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ORIGINAL PAPER

Distributional patterns of freshwater ascomycetes communities along an Andes to Amazon elevational gradient in Peru

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Abstract Freshwater ascomycetes are the predominant fungal colonizers of ligno-cellulosic substrates submerged in freshwater habitats. Although considered important decomposers and a food resource in freshwater food webs, little is known about the influence of environmental factors on their geographical distribution patterns, species richness and community structure. We undertook a study of the distribution of freshwater lignolytic ascomycetes in the Madre de Dios River basin in Peru along an elevational gradient from the headwater regions dominated by the Inambari and Araza Rivers to the lowlands of the Madre de Dios River. The gradient extended from 218 to 3870 m; collections were made at low (<300 m), medium (300–1000 m) and high (>1000 m) elevations. Three separate collecting trips were conducted during the dry seasons over 3 years. Samples of submerged woody debris were returned to the University of Illinois where they were incubated in moist chambers and examined for the presence of sexual and asexual reproductive

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structures, which were used for identification. GPS location, altitude, water temperature and pH were measured at the time of collection. A total of 2187 vouchered fungal collections representing 268 fungal taxa were collected. One hundred and fifty-nine taxa were collected at low elevations, 201 at middle elevations and 56 at high elevations. Only 33 of 268 taxa occurred at all three elevational ranges. Canonical analyses of principal coordinates and Sørensons Similarity Index of species based on presence/absence data revealed different structuring of freshwater fungal communities at low, middle, and high elevations, indicating a change in species composition along the Andes to Amazon elevation gradient. Mantel's tests demonstrated that beta diversity is strongly impacted by both elevation and pH as rapid taxonomic turnover was associated with both these factors. Of 140 species found in their sexual reproductive state, only ten occurred at all three elevational ranges. The most commonly occurring species was *Annulatascus velatisporus*, a species with a worldwide distribution. Of 128 taxa found in their asexual reproductive state, 23 occurred at all three elevational ranges. The most commonly collected species was *Candelabrum broccchiatum*, also a species with a worldwide distribution. Most of the taxa reported from Peru have been reported previously from Asian and/or Australian freshwater tropical habitats. One hundred and three species are new records for South America and 137 species are new records for Peru. About 80 species found in Peru have a pan-tropical distribution. Whether these distribution patterns exist due to vicariance or geodispersal remains to be determined. This study indicates that the composition of fungal communities in mountainous areas is influenced by elevation and has implications for the effects of global warming.

Keywords Aquatic · Distribution · Elevation · Fungi · Neotropics · Submerged wood

Introduction

Since early organismal collections were made in the Ecuadorian Andes by Humboldt and Bonpland (1805–1834), in the Chilean Andes by Charles Darwin (1839, 1859) and in Indonesia by Alfred Russel Wallace (Wallace 1869, 1876), distinctive species distribution patterns with respect to elevational gradients have been recognized. Cox and Moore (2010) and Lomolino et al. (2010) have summarized the history of early studies on elevational distributional patterns of selected plant and animal species. Since these initial observations, numerous studies have documented the elevational distribution patterns of many types of organisms, including amphibians, bats, birds, ferns, fish, insects, plants, and reptiles (McCain and Grytnes 2010). However, studies addressing the elevational distribution patterns of microorganisms, such as bacteria and fungi, are largely absent from the scientific literature (Bryant et al. 2008; Fierer et al. 2011; Gómez-Hernández et al. 2012). Some exceptions for fungi include studies of aquatic hyphomycetes (Raviraja et al. 1998), mycorrhizal, dark septate fungi and root-associated fungi (Schmidt et al. 2008; Gorzelak et al. 2012), terrestrial wood colonizing fungi (Meier et al. 2010), wood colonizing fungi in streams (Sridhar et al. 2010), bryophyte associated fungi (Davey et al. 2012), ectomycorrhizal fungi (Ryberg et al. 2011; Bahram et al. 2012), macromycetes (Gómez-Hernández et al. 2012), endophytic fungi (Unterseher et al. 2013), and soil fungal communities (Geml et al. 2014). Since temperature changes along elevational gradients of

sufficient magnitude, such studies could have predictive value with respect to the distribution of fungal species in light of global warming.

Freshwater ascomycetes are an ecological assemblage of fungi that occur on submerged or partially submerged wood substrates in freshwater habitats and include both sexual and asexual species (Shearer 1993, 2001). These fungi play a key role in the conversion of organic carbon to inorganic forms, which ultimately end up as carbon dioxide (Gulis et al. 2006; Krauss et al. 2011). As decomposers of recalcitrant forms of submerged allochthonous plant material containing cellulose and lignin (Bucher et al. 2004; Simonis et al. 2008), freshwater ascomycetes may be critical functional elements in the processes driving the carbon cycle—yet they have not been incorporated into such tropical freshwater studies to date. Most studies of tropical freshwater ascomycetes have been conducted in the Paleotropics and are largely taxonomic and/or distributional in nature (Ho et al. 2001; Tsui et al. 2001a, b; Cai et al. 2003; Luo et al. 2004; Vijaykrishna and Hyde 2006). Refer to Raja et al. (2009) and Shearer and Raja (2014) for an extensive listing of taxa and references.

With respect to the South American tropics, a few taxonomic studies have been reported for asexually reproducing ascomycetes growing on plant debris in Amazonian waters (Nilsson 1962), including in the São Paulo region of Brazil (Schoenlein-Crusius 2002; Schoenlein-Crusius and Grandi 2003), the semi-arid region of northeastern Brazil (Barbosa et al. 2008, 2013a, b; Fiuza and Gusmao 2013) and on foam in swift waters of Peru (Matsushima 1993). However, no comprehensive studies of fungal diversity and distribution along an elevational gradient have been conducted in Neotropical aquatic habitats. The need to investigate the key fungal players—freshwater ascomycetes—that actively decompose submerged plant debris in the Amazon Basin is pressing from a number of standpoints: species identities, biodiversity, distribution patterns, enzyme function, role in food webs, and response to environmental change and habitat destruction.

To contribute to the existing base of knowledge about the diversity and distribution of freshwater lignolytic ascomycetes in the Neotropics, we undertook a study to examine the identities, distribution and frequency of these fungi along an Andean-Amazonian elevational gradient in Peru, which currently completely lacks such studies. The major questions we intended to answer with this study pertained to diversity and distribution of freshwater fungal communities: (1) Are freshwater ascomycetes habitat specialists resulting in rapid species turnover at transitions between cloud forest and lower montane vegetation types and between páramo and cloud forest vegetation types and (2) How taxonomically similar are freshwater lignicolous ascomycetes in neotropical and paleotropical aquatic habitats?

Methods

Selection of study area

The geographical focus of this study was the tropical Andes, a biodiversity hotspot extending down into the Amazon lowlands (Myers et al. 2000, http://www.biodiversityhotspots.org/xp/Hotspots/andes/). We selected this region for several reasons: (1) the elevational gradient of the Andean mountains provides a variety of physiographic regions and aquatic habitats to study and test hypotheses about freshwater fungal diversity and distribution; (2) the high plant species diversity in this area provides high substrate diversity for aquatic decomposer fungi; (3) the overall high species diversity of other taxa

(Foster 1990; Brako and Zarucchi 1993; Foster et al. 1994; Terborgh and Andresen 1998; Pitman et al.1999; Young and Leon 2000; Pitman et al. 2001; Majestyk and Janovec 2004; Cornejo et al. 2006; Tobler et al. 2010; von May et al. 2010; Ignatov et al. 2011; Carvalho et al. 2012; Householder et al. 2012) portended high fungal species diversity; and (4) except for numerous collections of hyphomycetes from Peruvian floodplains (Matsushima 1993) and two aquatic hyphomycetes reported by Schoenlein-Crusius and Grandi (2003), the aquatic ascomycota of Peru has not been sampled in this region.

Study sites

This study was carried out in southeastern Peru at selected sites along an elevational gradient between 218 and 3870 m extending from the Madre de Dios River watershed in the Department of Madre de Dios up into the Andes Mountains in the Department of Cuzco (Fig. 1). The Madre de Dios River basin beginning with its headwater region in the Andean highlands ultimately drains into the Amazon River via the Madeira River Basin of southern Brazil. Collections were made in the lowlands of the Madre de Dios basin and one of its upland headwater regions dominated by the Inambari and Araza Rivers.

Fig. 1 Map of sampling locations

We conducted three collecting trips focused on three main areas along the elevational gradient during the following time periods: (1) 05/14/2010–06/05/2010; (2) 09/24/2010–10/10/2010; and (3) 04/02/11–04/20/2011 (Table 1, Supporting Information). We collected all samples during the dry season due to general safety and logistical restrictions.

The three main areas of sampling are characterized by a number of general vegetation types found along this specific Andes to Amazon elevational gradient. The lowland Amazonian collection sites are characterized by a tropical climate with a dry season from May to September and a rainy season from November to April, with a mean annual rainfall between 2500 and 3500 mm, a mean annual temperature of 24 °C, and a temperature range from about 10–38 °C. The area is dominated by continuous moist semi-deciduous lowland Amazonian forest with three major vegetation formations: (1) predominating terra firma forests on high terraces, (2) floodplain forests that are inundated seasonally in times of high precipitation, and (3) peat lands dominated by the palm *Mauritia flexuosa* (Arecaceae). Dominant tree families in terra firma and floodplain forest formations include the families Annonaceae, Fabaceae, Flacourtiaceae, Lauraceae, Lecythidaceae, Moraceae, Myristicaceae, Sapotaceae and others.

Hilly relief dissected by narrow to broad river valleys characterizes the middle elevation collection sites. The climate is very humid with more than 6000 mm of precipitation per year as recorded around the town of Quincemil in the District of Camanti, Department of Cuzco. The average temperature is 25 °C. In this region of high precipitation the vegetation is dominated by lower montane pluvial forest that represents a transition between the lowland Amazonian flora and upland montane forest. Dominant tree families include some of the same mentioned above for the lowland flora, as well as more montane families such as Clusiaceae, Melastomataceae, and Rubiaceae.

The high elevation collection sites are characterized by montane cloud forest around tree line, which transitions into high elevation pluvial puna and paramo vegetation dominated by grasslands on mountainous slopes and plateaus, and deep bofedal wetlands (high altitude peat-bog like habitat) and associated stream networks in the valleys. The average annual temperature in this high elevation zone ranges between 6 and 12 °C. The pluvial montane forest is located within a range of about 2700–3700 m elevation and is characterized by an average annual rainfall between 2000 and 4000 mm. Dominant tree families include the Clusiaceae, Cunoniaceae, Juglandaceae, Podocarpaceae, Melastomataceae and Theaceae, among others. These highland forests are also characterized by an abundance of bamboo species in the genus *Chusquea* (Poaceae), as well as a high abundance of epiphytes.

The grasslands and bofedal wetlands are found in mosaics along and above the tree line between 3500 and 4000 m elevation, an area characterized by an average annual rainfall between 800 and 1400 mm. Dominant plants include mostly herbs and shrubs of such families as the Asteraceae, Cyperaceae, and Poaceae, among others, as well as a number of Pteridophyte families.

Collecting methods

(1) Physical parameters, elevation, latitude and longitude were measured with a GPSMAP 60CS instrument (Garmin Ltd.). Water temperature and pH were measured with an HI 98129 Waterproof pH/Conductivity/TDS Tester (Hanna Instruments, Inc.). The type of aquatic habitat, size, stream bottom composition and surrounding vegetation was recorded.

(2) Submerged dead woody debris, a good substrate for freshwater ascomycetes (Shearer et al. 2004), was collected randomly from a variety of freshwater habitats that included rivers, streams, backwaters, swamps and a few seasonally inundated floodplain forests. Each collection comprised 30 approximately 20–30 cm long pieces of dead, submerged, woody debris gathered at each collection site and placed in sealable plastic bags. Collection bags were then placed in a larger plastic bag and transported to a holding facility in the study area. Efforts were made to select pieces of woody debris that appeared to have been submerged for a time period sufficient to enable colonization by aquatic fungi. This was accomplished by observing the degree of decortication, wood softness, and presence of other aquatic organisms. All collections were made during the dry season because collecting in streams in the rainy season is dangerous and most wood in the rivers at this time is newly introduced from the floodplain and colonized mainly by terrestrial rather than aquatic species.

(3) At the University of Illinois, wood samples were rinsed in sterile tap water and divided into sets of six twigs that were placed in sealable plastic refrigerator boxes containing two sheets of moistened paper towels. Each collection consisted of 30 pieces of sticks evenly divided between five boxes.

(4) Samples were incubated in plastic boxes at ambient room light (ca. 12 h/12 h light/dark) and temperature (ca. 25 °C) for 2 weeks, at which time they were examined with a dissecting microscope for the presence of reproductive structures used to identify the fungal species in question. Samples were examined again after 2 and 8 months. Incubation is required because the fruiting bodies needed for species identification are usually scoured off by flowing water and grazing by stream invertebrates and thus need to develop anew.

(5) Fungal reproductive structures were removed with sterile dissecting needles and placed on a microscope slide for examination and identification using the compound microscope. Digital images of fruiting structures on wood were taken with an Olympus SZX7 stereomicroscope (Olympus Optical Co. Ltd, Tokyo, Japan) fitted with a SPOT RT color camera using SPOT Advanced Software (Diagnostics instruments Inc., Sterling Hts., MI). Digital images of fungal reproductive structures mounted on microscope slides were taken with an Olympus BHS microscope (Olympus Optical Co. Ltd, Tokyo, Japan) equipped with brightfield, Nomarski and phase optics and a SPOT Insight 12 Mp color camera and SPOT Advanced Software.

(6) Slides of identified fungi were sealed according to the methods of Volkmann-Kohlmeyer and Kohlmeyer (1996) and deposited in duplicate in the ILL, USM, and MOL herbaria. All fungal taxa were vouchered with slides.

(7) Taxa were identified to species, when possible, and data about their presence/absence at each sampling site were recorded.

Statistical analyses

Multivariate statistical analysis of data was performed using Canonical Analysis of Principal Coordinates (CAP) (Anderson and Wills 2003). This software is freely available at the Ecological Society of America's Ecological Archives (E084-011-S1; http://esapubs.org/archive/ecol/E084/011/suppl-1.htm). A Canonical Discriminant Analysis was used to test the hypothesis that differences in freshwater ascomycetes occur among fungal

communities at different elevations along the Andes to Amazon elevational gradient in Peru. Based on the general vegetation zones described above, the elevational gradient was divided into low (L; <300 m), medium (M; 300–1000 m) and high (H; >1000 m) ranges (Table 1, Supporting Information).

We also conducted a separate CAP analysis with equal number of sites on a subset of the data where equal sampling effort was assumed (i.e. randomly selected 11 samples from each elevation range).

Species accumulation curves

Species accumulation curves were generated with EstimateS v. 9.0 (Colwell 2013; http://viceroy.eeb.uconn.edu/EstimateS) using 50 randomizations of sample order. Sørenson's index of similarity index (Sørenson 1948; Magurran 2004) was used to assess species similarities at low, medium and high elevations.

Mantel's test

We also wished to determine if sites that have large differences in elevation also have large differences in their fungal communities. That is, is beta diversity higher between pairs of sites that are far apart in elevation as compared to pairs with similar elevations? Our data also revealed an imperfect correlation between pH and elevation, which had the potential to confound our analysis. Thus, we decided to also examine the role of pH in beta diversity.

We determined the difference between fungal communities by calculating the Jaccard's distance based on presence-absence data between each pair of sites using the vegan package (Oksanen et al. 2015) for R 3.12 (R core team 2014). We then examined if the Jaccard's distance between pairs of sites is related to their differences in altitude and/or pH. Due to issues with independence, we cannot simply test for correlation between these distance measures. Instead we used Mantel's tests to determine the relationship between Jaccard's distance and differences in elevation and pH. The Mantel's test is a permutation test (Mantel 1967; Legendre and Legendre 1988) that compares the observed correlation between two observed distance matrices (e.g. Jaccard's distance and differences in altitude) to that obtained by randomly pairing the two distance measures. As we were concerned that correlation between a site's elevation and its pH could influence our analysis we also performed partial Mantel's tests (Smouse et al. 1986), which allowed us to test for both a relationship between the Jaccard's distance and elevation while controlling for the effect of pH, and for a relationship between Jaccard's distance and pH while controlling for elevation.

All Mantel and partial-Mantel tests were performed using the vegan package for R, utilizing Pearson correlations and 10,000 permutations.

Results

Study sites

The collection sites visited on each trip and their respective elevational, chemical, and physical data are presented in Table 1, Supporting Information. Unfortunately, high elevation samples were obtained only in the third sampling trip. Generally pH was similar

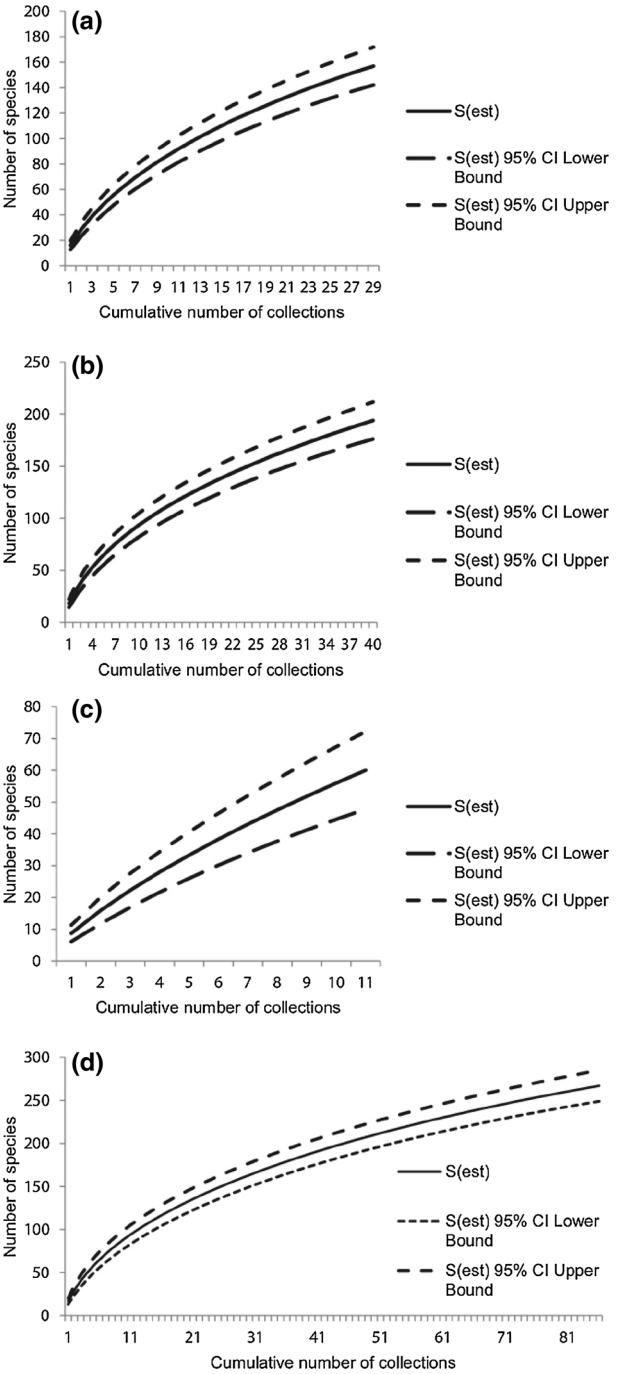


Fig. 2 **a** Species accumulation curve for low elevation sites (n = 29) **b** Species accumulation curve for middle elevation sites (n = 46) **c** Species accumulation curve for high elevation sites (n = 11) **d** Species accumulation curve for all sites (n = 86)

at low and middle elevations but was higher at high elevations (Table 1, Supporting Information). Average temperatures decreased with increasing elevation (Table 1, Supporting Information).

Fungal collections

Wood collections from 86 sampling sites (total of 2580 wood sticks) yielded a total of 2187 fungal collections representing 268 fungal taxa, of which 140 are sexual states and 128 are asexual states (Table 2, Supporting Information). A total of 159 taxa were collected at low elevation sites, 201 taxa at middle elevation sites, and 56 taxa at high elevation sites. Only 33 of the 268 fungal taxa collected occurred at all three sites (Table 2, Supporting Information). The curves representing the cumulative number of species with respect to number of samples collected at each elevation are similar in shape for high, medium, and low elevations despite unequal collection effort (Fig. 2a–d). Although curves for all elevation categories exhibit a weak asymptotic leveling, they all indicate that more species await collection in the region.

A total of 104 taxa occurred at both low and middle elevation sites, while low and middle elevation sites shared 39 and 44 taxa, respectively, with high elevation sites (Table 3, Supporting Information). Sørenson's coefficient of similarity among the three sites (Table 3, Supporting Information) revealed that taxa at low and middle elevation sites were more similar (0.579) than either of those sites were to high elevation sites, 0.363 and 0.333, respectively. The same pattern was observed when using Jaccard's index of similarity coefficient (Table 3, Supporting Information).

Analysis using CAP revealed a significant structuring of freshwater fungal communities along the elevational gradient. Communities at low, middle, and high elevation sites formed three clusters on the ordination graph (Fig. 3). The low and middle elevation communities were closer to one another (and in some cases overlapping) than either was to the high elevation cluster. The analysis found two canonical axes. Permutation tests provided significant statistical support for the hypothesis of elevation structuring of freshwater ascomycetes communities (trace statistic = 1.386, $p < 0.01$: 1st squared canonical correlation = 0.77, $p < 0.01$).

The CAP analysis using equal number of sites also revealed a similar structure as Fig. 3. The communities at low, middle, and high elevation sites formed three clusters on the ordination graph (Fig. 1, Supporting Information) and the low and middle elevation

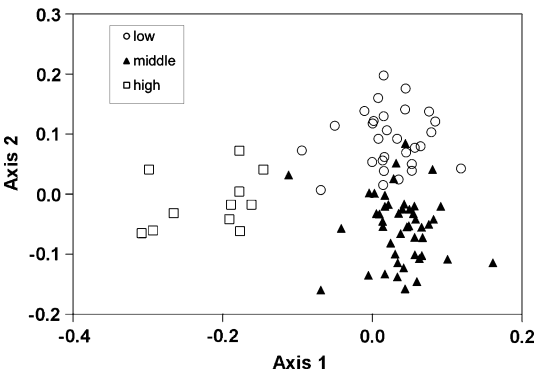
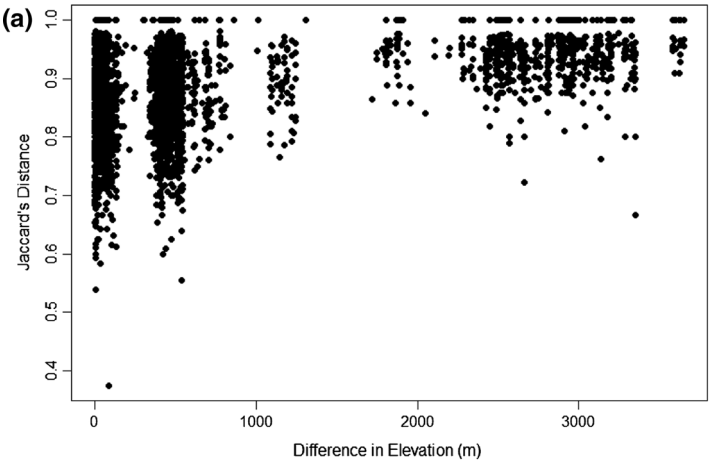
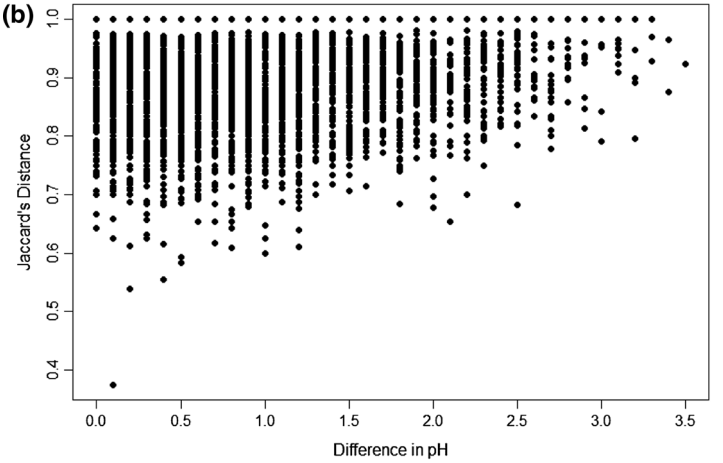
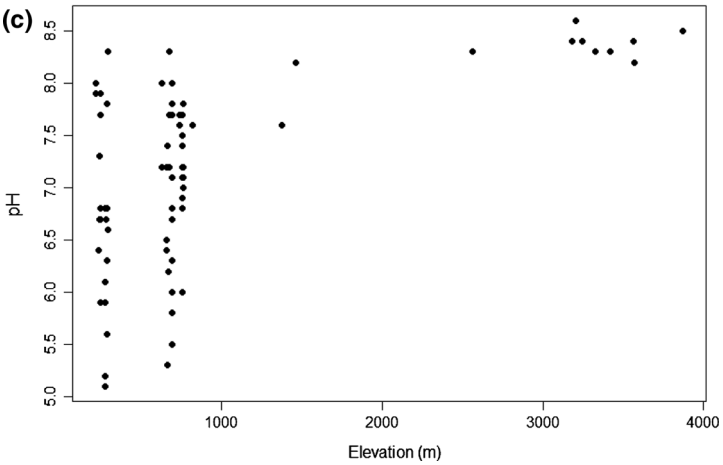


Fig. 3 Canonical analysis of principle coordinates (PCA) of freshwater fungal communities based on elevational gradient in Peru


(a)
Jaccard's Distance
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
1000
2000
3000
Difference in Elevation (m)


(b)
Jaccard's Distance
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Difference in pH


(c)
pH
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
1000
2000
3000
4000
Elevation (m)

◀**Fig. 4** **a** Jaccard's distance versus difference in elevation for every pair of sites. Note that sites that are within 1000 m of each other have a range of Jaccard's distance from ~0.6 to 1.0 (no species in common). Sites that are further apart in elevation generally have Jaccard's distance of 0.8 or greater. Each *dot* on the graph represents a pair of sites **b** Jaccard's distance versus difference in pH for every pair of sites. Note that pairs of sites with a large difference in pH tend to exclusively have high Jaccard's distances, whereas site pair with small differences in pH have a wide range of Jaccard's distances. Each *dot* on the graph represents a pair of sites **c** pH versus elevation (m) for all sites. Low elevation sites have a wide range of pH, whereas higher elevation sites have a pH above 7.5. Each *dot* on the graph represents a site

communities were closer to one another than either was to the high elevation cluster. The analysis found two canonical axes. Permutation tests provided mixed t statistical support for the hypothesis of elevation structuring of freshwater ascomycetes communities (trace statistic = 1.6080, $p < 0.02$, however 1st squared canonical correlation = 0.856, $p = 0.11$). Lower statistical support is not surprising given that this analysis uses fewer sites.

A plot of Jaccard's distance versus difference in elevation (Fig. 4a) shows a wide range of Jaccard's distances associated with pairs of sites with similar elevations. Pairs of sites with large differences in elevation, however, have large Jaccard's distances. Similarly, pairs of sites with a large difference in pH have high Jaccard's distances (Fig. 4b).

The Mantel test on Jaccard's distance and difference in elevation indicated a significant correlation (Fig. 4a; Mantel $r = 0.43$, $p < 0.0001$), as did a test on Jaccard's distance and differences in pH (Fig. 4b; Mantel $r = 0.25$, $p < 0.0001$). A plot of elevation versus pH (Fig. 4c) shows that low elevation sites have a wide range of pH values, whereas sites at high elevation have uniformly high pH. A Pearson's correlation shows a significant positive relationship between the two ($r = 0.50$, $t = 5.14$, $df = 79$, $p < 0.0001$). In light of this result, partial Mantel-s test were also performed.

A partial Mantel's test on Jaccard's distance and difference in elevation, conditioning on pH, confirms the relationship between Jaccard's distance and elevation (Fig. 4a; Mantel $r = 0.39$, $p < 0.0001$). The relationship between Jaccard's distance and pH is also confirmed by a partial Mantel's test conditioning on elevation (Fig. 4b; Mantel $r = 0.16$, $p < 0.0007$).

Discussion

Distribution: changes in species composition of freshwater fungi along the elevation gradient

This study demonstrates that species composition of freshwater ascomycetes communities differs along the elevation gradient in Peru. In terms of community structure, the ordination graph shows three clusters of sites—low, medium and high (Fig. 3). Species composition in the low and middle sites was more similar to one another than either is to the higher elevation sites. High turnover in species composition is also indicated by the lower similarity values between the higher and lower elevation sites, and between the higher and middle sites (Table 3, Supporting Information). CAP analysis with equal number of sites (Fig. 1, Supporting Information) also provided results similar to Fig. 3. These data thus provide much stronger argument that the overlap in freshwater ascomycete communities between lower and middle elevation sites is biologically meaningful and not an artifact of higher sampling effort at low and middle elevation sites.

Additionally, the Mantel's tests demonstrate that beta diversity between pairs of sites is strongly impacted by both elevation and pH (Fig. 4a, b). Rapid taxonomic turnover is associated with both of these factors.

Since, in our study, pH, temperature and vegetation varied with elevation, (Table 1, Supporting information; Fig. 4a–c), it is impossible to attribute the distribution patterns we found to one of these factors alone. Certainly the paucity of woody debris at high elevations plays an important role, but the effects of pH and temperature cannot be ruled out. It is unclear if the communities of fungi found at high elevation are truly distinct from those at lower elevation or are a subset of low elevation species. With the constant downstream displacement of woody debris, it might be expected that any species surviving at high elevation would also be found at low elevation. Numerous species were found only at high elevations but with the exception of *Luttrellia estuarina,* these were typically found at only one or two sites. More work must be done at high elevation sites to determine if there are many species common at high elevation but absent at lower elevations. It may also be that some low elevation sites are basically a sink for high elevational species; these species maybe found only on the wood that has washed down from higher up. This additive effect could play a role in structuring communities in a downstream direction.

Changes in species composition along elevation gradients have also been reported previously for other fungal studies. Geml et al. (2014) sampled soil fungi along an elevation gradient in the Yungas, a system of tropical and subtropical montane forests on the eastern slopes of the Andes in Argentina. Using semiconductor Ion Torrent sequencing of ITS2 nrDNA, the authors found that fungal community composition correlated most strongly with elevation. In a study of aquatic hyphomycetes on submerged leaf litter in Australia, Bärlocher et al. (2011) found that percentage similarities of fungal communities was significantly correlated with altitude along with temperature and geographic distance of stream.

Water pH was shown to be significant in explaining the variation in community composition of freshwater fungi in our study (Fig. 4b). Sites at low and middle elevation have a wide range in pH (Fig. 4c). This variation is likely one of the reason these elevation zones have a high species richness. Earlier studies of freshwater fungi have also demonstrated that pH is an important factor in the distribution of freshwater ascomycetes (Fallah 1999; Raja et al. 2009), as well as freshwater Ingoldian aquatic hyphomycetes (Bärlocher and Rosset 1981; Wood-Eggenschwiler and Bärlocher 1985; Shearer and Webster 1985; Bärlocher 1987). For freshwater Ingoldian mitosporic ascomycetes, Chamier (1992) concluded that pH might have an indirect effect on the distribution of freshwater mitosporic fungi by affecting the solubility of aluminum or other metals in freshwater habitats.

Despite the effects of pH and elevation, 33 of the total 268 taxa found occurred at all three elevation levels (Table 2, Supporting Information). This suggests that the fungal community may be comprised of both habitat specialists and generalists. The 33 species collected throughout the elevational gradient (Table 2, Supporting Information) apparently are able to grow and sporulate on a wide taxonomic range of woody substrates and over a wide range of pH and temperature (Table 1, Supporting Information).

Species richness (Table 3, Supporting Information), which has a slight peak at mid-elevations and a decline at high elevations, fall within the range of curves reported most commonly for other organisms in the Southern Hemisphere (Guo et al. 2013). Rahbek (2005) also showed that the most commonly occurring species richness pattern is a peak of diversity at mid-elevations. Our elevational distribution patterns are similar to those found for soil fungi colonizing popsicle sticks (birch wood) along a terrestrial elevational gradient in Peru (Meier et al. 2010). In that molecular study, most of the wood colonizers were

ascomycetes. This finding is contrary to most studies of terrestrial wood decomposition wherein Basidiomycetes play a major role (Rayner and Boddy 1988). It is possible that the Meier et al. (2010) study approximated the later stages in wood decomposition where ascomycetes play a relatively large role. Also it is not clear how using a non-native wood (birch wood) might have influenced the results of their study. Another study, which focused on patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian Forests of northern Iran (Bahram et al. 2012), found that species richness declined monotonically with increasing altitude. The authors attributed this pattern to the distribution of host species and the general decline in availability of energy with increasing altitude. Gómez-Hernández et al. (2012) studied the distribution of fungal macromycete and ectomycorrhizal communities along an elevational gradient from 100 to 3500 m, spanning tropical dry forest, tropical montane cloud forest and conifer forest in Veracruz, Mexico. Their models for richness and diversity displayed peaks in the mid-part of the gradient. Xylophagus fungal diversity, however, peaked in the mid-lower part of the gradient and tended to decrease with elevation. Unterseher et al. (2013) studied endophytic fungi from Peruvian highland and lowland habitats. Endophytic fungi, although microscopic, are quite different ecologically from aquatic saprobic fungi because many endophytes are host-specific and they generally do not decompose living hosts. Their study revealed considerable under-sampling for all host plants. However, species richness for all lowland and mid-elevation samples of *Hevea* and *Tillandsia* exceeded that for *Vasconcellea* in the highland site. Whether this difference in species richness is due to differences among hosts or elevation is not clear. It is likely that our study showed higher species richness due to bias in sampling regimes, which was higher at mid elevations compared to either low and high elevations (Table 3, Supporting Information). Additional research is needed for this group of fungi before any conclusions can be drawn about the influence of elevation on species richness peaking at mid altitudes.

From our study and others, it is clear that altitude needs to be considered in fungal diversity studies in mountainous areas, especially in light of global warming, which could result in the loss of species at higher elevations. The aforementioned studies and results of our study indicate that fungal species richness and community composition change along elevational gradients, although the patterns of variation are not identical. Some patterns appear to be host related (endophytes, ectomycorrhizal), while others are related to function (xylophagus, saprophytic). Elevational studies of other ecological and/or taxonomic fungal groups are warranted to determine whether similar distribution patterns occur. Additional work also is needed to determine how temperature might affect fungal growth, reproduction and processing rates of submerged ligno-cellulosic substrates in order to further predict the effects of global warming on these processes at different elevations.

Diversity of freshwater fungi

The rivers of Peru are mostly unstudied for freshwater ascomycetes and about 10 % of the taxa we encountered appear to be new to science. Among these are 2 new genera (Zelski et al. 2011a, b), one new species (Zelski et al. 2015); a new family, Natipusillaceae, (Raja et al. 2012, 2013) and an order of freshwater ascomycetes, Natipusillales, which contained a species from our study, were introduced recently (Hyde et al. 2013). Some commonly occurring freshwater asexual fungi from Peru, which were also frequently reported from other freshwater habitats worldwide were recently sequenced and placed within a phylogenetic framework among the Ascomycota (Zelski et al. 2014). Other new species will be described in future papers along with descriptions of rare tropical species. In addition, 103

species are new records for South America and 137 species are reported from Peru for the first time (Table 2, Supporting Information).

Matsushima (1975, 1993) described and/or reported about 415 ascomycete species (mostly as asexual forms) from rivers in Peru and Ecuador, i.e. the collection records indicated the sites were located at rivers. Almost all of these taxa were found on leaves, especially palm leaves. There is no indication that Matsushima used any techniques to target aquatic taxa such as collecting leaves from water or incubating them in water or moist chambers after collection from aquatic habitats. For the most part the species he described and reported would be considered terrestrial taxa. Consequently, only 14 of the taxa he reported were common to both his study and ours.

The two most frequently occurring species in our study, *Candelabrum brocchiatum* and *Cancellidium applanatum*, are both asexual fungi that have been reported in numerous studies of lignicolous freshwater ascomycetes in the Asian tropics (Goh and Hyde 1996; Hyde and Goh 1998a, b; Tsui et al. 2000; Ho et al. 2001; Zhang et al. 2011; Shearer and Raja 2014). *Cancellidium applanatum*, however, was not found at high elevation sites (Table 2, Supporting Information) and may not tolerate low temperatures and/or high pH. These two species are aero aquatic fungi, which may facilitate their dispersal and explain, in part, their widespread global distribution and commonality in our study. Aero aquatic fungi are morphologically adapted for flotation. Their propagules are hydrophobic and trap air bubbles in their spores, which keeps them from sinking out of the water column (Voglymayr 2000; Shearer et al. 2007). Thus they can be dispersed long distances on the water surface or on the surface of air bubbles in foam formed in aquatic habitats.

Of the 140 species found in their sexual reproductive state, only ten occurred at all three elevational ranges (Table 2, Supporting Information). The most commonly occurring species, *Annulatascus velatisporus*, has a widespread global distribution, especially in the tropics and warm temperate habitats (For world records see Shearer and Raja 2014). The remaining six species (in order of decreasing frequency of occurrence) include: *Jahnula appendiculata, Annulatascus citriosporus, Cataractispora appendiculata, Ophioceras commune, Savoryella lignicola,* and *Paraniesslia tuberculata.* With the exception of *O. commune* and *S. lignicola*, these ascomycetes have been reported exclusively from tropical freshwater habitats (For distribution records, see Shearer and Raja 2014). Of note, some of the species found at high elevations in this study also have been reported from warm temperate regions of the USA (Shearer and Raja 2014). These include: *Annulatascus velatisporus*, *Acrogenospora sphaerocephala*, *Exserticlava triseptata, Sporidesmiella hyalosperma*, and *Luttrellia estuarina.* These fungi may grow and survive along wider temperature and/or pH ranges compared to other species found exclusively in the tropics.

Among the 128 asexual taxa found, 23 occurred at all three elevations (Table 2, Supporting Information). Arranged by decreasing frequency of occurrence, these include: *Candelabrum brocchiatum, Monotosporella setosa, Pleurothecium recurvatum, Bactrodesmium longisporum, Sporodesmium adscendens, Phaeoisaria clematidis, Acrogenospora sphaerocephala, Helicosporium guianense, Pleurophragmium bicolor, Exserticlava triseptata, Sporoschisma uniseptata, Conioscypha peruviana, Brachysporiella gayana, Sporoschisma juvenile, Gangliostilbe* cf. *indica, Pseudobotrytis terrestris, Sporidesmiella hyalosperma, Dictyosporium elegans, Dictyosporium elatum,* and *Trichocladium* sp. PE0318. Some of these species have been found in temperate and tropical climates and terrestrial and aquatic habitats (Goh and Tsui 2003; Cai et al. 2006; Shearer et al. 2007; Seifert et al. 2011; Shearer and Raja 2014). Given the ubiquity of these species, their biological role in aquatic and damp habitats is worthy of study.

Two species found on many pieces of incubated wood from all three sites, *Trichoderma* sp. and *Verticillium* sp., occur commonly in soils worldwide, and strictly speaking, are not considered aquatic species. Species of *Trichoderma* are ubiquitous in the environment (Samuels 1996) and appear commonly on wood samples that have been submerged in water and then incubated in moist chambers (Shearer C.A. Pers. obs.). *Verticillium* spp. are plant pathogens (Inderbitzin et al. 2011; Inderbitzin and Subbarao 2014) and occurred on wood samples in this study less frequently than *Trichoderma* spp. Whether or not species of these two genera are physiologically active on submerged wood or simply grow and sporulate when wood is removed from water and incubated in moist chambers is not known. *Trichoderma aeroaquaticum*, however, was recently described as a new aeroaquatic species from Thailand (Yamaguchi et al. 2012).

Biogeographical and global species patterns of neotropical versus paleotropical freshwater fungi

Our research group has previously collected freshwater ascomycetes from Central American countries, such as Costa Rica and Panama and we have found that a number of freshwater ascomycetes found in the Central American tropics have heretofore been reported from the eastern tropics (Shearer et al. 2001; Ferrer and Shearer 2005). In this study, the sexual states of ten species and the asexual states of 23 species, excluding *Trichoderma* spp. and *Verticillium* spp. discussed above, occurred at all elevations (Table 2, Supporting Information). Most of these species have been found in other studies conducted in the paleotropics (see Table 2, Supporting Information and references therein) and were reported in a recent study of aquatic ascomycetes in tropical Brazil (Barbosa et al. 2013b). Data from this study (Table 2, Supporting Information) and that of Barbosa et al. (2013b) strongly indicate a pantropical distribution for tropical freshwater ascomycetes.

With respect to global distributional patterns of tropical Peruvian species, 20 have been reported also from Africa and/or the Seychelles as well as the Asian-Australian paleotropics (Table 2, Supporting Information). Sixty additional taxa have been reported from Peru and the Asian-Australian paleotropics (Table 2, Supporting Information). These reports also suggest a pantropical distribution but with a major gap for the relatively unstudied African continent.

The origins of these pantropical distribution patterns stimulate some interesting speculation. Did the freshwater ascomycetes disperse from landmass to landmass via ocean or air currents (geodisperal), or did they disperse throughout freshwater tropical habitats during the era of the Gondwanan formation (510–180 Mya) and/or the Pangaean supercontinent (300–100 Mya) and thus are widespread via vicariance? Vijaykrishna and Hyde (2006) studied the origins of freshwater ascomycetes; in their study, the authors concluded that the earliest possible date when fungi became adapted to freshwater habitats was about 390 Mya. A study of an estuary in Maryland, USA (Shearer 1972) indicated that aquatic wood-inhabiting fungal communities changed dramatically in species composition at sites where fresh water meets seawater. Marine fungi replaced freshwater fungi where fresh water and seawater mixed; Fryar et al. (2004a, b) found similar results. These studies suggest that freshwater fungi may not tolerate salinity. Many studies have been conducted on the systematics and distribution marine fungi (Jones et al. 2009; Jones and Pang 2012) but only a few of the marine species e.g. *Aniptodera chesapeakensis*, *Nais inornata*, and *Natantispora retorquens,* appear to occur in both fresh water and seawater (Jones et al. 2009). These studies also support the idea that seawater might be a barrier to the migration of freshwater ascomycetes. Also, one would expect that if a species was dispersed to a new

continent via geodispersal, that rapid speciation might follow. This does not seem to be the case for the tropical aquatic ascomycetes, since, except for the Jahnulales (Dothideomycetes) and Annulatascaceae (Sordariomycetes) (Shearer and Raja 2014), clusters of many, closely related species do not occur. In addition, the Andes Mountains, although relatively young geologically, form a large barrier to freshwater species invading by ocean from the west, and the large, nutrient poor streams in the east of South America form a barrier to fungal migrants from the east. Clearly, additional distributional and molecular studies of multi-continental taxa are warranted to better understand their evolutionary history.

Conclusions

Technical difficulties always exist in the sampling of fungal communities based on morphological and/or molecular methods. Despite these difficulties, our investigation and those of previously cited authors clearly indicate an elevational response in fungal community structure and species richness, although the responses differ across studies. Water pH was also a significant factor in explaining species composition and distribution patterns.

As Colwell et al. (2008) suggested, communities along elevation gradients could be affected by future climate change. While it is difficult to predict what specific changes will occur, for aquatic lignolytic fungi, our data suggest that some species could disappear at high elevations due to replacement by species from lower elevations and species at low elevations might disappear due high temperatures and/or changes in the composition of riparian vegetation. Autecological studies of these fungi could provide important new insights into the short and long-term effects of climate change on species and ecosystems.

While the fungal diversity of the selected sites on the river system we studied is relatively high, additional species are likely to be discovered in the many rivers, lakes and swamps in Peru that have not yet been sampled. About 10 % of the fungal species we found appear to be new to science and are currently under study or in the process of being published in future taxonomic papers.

Aquatic fungal sampling should be part of environmental baseline, monitoring, and impact studies associated with the rise of mineral, gas, and oil extraction activities in the Andes-Amazon region. This is especially important because aquatic fungi are essential to processing ligno-cellulosic material in aquatic habitats (Bucher et al. 2004; Simonis et al. 2008).

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