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Biogeography of plant-associated fungal symbionts in mountain ecosystems: A meta-analysis

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Abstract

Aim: Predicting the potential for climate change to disrupt host–microbe symbioses requires basic knowledge of the biogeography of these consortia. In plants, fungal symbionts can ameliorate the abiotic stressors that accompany climate warming and thus could influence plants under a changing climate. Forecasting future plant–microbe interactions first requires knowledge of current fungal symbiont distributions, which are poorly resolved relative to the distributions of plants.

Location: We used meta-analysis to summarize the biogeographic distributions of plant-fungal symbionts in mountain ecosystems worldwide, because these ecosystems are likely to be among the first to experience climate change-induced range shifts.

Methods: We analysed 374 records from 53 publications to identify general trends, pinpoint areas in need of greater study and develop reporting guidelines to facilitate future syntheses.

Results: Elevational patterns varied strongly among fungal and plant functional groups. Fungal diversity and abundance increased with altitude for the ectomycorrhizal fungi. However, arbuscular mycorrhizal fungi and localized foliar endophytes declined in either abundance or diversity with altitude. In shrubs, fungal abundance increased with elevation, but in C_3 grasses, fungal abundance declined with elevation. Altitudinal patterns in fungal composition were stronger than gradients in fungal abundance or diversity, suggesting that species turnover contributes more to elevational gradients in fungal symbionts than does variation in abundance or richness. Plant functional groups were overrepresented by C_3 grasses and trees, with surprisingly few data on sedges or shrubs, despite their ecological dominance in mountain ecosystems. Similarly, epichloae, ericoid mycorrhizal fungi and root endophytes were understudied relative to other fungal groups.

Main Conclusions: Meta-analysis revealed broad biogeographic patterns in plant-fungal symbiont abundance, diversity and composition that inform predictions of future distributions.

KEYWORDS

altitudinal gradients, arbuscular mycorrhizal fungi, ectomycorrhizal fungi, ericoid mycorrhizal fungi, foliar endophytes, fungal distributions, root endophytes

1 | INTRODUCTION

Climate change can cause divergent responses among species, disrupting species interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008) and creating communities that lack contemporary analogs (van der Putten, 2012; van der Putten, Bradford, Brinkman, van de Voorde, & Veen, 2016). Furthermore, the coupled dynamics arising from species interactions can produce complex and unanticipated ecological responses to climate change (Walther, 2010). Among these effects, climate change can perturb the consortia of microbes living inside of host organisms (Classen et al., 2015; Hughes et al., 2003).

Fungal symbionts can benefit plants by ameliorating abiotic stressors associated with climate change, such as heat and drought (Kivlin, Emery, & Rudgers, 2013; Lenoir, Fontaine, & Lounes-Hadj Sahraoui, 2016; Redman, Sheehan, Stout, Rodriguez, & Henson, 2002; Worchel, Giauque, & Kivlin, 2013). Therefore, the ability to predict shifts in fungal distributions under future climates could be useful for understanding general changes in terrestrial communities. To forecast future patterns, it is first necessary to elucidate current fungal distributions. However, the geographic distributions of fungi, especially at local to regional scales, are poorly resolved relative to plants (Peay, Kennedy, & Talbot, 2016; Tedersoo et al., 2014). Belowground, arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (ECM), ericoid mycorrhizal fungi (ERM) and root endophytes (RE) colonize the roots of up to 80% of plant species, often improving nutrient uptake or stress tolerance (Porras-Alfaro & Bayman, 2011; Smith & Read, 2008). Aboveground, plants host vertically transmitted fungi such as the epichloid endophytes as well as horizontally transmitted, localized foliar endophytes (LFE), both of which protect plants against abiotic stress (Rodriguez, White, Arnold, & Redman, 2009; Rudgers & Clay, 2012).

Mountain ecosystems provide distinct natural gradients of temperature as well as geographically variable gradients of precipitation and soil nutrients (Koerner, 2007), making them tractable platforms for predicting possible climate-related shifts in host and symbiont distributions. Elevational gradients can improve the ability to detect climate-related drivers of fungal distributions because gradients span short distances (~2–3 km) that fall within the potential dispersal ranges of many fungi (Lekberg, Koide, Rohr, Aldrich-Wolfe, & Morton, 2007; Wolfe, Richard, Cross, & Pringle, 2010). Furthermore, many plant species have shifted their altitudinal range limits upward under climate change (Davis & Shaw, 2001; Pauli et al., 2012; Walther et al., 2002), but range shifts may also be influenced by interactions with beneficial or pathogenic symbionts (van der Putten, Macel, & Visser, 2010; van der Putten et al., 2016).

Environmental stress changes along elevational gradients and can influence interactions among plants and between plants and their fungal symbionts. Whereas interactions among plants are well documented (Bertness & Callaway, 1994), interactions among plants and fungal symbionts along the same gradients have received less empirical attention. In one case where plants and ECM fungi were manipulated in reciprocal transplants among high and low elevations, high-elevation ECM improved plant growth relative to low-elevation ECM (Wagg, Husband, Green, Massicotte, & Peterson, 2011). Yet, the universality of this trend is unknown, as studies typically focus on one fungal group sampled along a single gradient.

Fungal symbiont groups differ in the environmental drivers of their local distributions, despite their association with the same host species (Ranelli, Hendricks, Lynn, Kivlin, & Rudgers, 2015). For example, RE increase with elevation (e.g., Read & Haselwandter, 1981), whereas AMF can decline (e.g., Gardes & Dahlberg, 1996). However, these findings are highly variable, ranging from increases in abundance or richness (Zubek, Błaszkowski, Delimat, & Turnau, 2009), decreases (Shi, Wang, Zhang, & Chen, 2014) or no pattern (De Beenhouwer et al., 2015) with elevation for the same fungal group. This variation has inhibited development of a generalizable framework of how fungal symbionts vary with elevation or might shift distributions under future conditions. To our knowledge, despite a number of individual reports, no comprehensive effort has synthesized existing fungal symbiont datasets for mountain ecosystems.

We used meta-analysis to summarize shifts in the distributions of fungal symbionts along altitudinal gradients in mountain ecosystems. We analysed data from 374 records from 53 published papers to report general trends for mountain ecosystems and identify areas that need greater study. Specifically, we addressed: (1) How do abundance, diversity and composition of fungal symbionts vary with elevation, and to what degree are patterns specific to fungal or plant functional groups? (2) Do altitudinal patterns in fungal abundance, diversity or composition vary geographically, with the spatial resolution of sampling, or among major biomes? For instance, are altitudinal gradients stronger or weaker at higher latitudes? (3) Do key aspects of study design, such as the elevation range, survey method, season of sampling or material source, influence the detection of altitudinal patterns? We used our results to make recommendations to facilitate future syntheses.

2 | METHODS

We used meta-analysis to examine patterns in fungal symbiont abundance, diversity and composition along altitudinal gradients. We followed guidelines outlined in PRISMA for systematic reviews and meta-analyses (Moher, Liberati, Tetzlaff, Altman, & Grp, 2009; Shamseer et al., 2015).

2.1 | Search terms

We performed a literature search in Thomson Reuters Web of Science through 17 December 2015 using the search terms: mycorrhiz* AND elevation* OR mycorrhiz* AND altitud*; endophyt* AND elevation* OR endophyt* AND altitud*; fungal symbiont* AND plant* AND elevation* OR fungal symbiont* AND plant* AND altitud*; root fung* AND elevation* OR root fung* AND altitud*; epichlo* AND elevation* OR epichlo* AND altitud*; neotypho* AND elevation* OR neotypho* AND altitud*. This search resulted in a total of 376 unique

publications. We also screened the NCBI Short Read Archive (SRA) with the same terms to obtain additional compositional studies, resulting in two extra records.

2.2 | Filtering search results

We screened the 376 unique publications for studies that reported data in natural (not agricultural) ecosystems and only included studies conducted on mountains that sampled >2 elevations. This resulted in 65 studies. However, we excluded five publications due to insufficient elevation range, one because the fungi were studied in litter, not in live plants, and one because authors manipulated the mycorrhizal fungi. We also excluded one additional publication on wetlands because it was an outlier among biomes, but this identified that wetlands were an understudied habitat. Finally, we excluded four more publications because key data were not published. For six publications, we contacted the authors to obtain original OTU composition data and thus were able to include those in the meta-analysis. The filtering process resulted in 53 publications, from which 374 records were used for meta-analyses (Tables S1 and S2). A record refers to a single report of a correlation coefficient between a fungal response variable and elevation. Most individual studies included multiple records that reflected either different response variables (fungal diversity vs. fungal abundance, which were analysed separately – see Section 2.5), different fungal types examined within the same study (e.g., AMF vs. ECM) or fungal responses that were measured on different plant species included within the same publication (summarized in Table S1).

2.3 | Data collection

For each record, we recorded geographic data including latitude in decimal degrees, continent, minimum elevation, maximum elevation and elevation range (m). We recorded host and symbiont information including biome type (e.g., forest vs. grassland), plant functional group and fungal functional group as designated by the original authors. Fungal functional groups included arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (ECM), ericoid mycorrhizal fungi (Ericoid), root endophytes (RE) including the dark septate endophytes (DSE), systemic, foliar endophytes in the Clavicipitaceae (Epichloae), and localized foliar endophytes (LFE). We collected data on the sample size (number of sites) and replication of gradients (number of independent altitudinal gradients sampled). We designated the spatial sampling scale as local if the study included only one gradient or regional if multiple gradients were sampled within ~500 × 500 km. In cases where publications included records at both local and regional scales ($N = 5$), we included only regional data because it provided stronger replication of elevation patterns. In mountain ecosystems, microbial communities change across seasons (Wu et al., 2016), and sampling time could affect the strength of altitudinal patterns. We designated the temporal sampling scale as summer, fall, winter, spring or multiple, for studies that combined samples collected over multiple seasons. We recorded data on the tissue type sampled: leaves, roots or soil (which included studies analysing spores or sporocarps). Because studies did not always surface-sterilize plant tissues, our meta-analysis likely included both epiphytic and endophytic fungi.

We categorized fungal response variables as abundance (plant tissue colonization, spore counts or fungal biomass estimates), richness, diversity (Shannon's index) or composition (OTU matrix), all derived from culture-based or culture-independent methods. Richness and diversity metrics were calculated using OTU tables provided in the original manuscript or subsequently from the authors. Studies reported either presence/absence or abundance. We only included studies that reported abundance when calculating Shannon's diversity index. We did not account for variation among studies in sequence similarity for OTU designations, primer choice or sequence processing. Therefore, ours was a conservative approach because variance in sequence analysis could possibly obscure trends. Because this meta-analysis spans studies performed over 30 years, it was not possible to obtain raw sequence data for a more comprehensive analysis using one pipeline. We additionally classified the survey method used to estimate fungal abundance (microscopy, biomass, culturing followed by Sanger sequencing, direct Sanger sequencing from PCR and cloning of environmental samples, or immunoblot), or fungal diversity/composition (culturing followed by Sanger sequencing, direct Sanger sequencing from cloning of environmental samples, next-generation sequencing, microscopy, morphology or t-RFLP).

2.4 | Fungal response metrics

We used the Pearson correlation coefficient (r) for the effect size metric calculated from raw data. Although the correlation coefficient is not as informative as a slope or covariance, we chose it for several reasons: it was commonly reported, it is insensitive to the units of measurement (e.g., allowing us to compare the magnitude of gradients among studies using different units of measurement), and it is constrained between −1.0 and 1.0, making it an easily interpretable effect size metric. We also recorded the p-value for the correlation coefficient and the net outcome: increase, decrease or neutral (non-significant) with increasing elevation. For composition, each OTU matrix was transformed into either a Bray–Curtis (abundance) or Sorensen (presence/absence) dissimilarity matrix. These scores were then used calculate the Pearson correlation coefficient for changes in composition against elevation using Mantel tests (Mantel, 1967) in the vegan package in R (Oksanen et al., 2016).

2.5 | Meta-analysis

We conducted mixed effects meta-analysis using the package "metafor" (Viechtbauer, 2010) in R (R Core Team 2016). Statistical models to address the influence of fungal vs. plant functional group on altitudinal patterns of fungal abundance, diversity and composition (*Question 1*) included the fixed factor of either fungal functional group or plant functional group, the random effect of publication identity, which accounted for the non-independence of records from the same

publication/author group, and the random effect of individual record nested within publication. We could not include fungal and plant functional group in the same model because ECM studies occurred only on trees. In addition, some functional groups were represented by too few records to include in meta-analysis (Table 1). *p*-values from likelihood ratio tests were obtained by comparing the full model that included the fixed factor(s) of interest to a null model that included only the random effect (Viechtbauer, 2010). Pairwise contrasts (e.g., among different fungal functional groups) were adjusted using the Holm method to reduce the likelihood of Type I error (see code in Appendix S1).

Statistical models to address geographic patterns in the magnitude of altitudinal gradients in fungal abundance, diversity and composition (*Question 2*) separately examined the fixed factors of biome (forest vs. grassland), spatial scale (local vs. regional) or continuous variation in latitude. We also tested three aspects of methodology (*Question 3*): elevation range sampled, sampling season (spring, summer or fall), survey method (microscopy, culturing or sequencing method) or source of sampled material (leaves, roots or soil). When there was sufficient replication for a given fungal group, models included the interaction with fungal functional group to determine if patterns varied among fungal groups. Exceptions were tests for the effect of the material sampled, which overlapped with fungal functional group (e.g., LFE are only in leaves) and comparison of alternative sampling methods (e.g., RE diversity was examined only with next-generation sequencing). In all other cases, fungal functional group was included additively in the model, but we lacked sample size to test for an interactive effect with methodology. Statistical significance was evaluated via likelihood ratio tests against a reduced model that did not include the factor, as above. Finally, because AMF were the most commonly sampled group, when possible, we also tested for an influence of geographic and methodological factors only within this fungal group.

3 | RESULTS

Across 374 records, foliar endophytes in the epichloae clade were the least studied, followed by ericoid mycorrhizal fungi, then root endophytes (RE) (Table 1). AMF received the most attention, representing ~60% of records. More studies examined patterns in fungal abundance ($N = 144$) than in fungal composition ($N = 78$) or diversity/richness ($N = 67–85$; Table 1), likely reflecting the increasing use of sequencing methods in recent years. Composition and richness/diversity data represented sufficient coverage of just three fungal groups (AMF, ECM, LFE; Table 1), heavily weighted towards AMF (67% of 78 composition records). Diversity indices were the smallest set of records (Table 1), because studies that only reported presence/absence OTU matrices precluded calculation of Shannon's index.

Trees (37% of records; Table 1) in forest biomes (54% of records) were the main plant functional group studied. In addition, studies on grasses were more likely to measure fungal abundance, while work on trees focused on fungal diversity and composition (Table 1). Approximately 20% of records sampled different plant functional groups at different elevations (Table 1, Plant functional group:

TABLE 1 Counts of the number of records ($N = 374$) of each fungal symbiont metric (abundance, richness, Shannon diversity index or composition) summarized separately by fungal functional group or plant functional group. For plants, "Multiple" indicates studies that examined different plant functional groups at different parts of the elevational gradients or combined data across plant groups. Column and row sums are shown in bold font

	Fungal Symbiont Metric				
	Abundance	**Richness**	**Shannon**	**Composition**	***Sum***
Fungal group					
AMF	71	53	49	52	**225**
RE	27	3	0	1	**31**
ECM	16	13	7	11	**47**
Epichloe	9	0	0	0	**9**
Ericoid	3	5	2	4	**14**
LFE	18	11	9	10	**48**
	144	**85**	**67**	**78**	***374***
Plant group					
C_3 grass	61	1	0	1	**66**
C_4 grass	6	1	1	1	**11**
Fern	4	0	0	0	**4**
Forb	24	8	7	8	**64**
Sedge	5	3	3	3	**20**
Shrub	10	5	5	6	**35**
Tree	13	44	41	42	**226**
Multiple	21	23	10	17	**107**
	144	**85**	**67**	**78**	***374***

Multiple), making it impossible to disentangle host roles in altitudinal patterns.

3.1 | How do abundance, diversity and composition of fungal symbionts vary with elevation, and to what degree are patterns specific to fungal or plant functional groups?

3.1.1 | Fungal functional group

Fungal functional groups differed in altitudinal patterns of abundance (QM_5 = 26.24, p < .0001; likelihood ratio X^2 = 11.62, p = .0204). The abundance of AMF (r = −.17 ± .05 SE, p = .0002) and LFE significantly declined with elevation (r = −.19 ± .07 SE, p = .0111; Figure 1a). In contrast, ECM abundance tended to increase with elevation (r = .23 ± .12 SE, p = .0649) and significantly differed from both AMF and LFE (Figure 1a). Residual heterogeneity was large (QE_{136} = 187.51, p = .0023), suggesting that other spatial, environmental or biotic variables contribute to the influence of altitudinal gradients on fungal symbiont abundance.

Results for fungal richness were similar to those for fungal abundance, with significant altitudinal effect sizes (QM_3 = 20.75, p = .0001) as well as divergence among fungal functional groups (likelihood ratio X^2 = 12.50, p = .0019). Whereas AMF richness declined with elevation (r = −.22 ± .10 SE, p = .0242), ECM richness significantly increased (r = .37 ± .12 SE, p = .0019; Figure 1b), mirroring abundance patterns. In contrast, LFE showed no significant change in richness with elevation (p = .1291). Shannon diversity for fungal OTUs had no significant altitudinal pattern (QM_3 = 3.00, p = .3913) and did not differ among fungal groups (likelihood ratio X^2 = 2.54, p = .2808).

Among the three fungal groups with sufficient data, AMF, ECM and LFE all showed strong elevational patterns in OTU composition (QM_3 = 143.16, p < .0001; Figure 2a), which did not differ among fungal groups (likelihood ratio X^2 = 4.08, p = .1303). Altitudinal patterns in composition were up to 12× larger (r^2 range across fungal functional groups: .42–.67) than altitudinal gradients in abundance (r^2 range: −.03 to .23) and were up to 2× larger than shifts in diversity (r^2 range: −.22 to .37).

3.1.2 | Plant functional group

Like fungal groups, plant functional groups significantly differed in elevational patterns of fungal symbiont abundance (QM_4 = 19.73, p = .0006; likelihood ratio X^2 = 14.89, p = .0019). C_3 grasses showed significant altitudinal declines (r = −.11 ± .04 SE, p = .0072), whereas shrubs showed altitudinal increases (r = .60 ± .18 SE, p = .0008; Figure 3a). Both forbs and trees had altitudinal declines that were not significantly different from zero but did differ from the shrub pattern (p = .0100; Figure 3a). In contrast to their differences in fungal abundance, plant functional groups did not have strong altitudinal patterns in fungal symbiont richness (QM_2 = 0.18, p = .9119; likelihood ratio X^2 = 0.17, p = .6823) or diversity (QM_2 = 0.55, p = .7602; likelihood ratio X^2 = 0.54, p = .4611). Altitudinal patterns in fungal composition were strong when divided by plant functional group (Figure 2b; QM_2 = 63.99, p < .0001), but were overwhelmingly represented by trees (N = 42 of 78 cases). Fungal composition in trees did not significantly differ from forbs (N = 8) in the strength of altitudinal pattern (likelihood ratio X^2 = 0.02, p = .8899; Figure 2b), and there were too few studies on other plant groups to permit meta-analysis (Table 1).

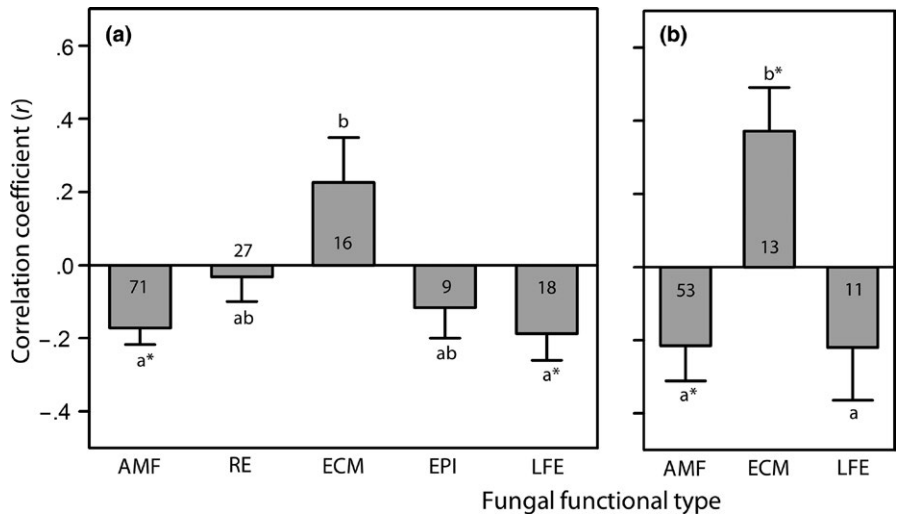

FIGURE 1 Differences among fungal functional groups in the altitudinal gradients for (a) fungal abundance metrics and (b) fungal richness metrics. Fungal functional types included AMF, arbuscular mycorrhizal fungi; RE, root endophytes; ECM, ectomycorrhizal fungi; EPI, systemic foliar endophytes in the epichloae clade; and LFE, localized, foliar endophytes. Meta-analysis used the correlation coefficient with elevation (r) as the effect size metric (range: −1 to 1); bars show means + SE. Asterisks indicate cases where r significantly differed from zero. Different letters show significant differences among fungal functional groups. Numbers on bars indicate the number of records per group

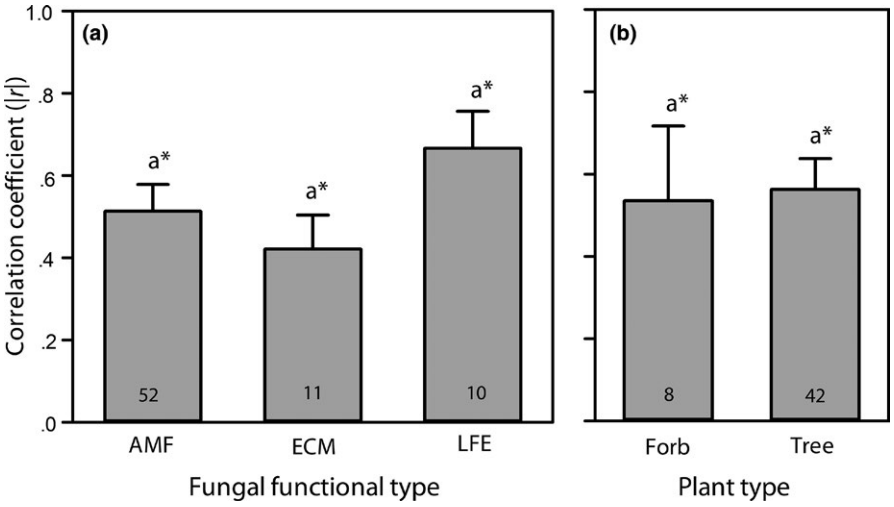

FIGURE 2 Altitudinal patterns in fungal composition from OTU tables across (a) fungal functional groups with sufficient data for analysis: AMF, arbuscular mycorrhizal fungi; ECM, ectomycorrhizal fungi; LFE, localized, foliar endophytes; and (b) plant functional groups with sufficient data for analysis. Meta-analysis used the absolute value of the correlation coefficient with elevation (*r*) as the effect size metric (range: 0 to 1, because compositional changes are non-directional). Bars show mean *r* + SE. Asterisks indicate cases where *r* significantly differed from zero. The lack of different letters indicates no significant differences among fungal or plant functional groups in the magnitude of *r*. Numbers on bars indicate the number of records per group

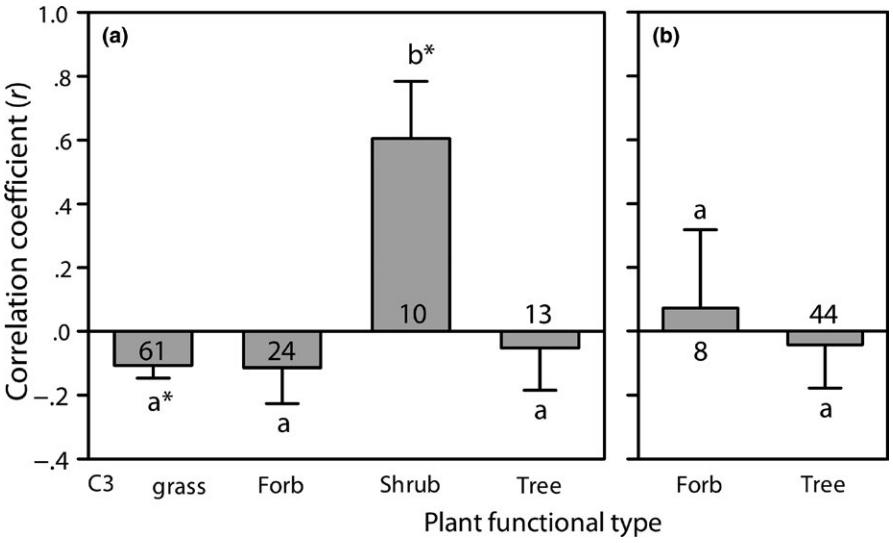

FIGURE 3 Altitudinal patterns in (a) fungal abundance and (b) fungal richness across plant functional groups. Meta-analysis used the correlation coefficient with elevation (*r*) as the effect size metric (range: −1 to 1); bars show mean + SE. Asterisks indicate cases where *r* significantly differed from zero. Different letters show significant differences among plant functional groups within a fungal response variable. Numbers on bars indicate the number of records per group

3.2 | Do altitudinal patterns in fungal abundance, diversity or composition vary geographically, with the spatial resolution of the sampling effort, or among major biomes?

3.2.1 | Biogeography

The strength of altitudinal gradients of fungal symbiont abundance did not vary with any spatial variable. In contrast, richness gradients became more negative for all fungal functional groups at higher latitudes (estimate of the slope of *r* vs. latitude = −.01 ±.0022 SE, $p = .0028$). Because ECM richness patterns along elevational gradients were positive, they weakened at higher latitudes, whereas AMF and LFE elevational richness gradients, which were already negative, strengthened. The strength of compositional patterns differed with latitude separately for each fungal group (Table 2). Latitudinal AMF compositional patterns with elevation did not vary ($p = .4705$), whereas turnover in ECM with altitude weakened with increasing latitude (estimate of the slope of *r* vs. latitude = −.01 ± 0.0037 SE, $p = .0298$), and LFE compositional turnover marginally intensified at the highest latitudes (estimate of the slope of *r* vs. latitude = .01 ± 0.01 SE, $p = .0668$). Altitudinal patterns in fungal richness (Table 2) varied across continents, but this likely reflected differences in which fungal groups were sampled in each continent. Within fungal groups, only AMF altitudinal gradients were sampled enough to compare abundance, richness and composition patterns across continents, with no significant differences ($p > .1100$).

TABLE 2 Results of likelihood ratio tests of the influence of geography and spatial factors, including latitude, continent, biome type (forest vs. grassland) and spatial scale (local vs. regional) on the strength of altitudinal gradients in fungal abundance, richness or composition. *p*-values <.05 are shown in bold. Only latitude had sufficient replication to test for interactions with fungal functional group, and functional group was included as an additive effect in all other models (no interaction tested)

	Fungal abundance		Fungal richness		Fungal composition	
	X^2	*p*	X^2	*p*	X^2	*p*
Latitude	0.00	.9502	6.30	**.0120**	0.99	.3199
Latitude × fungal group	1.31	.7269	0.47	.9246	7.61	**.0222**
Continent	4.71	.1941	9.08	**.0282**	1.28	.5266
Biome	1.57	.2103	N/a	N/a	N/a	N/a
Spatial scale	2.05	.1527	0.23	.6299	0.93	.3341

3.2.2 | Biome type

The influence of altitude on fungal abundance did not differ between forests and grasslands ($p = .2103$); the two biome types with sufficient replication (Table 2). Generally, there was insufficient replication of fungal functional groups to permit evaluation of fungal group × biome interactions (Table 2, Fig. S1). For fungal diversity and composition, biome type was highly overlapping with fungal functional group. However, we could test for differences in the strength of altitudinal patterns for AMF in forests vs. grasslands, which was non-significant for all metrics: abundance ($X^2 = 1.75$, $p = .1853$), richness ($X^2 = 0.04$, $p = .8499$) and composition ($X^2 = 0.66$, $p = .4172$).

3.2.3 | Spatial scale

Spatial scale had no influence on the magnitude of gradients in fungal abundance, richness, or composition (Table 2).

3.3 | Do key aspects of study design influence the ability to detect altitudinal patterns?

Sampling was biased towards the Northern Hemisphere (Fig. S1). Sampling of AMF was the most consistent across latitudes, with approximately one-third of studies occurring in the Southern Hemisphere. In general, Africa and Australia were under sampled compared to other continents, whereas North America, Europe and Asia had higher coverage (Fig. S1).

3.3.1 | Elevation range

Studies varied in the elevation range sampled, from a minimum span of 150 m [850–1000 m] to a maximum of ~2750 m [1900–4648 m]. In addition, different fungal groups were sampled across different elevation ranges. In particular, LFE studies sampled elevation ranges that were ~200 m larger than for any other functional group. Furthermore, ECM (701–1501 m) and ericoid (808–1607 m) studies sampled lower elevation ranges than AMF studies (1567–2471 m). We expected studies that investigated a wider elevation range would uncover stronger correlation coefficients between fungal symbionts and elevation and that fungal groups that were sampled over different elevation ranges might have contrasting altitudinal trends. However, there was no significant influence of elevation range or its interaction with fungal functional group on any fungal metric (all $p > .2922$; Table S1).

3.3.2 | Methodology

In 97% of cases, fungal abundance ($N = 137$) data originated by colonization via microscopy, with 1% via qPCR and <1% via culturing, immunoblot or PLFA. Thus, we were unable to compare the strength of altitudinal gradients in fungal abundance among sampling methods (Table S1). Fungal richness ($N = 82$) data came 57% via direct Sanger sequencing, 21% via next-generation sequencing, 7% via culturing followed by Sanger sequencing, 5% by morphology of spores or cultures using microscopy and 4% via t-RFLP. Analysis across fungal groups showed no significant effect of method on the ability to detect altitudinal gradients in fungal richness ($p = .8515$; Table S1). Fungal composition ($N = 73$) consisted of 65% records using direct Sanger sequencing, 15% using next-generation sequencing, 11% by some form of morphotyping, 5% by culturing followed by Sanger sequencing and 4% via t-RFLP. Methodologies with adequate replication did not return different altitudinal patterns across fungal groups ($p = .2954$; Table S1).

For fungal richness, ECM and AMF had sufficient replication to compare the influence of methods. We compared two methods with sufficient replication: direct Sanger sequencing and next-generation sequencing. Methodology affected fungal richness responses differently for ECM and AMF (method × fungal group, $X^2 = 8.60$, $p = .0034$). For ECM richness, alternative methods returned different altitudinal patterns ($QM_2 = 13.65$, $p = .0011$), with strong elevational signal for next-generation sequencing ($r = .49 \pm .13$ SE, $p = .0002$) and no significant correlation for direct Sanger sequencing ($r = .00 \pm .14$, $p = .9745$). For AMF richness, there were no significant differences between methods ($QM_2 = 2.97$, $p = .2268$, although next-generation sequencing had a more negative average altitudinal trend ($r = -.29 \pm .18$, $p = .1112$), consistent with the overall pattern from AMF as compared to results from direct Sanger sequencing ($r = .08 \pm .12$, $p = .5120$).

3.3.3 | Sampling season

Only patterns of fungal abundance were measured across enough different seasons to compare seasonal effects, and they did not vary ($X^2 = 2.57$, $p = .2760$).

3.3.4 | Plant material sampled

Despite clear differences in altitudinal patterns among fungal functional groups, the type of material sampled (leaves, roots or

plant-associated soil) had no detectable influence on the strength of the effect of altitudinal gradients on fungal symbiont abundance, richness or composition (all $p > .1056$).

4 | DISCUSSION

4.1 | Altitudinal patterns of fungal abundance, richness and composition differ among fungal and plant functional groups

Meta-analysis revealed striking variation among fungal groups in the strength and direction of altitudinal gradients. This variation occurred even among fungi that occupy similar plant tissues and can have similar functional roles in plant nutrient acquisition. For example, ECM fungal richness significantly increased with elevation, whereas AMF richness declined with elevation. Increases in ECM fungal richness with elevation were found in locations as diverse as tropical and subtropical montane dry forests in the Andes of Argentina (Geml et al., 2014), a temperate forest in Nepal (Christensen & Heilmann-Clausen, 2009) and tropical montane cloud forests in Costa Rica (Looby, Maltz, & Treseder, 2016). Studies documented strong altitudinal declines in the richness of AMF in trees in Brazil (Bonfim, Vasconcellos, Baldesin, Sieber, & Cardoso, 2016) and in multiplant species communities in China (Shi et al., 2014). Interestingly, fungal diversity, measured as Shannon's index, did not vary with elevation. This suggests that rare fungal taxa may be contributing to the observed richness patterns and warrants further investigation.

Altitudinal changes in fungal abundance also varied among fungal and plant functional groups, but were weaker than altitudinal shifts in fungal diversity or composition, ranging from elevational declines for the LFE and AMF to increases for the ECM. Other studies showed similar correlation coefficient sizes for AMF abundance across temperature (Wilson et al., 2016) and nutrient gradients (Hu, Rillig, Xiang, Hao, & Chen, 2013), and sensitivity of AMF composition to both climate and soil nutrients (Kivlin, Hawkes, & Treseder, 2011). Similarly, ECM diversity and composition are often correlated with climate and plant host diversity (Tedersoo et al., 2012, 2014). Root and leaf endophytes are less well characterized over environmental gradients, but both are known to vary with precipitation (Giauque & Hawkes, 2013; Herrera, Poudel, Nebel, & Collins, 2011). Altogether, these patterns suggest that both climatic and edaphic variables could be driving the elevation patterns described here. However, studies in the current meta-analysis rarely contained enough metadata to attribute causality to the altitudinal trends. Nevertheless, because AMF and ECM fungal groups varied along altitudinal gradients more than other groups, these fungi may be more responsive to the direct effects of global change and therefore good targets for understanding how fungal symbionts affect plant responses to climate (e.g., Wagg et al., 2011). In addition, larger altitudinal variation in fungal composition than in abundance or richness suggests that shifts in the presence of particular species may be the highest impact of future climate, rather than changes in abundance per se.

Plant functional groups were most strongly represented by C_3 grasses and trees, with surprisingly few studies on sedges or shrubs, despite their dominance in mountain ecosystems. Fungal symbionts increased in abundance at higher elevations in shrubs but decreased in C_3 grasses. For instance, in northern Japan, the abundance of ECM fungi increased with altitude in roots of the shrubs *Weigela hortensis*, *Gaultheria miqueliana* and *Salix bakko* (Tsuyuzaki, Hase, & Niinuma, 2005), and a similar pattern was present in the southern Appalachian Mountains of the U.S. for ericoid colonization of *Rhododendron maximum* (Parker, 2013). Fungal composition, however, consistently varied along elevational gradients in both trees and forbs, the two plant functional groups with sufficient replication. Differences in abundance, diversity and composition of fungal symbionts among plant functional groups are not surprising. The plant functional groups we surveyed here generally differ in traits such as biomass, chemical recalcitrance and secondary metabolites (Eviner & Chapin, 2003; Pichersky & Gang, 2000), which could influence fungal symbiont colonization. Indeed, AMF (Kivlin et al., 2011), LFE (Giauque & Hawkes, 2016) and ECM fungi (Peay et al., 2016) all can differ in composition among plant functional groups. Little is known about host preferences of RE, representing an open avenue for future research (e.g., Kia et al., 2017).

Few studies ($n = 9$) in our meta-analysis sampled across enough elevations to examine nonlinearity in elevation responses. Limited sampling also precluded analysis at the level of plant species. However, in one case where multiple plant hosts and fungal groups were sampled across the same elevations, altitudinal trends differed among fungal groups and plant species (Ranelli et al., 2015). In some cases, opposite colonization–elevation relationships occurred for the same fungal functional group colonizing plant species within the same genus. This small snapshot suggests that general patterns described here may be context-dependent on host resources or density, or may depend on host-specificity relationships (e.g., specialist epichloae vs. generalist AMF).

4.2 | Altitudinal gradients in fungal symbionts vary geographically

Fungal groups exhibited some geographic variation in the magnitude of altitudinal gradients. ECM fungi had a positive correlation of richness with elevation at low latitudes that weakened at higher latitudes, whereas AMF and LFE exhibited negative correlations of richness with elevation at lower latitudes that strengthened at higher latitudes. In contrast, turnover in ECM composition along altitudinal gradients weakened at higher latitudes, whereas AMF turnover did not change and LFE turnover increased. These patterns may reflect differences in host specificity for ECM, AMF and LFE fungi. Because ECM fungi are typically more host-specific than AMF (Allen et al., 1995; Tedersoo et al., 2014), host specificity could contribute to geographic variability in the magnitude of elevational gradients, particularly if there is strong geographic variation in the altitudinal patterns of key host plants. Alternatively, the thermal optima of these fungal groups may vary such that AMF and LFE prefer warmer climates (Kivlin et al., 2011), and ECM function best under colder conditions (Tedersoo et al., 2012). Because host plant abundance is confounded with elevation

Box 1 List of recommendations for future studies to facilitate synthesis

(1) Sample the same host plant species across the gradient. There is strong evidence for host-specific biogeographic patterns (e.g., Ranelli et al., 2015); studies that sample different species or functional types at different elevations may confound host identity with symbiont biogeographic pattern.
(2) Report sample sizes (sites and gradients) and simple statistics (correlation coefficients and associated *p*-values). Alternatively, studies that provide open-access data would enable the comparison of alternative analysis frameworks in future syntheses. Using standardized data in analyses, including reporting elevation in metres, colonization as a percentage, taxonomic richness and a standard diversity metric (e.g., Shannon–Wiener), would allow for direct comparison of slopes across studies, which could deepen quantitative prediction over using correlation coefficients alone.
(3) Replicate elevation. Points at the ends of a gradient can have undue leverage on the slope, but may vary for reasons other than elevation. True replication of elevation—achieved by sampling multiple, independent altitudinal gradients—is the best solution to this issue.
(4) Consider nonlinear analyses. While environmental gradients over altitude may be nonlinear, the majority of studies have only employed linear analysis methods. Evaluation of quadratic or cubic terms or alternative nonlinear functions via model selection procedures could provide new insight into fungal biogeography.
(5) Report underlying environmental variables. Elevational gradients are excellent platforms to investigate strong environmental variation over short distances. However, studies rarely report climatic, resource or edaphic (soil pH) factors that may influence fungal symbionts. Variance partitioning of these abiotic factors can suggest when and where fungi may be sensitive to altered climates or resources under global change.

(see Box 1), our meta-analysis cannot separate these two alternative scenarios. Local adaptation of fungi to both climate and plant hosts would be a useful target for future research.

4.3 | Study design rarely influences the ability to detect altitudinal patterns of fungi

Overall patterns of fungal abundance, richness and composition along altitudinal gradients were not influenced by the elevation range sampled, study methodology, the plant material sampled or the sampling season. The availability of host plants along elevational gradients likely influenced sampling patterns, including that AMF studies sampled higher elevations than ECM studies, and LFE studies sampled larger elevation ranges. Most studies measured fungal abundance microscopically, which may bias biomass estimates owing to differences among observers and in sample preparation among laboratories. Yet, a comparison of microscopic versus chemical approaches to detect fungal biomass generated largely congruent results (Stahl, Parkin, & Eash, 1995). Variance in sequencing technologies or analysis may have affected detection of patterns, as trends in ECM richness along altitudinal gradients were sensitive to sequencing technology. This is expected when differences in sequencing technology range from capturing 1% (culturing and sequencing) to >90% (Illumina sequencing) of the composition at a given site (Allen, Millar, Berch, & Berbee, 2003; Arnold, 2007). Trends captured from Illumina sequencing matched the overall richness patterns better than those from Sanger sequencing, despite containing 60% fewer records, suggesting that newer sequencing technologies better represent the entire fungal community. We were not able to analyse differences in analysis pipelines among studies, but these affect results. Differences in primer choice, the classification of OTUs, pipeline quality control, chimera filtering and rarefaction techniques can each bias resulting composition and richness (Lindahl et al., 2013). However, because our meta-analysis used a standardized effect size for each study, these methodological issues may add noise to our analysis, but are not likely to fundamentally change the results.

4.4 | Recommendations for future research

Based on our experience assembling data for meta-analysis, we compiled a list of recommendations to future researchers (Box 1). Despite amassing 374 records, our dataset lacked sufficient replication to compare fungal functional groups within plant functional groups. Future surveys that examine the full mycobiome of individuals of the same species, including both roots and leaves, would enable such analysis (Recommendation 1). As with other ecological meta-analyses (Gurevitch, Curtis, & Jones, 2001; Koricheva & Gurevitch, 2014), a key recommendation for future work is greater accuracy of data reporting (Recommendation 2). Following our initial search, we discarded 12 publications due to lack of presentation of appropriate statistics, data or sample sizes to enable meta-analysis. Additionally, regression slopes (β) are better suited to predict quantitative changes in abundance, diversity and composition over an elevational gradient compared to the correlation coefficient, *r*. However, a lack of reporting of standardized slopes has hampered such analysis. We also recommend true replication of elevation (Recommendation 3). Studies that do not independently replicate elevation have high risk of detecting patterns driven by confounding factors (such as land use history or local edaphic factors) rather than by elevation per se, particularly if the number of sites sampled is small or the highest/lowest sites diverge for reasons other than elevation. For example, of the 53 publications we examined, only 11 studied more than one elevational gradient (one publication used 8, three used 6, one each used 4 or 5, two used 3, three used 2). Although

we found no influence of the elevation range sampled on the magnitude of linear altitudinal gradients, we also recommend sampling the widest range possible to enable the detection of nonlinearities in altitudinal patterns (Recommendation 4). In our survey, >95% of records only tested for linear relationships with elevation. Nonlinearities, such as mid-elevation peaks in fungal diversity, will create bigger challenges for forecasting future distributions. Finally, one of the main reasons that elevational studies are tractable is that they provide multiple climatic, resource and edaphic gradients that can simultaneously influence symbiotic fungi at scales where dispersal limitation is minimal. However, these environmental variables are often not reported. Therefore, we recommend that studies aim to include underlying abiotic variation in soils and climate to attribute causality to altitudinal trends (Recommendation 5). Ultimately, studies that sample the same host species using the same methodologies across replicated elevational gradients at continental to global scales are necessary to determine the global biogeography of mountain fungal symbiont communities. When combined with global change experiments and reciprocal transplants of fungal symbiont communities among elevations, these studies will help to elucidate when and where the abundance, diversity and composition of fungal symbionts will be sensitive to changing climates.

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REFERENCES

Allen, E. B., Allen, M. F., Helm, D. J., Trappe, J. M., Molina, R., & Rincon, E. (1995). Patterns and regulation of mycorrhizal plant and fungal diversity. *Plant and Soil*, *170*, 47–62.

Allen, T. R., Millar, T., Berch, S. M., & Berbee, M. L. (2003). Culturing and direct DNA extraction find different fungi from the same ericoid mycorrhizal roots. *New Phytologist*, *160*, 255–272.

Arnold, E. A. (2007). Understanding the diversity of foliar endophytic fungi: Progress, challenges, and frontiers. *Fungal Biology Reviews*, *21*, 51–66.

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology and Evolution*, *9*, 191–193.

Bonfim, J. A., Vasconcellos, R. L. F., Baldesin, L. F., Sieber, T. N., & Cardoso, E. (2016). Dark septate endophytic fungi of native plants along an altitudinal gradient in the Brazilian Atlantic forest. *Fungal Ecology*, *20*, 202–210.

Christensen, M., & Heilmann-Clausen, J. (2009). Forest biodiversity gradients and the human impact in Annapurna Conservation Area, Nepal. *Biodiversity and Conservation*, *18*, 2205–2221.

Classen, A. T., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M. A., … Patterson, C. M. (2015). Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*, *6*, 130.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, *292*, 673–679.

De Beenhouwer, M., Van Geel, M., Ceulemans, T., Muleta, D., Lievens, B., & Honnay, O. (2015). Changing soil characteristics alter the arbuscular mycorrhizal fungi communities of Arabica coffee (*Coffea arabica*) in Ethiopia across a management intensity gradient. *Soil Biology and Biochemistry*, *91*, 133–139.

Eviner, V. T., & Chapin, F. S. (2003). Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology Evolution and Systematics*, *34*, 455–485.

Gardes, M., & Dahlberg, A. (1996). Mycorrhizal diversity in arctic and alpine tundra: An open question. *New Phytologist*, *133*, 147–157.

Geml, J., Pastor, N., Fernandez, L., Pacheco, S., Semenova, T. A., Becerra, A. G., … Nouhra, E. R. (2014). Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover among forest types along an altitudinal gradient. *Molecular Ecology*, *23*, 2452–2472.

Giauque, H., & Hawkes, C. V. (2013). Climate affects symbiotic fungal endophyte diversity and performance. *American Journal of Botany*, *100*, 1435–1444.

Giauque, H., & Hawkes, C. V. (2016). Historical and current climate drive spatial and temporal patterns in fungal endophyte diversity. *Fungal Ecology*, *20*, 108–114.

Gurevitch, J., Curtis, P. S., & Jones, M. H. (2001). Meta-analysis in ecology. *Advances in Ecological Research*, *32*(32), 199–247.

Herrera, J., Poudel, R., Nebel, K. A., & Collins, S. L. (2011). recipitation increases the abundance of some groups of root-associated fungal endophytes in a semiarid grassland. *Ecosphere*, *2*, art50.

Hu, Y. J., Rillig, M. C., Xiang, D., Hao, Z. P., & Chen, B. D. (2013). Changes of AM fungal abundance along environmental gradients in the arid and semi-arid grasslands of Northern China. *PLoS ONE*, *8*, e57593.

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., … Roughgarden, J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, *301*, 929–933.

Kia, S. H., Glynou, K., Nau, T., Things, M., Piepenbring, M., & Macia-Vicente, J. G. (2017). Influence of phylogenetic conservatism and trait convergence on the interactions between fungal root endophytes and plants. *ISME Journal*, *11*, 777–790.

Kivlin, S. N., Emery, S. M., & Rudgers, J. A. (2013). Fungal symbionts alter plant responses to global change. *American Journal of Botany*, *100*, 1445–1457.

Kivlin, S. N., Hawkes, C. V., & Treseder, K. K. (2011). Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry*, *43*, 2294–2303.

Koerner, C. (2007). The use of 'altitude' in ecological research. *TRENDS in Ecology and Evolution*, *22*, 570–574.

Koricheva, J., & Gurevitch, J. (2014). Uses and misuses of meta-analysis in plant ecology. *Journal of Ecology*, *102*, 828–844.

Lekberg, Y., Koide, R. T., Rohr, J. R., Aldrich-Wolfe, L., & Morton, J. B. (2007). Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. *Journal of Ecology*, *95*, 95–105.

Lenoir, I., Fontaine, J., & Lounes-Hadj Sahraoui, A. (2016). Arbuscular mycorrhizal fungal responses to abiotic stresses: A review. *Phytochemistry*, *123*, 4–15.

Lindahl, B. D., Nilsson, R. H., Tedersoo, L., Abarenkov, K., Carlsen, T., Kjoller, R., … Kauserud, H. (2013). Fungal community analysis by high-throughput sequencing of amplified markers – a user's guide. *New Phytologist*, *199*, 288–299.

Looby, C. I., Maltz, M. R., & Treseder, K. K. (2016). Belowground responses to elevation in a changing cloud forest. *Ecology and Evolution*, *6*, 1996–2009.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*, 209–220.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & Grp, P. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Journal of Clinical Epidemiology*, *62*, 1006–1012.

Oksanen, J., Blanchet, J. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2016). Vegan: Community Ecology Package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

Parker, D. C. (2013). *Diversity and rate of infection of ericoid mycorrhizal fungi that colonize rhododendron maximum along an elevational gradient and their potential to degrade poly-aromatic hydrocarbons using lignin degrading enzymes*. Boone, NC: Appalachian State University.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J. L., … Grabherr, G. (2012). Recent plant diversity changes on Europe's mountain summits. *Science*, *336*, 353–355.

Peay, K. G., Kennedy, P. G., & Talbot, J. M. (2016). Dimensions of biodiversity in the Earth mycobiome. *Nature Reviews Microbiology*, *14*, 434–447.

Pichersky, E., & Gang, D. R. (2000). Genetics and biochemistry of secondary metabolites in plants: An evolutionary perspective. *Trends in Plant Science*, *5*, 439–445.

Porras-Alfaro, A., & Bayman, P. (2011). Hidden fungi, emergent properties: Endophytes and microbiomes. *Annual Review of Phytopathology*, *49*, 291–315.

van der Putten, W. H. (2012). Climate change, aboveground-belowground interactions, and species' range shifts. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 365–383.

van der Putten, W. H., Bradford, M. A., Brinkman, E. P., van de Voorde, T. F. J., & Veen, G. F. (2016). Where, when and how plant-soil feedback matters in a changing world. *Functional Ecology*, *30*, 1109–1121.

van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *365*,2025–2034.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ranelli, L. B., Hendricks, W. Q., Lynn, J. S., Kivlin, S. N., & Rudgers, J. A. (2015). Biotic and abiotic predictors of fungal colonization in grasses of the Colorado Rockies. *Diversity and Distributions*, *21*, 962–976.

Read, D. J., & Haselwandter, K. (1981). Observations on the mycorrhizal status of some alpine plant communities. *New Phytologist*, *88*, 341–352.

Redman, R. S., Sheehan, K. B., Stout, R. G., Rodriguez, R. J., & Henson, J. M. (2002). Thermotolerance generated by plant/fungal symbiosis. *Science*, *298*, 1581.

Rodriguez, R. J., White, J. F., Arnold, A. E., & Redman, R. S. (2009). Fungal endophytes: Diversity and functional roles. *New Phytologist*, *182*, 314–330.

Rudgers, J. A., & Clay, K. (2012) Microbial mutualists and biodiversity in ecosystems. In: T. Ogushi, O. Schmitz & R. D. Holt (Eds.), *Ecology and evolution of trait-mediated indirect interactions: linking evolution, community, and ecosystem* (pp. 391–413). Cambridge: Cambridge University Press

Shamseer, L., Moher, D., Clarke, M., Ghersi, D., Liberati, A., Petticrew, M., … Stewart, L. A. (2015). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015: Elaboration and explanation. *BMJ-British Medical Journal*, *349*, g7647.

Shi, Z. Y., Wang, F. Y., Zhang, K., & Chen, Y. L. (2014). Diversity and distribution of arbuscular mycorrhizal fungi along altitudinal gradients in Mount Taibai of the Qinling Mountains. *Canadian Journal of Microbiology*, *60*, 811–818.

Smith, S. E., & Read, D. J. (2008). *Mycorrhizal symbiosis*, 3rd ed. London: Academic Press.

Stahl, P. D., Parkin, T. B., & Eash, N. S. (1995). Sources of error in direct microscopic methods for estimation of fungal biomass in soil. *Soil Biology and Biochemistry*, *8*, 1091–1097.

Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N. S., Wijesundera, R., … Abarenkov, K. (2014). Global diversity and geography of soil fungi. *Science*, *346*, 1078.

Tedersoo, L., Bahram, M., Toots, M., Diedhiou, A. G., Henkel, T. W., Kjoller, R., … Koljalg, U. (2012). Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Molecular Ecology*, *21*, 4160–4170.

Tsuyuzaki, S., Hase, A., & Niinuma, H. (2005). Distribution of different mycorrhizal classes on Mount Koma, northern Japan. *Mycorrhiza*, *15*, 93–100.

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*, 1351–1363.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*, 1–48.

Wagg, C., Husband, B. C., Green, D. S., Massicotte, H. B., & Peterson, R. L. (2011). Soil microbial communities from an elevational cline differ in their effect on conifer seedling growth. *Plant and Soil*, *340*, 491–504.

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *365*, 2019–2024.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., … Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.

Wilson, H., Johnson, B. R., Bohannan, B., Pfeifer-Meister, L., Mueller, R., & Bridgham, S. D. (2016). Experimental warming decreases arbuscular mycorrhizal fungal colonization in prairie plants along a Mediterranean climate gradient. *Peerj*, *4*, e2083.

Wolfe, B. E., Richard, F., Cross, H. B., & Pringle, A. (2010). Distribution and abundance of the introduced ectomycorrhizal fungus *Amanita phalloides* in North America. *New Phytologist*, *185*, 803–816.

Worchel, E. R., Giauque, H. E., & Kivlin, S. N. (2013). Fungal symbionts alter plant drought response. *Microbial Ecology*, *65*, 671–678.

Wu, Z.-Y., Lin, W.-X., Li, J.-J., Li, B.-L., Wu, L.-K., Fang, C.-X., & Zhang, Z.-X. (2016). Effects of seasonal variance on soil microbial community composition of two typical zonal vegetation types in the Wuyi Mountains. *Journal of Mountain Science*, *13*, 1056–1065.

Zubek, S., Błaszkowski, J., Delimat, A., & Turnau, K. (2009). Arbuscular mycorrhizal and dark septate endophyte colonization along altitudinal gradients in the Tatra Mountains. *Arctic, Antarctic, and Alpine Research*, *41*, 272–279.

BIOSKETCH

This research team focuses on understanding the responses of plant-fungal symbiosis to climate change, with a concentration on mountain ecosystems.

Author Contributions: SNK and JAR conceived the study. All authors collected data. SNK and JAR analysed the data, and all authors contributed to writing the manuscript.

SUPPORTING INFORMATION

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

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