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Phylogenetic diversity of macromycetes and woody plants along an elevational gradient in Eastern Mexico

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ABSTRACT

Phylogenetic information provides insight into the ecological and evolutionary processes that organize species assemblages. We compared patterns of phylogenetic diversity among macromycete and woody plant communities along a steep elevational gradient in eastern Mexico to better understand the evolutionary processes that structure their communities. Macrofungi and trees were counted and identified in eight sites from 100 to 3500 m asl, and sequence data retrieved from GenBank for the same or closely related species were used to reconstruct their phylogenies. Patterns of species richness and phylogenetic diversity were similar for both macrofungi and trees, but macromycete richness and diversity peaked at mid-elevations, whereas woody plant richness and diversity did not show significant trends with elevation. Phylogenetic similarity among sites was low for both groups and decreased as elevational distance between sites increased. Macromycete communities displayed phylogenetic overdispersion at low elevations and phylogenetic clustering at high elevations; the latter is consistent with environmental filtering at high elevation sites. Woody plants generally exhibited phylogenetic clustering, consistent with the potential importance of environmental filtering throughout the elevational gradient.

Abstract in Spanish is available with online material.

Key words: cloud forest; coniferous forest; dry forest; macrofungi; Mexico; phylogenetic turnover; trees.

UNDERSTANDING HOW COMMUNITIES ARE ORGANIZED AND THE FORCES THAT INFLUENCE THEIR DYNAMICS AND DIVERSITY IS A PRIORITY FOR MANAGING AND RESTORING THE EARTH'S BIOTA (Cavender-Bares *et al.* 2009). Researchers have become increasingly aware that the conservation of many traits during the evolution of a lineage may influence the resulting distribution of species (Webb 2000, Cavender-Bares *et al.* 2006), and the interaction of ecological processes with evolution in some taxa may affect the structure of communities (Webb *et al.* 2002). Metrics of diversity derived from phylogenetic information, such as phylogenetic diversity (total phylogenetic branch length spanned by the species in a given community; Faith *et al.* 2004) and phylogenetic turnover (the additional branch length collectively contributed by those species in the area but not in a reference set; Faith *et al.* 2004), provide an evolutionary and hierarchical context for understanding the current coexistence within communities (Nipperess *et al.* 2010). Yet these topics can be difficult to address using only traditional metrics such as species richness and composition, and diversity indexes based solely on taxon lists (Bryant *et al.* 2008, Swenson 2009, Gonzalez *et al.* 2010, Morlon *et al.* 2011).

Measures of the phylogenetic structure of communities may reveal the relative importance of the different ecological processes that organize assemblages (Kembel & Hubbell 2006). Two main processes have been suggested to influence the phylogenetic structure of co-occurring species. Phylogenetically clustered communities with an inferred high degree of functional similarity are thought to result from environmental filtering (tolerance of taxa for abiotic conditions due to their ecological traits), whereas phylogenetically overdispersed communities are thought to be structured by the competitive exclusion of functionally similar species (Webb *et al.* 2002).

Several studies have placed phylogenetic diversity measures into ecological and biogeographic contexts (Webb 2000, Faith *et al.* 2004, Fine & Kembel 2011), suggesting that phylogenetic similarity of communities often decreases as a function of geographic distance between communities and phylogenetic distances among taxa may decrease at higher elevations and increase with

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sample area (Graham *et al.* 2009, Machac *et al.* 2011). Ecological studies of communities carried out from an evolutionary perspective may help us understand how evolution interacts with biotic and abiotic factors to structure species assemblages at the local scale. In addition, comparing taxonomically distant groups, like trees and fungi, is of great interest for understanding the distribution of species along major environmental gradients and for predicting the ecological responses of organisms to changing climate (Bryant *et al.* 2008).

Here, we evaluate the diversity of phylogenetically distant but ecologically related organisms—woody plants and macromycetes—along an elevational gradient in eastern Mexico, with the broad aim of determining how communities are phylogenetically structured at different environmental conditions. Specifically, we (1) evaluate patterns of species richness and phylogenetic diversity; (2) determine the efficacy of species richness as a proxy for estimating phylogenetic diversity; and (3) discuss potential evolutionary processes determining the phylogenetic relatedness of coexisting taxa within macrofungal and tree assemblages. In previous work along the same elevational gradient analyzed here, Gómez-Hernández *et al.* (2012) found that the species richness of macromycetes peaked at mid-elevations and that of woody plants decreased with increasing elevation. Thus, we predicted that the variation in phylogenetic diversity for macromycete and woody plant communities would correspond to variation in species richness. We also expected high phylogenetic turnover between adjacent communities, and a positive correlation between phylogenetic turnover and the difference in elevation among sites. Finally, we predicted that communities would demonstrate phylogenetic clustering at high elevation sites, where conditions are relatively severe, but would be phylogenetically overdispersed at low elevations (Webb *et al.* 2002, Graham *et al.* 2009).

METHODS

Study area.—The study area is located in central Veracruz, Mexico, along a steep elevational gradient from the Gulf of Mexico to the summit of Cofre de Perote Volcano at 4282 m asl. In this area, eight study sites were selected from *ca.* 100–3500 m asl, and about every 500 m elevation (Fig. S1). Sites include seasonally dry tropical forest (97 and 501 m asl), a transition zone or ecotone between dry tropical and montane cloud forest (986 m), cloud forest (1630 and 1950 m asl), an ecotone between cloud and coniferous forest (2650 m asl), and coniferous forest (3020 and 3460 m asl) (Table 1). Ecotones were identified by the presence of woody species belonging to adjacent types of vegetation. The selected sites are conserved forests representative of the vegetation types in the study area. Sites from 97 to 986 m elevation are not under apparent conservation management. The site at 1630 m is private land destined for conservation. Sites at 1950 and 2650 m are private lands managed for controlled logging. Sites at 3020 and 3460 m are protected areas within a private park and a National Park, respectively.

In each site, a 1 ha parcel was delimited at least 30 m from the forest edge, and haphazardly set up 10 permanent 10 × 10 m plots separated by at least 10 m. In each plot, trees ≥5 cm diameter at 1.3 m above ground were measured and identified, and macromycete fruiting bodies were counted and collected monthly during the rainy seasons (May to October) of 2010 and 2011. Macrofungal specimens were determined by their micro- and macro-morphological characters (see Gómez-Hernández & Williams-Linera 2011). Unidentified taxa were classified as numbered morphospecies within a genus and the putative nearest species. Observed species richness for both macromycetes and woody plants was defined as the number of species recorded.

Phylogenetic analyses were carried out to determine the evolutionary relatedness of tree and macromycete species within and across communities. The analysis for macromycetes included three nrDNA regions: 5.8S, 18S, and 28S. For the woody plant analysis, the cpDNA regions were *matK* and *rbcL*. In this study, sequences of surrogates obtained from GenBank (http://www.ncbi.nlm.nih.gov/genbank/) were used to estimate the phylogenetic distance for both macrofungal and woody plant taxa (same species, sister species, or species hypothesis in UNITE database; accessions are provided in Appendices S1 and S2). BLAST searches were used to validate the taxonomy of potential surrogate sequences from GenBank. For samples identified only to genus and section, and for species not available in GenBank,

TABLE 1. *Study sites and geographical coordinates, elevation (m asl), vegetation type, species richness of macromycetes ($S_{obs}m$) and woody plants ($S_{obs}p$), phylogenetic diversity of macromycetes (PDm) and woody plants (PDp), and net related index values of macrofungi (NRIm) and woody plants (NRIp) for the eight study sites along the elevation gradient. NRI > 0 means phylogenetically clustered, NRI < 0 means overdispersed.*

Site	N Latitude	W Longitude	Elevation	Vegetation	S_{obs}m	PDm	NRIm	S_{obs}p	PDp	NRIp
1	19°16′11″	96°29′ 38″	97	Dry forest	11	1.603	−0.28	13	1.03	0.27
2	19°27′15″	96°41′37″	501	Dry forest	22	2.299	−0.19	24	2.17	0.21
3	19°30′34″	96°49′51″	986	Ecotone	48	3.549	−0.29	13	1.4	0.72
4	19°31′03″	97°00′14″	1630	Cloud forest	38	3.461	−0.18	19	1.88	0.5
5	19°29′23″	97°01′53″	1950	Cloud forest	30	3.092	0.21	23	1.9	0.78
6	19°30′59″	97°03′36″	2650	Ecotone	44	3.427	0.24	13	1.43	−0.52
7	19°33′46″	97°05′34″	3020	Coniferous	27	2.333	0.27	3	0.66	1.21
8	19°31′13″	97°08′51″	3460	Coniferous	27	2.436	0.64	2	0.65	0.95

sequences from closely related species (belonging to the same section, often a putative sister species based on morphology) were used as surrogates. Since species are assumed to represent monophyletic lineages, using sequences from different individuals is appropriate for this broad scale of phylogenetic analysis. The selected gene regions are highly conserved and are primarily used for phylogenetic analyses above the species level. Furthermore, likelihood-based phylogenetic analyses such as ours in which some species have missing data have proved to be robust (Appendix S3).

Sequences were aligned using PhyDe v.0.99 (Müller *et al.* 2010). The gene regions were concatenated as single matrices for macomycetes and woody plants, and analyzed. Then, jModelTest 2.1.6 (Darriba *et al.* 2012) was used to identify the model of molecular evolution that best fit the data matrix of concatenated data matrices for both macromycetes and woody plants under the Akaike Information Criterion (AIC).

The best-fit model obtained for both the nrDNA and cpDNA concatenated regions was GTR + I + G. The phylogenetic analyses did not include macrofungal and woody plant species identified only to family or higher taxonomic levels; thus, we used 163 terminal taxa for macromycetes and 93 for woody plants (Appendices S1 and S2; Figs. S2 and S3). Alignments were deposited in TreeBASE (www.treebase.org) (Submission ID 17742). Phylogenetic analyses were performed for Maximum Likelihood (ML) using Garli v.2.0 (http://garli.googlecode.com).

A backbone constraint tree to the family level was estimated using Phylomatic v.3 web service (http://phylodiversity.net/phylomatic/), and the resulting phylogeny was used as a constraint tree for the ML analysis followed by 500 parametric bootstrap replicates. ML analyses for both macromycetes and woody plants were performed using the GTR+I+G model with two independent replicates and default settings in Garli v.2.0. The minimum linking path between pairs of taxa in the phylogenetic tree and phylogenetic diversity of macromycete and woody plant communities were calculated in Mesquite v.2.75 (Maddison & Maddison 2011), the latter with the Tuatara package v.1.0 (Maddison & Mooers 2007). Phylogenetic diversity was estimated by proxy based on the phylogeny of sequences of the same species or from closely related taxa rather than from specimens collected in the communities.

To determine whether the phylogenetic diversity along the elevational gradient differed from that expected by chance, the observed phylogenetic diversity of communities was compared to a null model obtained by randomly sampling the phylogenetic pool 1000 times. The relationship between species richness, phylogenetic diversity, and elevation was determined by fitting linear and polynomial regressions. To select the best-fit model, we used the AIC. A two-sample Kolmogorov–Smirnov test was performed in R v. 2.15.2. (R Core Team 2012) to define differences between distributions of phylogenetic diversity and species richness. The null hypothesis for this test is that both data samples come from identical distributions, where the statistic D is the maximum difference between the theoretical and the empirical cumulative frequencies of the variable.

The similarity in species composition between study sites was estimated with the Sørensen similarity index, run in the program EstimateS v. 8.2 (Colwell 2006). As a measure of phylogenetic turnover, phylogenetic similarity between communities was determined with the metric analog of the Sørensen similarity index, termed PhyloSor (Bryant *et al.* 2008). Linear regression analyses were carried out to determine the relationship between phylogenetic and species turnover. Mantel tests with Pearson's correlation coefficient based on 9999 replicates were performed in R v. 2.15.2. (R Core Team 2012) to determine differences in phylogenetic and species composition similarity between macromycete communities, and elevational and geographic distance between sites. Since phylogenetic and species composition similarity data for woody plants were not normally distributed and transformations were not successful in normalizing the data, the non-parametric Spearman's test was used to determine differences between them and elevational and geographic distance. A chi-square test was carried out to determine the independence between elevational and geographic distance variables. Singletons (species recorded only once) were removed prior to analyses to avoid underestimating phylogenetic and species similarity among communities.

The overall clustering of taxa in the communities' phylogeny along the elevational gradient was quantified with the net relatedness index (NRI) calculated as in Webb *et al.* 2002. This index is a standardized measure of the mean pairwise phylogenetic distance of taxa in a sample, relative to a phylogeny of a species pool. Negative values of NRI indicate that taxa are phylogenetically overdispersed, and positive values indicate that they are clustered in the pool of the phylogeny. The relationship between NRI and elevation was determined by fitting linear and polynomial regressions. We used the AIC to select the best-fit model. Since the phenology of macromycetes and ephemeral fruiting bodies makes it difficult to record all of the species in a site, the effect of undersampling on NRI was estimated by simulating two mechanisms: (1) subsampling of the community when the less abundant species are missed, and (2) random subsampling when species are missed regardless of whether they are common or rare. The analyses were run to simulate a whole gradient of subsampling, from ~1 percent to ~95 percent. Percentage of subsampling is measured as a proportion of the lost taxa in each run relative to the pool of taxa recorded. All statistical analyses were run in R v. 2.15.2. (R Core Team 2012).

RESULTS

A total of 202 macromycete species and 112 woody plant species were recorded in the eight study sites. The nrDNA multigene analysis for macromycetes resulted in an aligned matrix of 2,184 bp for 163 taxa. The cpDNA gene analysis for the woody plants resulted in an aligned matrix of 1420 bp for 93 taxa.

The best-fit model for both species richness and phylogenetic diversity of macromycetes showed a trend to increase with elevation with a peak at intermediate part of the gradient (Fig. 1A). However, the relationship with elevation was significant

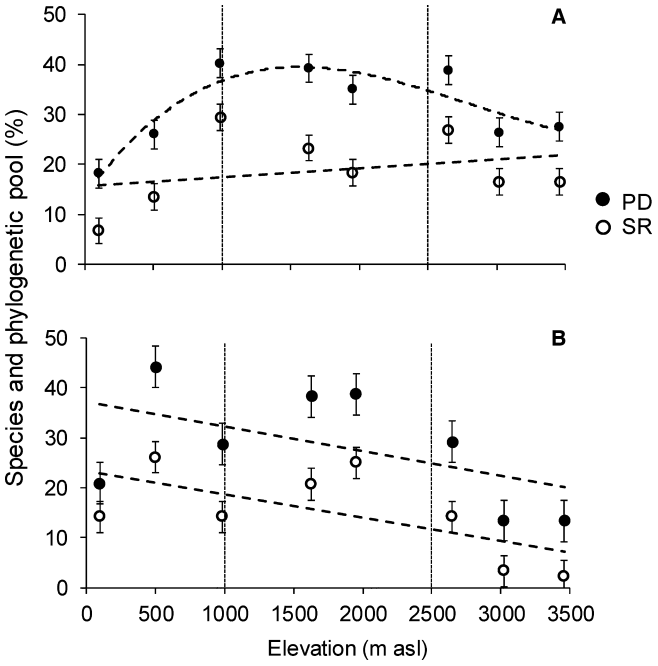

FIGURE 1. Patterns of species richness (SR) and phylogenetic diversity (PD) for macromycetes (A) and woody plants (B) along an elevational gradient. PD and SR trends are represented by solid and dashed lines, respectively. Vertical dotted lines represent the dry–cloud and cloud–coniferous forest ecotones. Note, to homogenize the scale, *y*-axis values are the percentage of species richness and phylogenetic diversity for each community with respect to species and to the phylogenetic pool.

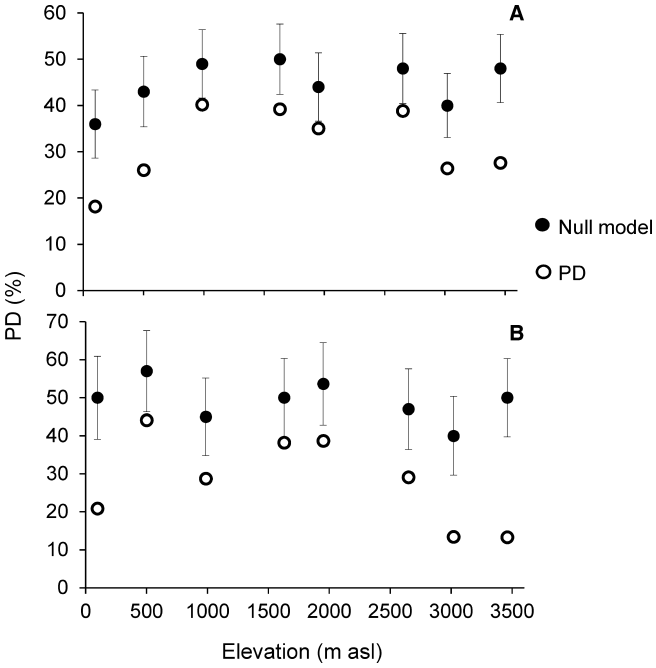

FIGURE 2. Phylogenetic diversity of macromycetes (A) and woody plants (B) compared to a null model. Open circles represent the observed phylogenetic diversity and solid circles represent the null phylogenetic diversity. Error bars are standard error. Note, to homogenize the scale, *y*-axis values are the percentage of phylogenetic diversity for each community with respect to the phylogenetic pool.

only for phylogenetic diversity (Polynomial regression, $F = 9.48$, $r^2 = 0.87$, df = 4, $P = 0.027$), and only suggestive for species richness (Linear regression, $F = 0.4$, $r^2 = 0.07$, df = 6, $P = 0.055$). For woody plants, the best-fit model for both phylogenetic diversity and species richness indicated non-significant trends with elevation (Linear regression, $F = 2.3$, $r^2 = 0.27$, df = 6, $P = 0.17$, and $F = 4.22$, $r^2 = 0.41$, df = 6, $P > 0.085$, respectively; Fig. 1B). The elevational patterns of species richness versus phylogenetic diversity did not differ significantly, either for macromycetes or woody plants (Kolmogorov–Smirnov test, $D = 0.62$, $P = 0.085$, and $D = 0.6$, $P > 0.08$, respectively). Phylogenetic diversity for both macromycete and woody plant communities along the elevational gradient significantly differed from the null prediction ($P < 0.05$; Figs. 2A and B).

Distributions of elevational and geographic distances among sites are independent ($X^2 = 168$, df = 162, $P > 0.05$). Geographic distance between adjacent sites decreased with elevation, whereas elevational distance remained about 500 m asl between adjacent sites. For macromycetes, PhyloSor and Sørensen similarity indexes ranged from 0 to 0.61, and from 0 to 0.39, respectively (Table S1 A, C), and were positively related (Linear regression, $F = 163$, $r^2 = 0.86$, df = 26, $P = 1.04^{-12}$; Fig. 3A). However, the difference in phylogenetic similarity between macromycete communities was not significantly correlated with the elevational distance between sites (Mantel test, $r = 0.11$, $P = 0.12$; Fig. 4A), but was significantly correlated with geographic distance (Mantel test, $r = 0.3$, $P = 0.004$). The difference in species composition similarity for macromycete communities was significantly correlated with elevational and geographic distance between sites (Mantel test, $r = 0.19$, $P = 0.03$; Fig. 4B, and $r = 0.18$, $P < 0.03$, respectively). Most macromycete communities shared species and showed phylogenetic similarity (PhyloSor). By contrast, woody plant communities shared species and showed phylogenetic similarity only between sites with *ca.* 500 or 1000 m elevational difference. PhyloSor and Sørensen similarity indexes for woody plants ranged from 0 to 0.42, and from 0 to 0.8, respectively (Table S1B, D), and were positively related (Spearman's test, $\rho = 0.9946$, $P = 2.2^{-6}$; Fig. 3B). Similarly to macromycetes, the difference in phylogenetic similarity between woody plant communities was significantly correlated with elevational and geographic distance (Spearman's test, $\rho = -0.77$, $P = 1.6^{-6}$; Fig. 4C, and $\rho = -0.51$, $P = 0.005$, respectively). The difference in species composition similarity was significantly correlated with elevational and geographic distance of sites (Spearman's test, $\rho = -0.78$, $P = 9.05^{-7}$; Fig. 4D, and $\rho = -0.54$, $P = 0.002$, respectively).

Net relatedness index values for macromycetes changed from <0 at low elevations (phylogenetically overdispersed) to >0 at high elevations (phylogenetically clustered) (Table 1). The best-

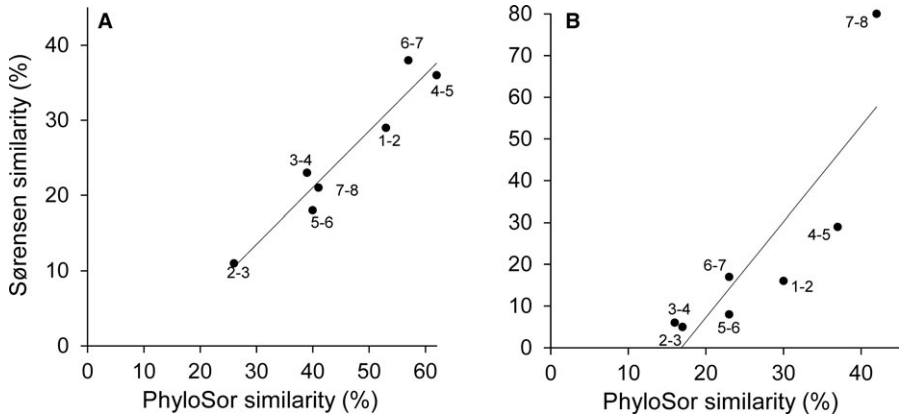

FIGURE 3. Relationship between the percentage of phylogenetic (PhyloSor) and species composition (Sørensen) similarity indexes for macromycetes (A) and woody plants (B) at adjacent sites. Lines represent the relation trend.

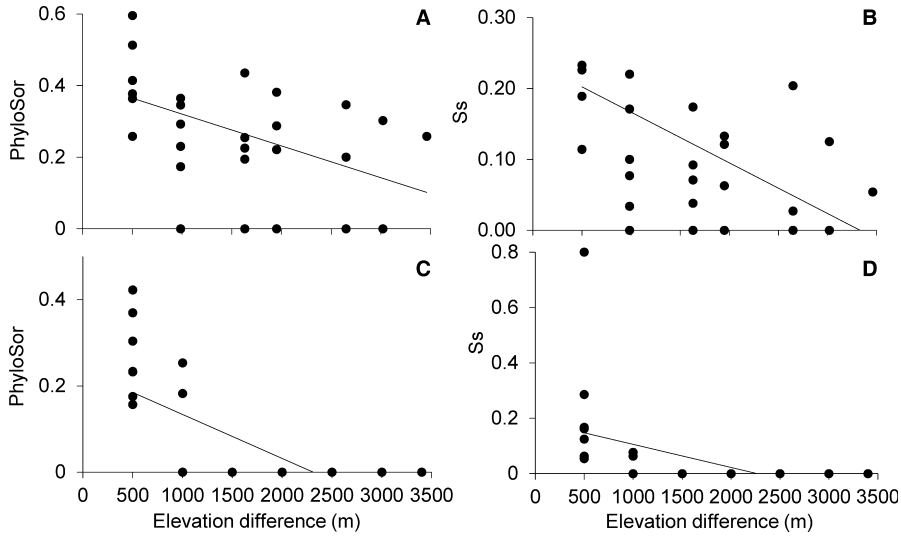

FIGURE 4. Variation in phylogenetic similarity (PhyloSor) and Sørensen's similarity index (Ss) for macromycetes (A, B) and woody plants (C, D) with difference in elevation between sites. Lines in A, B, and C represent significant trends.

fit model showed a monotonic and significant trend of increasing phylogenetic relatedness among macromycete taxa with elevation (Linear regression, $F = 39.9$, $r^2 = 0.86$, df = 6, $P = 0.001$; Fig. 5A). By contrast, the NRIs of woody plant communities were >0 across the elevational gradient except for the ecotone site at 2650 m asl, which showed a marked overdispersion. The best-fit model for woody plants showed a non-significant increase in phylogenetic relatedness with elevation (Linear regression, $F = 0.8$, $r^2 = 0.11$, df = 6, $P = 0.4$; Fig. 5B). However, the best-fit model excluding the site at 2500 m asl showed a significant, monotonic increase in phylogenetic clustering with elevation (Linear regression, $F = 18.21$, $r^2 = 0.78$, df = 5, $P = 0.007$). Simulation analysis revealed that the NRI of macromycetes and woody plant species was a robust metric not influenced when undersampling by 50–75 percent of the total number of species recorded (*i.e.*, sampling only 25–50% of the total), and this was independent of losses occurring among the rare species or random losses (Figs. S4A and B).

DISCUSSION

PATTERNS OF SPECIES RICHNESS AND PHYLOGENETIC DIVERSITY.—The relationships found in our macromycete ML tree resemble those found in previous studies (Hibbett 2006, Hibbett *et al.* 2007), and the woody plant ML tree is concordant with the most recent Angiosperm phylogeny (APG III 2009, Chase & Reveal 2009).

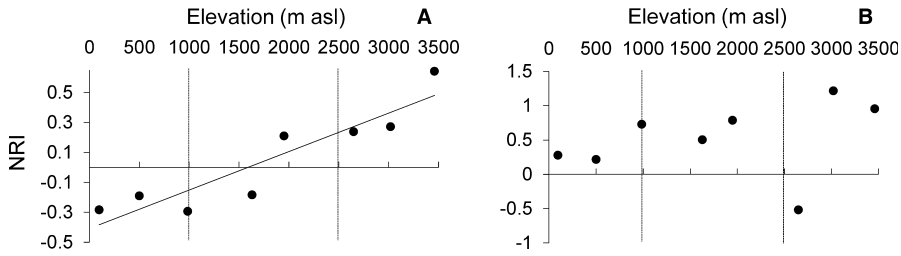

FIGURE 5. Regression analyses for the net relatedness index (NRI) of macromycete (A) and woody plant (B) communities along the elevational gradient. Solid lines in represent the trend of NRI values along the elevational gradient. Vertical dotted lines represent the dry–cloud and cloud–coniferous forest ecotones. The site at 3500 m asl is not represented in panel B because of the scale and its high NRI value (see Table S1).

Elevational patterns of phylogenetic diversity corresponded to patterns of species richness for both macromycetes and woody plants (Fig. 1). Our results do not support the claim that granting all species the same weight makes species richness a poorer measure of biodiversity as compared to phylogenetic diversity, which is thought to be a more robust metric since it is based on evolutionary novelties (Vane-Wright *et al.* 1991, Faith 1992, Forest *et al.* 2007). Our findings were concordant with those of Polasky *et al.* (2001), Rodrigues and Gaston (2002), and Bryant *et al.* (2008) who reported that phylogenetic diversity and the richness of species and genera follow similar spatial patterns. Global patterns of species/genus and species/family ratios have shown a relationship between the number of genera or families and the number of species, suggesting the influence of evolutionary forces on phylogenetic structure (Enquist *et al.* 2002). Taxonomic similarities among lineages reflect the number of conserved traits, so the phylogenetic distance among species is expected to be higher in taxonomically rich communities than in taxonomically poor communities.

Our results showed that phylogenetic diversity and species richness in macromycete communities along the elevational gradient were higher at mid-elevation. A literature review by Rahbek (1995) found that approximately half the studies on elevational gradients report mid-elevation peaks in species richness, which is thought to result from the overlap of distribution ranges of lowland and highland specialist species when the complete gradient has been sampled (Colwell *et al.* 2004, Nogués-Bravo *et al.* 2008).

For woody plants, our results showed that phylogenetic diversity and species richness neither increase nor decrease with elevation (Fig. 1B) in contrast to many studies on plant communities (Lieberman *et al.* 1996, Givnish 1999, Behera & Kushwaha 2007, Mwaura & Kaburu 2009), and the ecological theory that temperature declines associated with increasing elevation leads to a lower productivity and consequently to a reduced number of biotic interactions (Lovett *et al.* 2006). Although our results did not show a significant trend, there was an overall pattern of decreasing woody plant richness and phylogenetic diversity with elevation, with a major peak at low elevations and a minor peak at mid-elevations (Fig. 1B). This may result from the repeated minor peaks that species richness can exhibit at the transitions between zonal communities along elevational gradients, and this is consistent with patterns resulting from the climate gradients and biotic interactions between adjacent communities (Lomolino 2001).

PHYLOGENETIC AND SPECIES TURNOVER.—While several studies have documented the turnover of macromycete species along environmental, geographic, and elevational gradients (*e.g.,* Lodge *et al.* 1995, Brown *et al.* 2006, Durall *et al.* 2006, Braga-Neto *et al.* 2008), no previous studies have addressed the turnover along an elevational gradient using a phylogenetic approach. Our results for macrofungal communities showed that both phylogenetic and species similarities were low between adjacent elevational zones (<59%; Fig. 3A). Local processes such as dispersal limitation and habitat specialization can interact with biogeographic history and evolutionary processes, increasing the species turnover between communities (Fine & Kembel 2011), and leading to adjacent communities with species from lineages with long-standing and divergent evolutionary histories (Graham & Fine 2008). Consequently, the composition of host-generalist and host-specialist macrofungi can strongly differ among forests with similar tree species (Nantel & Neumann 1992, Ferrer & Gilbert 2003, Kujawa & Kujawa 2008). Although the distributions of macrofungi and their host trees differ and these two groups are phylogenetically distant, the ecological link between fungal and plant communities is widely recognized, with fungus–plant feedback being important for ecosystem functioning. The resources provided by plant communities strongly influence the communities' composition of root-associated organisms (*e.g.,* mycorrihzal fungi) (Yeates 1999, Saetre & Bååth 2000). Similarly, mycorrhizal fungi may markedly influence the structure of plant communities. Perry *et al.* (1989) suggested that mycorrhizal diversity raises plant productivity more than variation in species composition, since the interspecific competition between tree species increases as the number of mycorrhizal fungi increases. In the case of wood-decaying fungi, different groups of decomposer macromycetes act as parasites and/or saprophytes (Borba-Silva *et al.* 2015). The decomposer subsystem in forests indirectly regulates plant growth and community composition by determining the supply of available soil nutrients (Wardle *et al.* 2004).

PhyloSor and Sørensen index values among communities were low for both macromycetes and woody plants. However, our results indicate that macromycete communities along the elevational gradient share more evolutionary history than do tree communities. While most elevational zones share some macromycete species and show phylogenetic similitude, for woody plants this was found only among sites differing in elevation by less than *ca*. 1000 m (Fig. 4). The high phylogenetic turnover between adjacent communities and the marked decrease in phylogenetic similarity with elevational distance may be a consequence of the strong variability in relevant conserved traits leading to species specialization for particular habitats as a function of the abiotic environment, which has a stronger effect on community structure than does dispersal limitation (Hardy & Senterre 2007, Bryant *et al*. 2008, Graham *et al*. 2009, Fine & Kembel 2011).

Phylogenetic structure of communities.—For both macromycetes and trees, species within communities at high elevation were more closely related than those at lower elevations (Figs. 5A and B), as was also found by Graham *et al*. (2009) and Machac *et al*. (2011). Inferring that phylogenetic clustering at high elevation resulted from historical filtering based on conserved traits, agrees with the study by Merckx *et al*. (2015) in East Malaysia, showing strong niche conservatism in lineages of fungi, plants, and animals. In that study, endemic high-elevation species on a recent volcanic tropical mountain were mostly derived from high-elevation species that colonized from elsewhere, while a few evolved locally from species at lower elevation, mostly in the same forest type. While forest fungi are irrevocably linked with plants for their nutrition, the environment has also been reported to influence macromycete species richness and distribution, with temperature and precipitation being the main factors involved (Lange 1978, O'Dell 1999, Ohenoja 1995, Salerni *et al*. 2002). A previous study along the same elevational gradient found that humidity and temperature are the factors most strongly related to macromycete distributions at mid and high elevations (Gómez-Hernández *et al*. 2012), consistent with environmental filtering structuring macromycete communities at high elevation.

In contrast to macromycete communities, the structure of woody plant communities was phylogenetically clustered along the entire elevational gradient except for the ecotone at 2650 m asl, and clustering was especially strong at the two highest sites (Fig. 5B). Several studies have shown similar patterns of increasingly close phylogenetic relatedness of taxa with elevation, suggesting more stressful conditions in high elevation environments (Graham *et al*. 2009, Kluge & Kessler 2011, Machac *et al*. 2011). Evidence for phylogenetic clustering was found in 59 percent of the studies of contemporary communities, with plant systems representing most of the published studies (Vamosi *et al*. 2009). A study to test the increasing phylogenetic relatedness of species with elevation as a function of trait conservatism indicated that the traits are phylogenetically conserved, leaving only the species that have evolved the ability to tolerate cold climates at high elevations (Machac *et al*. 2011). Their results suggested that interspecific competition might be structuring the lowland communities, but competition is secondary to the effect of habitat filtering under extreme conditions. The phylogenetic distance among taxa within the ecotone at 2500 m asl in our study resulted in a sharp drop of NRI for this site (Fig. 5B). This result along with the woody plant taxa recorded in the site, which are representative of cloud forest (*e.g., Carpinus*, *Cinnamomum*, *Liquidambar*, *Turpinia*) and coniferous (*i.e.*, *Pinus*), suggest that the highly overdispersed structure of the community most likely resulted from the overlapping of two different communities at the ecotone where neither could dominate.

Studies of macromycetes at local scales have shown that sampling over several years is needed to record the majority of the species in a site (Bills *et al*. 1986, Straatsma *et al*. 2001, Durall *et al*. 2006). However, it is rarely possible to sample over the many years required to document most of the species (Gabel & Gabel 2007), so undersampling macromycetes is likely a common issue. Our simulations of random undersampling resulting from unobserved and rare species showed that undersampling by up to 50–75 percent had no effect on the calculations of phylogenetic structure for either the woody plant or macromycete communities (Fig. S4). The Net Relatedness Index thus appears to be a useful and robust metric for characterizing and comparing macromycetes communities.

CONCLUSIONS

Our results indicate that variations in the number of macromycete and woody plant species within communities along the elevational gradient are concordant with variations in phylogenetic diversity. Thus, species richness is likely to be as efficient as phylogenetically based metrics for measuring local diversity, which could facilitate the identification of differences in the proportion of evolutionary history between assemblages based on the number of species. The results of phylogeny-based metrics of turnover, however, do not always correspond to metrics based on species composition. Moreover, our results suggest that environment interacting with evolution may strongly affect the structuring of contemporary macromycete and woody plant assemblages. It is worth highlighting that inferences of community-structuring processes were based on the literature and the NRI results, so analyses such as ancestral character state evolution, niche conservatism, and phylogenetic signal are needed to accurately determine the primary processes that organize species assemblages. Taxonomically distant groups (*e.g.,* macromycetes and woody plants) must be compared to better understand the evolutionary forces generating the observed species assemblages. In developing countries such as Mexico, it can be difficult to obtain sequences directly from collected specimens due to the lack of economic resources and/or limited access to suitable labs. It is crucial to develop methods and tools for accurate phylogenetic analyses using sequences of surrogate species from databases, as done in this study. Furthermore, the phylogeny-based metrics were much more robust to undersampling than species richness, and the method may therefore aid studies of macromycete fungi that are difficult to sample thoroughly.

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SUPPORTING INFORMATION

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

TABLE S1. *PhyloSor and Sørensen similarity indexes for macromycetes and woody plants between pairs of communities along an elevational gradient in central Veracruz, Mexico.*

FIGURE S1. Study area in central Veracruz, Mexico.

FIGURE S2. Phylogeny of macromycete species sampled in eight sites along an elevational gradient.

FIGURE S3. Phylogeny of woody plant species sampled in eight sites along an elevational gradient.

FIGURE S4. Effect of undersampling on net relatedness index for macromycetes and woody plants along the elevational gradient.

APPENDIX S1. GenBank accession numbers for the macromycete sequences used in the phylogenetic analysis.

APPENDIX S2. GenBank accession numbers for the woody plant sequences used in the phylogenetic analysis.

APPENDIX S3. Support for the use of surrogate sequences from different individuals, and missing genes in the phylogenetic analyses.

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