

# Patterns of macromycete community assemblage along an elevation gradient: options for fungal gradient and metacommunity analyses

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**Abstract** Gradient analysis is rarely used in studies of fungal communities. Data on macromycetes from eight sites along an elevation gradient in central Veracruz, Mexico, were used to demonstrate methods for gradient analysis that can be applied to studies of communities of fungi. Selected sites from 100 to 3,500 m altitude represent tropical dry forest, tropical montane cloud forest, conifer forest, and their ecotones. From May to October 2010, macromycetes were collected monthly within ten 10 × 10 m permanent plots per site. In total, 672 individuals of 213 species of macromycetes were recorded. Models for richness and diversity for all macromycete and ectomycorrhizal communities displayed peaks in the mid-part of the gradient, and a tendency to increase with elevation, whereas xylophagous fungi displayed a peak in the mid-lower part but tended to decrease with elevation. Cluster and Maximum Likelihood analyses distinguished four communities for both macromycetes and trees, but plant and fungal communities were only partly concordant. Canonical correspondence analysis indicated that macromycete distribution along the gradient is related to slope, relative humidity, soil temperature, soil water content, canopy openness, and litter depth. Spearman's correlation and regression trees suggested that air and soil temperature, relative humidity, soil water content, canopy openness, vegetation structure and tree species richness were most strongly related to macrofungal functional groups, but these environmental variables were often correlated to the forest type and may not be causal. Variation in the environment along the elevation gradient differentially affected macromycete functional groups. Results from the different methods used in this work were concordant and showed significant patterns.

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### Abbreviations

AIC	Akaike information criterion
CCA	Canonical correspondence analysis
CF	Conifer forest
ECM	Ectomycorrhizal fungi
H'	Shannon diversity index
ML	Maximum likelihood
Sobs	Species richness observed
TDF	Tropical dry forest
TMCF	Tropical montane cloud forest

### Introduction

In this paper, data on macromycetes from an elevation gradient in Veracruz, Mexico, were used to demonstrate methods for gradient and metacommunity analysis that can be applied to studies of turnover of species assemblages in macromycetes. Macrofungi (those producing visible sporomes) are primarily Ascomycota and Basidiomycota and comprise about 10% of total fungal biodiversity (Rossman 1994). Biodiversity has scale-dependant components known as alpha, beta and gamma diversity. The majority of macrofungal studies are at the level of alpha diversity, which is frequently expressed as species richness at a local scale. Beta diversity is often defined as the extent of species replacement or turnover along environmental gradients (Whittaker 1972; Wilson and Shmida 1984) at a landscape scale, but it has also been used to describe changes in composition between samples from different habitats (Heilmann-Clausen et al. 2005) as well as the reduction of sample similarity with distance attributable to dispersal limitations (Condit et al. 2002; McCune and Grace 2002). Studies of fungal species turnover are important for management and conservation as they can indicate which habitats have the highest diversity and how fungi respond to natural and anthropogenic disturbances and management regimes (e.g. Braga-Neto et al. 2008; Durall et al. 2006; Gates et al. 2011a, b, c; McMullan-Fisher et al. 2010; Sysouphanthong et al. 2010). The turnover of species between habitats along environmental gradients is thought to be one of the dominant factors affecting macrofungal species richness at landscape scales (Braga-Neto et al. 2008; Brown et al. 2006; Lodge et al. 1995; Nantel and Neumann 1992), and it has been demonstrated that environmental gradients related to altitude affect the diversity and distribution of macromycetes (O'Dell et al. 1999; Zhang et al. 2010). A literature review on species richness patterns showed that about half of the elevation gradient studies detected a mid-altitude peak in species richness (Rahbek 1995). Gradient analysis is frequently used in ecological studies of plant and animal assemblages but examples of their use for fungi are few.

Published gradient analyses of macromycete data are mostly from temperate and boreal zones (e.g. Alfredsen and Høiland 2001; Edwards and Zak 2010; Gates et al. 2011a, b, c; Nantel and Neumann 1992), and fewer from the tropics (Braga-Neto et al. 2008; Brown

et al. 2006; Gómez-Hernández and Williams-Linera 2011). Data from macrofungal surveys often have characteristics that restrict the types of gradient and meta-community analyses that can be applied to them, or additional steps to edit the data are required. Fungal assemblages resemble those of plants and animals in having many rare species that result in a sparse sample per species data matrix and non-normal distributions (McCune and Grace 2002). Macrofungal data that are based on collections of fruit bodies differ, however, in having many ‘false absences’ (failure of a species that is present to fruit during a survey). Here, criteria were compared for exclusion of ‘unreliable’ species from the data matrix by back-casting the species composition of a nearby plot that was studied previously. A data matrix that was edited using the best criterion from the back-casts with other criteria was used to explore meta-community structure along the gradient, specifically clumping of distribution boundaries (i.e. a greater frequency of distributions that end or begin at a point along the gradient than expected by chance; Leibold and Mikkelsen 2002). As in Nantel and Neumann (1992), canonical correspondence analysis (CCA) was used because it can detect unimodal relationships between species and environmental variables. Richness and diversity patterns along the elevation gradient were analyzed by fitting linear and polynomial regressions and selecting the best model using the Akaike information criterion (AIC). Distance-based Cluster analyses, graphical display of fungal and plant Chao-Jaccard similarities between adjacent sites along the gradient, and maximum likelihood (ML) with bootstrap analysis were used to determine the number of distinct communities, followed by visual comparisons to determine if there was concordance between plant and fungal community boundaries. These latter methods are most familiar to mycologists as they are used in phylogenetic analyses of molecular data. Regression tree analysis was used instead of discriminant function analysis to determine which environmental variables were predictive for species richness of all macromycetes and specific fungal functional groups (ectomycorrhizal, xylophagous) as it is not dependant on normally distributed data or linearity of relationships between all pairs of variables.

The specific hypotheses tested with these data were that (1) species richness and diversity of macromycetes is higher in the middle of the altitudinal gradient, (2) species richness correlates with environmental changes along the altitudinal gradient, (3) species richness and diversity of ectomycorrhizal (ECM) and xylophagous fungi are distributed differently along the altitudinal gradient because they are influenced by different environmental factors, and (4) species composition of macromycetes differs among vegetation types more than among sites within the same vegetation type.

## Methods

### Study area

The study area is located in central Veracruz, Mexico, where the altitude changes from 0 to 4,282 m in less than 100 km. In this area, eight study sites were selected at ca. 100, 500, 1,000, 1,500, 2,000, 2,500, 3,000, and 3,500 m altitude corresponding to seasonally dry tropical forest (TDF, sites 1 and 2), an ecotone dry forest-tropical montane cloud forest (site 3), tropical montane cloud forest (TMCF, sites 4 and 5), an ecotone TMCF-conifer forest (site 6), and conifer forest (CF, sites 7 and 8) (Table S1).

In the TDF sites (1 and 2), mean annual precipitation is 878 and 892 mm, and mean annual temperature is 25.4 and 23°C, respectively. Considering as dominant those tree species with a density higher than 15% of all individuals recorded in each forest type, the

dominant tree species in TDF are *Bursera simaruba*, *Guazuma ulmifolia*, *Ipomoea wolcottiana*, *Luehea candida*, and *Tabebuia chrysantha*. The common macromycete genera are *Auricularia*, *Geastrum*, *Lentinus*, *Pleurotus*, *Polyporus*, *Psilocybe*, *Pycnoporus*, *Trametes*, *Volvariella*, and *Xylaria*. In the ecotone TDF-TMCF (site 3), mean annual precipitation is 1,421 mm, and average annual temperature is 20°C. The dominant tree species is *Quercus sapotifolia*. Common macromycete genera are *Amanita*, *Boletus*, *Lactarius*, *Lentinus*, *Polyporus*, *Pycnoporus*, and *Trametes*. In TMCF sites (4 and 5), mean annual precipitation is 1,685 and 3,000 mm, and mean annual temperature is 17.7 and 14.1°C, respectively. The dominant tree species are *Carpinus tropicalis*, *Cinnamomum effusum*, *Liquidambar styraciflua*, *Oreopanax xalapensis*, *Quercus* spp., and *Turpina insignis*. Common macrofungus genera are *Agaricus*, *Amanita*, *Gymnopus*, *Gymnopilus*, *Hypoxylon*, *Inocybe*, *Lactarius*, *Marasmius*, *Psathyrella*, *Psilocybe*, *Trametes*, and *Xylaria*. In the ecotone TMCF-CF (site 6), mean annual precipitation is 1,678 mm, and mean temperature is 11.1°C. The dominant tree species are *Pinus patula* and *Quercus* spp. Dominant macromycete genera are *Amanita*, *Clitocybe*, *Helvella*, *Hygrophoropsis*, *Lactarius*, and *Tricholoma*. In CF sites (7 and 8), mean annual precipitation is 860 and 456 mm, and mean annual temperature is 8 and 11.8°C, respectively. Dominant genera in CF are *Pinus* and *Abies*. The common genera of macromycetes in CF are *Amanita*, *Boletopsis*, *Boletus*, *Clitocybe*, *Hygrophorus*, *Lycoperdon*, *Morchella*, and *Russula*. The most common taxa of macromycetes and tree species were documented in the Herbarium XAL database and Guzmán et al. (2003).

### Vegetation sampling

In each site, 10 permanent 10 × 10 m plots were established arbitrarily without pre-conceived bias. Plots were located at least 10 m apart from each other, and at least 30 m from the forest edge. In each plot, trees with diameter at breast height (1.3 m above ground) ≥ 5 cm were counted and identified as part of a parallel study carried out in the same study sites. Vegetation structure for each site was described as density (trees ha<sup>-1</sup>), basal area (m<sup>2</sup> ha<sup>-1</sup>), and mean and maximum height of canopy trees (m).

### Macromycete sampling

This study was carried out during a single year's sampling season. Each study site was sampled monthly between May and October 2010 since most macromycete sporome production is restricted to the rainy part of the year. Every month the sporomes of macromycetes growing within each of the ten 10 × 10 m plots were counted and collected. Macromycetes with a caespitose growth form, two or more sporomes belonging to the same species growing <50 cm apart or in fairy rings were recorded as one individual. Fruit bodies were collected and each specimen was macromorphologically described when fresh and then dried for 24 h. Specimens were mostly identified to species by their micro- and macromorphological characters (see Gómez-Hernández and Williams-Linera 2011 for details). As the use of genera and families as surrogate of species to determine species richness, rarity, and composition gives reliable results at local scale (Balmford et al. 2000; Bertrand et al. 2006; Mandelík et al. 2007), we classified as numbered morpho-species a few unidentified taxa using a higher-taxonomic level approach. Fungal communities were analysed as all macromycetes together, and separated into the functional groups of ECM and xylophagous species. Specimens are deposited at the Herbarium XAL of the Institute of Ecology, Mexico.

## Macromycete richness and diversity

Richness was determined as the total number of species observed (Sobs) in each study site. Species richness was compared among the eight study sites using rarefaction curves with the Mao Tau function, reducing the samples to a common number of individuals. Diversity was calculated using the Shannon diversity index (Magurran 2004).

Tree and macrofungal species composition similarity among study sites was estimated using Chao's Jaccard abundance-based index in the program EstimateS (Colwell 2006), where 0 indicates complete dissimilarity and 1 means identical species composition assemblages between two sites.

## Microenvironmental explanatory variables

The explanatory variables recorded one time at each plot in each study site were geographical coordinates, altitude, slope, aspect, percentage of canopy openness (see details of site measurements in Gómez-Hernández and Williams-Linera 2011). Additionally, we measured litter depth, soil cover, presence of dead wood and decay level, surface unevenness, and wind exposure of the plots. Litter depth was measured with a ruler at the beginning, middle, and the end of the sampling season at the center of every plot, and percentage cover was estimated for wood, immovable rocks (rockiness), moss, exposed soil, and loose gravel (stoniness) on the soil surface. Wood decay stage of logs >5 cm diameter was classified by criteria in Table S2a. The surface unevenness was classified as flat, concave and convex (Table S2b). Wind exposure was classified according to forest openness and understory density (Table S2c).

Microclimate variables were measured monthly at a permanent point (between 1,100 and 1,200 h) in each plot in the same date that the macromycetes were sampled. Microclimate variables were air temperature, air relative humidity, soil temperature, and soil water content following the same procedures as in Gómez-Hernández and Williams-Linera (2011).

## Statistical analyses

The relationship between all macrofungal species, ECM and xylophagous richness and the explanatory variables was determined using the Spearman's rho correlation coefficient (JMP, version 3.2.2, SAS 1997).

Regression tree analysis was used to explain variation of macrofungal species richness related to microclimate and microenvironmental variables. Response variables were all macromycete, ECM and xylophagous species richness. Explanatory variables used in the models were slope, aspect, air and soil temperatures, relative humidity, soil water content, tree species richness, canopy openness, vegetation structural variables (basal area, density and mean and maximum height of overstorey trees >5 cm dbh), litter depth, surface unevenness, and cover of soil, rock, stone, moss and dead wood and its decay level. We generated 1,000 regression tree models based on random sub-samples of the database, and then reconstructed the most parsimonious tree.

We used CCA to facilitate the interpretation of the macromycete species distribution with regard to a set of explanatory variables, with the program CANOCO, version 4.5 (ter Braak and Smilauer 1998). CCA was conducted on macromycete abundance for all species, ECM species and xylophagous species on a set of microenvironmental variables (same as in regression tree analysis). We used forward selection for ranking explanatory

variables in importance, and their statistical significance was tested using a Monte Carlo permutation test (ter Braak and Smilauer 1998).

Patterns of species richness and diversity along the elevation gradient were analyzed by fitting linear and polynomial regressions and selecting the best model using the AIC. The altitudinal patterns were explored for all macromycetes and functional groups separately. Model selection was conducted using nonlinear fittings in R project software version 2.6.2 with the package “gmodels” (R Development Core Team (R 2008)).

Analyses based on sporome production of macromycetes are plagued by ‘noisy data’ (McCune and Grace 2002) from false negatives (absences from sites owing to unfavorable conditions for fruiting). Methods for selecting the most ‘reliable’ species (those most likely to be represented by sporomes, if present) for analysis were evaluated as follows. Patterns of occurrence for species in the cloud forest plots in this study (sites 3–5) were used to back-cast occurrence in another cloud forest plot (site 2 in Gómez-Hernández and Williams-Linera 2011) that was sampled during a period of higher sporome abundance. Criteria for selecting reliable species were coherence (appearance in adjacent sites; Leibold and Mikkelsen 2002), maximum frequency of occurrence among plots within sites, and maximum frequency of fruiting mycelia summed across plots within sites. For maximum frequency of occurrence among plots within sites, species were grouped into the following four classes according to the maximum number of plots in which the species was recorded among the three cloud forest sites: present in five of 10 plots, present in three or four plots (mean 3.5), present in two plots, or present in one plot. The plot frequency was regressed against the percentage of species in each class that occurred in the back-cast site. For maximum number of fruiting mycelia per site, species were grouped into three frequency classes: 4 or 5 fruiting mycelia (mean 4.5), 2 or 3 fruiting mycelia (mean 2.5) or 1 fruiting mycelium. The mean maximum frequency of fruiting mycelia was regressed against the percentage of species that occurred in the back-cast site in each of the frequency classes.

Cluster analyses were carried out to identify types of vegetation and ecotones according to fungal and tree species composition. Based on the back-casting described above to select reliable species, cluster analyses were carried out for all macromycete and tree species matrices represented by three or more individuals among the eight study sites. Distance was determined with Sørensen (Bray-Curtis) and linkage with Ward’s Method (PC-ORD for Windows, McCune and Mefford 1999). ML analysis was performed on the same data set using R (2008), with 1,000 Monte Carlo replications in order to obtain bootstrap probabilities for each node.

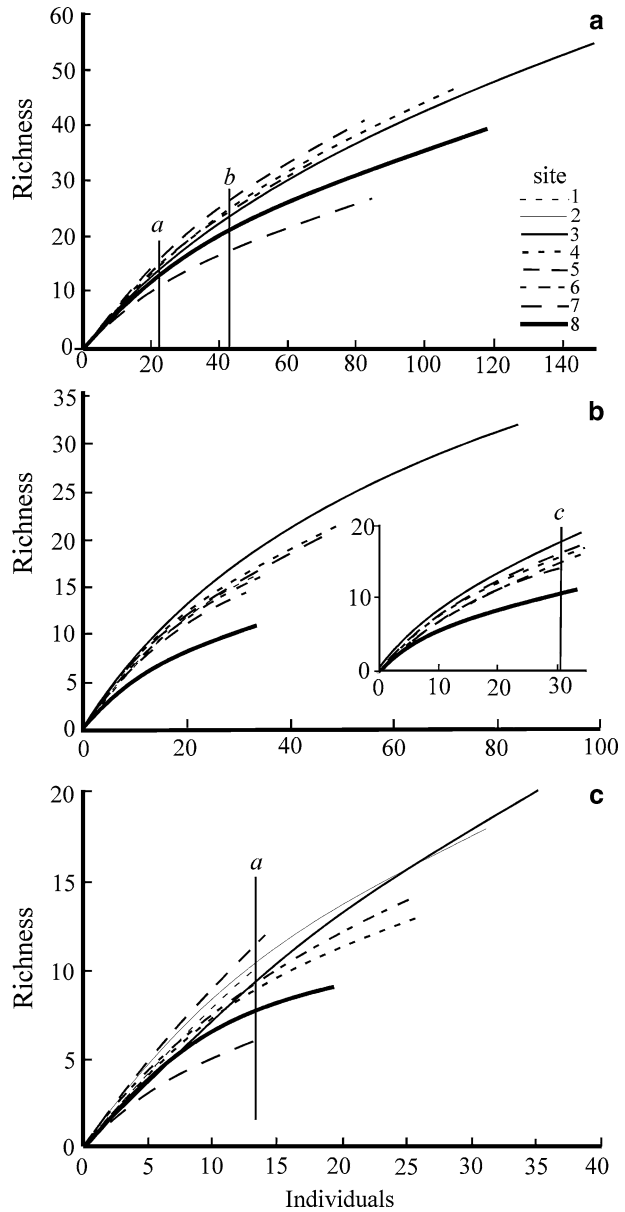
## Results

### Richness and diversity patterns along the gradient

Along the elevation gradient, 672 individuals of 213 species of macromycetes were recorded during the growing season of 2010 at the eight study sites. Number of individuals and species varied in each study site (Table S1).

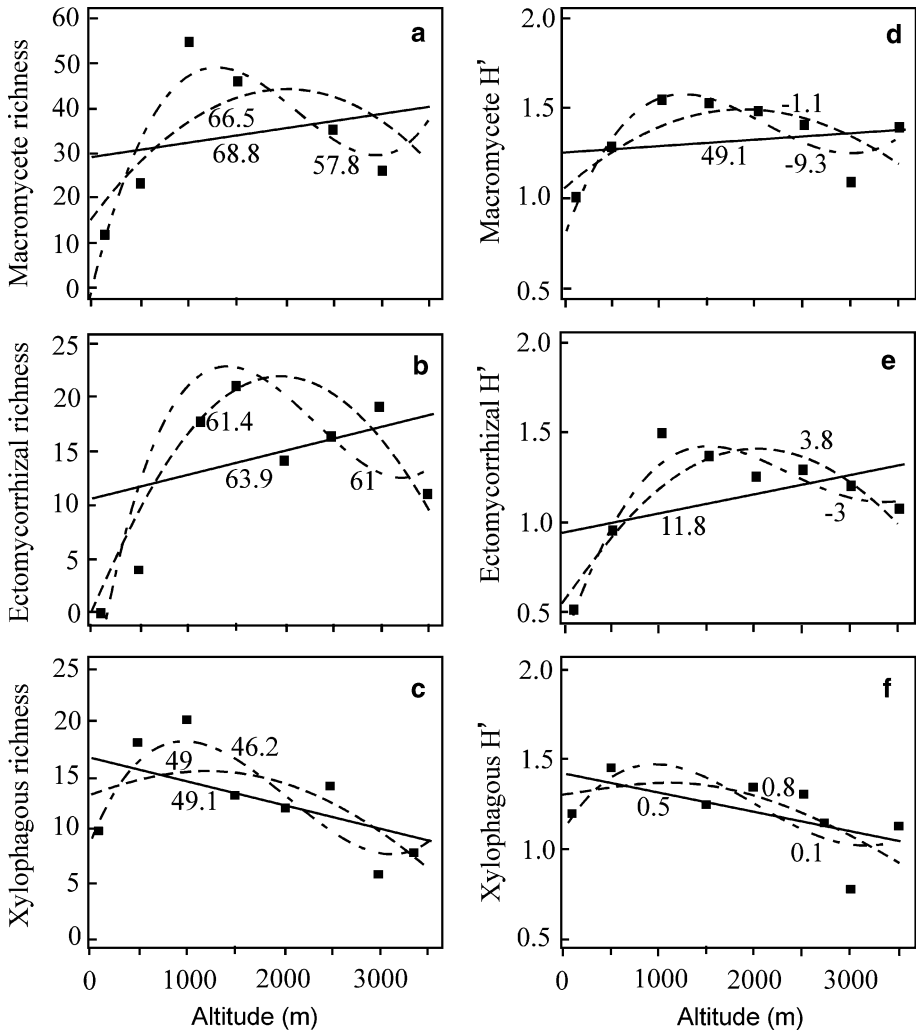
The species rarefaction curves for all macromycetes showed that the highest richness occurred in sites located between 1,500 and 2,500 m elevation; the same trend was found when site 1, with very few species, was excluded, indicating that the lowest richness occurred in the highest elevation sites (Fig. 1a). Rarefaction curves for ECM species showed that the lowest richness occurred in low elevation TDF. Even when site 2 was excluded, rarefaction curves indicated the higher richness between 1,000 and 3,000 m

**Fig. 1** Rarefaction species accumulation curves (function Mao Tau) for individuals of **a** all macromycetes, **b** ectomycorrhizal, and **c** xylophagous species recorded at eight sites on the elevation gradient of central Veracruz, Mexico. Note that *vertical line a* indicates species richness for the common number of individuals including site 1, *b* indicates species richness excluding site 1, and *c* indicates species richness excluding sites 1 and 2



elevation, the highest elevation site displayed the lowest richness in ECM species (Fig. 1b), and site 1 did not have ECM species. Rarefaction curves for xylophagous species indicated the highest richness in both TDF sites and one TMCF (sites 1, 2 and 5), and the lowest xylophagous rarified richness in the highest elevation sites (Fig. 1c).

Along the elevation gradient, we observed similar patterns of richness and Shannon diversity index distribution for macromycete species and functional groups when linear and polynomial models were fitted (Fig. 2). Richness and diversity for the overall fungal



**Fig. 2** Models fitted to macromycete species richness (a–c) and Shannon diversity index (d–f) along the elevation gradient in central Veracruz, Mexico. **a, d** All macromycetes, **b, e** ectomycorrhizal, and **c, f** xylophagous species. Numbers are the AIC for each model fitted in each case, where the first degree model is a solid line, second degree polynomial is a dashed line, and third degree polynomial is a dot-dash line (see Table 3)

community and ECM community showed a tendency to increase with elevation, but many species in all groups tended to display a peak in the mid-part of the altitudinal gradient, mainly within the cloud forest region. In contrast, the two metrics of diversity showed peaks in the lower part of the gradient and decreased with elevation for the xylophagous community. The best fitted model indicates the highest richness and diversity at 1,000 m for all species and xylophagous, but ECM showed a richness peak at 2,000 m and a diversity peak at 1,500 m (Fig. 2; Table 1).

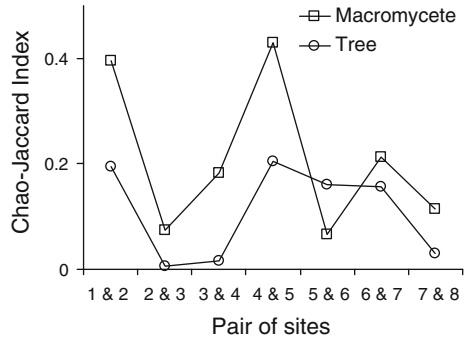


**Table 1** Models used to describe changes in macromycete species richness (S) and diversity (H') along the elevation gradient in central Veracruz, Mexico, for all macromycete (ALL), ectomycorrhizal (ECM) and xylophagous (XY) species, and AIC values

Models	ALL			ECM			XY				
	H'			H'			S				
	AIC	AIC	AIC	AIC	AIC	AIC	AIC	AIC	AIC		
$y = a + bx$	68.8	11.0	1.9	11.2	63.9	2.9	11.8	14.8	49.1	2.9	0.5
$y = a + bx + cx^2$	66.5	8.7	-1.1	8.2	61.4	0.4	3.8	6.8	49	2.8	0.7
$y = a + bx + cx + dx^3$	57.8	0	-9.3	0	61	0	-3	0	46.2	0	0.1

AIC = 0 for best model; when AIC less than 2, we chose the simplest possible model (Burnham and Anderson 2002)

**Fig. 3** Chao-Jaccard index for macromycete and tree species comparisons between adjacent sites along the elevation gradient in central Veracruz, Mexico



### Altitudinal turnover or beta diversity

Chao-Jaccard index varied between 0 and 0.43 for macromycetes and between 0 and 0.20 for tree species assemblages (Fig. 3). Beta diversity showed a high turnover in species composition among study sites located along the altitudinal gradient, and indicated four distinct macromycete communities. The four distinct macromycete communities based on the similarity index, cluster and ML analyses comprised sites 1 and 2 located in TDF (0.40), sites 3–5 located in ecotone TDF-TMCF and TMCF (0.18–0.43), sites 6 and 7 located in ecotone TMCF-CF and CF (0.21), and site 8 in CF. The sharpest breaks between fungal communities, as indicated by similarities below 0.1, were between TDF and TMCF (sites 2 and 3), and between TMCF and CF (sites 5 and 6), while the similarity between the two CF sites was also low (0.11).

### Richness and explanatory variables

Correlations between all macromycete and ECM richness and explanatory variables suggested that along the gradient fungal richness increased with air relative humidity, soil water content, % cover by moss, and southern slope aspect (Table 2). Also the total macromycete group was positively correlated with density of trees, but ECM richness was negatively correlated with tree richness. Moreover, ECM were positively correlated with air relative humidity, soil water content, litter depth and moss, and negatively correlated with canopy openness, air and soil temperature, rockiness, stoniness and soil coverage (Table 2). Xylophagous richness was significantly and positively correlated to slope, and density and richness of tree species (Table 2). Correlations among explanatory variables are shown in Table S3.

A different approach was the use of regression trees (Fig. 4). In the regression tree model for all macrofungi (accounted deviance, 66%) a soil water content threshold of 17.4% separated the two most distinct groups (Fig. 4a). A mean of 1.3 species of macrofungi per plot was found when soil water content fell below 17.4% versus 7.3 species when soil water content exceeded 17.4%. This environmental threshold is strongly tied to SDTF as 20 out of 21 plots with soil water content below 17.4% belong to this biome and the additional site was in the SDTF-MTCF ecotone. Similarly, plots with soil water content above 17.4% and soil temperature above 16.5°C, had on average 10.5 fungal species and all nine plots belong to site 3 (ecotone SDTF-MTCF), whereas plots with cooler soils had

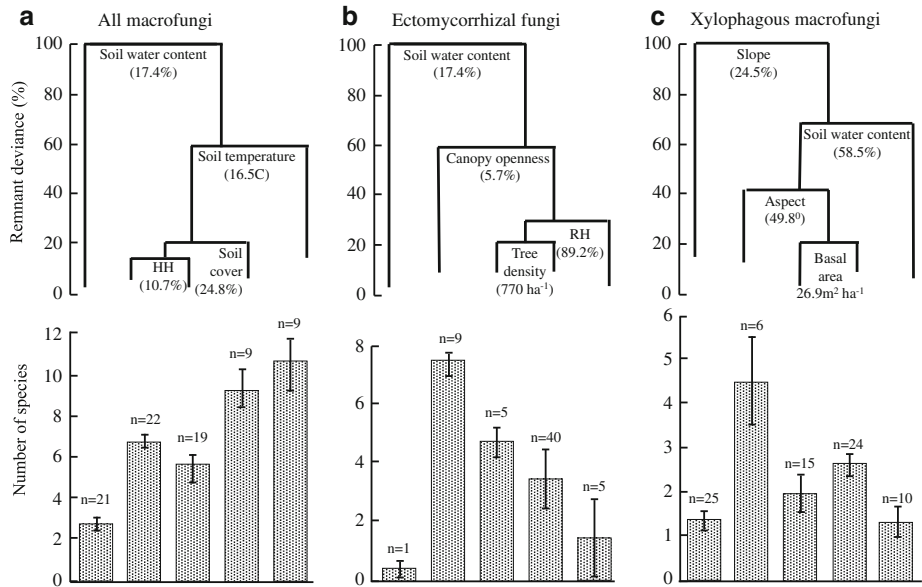
**Table 2** Correlation between macromycete (ALL), ectomycorrhizal (ECM) and xylophagous (XY) species richness, and the explanatory variables that were significant for at least one of the functional groups of macromycetes along the elevation gradient in central Veracruz, Mexico

Variable	ALL	ECM	XY
Slope	0.24*	0.03	0.33**
Aspect	0.26*	0.39***	-0.11
T air	-0.42***	-0.34**	0.05
RH	0.37**	0.22*	0.12
T soil	-0.41***	-0.33**	0.04
Soil water	0.38***	0.40***	-0.10
Tree density	0.28*	0.04	0.31**
Tree richness	-0.17	-0.28*	0.23*
Canopy openness	-0.58***	-0.61***	-0.00
Litter depth	0.21	0.28*	0.03
Moss cover	0.55***	0.46***	0.01
Rockiness	-0.25*	-0.33**	0.05
Stoniness	-0.16	-0.25*	0.14
Soil cover	-0.12	-0.30**	0.17
Soil surface	-0.25*	-0.29*	-0.06
Wind exposure	0.36***	0.05	0.05

*T air* Air temperature, *RH* air relative humidity, *T soil* soil temperature, *Soil water* soil water content. Values are Spearman's correlation coefficients

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

on average 6.7 species (Sites 4–8). Mean fungal species richness in plots was nine versus 6.2 with soil cover above versus below the 24.8% threshold, but 6.8 species if relative humidity was below 10.7% versus 5.4 species above this relative humidity threshold. The regression tree model for ectomycorrhizal fungi (accounted deviance, 71%) also showed a soil water content threshold of 17.4% that separated the two most distinct groups of plots (Fig. 4b). The mean number of species per plot was only 0.33 below this soil moisture threshold versus four per plot above the threshold. Also, when soil water content was above 17.4 and canopy openness was less than 5.7%, plots had over seven species on average; the nine plots in this branch of the tree belong to the SDTF-TMCF ecotone. In plots with canopy cover above 5.7% and relative humidity above 89.2% there was on average 1.4 species per plot, whereas plots with relative humidity below 89.2% had on average 3.5 species per plot, increasing to 4.5 species in plots with relatively low tree density. In the regression tree model for xylophagous fungi (accounted deviance, 40%), slope of the terrain was the main factor separating plots with contrasting species richness (Fig. 4c). Plots with mild slopes (<24.5%) had on average 1.3 species whereas those in steep slopes had on average 2.4 species. Also plots on steep slopes with soil water content above 58.5% had on average only 1.3 species; the 10 plots in this branch of the tree belong to the TMCF (site-5). Aspect was an important factor in plots with soil water content below 58%. Mean number of xylophagous species per plot was 4.5 in plots facing SE (sites 2 and 3) versus 2.3 in plots facing S-SW. In SW facing plots, species richness was 2.6 when basal area exceeded  $26.9 \text{ m}^2 \text{ ha}^{-1}$  versus 1.9 in plots with lower basal area.



**Fig. 4** Consensus Regression tree for macrofungal species richness along an elevation gradient in central Veracruz, Mexico: **a** all macrofungi, **b** ectomycorrhizal, and **c** xylophagous species. Trees show at each partition the explanatory variable and threshold at which the partition was made. In all cases plots on the left branches fall below the partition threshold while those in right branches exceed the *threshold*. Bar plots show mean and standard error of species richness for all plots included in each terminal branch

#### Direct gradient ordination analysis

The CCA was carried out for eight sites and abundance of all macrofungi (118 species), ECM (52 species) and xylophagous (46 species) with 18 explanatory variables in each case. All the CCA models retained only three explanatory variables (canopy openness, soil water content, litter depth) but other variables contributed to explaining ordinations in each group (Table S4; Fig. 5).

For all macrofungi, axis 1 (eigenvalue = 0.89) and axis 2 (eigenvalue = 0.81) described 12.3 and 11.2% of the species-environment relationship (Monte Carlo test, first axis,  $F = 2.24$ ,  $P = 0.02$ ; all canonical axes,  $F = 1.41$ ,  $P = 0.005$ ). CCA results showed that sites 1 and 2 were clearly separated from sites 3–5, and both groups were separated from the other sites along the first canonical axis. Some macrofungal species showed a strong association with specific type of vegetation along the altitudinal gradient (Fig. 5a).

CCA for ECM retained the explanatory variables: canopy openness, litter depth, moss cover, maximum and mean tree height, air humidity, soil water content, and air temperature (Table S4). Axis 1 (eigenvalue = 0.88) and axis 2 (eigenvalue = 0.76) accounted for 15.1 and 13% of the accumulated variance, respectively (Monte Carlo test of first axis,  $F = 2.83$ ,  $P = 0.005$ ; test of all canonical axes,  $F = 1.68$ ,  $P = 0.005$ ). Sites at lower altitude were not clearly separated in the CCA, although they seem related to air temperature and relative humidity. Sites 6–8 are clearly separated from the other sites. Some ECM species were strongly associated with specific vegetation types along the altitudinal gradient, but there were no ECM species associated with TDF (Fig. 5b).

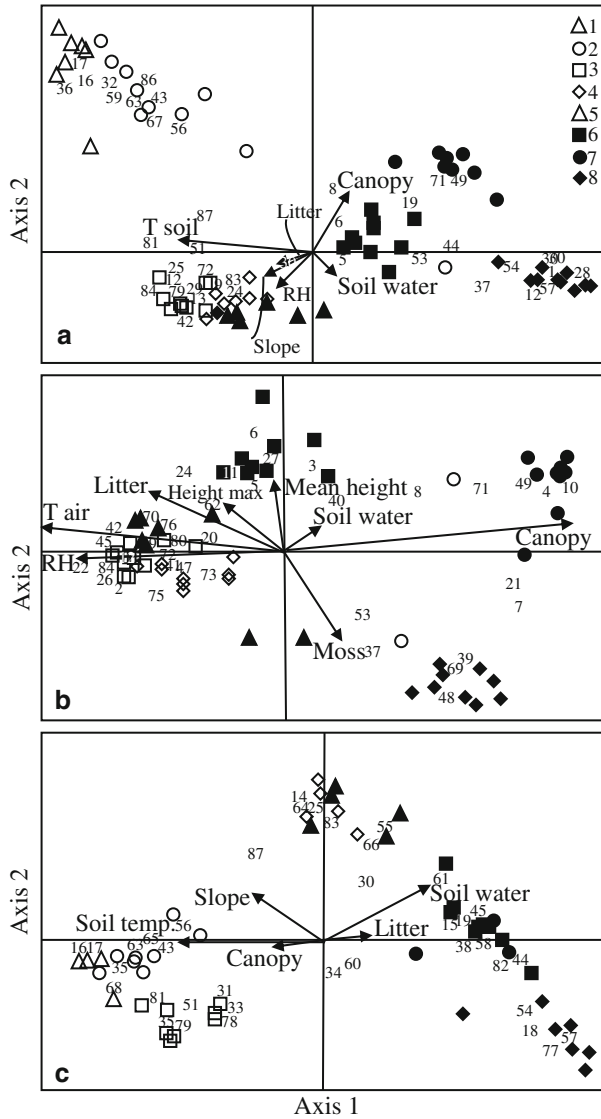
For xylophagous species the CCA retained the explanatory variables: slope, canopy openness, litter depth, soil temperature and soil water content (Table S4; Fig. 5c). Axis 1 (eigenvalue = 0.93) and axis 2 (eigenvalue = 0.86) accounted for 12.7 and 11.7% of the accumulated variance, respectively (Monte Carlo test of first axis,  $F = 2.02$ ,  $P = 0.005$ ; test of all canonical axes,  $F = 1.29$ ,  $P = 0.005$ ). The ordination separated upper altitude from lower altitude located sites. Xylophagous fungal distribution in the lowest altitude sites was related to soil temperature, slope, and canopy openness; the upper elevation sites were related to soil water content and litter depth. Several xylophagous species were strongly associated with lower and upper elevation (Fig. 5c).

#### Removal of unreliable fungal species for analysis of boundary clumping

Tests to determine the best criteria for selecting species with fewer false-negative occurrences showed that high abundance in sites from the same forest type was a good indicator of species occurrence when frequencies were used to back-cast species presence in a site that was sampled in a previous study (i.e. Gómez-Hernández and Williams-Linera 2011, site 2). Back-casting based on coherence gave very poor results and was rejected. Back-casting based on the maximum frequency of a given species' occurrence among plots within sites gave percentages of 50% for five or more plots, 47% for 2–3 plots, 7% for two plots and 11% for one plot. A perfect linear relationship was found in back-casts using the maximum frequency of fruiting mycelia observations per site: 61% for four or more observations per site, 38% for 2–3 observations per site, and 19% for one observation per site. The species listed for sites 3–5 in Table 3 were the most frequently recorded in a back-cast of species composition in a site from a previous study that was located between sites 3 and 4, so low frequency was taken as an indicator of unreliability and used to remove species likely to have false absences (species present but not observed fruiting). Coherence was not indicative of reliability in back-casts so species with semi-incoherent distributions (i.e. with gaps in their distribution along the elevation gradient) were retained.

The resulting set of species was ordered in Table 3 according to their distributions. There appeared to be a higher frequency of clumping of upper and lower boundaries of distributions than would be expected by chance. The most frequent distribution boundaries corresponded to those determined using Chao-Jaccard similarities between sites (Fig. 4) and the cluster analysis (Fig. 6d), but differed slightly from the ML analysis in grouping site 3 with sites 4 and 5 (Fig. 6b).

Cluster analyses were carried out separately for 72 species of trees and 107 species of macromycetes (Fig. 6). Only macromycete species for which there were three or more observations at a given site were included. In the case of tree species, TDF (sites 1 and 2), TMCF and TMCF-CF (sites 4–6), and CF sites (7 and 8) formed separate clusters, but ecotone TDF-TMCF (site 3) was loosely clustered with sites 7 and 8 (Fig. 6c). When macromycete species were analyzed, the cluster showed four types of communities along the elevation gradient. Sites 1 and 2 (TDFs) are clustered as well as sites 3 (ecotone TDF-TMCF) with 4 and 5 (TMCFs), sites 6 and 7 (ecotone TMCF-CF and CF) were clustered, and site 8 (CF) was apart from the other sites (Fig. 6d). ML analysis was used with Monte Carlo simulations to obtain bootstrap probabilities. Both for trees and macromycetes, there was a 100% probability that sites 1 and 2 were related, site 3 was unrelated to other sites, sites 4 and 5 were related, and sites 7 and 8 were related (Fig. 6a, b). The ML analysis for trees and macromycetes differed in that site 6 was related to sites 4 and 5 for trees, but to site 7 for fungi (100% probability).



### Discussion

#### Richness and diversity patterns along the gradient

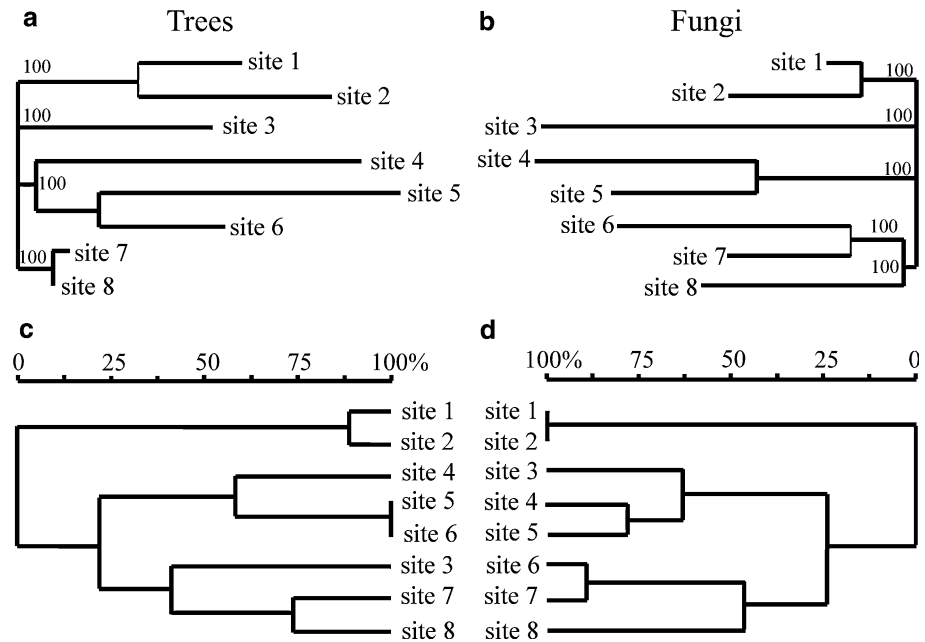
Although fungal diversity is thought to be greater in the tropics than at higher latitudes, temperate mycotas are better known (Lodge et al. 1995), so the discussion in this work strongly rests in a comparison with data from studies made in temperate regions. It may not be appropriate to assume that the fungal diversity or species richness recorded in a tropical region corresponds to that from a temperate region. However, when determining the environmental variables related in the diversity and distribution of ECM and xylophagous

**Fig. 5** Triplots of CCA for **a** all macromycetes, **b** ectomycorrhizal, and **c** xylophagous species in eight sites located along an elevation gradient in central Veracruz, Mexico. Symbols are sites, vectors are significant environmental explanatory variables, and numbers are species with higher weights in the ordinations; 1 *Agaricales* 4, 2 *Amanita* aff. *tecomate*; 3 *Amanita caesarea* complex 1, 4 *Amanita caesarea* complex 2, 5 *Amanita flavoconia*, 6 *Amanita gemmata*, 7 *Amanita muscaria*, 8 *Amanita rubescens*, 9 *Amanita* sp. 1, 10 *Amanita* sp. 4, 11 *Amanita* sp. 5, 12 *Amanita* *vaginata*, 13 *Amanita virosa*, 14 *Annulohyphoxylon thouarsianum* *thouarsianum*, 15 *Auricularia* aff. *delicata*, 16 *Auricularia auricula-judae*, 17 *Auricularia polytricha*, 18 *Auricularia* sp. 1, 19 *Baeospora* aff. *myosura*, 20 *Boletochaete* aff. *bicolor*, 21 *Boletus edulis*, 22 *Boletus* sp. 1, 23 *Boletus* sp. 2, 24 *Calostoma cinnabarinum*, 25 *Cantharellus cibarius*-like, 26 *Cantharellus cinnabarinus*, 27 *Clavulina cinerea*, 28 *Clitocybe* sp. 1, 29 *Coltricia montagnei*, 30 *Coltricia perennis*, 31 *Corylidia* sp. 1, 32 *Cyathus striatus*, 33 *Cyptotrama chrysopeplum*, 34 *Fomitopsis pinicola*, 35 *Ganoderma lucidum*, 36 *Geastrum* sp. 1, 37 *Gomphus floccosus*, 38 *Gymnopilus* sp. 1, 39 *Hebeloma fastibile*, 40 *Helvella macropus*, 41 *Hydnum* aff. *repandum*, 42 *Hydnum repandum*, 43 *Hygrophoropsis aurantiaca*, 44 *Hypholoma fasciculare*, 45 *Hypholoma subviride*, 46 *Lactarius* sp. 1, 47 *Lactarius* sp. 3, 48 *Lactarius* sp. 5, 49 *Lactarius tabidus*, 50 *Lentinula boryana*, 51 *Lentinus crinitus*, 52 *Leucoagaricus*? 1, 53 *Lycoperdon perlatum*, 54 *Marasmiellus* sp. 1, 55 *Mycena* aff. *pura*, 56 *Mycena chlorinosma*, 57 *Mycena pura*, 58 *Oligoporus* sp.1, 59 *Oudemansiella canarii*, 60 *Phellinus robustus*, 61 *Pholiota spumosa*, 62 *Phylloporus leucomycellinus*, 63 *Pleurotus djamor*, 64 *Pluteus cervinus*, 65 *Polyporus occidentalis*, 66 *Polyporus* sp. 1, 67 *Polyporus tricholoma*, 68 *Pycnoporus sanguineus*, 69 *Ramaria botrytis*, 70 *Rutiboletia retipes*, 71 *Russula cyanoxantha*, 72 *Russula* aff. *emetica*, 73 *Russula mephitica*, 74 *Russula* aff. *mephitica*, 75 *Russula* aff. *mexicana*, 76 *Scleroderma nitidum*, 77 *Sowerbyella rhenana*, 78 *Stereum* aff. *gausapatum*, 79 *Stereum ostrea*, 80 *Strobilomyces floccopus*, 81 *Trametes villosa*, 82 *Trichaptum abietinum*, 83 *Trogia* aff. *buccinalis*, 84 *Xerocomus* sp. 1, 85 *Xeromphalina tenuipes*, 86 *Xylaria filiformis*, 87 *Xylaria hypoxylon*

**Table 3** Frequency of fruiting mycelia that were recorded at more than one site along the elevation gradient in central Veracruz, Mexico

Fungal species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
<i>Auricularia polytricha</i>	<b>5</b>	1	0	0	0	0	0	0
<i>Pleurotus djamor</i>	1	<b>4</b>	0	0	0	0	0	0
<i>Mycena chlorinosma</i>	<u>0</u>	<u>6</u>	0	1	0	0	0	0
<i>Lentinus crinitus</i>	0	1	<b>4</b>	0	0	0	0	0
<i>Trametes villosa</i>	0	1	<b>4</b>	0	0	0	0	0
<i>Amanita vaginata</i>	0	0	<b>17</b>	1	0	0	0	0
<i>Russula</i> aff. <i>emetica</i>	0	0	<b>8</b>	<b>11</b>	0	0	0	0
<i>Hydnum</i> aff. <i>repandum</i>	0	0	2	0	<b>4</b>	0	0	0
<i>Hydnum repandum</i>	0	0	<b>7</b>	0	<b>6</b>	0	0	0
<i>Amanita virosa</i>	0	0	<b>11</b>	<b>8</b>	0	1	0	0
<i>Calostoma cinnabarinum</i>	0	0	0	1	<b>7</b>	0	0	0
<i>Coltricia montagnei</i>	0	0	0	<b>8</b>	1	0	0	0
<i>Hygrocybe coccinea</i>	0	0	1	<b>4</b>	0	0	0	0
<i>Lentinula boryana</i>	0	0	0	<b>4</b>	1	0	0	0
<i>Russula mephitica</i>	0	0	<u>0</u>	<u>7</u>	<u>1</u>	0	0	0
<i>Amanita flavoconia</i>	0	0	0	1	1	<b>7</b>	0	0
<i>Baeospora</i> aff. <i>myosura</i>	0	0	0	0	0	<b>8</b>	<b>12</b>	0
<i>Russula cyanoxantha</i>	0	0	0	0	1	<b>5</b>	0	0
<i>Marasmiellus</i> sp. 1	0	0	0	0	0	1	0	<b>5</b>
<i>Hebeloma fastibile</i>	0	0	0	0	0	<u>0</u>	<u>1</u>	<b>19</b>

Maximum frequency of at least four per site (>4 in bold). Underlines demarcate distinct fungal communities as determined using Chao-Jaccard similarities between adjacent sites, cluster and maximum likelihood analyses. A moderate to high degree of clumping can be seen for both the lower and upper species distribution boundaries



**Fig. 6** Relationships among sites along the elevation gradient in central Veracruz, Mexico, using maximum likelihood with percent bootstrap support for nodes (*above*) and aluster (*below*) analyses for tree (**a**, **c**) and macromycete (**b**, **d**) species that were represented by 3 or more individuals

fungi, as in this work, comparison between results from tropical and temperate regions can be made as such groups' requirements are the same regardless of latitude. Furthermore, about half of the macromycete species we recorded in these two functional groups are also found in temperate forests.

Model selection supported the hypothesis of higher macromycete species richness and diversity in the middle of the elevation gradient. Recent ecological studies have used the AIC for selection of models (e.g. Brehm et al. 2007; Gilbert 2010; Queenborough et al. 2009), but it has only rarely been employed in studies of fungal ecology (e.g. Gilbert et al. 2007). The best model selected using AIC indicated that macromycete richness peaked in the middle of the altitudinal gradient within the TMCF. Peaks in richness at mid-elevation occur mainly when the complete gradient has been sampled as it results from the overlapping of species ranges (Colwell et al. 2004; Nogués-Bravo et al. 2008). Moreover, overlap increases when there is a high frequency of species with large ranges (Colwell et al. 2004). Macromycete species within the TMCF showed the largest distribution range size, coinciding with the richness peak. Middle elevation peaks in mammal and plant species have been observed to correspond with peaks in precipitation and humidity, and with transitions between lowland and montane zones (Nor 2001). In our study, site 3 (ecotone TDF-TMCF) displayed a peak in macromycete richness, but this did not correspond to peaks in soil moisture or air humidity, and soil and air temperature decreased monotonically with altitude.



### Altitudinal turnover or beta diversity

The graph of Chao-Jaccard similarity index comparisons between adjacent sites was consistent with cluster analysis and ML results, indicating four distinct fungal communities. This index is based on the probability that two randomly chosen individuals, one from each of two samples, both belong to species shared by both samples. The estimators for this index take into account the contribution to the true value of this probability made by species actually present at both sites, but not detected in one or both samples (Chao et al. 2005). Our results indicated strongest dissimilarity in macromycetes between areas separated by plant ecotones, even though complementarity in macromycete species composition was high between sites with the same vegetation type. Similarly, Ferris et al. (2000) confirmed the site and plot-specific nature of fungal communities in 12 stands of planted *P. sylvestris* and *Picea abies* across lowland England by calculation of Jaccard similarity coefficients, and found few species in common between the sites.

Analysis of boundary clumping indicated that macromycetes were distributed in four communities, consistent with results of Chao-Jaccard, Cluster, and ML analyses. Boundaries in species distribution ranges along environmental gradients are of interest to identify different communities and determine turnover of species assemblages. Species ranges can be summarized by an incidence matrix, which documents which sites are occupied by which species (Leibold and Mikkelsen 2002). In the present work, the best results were obtained using a matrix restricted to species with at least three fruiting mycelia observations in at least one of the sites. Based on back-casting, low abundance of sporomes was found to be the best criterion for eliminating species from the data matrix that were likely to have false absences. Similarly, Straatsma and Krisai-Greilhuber (2003) found that fruit body abundance was the best predictor of reliable sporome production across years in a seven-year study in Austria.

### Richness and explanatory variables

Spearman's correlation and regression trees indicated that environmental variation along the elevation gradient differentially affected the macrofungal functional groups. Although Spearman's rho coefficient has often been used to estimate strength and direction of association between variables in ecological studies (e.g. Leski et al. 2010; Willig et al. 2011), regression trees are being increasingly used for analysis of complex ecological data (De'Ath and Fabricius 2000). Regression trees are especially robust if hundreds of trees are generated using random subsets of the original data, and only those partitions and branches that are consistent over a large proportion of trees are used (Breiman 2001; Karp and Guevara 2011). Results from our regression trees suggested that different functional groups of macrofungi respond differentially to environment factors. Species richness of ECM and xylophagous fungi was high in plots with moderate soil water content. Further, richness of ECM correlated with canopy openness, relative humidity and tree density, while slope, aspect and tree basal area correlated with species richness of xylophagous macrofungi. These findings are in agreement with other studies suggesting one or more of these factors as strong correlates with diversity of ECM (Cavender-Bares et al. 2009; Ferris et al. 2000; Nantel and Neumann 1992) and xylophagous macrofungi (Bonet et al. 2004; Osono 2007; Rubino and McCarthy 2003). Neither Spearman's correlation nor regression trees showed a direct relation between abundance of dead wood and xylophagous fungal species richness as the latter was similar among the sites. In contrast, others have found that the number of saprotrophic fungal species on wood increases with deadwood volume and log surface area

(Ferris et al. 2000; Pouska et al. 2010; Rubino and McCarthy 2003). Furthermore, Heilmann-Clausen et al. (2005) found that dead wood represents multiple niches for fungi, and that tree species diversity is a main factor in structuring fungal communities. At least two likely explanations exist to explain this apparent incongruence among results. First, turnover rate of decomposing wood could be faster in warmer and more humid sites resulting in effective high availability of substrates for xylophagous species but not detectable in snapshot estimates of wood cover. Microclimatic factors have previously been found to affect available wood on the floor of temperate forests (Heilmann-Clausen 2001; Heilmann-Clausen and Christensen 2003). Studies in tropical areas have shown higher abundance of termites in dry versus wet forests and this functional group can greatly increase the rate of wood turnover (Torres and González 2005). Our study sites include both a temperature and humidity gradient that are inversely correlated. To determine the impact of the temperature gradient on the incongruence reported, it would be necessary to assess the turnover rate variation of decomposing wood along the gradient in relation to microclimate. A second explanation is that there are differences among sites in the quality of available wood for xylophagous fungi (e.g. wood of tropical versus boreal broad leaved trees versus conifers). These two explanations are not mutually exclusive, and these aspects deserve further investigation. In this work, xylophagous richness was related to tree species richness, density and basal area, and this may reflect host-specificity.

#### Direct gradient ordination analysis

CCA results clearly showed a strong segregation of functional groups among sites along the elevation gradient. CCA is one of the most commonly used methods to test hypotheses given a site by species matrix and data on an environmental factor that it is believed to explain the differences in species presence or abundance between sites (Schmit and Lodge 2005). This method has been broadly used for macrofungal ecological studies (e.g. Alfredsen and Høiland 2001; Henkel et al. 2002). Our CCA results suggested that macromycete species distribution along the elevation gradient is influenced by environmental factors according to the functional group to which they belong. For all macromycete and ECM assemblages a clear separation of sites was observed along the elevation gradient. However, for xylophagous assemblages, sites were split into two groups defining upper and lower altitude sites. Variables related to the separation of these sites (i.e. slope and canopy openness) are related to moisture and temperature of soil. In temperate communities, greater canopy cover was reported as providing shade, increasing soil moisture and water-holding capacity that influences macrofungal species richness (Ferris et al. 2000; Gabel and Gabel 2007). Additionally, ECM richness, sporome production patterns, and composition depend on both the abiotic and biotic environments and can shift with changes in soil moisture as well as host plants (Cavender-Bares et al. 2009; O'Dell et al. 1999). For xylophagous species distribution, CCA suggests that slope, canopy openness, litter depth, and soil moisture and temperature were the main correlates. Rubino and McCarthy (2003) related individual species distributions to various plot and log parameters, and CCA revealed that aspect, percent slope, and woody stem density influenced epixylic species distributions.

#### Macromycete and tree communities

Results of this study strongly indicated an orderly turnover of macrofungal communities and functional groups along the altitudinal gradient. Communities were clearly defined by

cluster and ML analyses, suggesting four macrofungal communities and four tree communities, but the plant and fungal communities were not completely concordant. Cluster analysis is one of the most common multivariate techniques used to identify groups of fungal communities (Schmit and Lodge 2005), whereas ML has rarely been used in macrofungal ecology. ML and Bayesian analyses, techniques commonly used for phylogenetics, are now increasingly used in ecological analyses (O'Hara et al. 2002). In this work, ML followed by bootstrap analysis clarified relationships among sampled sites and assemblages that define macrofungal communities. The ML analysis classified site 3 as unrelated to any of the other sites, either for fungi or trees. The real difference between vegetation and fungi is that for trees, sites 4–6 are related and sites 7 and 8 are related, whereas for fungi, sites 4 and 5 are related, sites 6 and 7 are related, and site 8 is related to a lesser extent to sites 6 and 7. These differences reflect fungal responses to dominant tree species, conifers versus broadleaved trees and ECM hosts. Sites 1 and 2 share two *Bursera* species (non-ECM). Several *Quercus* species (ECM) dominate sites 3–6, but site 3 does not share its dominant *Quercus* (*Q. sapotifolia*) with other sites. Sites 6 and 7 share a dominant ECM pine, *P. patula*, whereas Site 8 is monodominated by an ECM fir, *Abies religiosa*. Similarly, Gabel and Gabel (2007) compared sites with cluster analysis using data for only macrofungi, only plants and combinations of macrofungi and plants, and found that species assemblages of fungi did not vary consistently with species assemblages of plants.

## Conclusions

In conclusion, macrofungal communities can be analyzed using methods used in plant community ecology, and some more commonly used for molecular sequences. These methods include gradient analyses but also more recently developed statistical methods such as regression trees, ML and Bayesian analysis, and metacommunity analyses such as Boundary Clumping. Results from the different methods we used in this work were largely concordant, and showed that environmental variation along an elevation gradient in Veracruz differentially affected macromycete functional groups. Furthermore, the various methods distinguished four macromycete assemblages that were only partly concordant with the four plant communities.

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