation gradient. The strength of the correlation between NRI and elevation for the full tree was similar to that for the non-Fabaceae subtree. However, deconstruction of statistical signal (Fig 3; Table 1) showed the full tree to differ

Table 1. Signal deconstruction

Model	NRI				NTI			
	1. Full	2. Fab	3. Non-Fab	4. BLADJ	5. Full	6. Fab	7. Non-Fab	8. BLADJ
1. Species-full res	30.1*** +	10.8* +	32.4*** +	7.0	0.6	3.6 –	0.2 +	3.3 –
2. Species-unres@g	20.0** +	10.7* +	32.8*** +	7.2	3.7 –	1.2 –	5.0 +	7.8 –
3. Species-unres@g&f	1.2 –	15.3** +	32.2*** +	6.1	0.5 –	10.5* +	7.7 +	0.3 –
4. Species-unres@f	2.6 –	N.A. +	32.6*** +	6.3	0.1 +	N.A. +	4.9 +	1.1 +
5. Genus-full res	21.3** +	5.2 +	7.7 +	1.5	6.9 +	1.1 +	5.9 +	0.2 +
6. Genus-unres@f	1.4 –	N.A. –	7.9 –	0.9	2.9 +	N.A. –	18.2** +	2.6 +
7. Family-full res	0.1 +	N.A. –	0.5 +	2.0	2.2 –	N.A. –	1.6 –	5.2 +

Note: r^2 values (%) for phylogenetic structural analysis of tree communities (transects) across an elevation gradient as measured by the net relatedness index (NRI) and nearest taxon index (NTI). Each model represents a level of phylogenetic resolution (res) or artificial lack of resolution (unres) where polytomies are imposed below a given taxonomic level (g, f = genus, family; see Fig. 2) to show sensitivity to structural changes. Analyses are shown for all taxa (full), taxa within the Fabaceae only (Fab), and all taxa *except* the Fabaceae (non-Fab) using branch length = 1 (i.e. counting nodes; see Methods).

Significance: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; ‘+’ or ‘–’ indicates direction of the slope between NRI and elevation; N.A., not applicable.

from the two subtrees in the pattern of change in NRI with loss of resolution and truncation of taxa (compare column 1 to columns 2 and 3, Table 1).

Analysis of the subtrees identified the location where phylogenetic structure was changing in response to the environmental gradient. We found that differences in strength of the NRI signal between the two subtrees were not accompanied by differences in the general pattern (i.e. direction) of that signal. In each subtree, the correlation of NRI with elevation lost significance only when we removed species weighting and made genus the terminal taxon. The deconstructed signal of the full tree could not be explained as a simple averaging or addition of the two subtrees. Rather, significant deconstruction effects on NRI for the full tree were due to loss of resolution of species within genera (Table 1: column 1, row 1 $\rightarrow$ 2; significance of loss in r^2 , $P < 0.025$) and of genera within families (column 1, rows 2 $\rightarrow$ 3 and 5 $\rightarrow$ 6; significance of loss in r^2 , $P < 0.005$ for each). Loss of resolution alone did not significantly change the NRI signal for either subtree.

At first glance, the positive NRI correlation with elevation seen in Fig. 4 may be interpreted as greater phylogenetic clustering at higher elevations. This is inconsistent, however, with the finding that the larger part of the variation in NRI with elevation was accounted for by increased clustering of species within genera at lower elevations. Individually and together, S/G and the SD of S/G accounted for all or the majority of the variation between NRI and elevation in the Fabaceae and full trees. In the non-Fabaceae clade, the GLM shows 60% of the variation in NRI with elevation is shared with S/G and the SD of S/G, but it also shows that a significant proportion of the positive correlation between NRI and elevation is independent of S/G in this clade (Table 2; Fig. 5). In contrast, neither G/F nor NTI shows an independent statistical relationship with elevation for any of

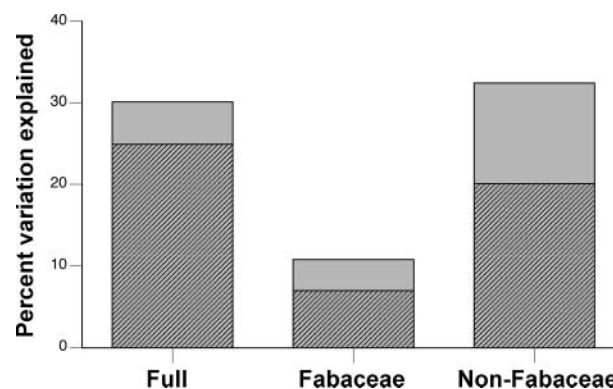


Fig. 5. The role of species distribution among genera in the correlation between NRI and elevation. The species-to-genus ratio (S/G) and the standard deviation (SD) of S/G account for much of the variation in NRI due to the elevation gradient. When entered separately into a general linear model, elevation accounts for a significant proportion of the variation among transects along the gradient. However, when indices of S/G and the SD of S/G are added to the model, these variables are able to account for a significant proportion of the variation initially explained by elevation alone. In the figure, the striped portion represents the variation in NRI accounted for jointly by elevation, S/G, and the SD of S/G (full tree: 24.2%, $P < 0.001$; Fabaceae: 8.05%, $P < 0.05$; non-Fabaceae: 20.1%, $P < 0.001$). The solid grey portion shows the variation in NRI that elevation accounts for independently (full tree: 5.9%, $P = 0.06$; Fabaceae: 2.7%, $P = 0.22$; non-Fabaceae: 12.3%, $P = 0.01$). See Appendix F, Table 1 (2794Appendix.pdf) for complete GLM tables.

Table 2. Assessing the effect of the distribution of species among genera on NRI signal

NRI versus:																
Full							Fabaceae					Non-Fabaceae				
Source	d.f.	Seq. SS	Adj. SS	Adj. MS	F	P	Seq. SS	Adj. SS	Adj. MS	F	P	Seq. SS	Adj. SS	Adj. MS	F	P
Elevation	1	20.116	3.672	3.672	3.97	0.053	103 277	26 254	26 254	1.42	0.240	308 434	123 234	123 234	8.40	0.006
S/G	1	80 499	80 499	80 499	5.50	0.002	110 632	110 632	110 632	5.99	0.055	57 627	57 627	57 627	3.93	0.036
Error	40	585 379	585 379	14 634			739 120	739 120	18 478			586 967	586 967	14 674		
Total	42	953 029					953 029					953 029				
r^2		44.6%					18.8%					39.5%				
Elevation	1	287 151	96 934	96 934	6.37	0.016	103 277	26 835	26 835	1.54	0.222	308 434	141 738	141 738	9.74	0.003
SD of S/G	1	57 155	57 155	57 155	3.76	0.011	151 203	151 203	151 203	8.66	0.139	62 446	62 446	62 446	4.29	0.100
Error	40	608 722	608 722	15 218			698 548	698 548	17 464			582 148	582 148	14 554		
Total	42	953 029					953 029					953 029				
r^2		40.6%					15.7%					36.8%				
Elevation	1	287 151	56 557	56 557	3.78	0.059	103 277	27 687	27 687	1.55	0.221	308 434	116 917	116 917	7.91	0.008
S/G	1	80 499	24 542	24 542	1.64	0.095	110 632	869	869	0.05	0.201	57 627	5 697	5 697	0.39	0.198
SD of S/G	1	1 199	1 199	1 199	0.08	0.726	41 440	41 440	41 440	2.32	0.678	10 516	10 516	10 516	0.71	0.922
Error	39	584 180	584 180	14 979			697 680	697 680	17 889			576 451	576 451	14 781		
Total	42	953 029					953 029					953 029				
r^2		44.7%					19.2%					39.5%				

Note: It is possible to calculate the percentage of the relationship between NRI and elevation explained by a subsequent factor by subtracting the difference between adjusted SS and sequential SS, then dividing the difference by the adjusted SS. For example, to determine the percentage of variation in the relationship between NRI and elevation in the non-Fabaceae accounted for by S/G and the standard deviation (SD) of S/G together, calculate from the bottom analysis: $(308,434 - 116,917)/308,434$ to find that 62% of the relationship is accounted for by the combined effects of S/G and the SD of S/G, leaving 38% of the relationship between NRI and elevation (12% of all variation in NRI) open for explanation by some other ecological effect not addressed by our hypothesis-based analyses. Inspection of the lower tables for the Fabaceae and full trees shows that S/G and the SD of S/G combined account for all of the significant effect of elevation on NRI for both trees (for the correlation between NRI and elevation, $P > 0.05$). See Table 1 for the results of simple correlation between NRI and elevation.

the three unmodified phylogenetic trees (all $P \geq 0.2$). We initially found a significant correlation between NRI and S/F, but this relationship disappeared when S/G was added to the model (without S/G, $P = 0.003$; with S/G, $P = 0.927$), signifying that S/F carries no independent explanatory value for NRI.

The impact of changing S/G on phylogenetic structure in response to the elevation gradient is further seen with the identification and elimination of large genera from the tree dataset. Seven of the nine most speciose genera have greater representation in transects found in the lower half of the elevation gradient ($P < 0.05$). No multi-species genus (i.e. ≥ 2 species) shows a significantly greater percentage of species occurrences in the upper than the lower half of the elevation gradient. Six genera support negative correlations between elevation and number of species per transect [$P < 0.02$; in order of strength of relationship: *Caesalpinia* (7 spp.), *Croton* (5 spp.), *Lonchocarpus* (7 spp.), *Bursera* (11 spp.), *Randia*

Table 3. The role of four key genera in determining changing pattern along the gradient

Dataset	S/G r^2	S/G P -value	NRI r^2	NRI P -value
Full (273 species)	32.9	<0.0005	30.6	<0.0005
Full – <i>Bursera</i>	28.6	<0.0005	29.8	<0.0005
Full – <i>Caesalpinia</i>	23.7	<0.001	27.6	<0.0005
Full – <i>Lonchocarpus</i>	29.7	<0.0005	26.9	<0.0005
Full – <i>Croton</i>	28.6	<0.0005	26.4	<0.0005
Full – Above genera	3.2	=0.25	17.6	=0.0052

Note: Removing the four speciose genera with a significant negative relationship between number of species and elevation showed these genera to have a major role in determining the observed patterns in species-to-genus ratio (S/G), standard deviation (SD) of S/G, and net relatedness index (NRI) for the 43 sample tree communities (transects) in the tropical dry forest of coastal Oaxaca. ‘Full’ refers to the full suite of 273 species sampled across all transects.

Table 4. Assessing the relationship between NRI and NTI relative to the distribution of species among genera (S/G)

	Sequential sum of squares (SS)	Adjusted SS (after S/G entry)	r^2 of NTI model	r^2 of S/G model	r^2 of combined model	P -value of adj. SS for NRI/NTI relationship after S/G entry
NRI_{Full}	2.381	10.813	3.57	39.06	55.26%	<0.001
$NRI_{Fabaceae}$	0.117	1.921	0.31	15.91	20.93%	=0.119
$NRI_{non-Fabaceae}$	1.5971	3.439	4.63	26.77	36.75%	=0.016

Note: NRI and NTI show no significant relationship in a simple linear regression in the full tree or either of the two subtrees. GLMs show that once S/G is entered into the model, NTI accounts for a greater proportion of the remaining variation in NRI for both the full and non-Fabaceae trees. In the Fabaceae, although the addition of S/G does not have a significant impact on the NRI–NTI relationship, there is still an increase in the proportion of variation in NRI for which NTI is able to account (shown as increase between sequential and adjusted sum of squares for NTI). These results suggest that the changing asymmetry of species with genera with elevation acts against the more regular – and less responsive – structure of the parent phylogenetic structure at higher organizational levels.

(4 spp.), and *Tabebuia* (3 spp.)] – the first four also passed a Dunn-Sidak multiple comparisons correction ($P < 0.013$) (Sokal and Rohlf, 2012). Together, the proportion of all species these four genera account for forms a significant negative correlation with elevation ($r^2 = 41.6$, $P < 0.001$; Fig. 4d).

By eliminating each genus from the dataset individually and then all four together, we found that this weakened the relationships between both S/G and elevation, and NRI and elevation. In the first instance, although no one genus accounts for a large part of the negative correlation between S/G and elevation, removal of all four genera eliminates the significant relationship between the two (Table 3). Similarly, removal individually of the four genera lowers between 3% and 14% of the variation accounted for by the relationship between NRI and elevation, but removing all four simultaneously lowers it by more than 40%, a quantity greater than the summed individual effects (Table 3).

Further support for the ecological impact of S/G on phylogenetic structure is provided by its effect on the relationship between NRI and NTI. Simple correlation between NRI and NTI shows no relationship for any of the trees. However, when the appropriate clade-specific S/G is added to the GLM model (i.e. the effect of S/G is eliminated from the relationship between NRI and NTI), the correlation between NRI and NTI increases – significantly so for the full and non-Fabaceae trees, less so for the Fabaceae tree (Table 4).

DISCUSSION

This study differs from recent research examining trait evolution to infer ecological processes (see citations in Vamosi *et al.*, 2009), in that we begin by considering an analytical model of ecological interaction – temporal niche dynamics – and evaluate whether the observed changes in phylogenetic structure across an elevation gradient provide empirical support for its action. The results obtained using this approach carry both conceptual and methodological implications.

Here we have determined that a tropical dry forest exhibits directional change in phylogenetic structure with increasing elevation. Our analyses of this pattern indicate that the observed structural change comes primarily from interactions occurring below the level of genus and in a manner consistent with the stable competition of temporal niche dynamics (Kelly and Bowler, 2009; Kelly *et al.*, 2010). While other studies have examined the response of plant or animal community structure to elevation (e.g. Bryant *et al.*, 2008; Parra *et al.*, 2010; Machac *et al.*, 2011), this study is novel in determining that changes occurring at the tips of the phylogenetic tree can be an important component of plant community response to changing environmental conditions. These findings, taken together with the results of Kelly *et al.* (2008, 2010), in which indicators of focused interaction were found to occur uniquely among pairs of congeneric tree species, indicate that what goes on within genera can play an important role in shaping community structure and response.

Our approach has implications for the determination of pattern in complex phylogenetic structure. We reached our conclusions by applying two different branch length algorithms – in effect, two different models of evolution. In one model, ecologically important change is assumed to be a linear correlate of evolutionary time; recent research shows that is not necessarily the case (Davies and Savolainen, 2006). In the other model, ecological information is subsumed into the occurrence of species divergence, the unit of change being that which allows the persistence of two otherwise similar taxa. This approach recognizes a node as a point of niche divergence, with an underlying assumption of species packing within the

community (MacArthur, 1970). Because there are multiple modes of evolution, speciation, and co-existence, no one algorithm is going to be right all the time (Cooper *et al.*, 2010; Losos, 2010). For the purposes of this investigation, the two models used here differ mechanically in a manner that reveals different aspects of the phylogenetic tree (see Methods). The evolutionary time model is more sensitive to structural changes involving higher taxa (e.g. family or order) to the extent that change among lower-level taxa may not be detected, as occurred here. In contrast, the node/branch counting model gives more equal weight to change at all organizational levels, and thus is better able to reflect pattern or pattern change among taxa at lower levels.

Three independent lines of evidence support the statistical pattern reflected in the node-counting algorithm. In the first instance, stepwise pruning and removal of resolution (deconstruction) from the landscape-level phylogeny weakened or fully eliminated significant correlation between elevation and phylogenetic structure at the genus level and below. Second, generalized linear models (GLMs) showed variation in species per genus (S/G) and the standard deviation of S/G in sample communities to account statistically for all or most of the relationship between elevation and phylogenetic structure in this forest. Lastly, removal from the dataset of four key speciose genera removed more than 40% of the correlation between phylogenetic structure and elevation change. By contrast, the evolutionary time model of estimating branch lengths was unable to detect pattern at any level of tree organization.

Looking in more detail at the phylogenetic tree, four genera show statistically significant correlation with elevation, the expected signature of temporal dynamics. These taxa form a substantial physical presence in the study forest, comprising less than 3% of the 171 genera present, but more than 20% of stems assayed. Of the remaining genera, none shows a distribution significantly different from the expectation of S/G pattern generated by the quantitative temporal niche dynamic model, but for many of the genera the number of species or occurrences is just too few for statistical analysis. We expect that some percentage of these genera will operate under a temporal dynamic; for example, although they do not show significant pattern in this study, we know from direct observation that both *Cordia* and *Tabebuia* can co-exist as inter-digitated populations of congeners, a strong indicator of temporal processes (C.K. Kelly, unpublished data). The numbers above indicate, however, that it is not necessary for temporal dynamics to affect all genera equally, or even to regulate all genera, in order to have a significant role in ecosystem function and structure.

The increasingly uneven distribution of species among genera stemming from changing congener co-existence patterns has ramifications for understanding the larger-scale patterns seen in the phylogenetic structure as it moves down along the elevation gradient. The result seen here – the NRI measure of phylogenetic structure being more negative at low elevations and more positive at higher elevations – would most commonly be interpreted in the context of phylogenetic trait conservatism, with decreasing elevation associated with increasing ‘overdispersion’ relative to the null expectation and co-existence mediated more by competitive exclusion. At upper elevations, the increasingly positive NRI would indicate that the samples are clustered relative to the null model, and that co-existence is constrained by environmental filtering (see studies reviewed in Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; and Vamosi *et al.*, 2009). In this study, however, the most salient abiotic gradients (i.e. temperature and precipitation) suggest the opposite pattern should exist – that the constraints of environmental filtering, if present, should be more evident at lower elevations where hotter, drier

conditions in this already hot, dry climate are expected to filter membership to the subset of species able to withstand more extreme conditions.

We explain this apparent anomaly as primarily a mechanical effect – in direct contrast to the more common inference of ecological process offered by Vamosi *et al.* (2009, and citations therein). In an asymmetric tree, species scattered as random clusters across the phylogeny can produce a more negative NRI value than the same number of species spread more evenly over the same breadth of phylogenetic distance, leading to an inference of greater dispersion (Webb *et al.*, 2002; Vamosi *et al.*, 2009). In previous work, this sort of pattern has been inferred to represent convergence of traits from distinct major clades (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006). However, the gross ecological differences between the four genera identified as consistent with temporal processes argue more strongly for multiple independent instances of species proliferation (Schluter *et al.*, 2004; Losos, 2010, 2011; Droissart *et al.*, 2011). Factors differentiating these genera include such fundamental traits as nitrogen fixation, wood density, growth form, and water retention habit (Barajas-Morales, 1985; Giller, 2001). We infer that these genera co-occur within a transect through different methods of persistence as a result of niche differentiation. This view coincides with recent determinations that a number of ecologically important characters differentiate at the level of genus (e.g. Chave *et al.*, 2006; Querejeta *et al.*, 2007; Queenborough *et al.*, 2009; He *et al.*, 2011; Soriano *et al.*, 2011), suggesting that patterns of co-occurrence or exclusion at the level of genus and above are likely to signify spatial niche differentiation rather than competitive exclusion. By contrast, the pattern of co-existence *within* genera may be the result of stable competition via the action of temporal niche dynamics.

These results carry additional implications for ecological inference. There is no significant decrease in number of either species or genera with decreasing elevation, even though maximum annual rainfall decreases by two-thirds and average daily temperature increases by 3°C between the highest and lowest elevations in the study. This lack of pattern goes against what one would expect from environmental filtering, either across taxa or with regard to phylogenetic structure. In both categories, there is turnover in species identity (Williams, 2008), but not in the number of taxa accommodated under markedly greater water-limitation, a classic indicator of environmental harshness (Woodward, 1987; Goldberg and Novoplansky, 1997).

In terms of methodology, looking at taxonomic subsets of a larger tree is not a new idea (e.g. Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2007). Here, however, rather than a general search for pattern, we were specifically interested in observable effects of the Fabaceae dominance across the larger community phylogeny. Our results differ from these previous studies in that we found the subtrees, when treated independently, showed similarly changing structure across the environmental gradient, with the full tree also agreeing in the direction if not the full pattern of the relationship. This may be attributed to each of these phylogenetic units harbouring more than one of the identified speciose genera, reflecting, perhaps, multiple instances of parallel evolution in each. As to the particular success of the Fabaceae, we speculate that it may be due partly to its ability to exploit temporal variability in environmental conditions, particularly of moisture, as suggested by its dominant presence across neotropical dry forests and other arid and semi-arid ecosystems (Gentry, 1995; Maggs *et al.*, 1998; Gillespie *et al.*, 2000; Goldblatt and Manning, 2002). The pattern that we have documented thus recommends research comparing the evolution of adaptations used by the Fabaceae to deal with such seasonality relative to other drought-adapted families.

Our stepwise deconstruction indicates an essential role of appropriate sampling as a determining factor in establishing pattern. In this study, the changing and uneven distribution of subtaxa among taxa is the primary community response to environmental change, and has a significant impact on NRI across the gradient. Incomplete sampling would have altered this determination, as was evident when we removed species within genera in our manipulations of tree structure. Reduced resolution has also been suggested to diminish or alter the phylogenetic structural pattern detected (Kress *et al.*, 2009; Swenson, 2009). In our analyses, the loss of resolution led to loss of significance with stepwise removal of structure in the full tree, but not within either the Fabaceae or non-Fabaceae subtrees. We surmise that these differences are related to the symmetry of change within, but not between, subtrees with loss of resolution, but we offer this idea only as a possibility, not as a tested hypothesis.

We developed the stepwise deconstruction applied here for the hypothesis-driven nature of our investigation, but the method could be generally useful for approaching questions of tip-based processes. Its effectiveness depends on fixed branch lengths and identification of non-arbitrary groupings in the phylogenetic tree, such as genus may be (Krug *et al.*, 2008; Jablonski and Finarelli, 2009a, 2009b). The observation that taxonomically determined genera generally correspond to monophyletic groupings applies here, and may travel up the phylogenetic tree to also identify monophyly at the family level or above. However, we suspect that the deeper the node, the more its identity (e.g. family, order) will be based on taxonomic decisions that depend on group-specific criteria, and the less it will resemble the cladistic structure of modern molecular phylogenetics.

We have focused here on congeneric species because the similarity required by competition has been found to be associated predictably with phylogeny only at this level. Competition, including the stable competition of a temporal dynamic, may also occur between distantly related species, but the similarity upon which it rests is not predictable from the phylogenetic relationship. Whether close or distant relatives, simple co-occurrence or the lack of it is not sufficient to infer interaction; either separation or co-existence could be due to niche differentiation rather than interaction (Connor and Simberloff, 1979). In this study, we subjected our results to an additional expectation of pattern – directional change in the species-to-genus ratio generated by an analytical model of temporal niche dynamics – and found agreement between model and data. We thereby simultaneously extend understanding of temporal niche dynamics to the landscape/regional level, and reveal the potential action of this process to impact phylogenetic structure and community response to environmental change in a major biome of the world, the tropical dry forest.

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