

REPORT

Dominance, diversity, and niche breadth in arbuscular mycorrhizal fungal communities

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Abstract

Classical theory identifies resource competition as the major structuring force of biotic communities and predicts that (i) levels of dominance and richness in communities are inversely related, (ii) narrow niches allow dense “packing” in niche space and thus promote diversity, and (iii) dominants are generalists with wide niches, such that locally abundant taxa also exhibit wide distributions. Current empirical support, however, is mixed. We tested these expectations using published data on arbuscular mycorrhizal (AM) fungal community composition worldwide. We recorded the expected negative relationship between dominance and richness and, to a degree, the positive association between local and global dominance. However, contrary to expectations, dominance was pronounced in

communities where more specialists were present and, conversely, richness was higher in communities with more generalists. Thus, resource competition and niche packing appear to be of limited importance in AM fungal community assembly; rather, patterns of dominance and diversity seem more consistent with habitat filtering and stochastic processes.

KEYWORDS

AM fungi, climatic zones, community richness, dominance, ecological niche, ecosystem type, metabarcoding, niche volume, soil microbes

INTRODUCTION

Community ecologists have considered the interconnections between dominance, diversity, and niche breadth for at least 50 years. Whittaker (1965) appreciated the potential links and suggested that the expression of dominance and diversity in communities mirrors patterns of competition and niche differentiation. Addressing aquatic and terrestrial communities, respectively, Margalef (1965) and McNaughton (1967) concluded that increasing species diversity is associated with decreasing dominance. Around the same time, McNaughton and Wolf (1970) showed that dominant species tend to have broader niches than subordinate species; and MacArthur and Levins (1967) argued that the total number of species in a community is proportional to the total range of the environment divided by the niche breadth of the species—hence, narrower niches allow denser “packing” of species. The emerging relationships linking broad niches with high dominance and low diversity were further confirmed by Odum (1969), who concluded that early successional communities are characterized by low diversity and broad niches and late stages by high diversity and narrow niches. At the wider scale, it has also been argued that species with broad niches tend to attain both higher local abundance and wider distributions than those with narrow niches (Brown, 1984; Hanski, 1982).

In principle, the relationships between dominance, diversity, and niche breadth encapsulate our mechanistic understanding of how resource competition structures communities (Carscadden et al., 2020). Species with wide niches use more of the niche space, achieve high abundance, leave few resources to others, and, thus, limit the number of potentially coexisting species (MacArthur & Levins, 1967). The relationships sound simple and universal, yet empirical support is mixed. A multitaxon meta-analysis by Granot and Belmaker (2020) found that a strong negative relationship between richness and niche width is indeed generally apparent. Conversely, another meta-analysis revealed that plant richness and evenness are always negatively related (i.e., richness is positively associated with dominance; Stirling & Wilsey, 2001). Likewise, there are examples of community

dominants that are habitat specialists (Boulangeat et al., 2012; Ter Steege et al., 2013), while there is mixed evidence concerning the relationship between regional distribution and local abundance (Gaston et al., 2000; Kambach et al., 2019).

The gap between theoretical expectation and observed data may reflect limitations of classical niche theory in explaining the mechanisms of community assembly. Besides resource competition, communities are shaped by other biotic interactions, such as predation (Hillebrand et al., 2007) and mutualism (Tedersoo et al., 2020), as well as interactions with the abiotic environment and stochastic, dispersal-related, and regional historical processes (Pärtel et al., 2011). Alternatively, mismatch with classical theory could reflect the specific characteristics of study objects or the scale of empirical observations, for example concerning niche dimensions (Mi et al., 2021), taxonomic resolution (Bay et al., 2020), or spatial scale (Czarniecka-Wiera et al., 2019). Because the relationships between dominance, diversity, and niche width represent universal foundations for understanding ecological community assembly, clearer insight would be highly valuable. However, collecting suitable data to study these parameters poses a major challenge, and full environmental gradients and species lists (within a given taxonomic group) have rarely been studied together in detail.

Here, we consider the relationships between dominance, diversity, and niche breadth in communities of arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota)—a widespread group of root symbionts that associate with more than 80% of plants in terrestrial ecosystems (Smith & Read, 2008). In practical terms, AM fungal communities can be extensively described using environmental DNA and metabarcoding techniques. There exists a molecular operational taxonomic unit nomenclature for AM fungi: virtual taxa (VT) are phylogenetically defined sequence groups roughly corresponding to species-level taxa (Öpik et al., 2014). Moreover, information about distributions and niches of AM fungi is accumulating (Kivlin, 2020; Kivlin et al., 2017), and realized niche optima and breadth estimates were recently published for 230 VT along 9 environmental gradients (Davison et al., 2021). However, relatively little is known about dominance, diversity, and niche

breadth relationships in AM fungal communities. Studying multiple data sets, Dumbrell et al. (2010) found that AM fungal communities were typically dominated by a single taxon. Because the identity of the dominant differed among communities, the authors concluded that they were not widespread generalists.

We used published data from Davison et al. (2021) describing AM fungal communities in 327 soil samples collected worldwide, along with environmental metadata and VT niche breadth estimates. We hypothesized that the structure of AM fungal communities matches the expectations of classical community theory: (1) community dominance and richness are negatively related; (2) narrower niches allow “packing” of more species into communities, such that levels of specialism in a community are positively related to diversity; and (3) dominants are generalists with broad niches, such that locally abundant taxa also exhibit wide distributions.

METHODS

A brief description of data collection and laboratory methods is provided in Appendix S1; for a full description see Davison et al. (2021). The final data set from Davison et al. consisted of read counts for 268 VT in 286 samples. Niche volume estimates—the product of niche breadths along a series of climatic and edaphic axes: mean annual temperature, mean annual precipitation, pH, N, P, K, Ca, Mg—were available for 230 VT (representing 86% of all recorded VT and >99% of reads).

We used several measures to define dominance, using as a basis the relative abundance of reads in samples. To describe VT-level dominance, we calculated the mean relative abundance of VT at sites where they were present and the global frequency of VT (the proportion of sites at which a VT was present). To describe community-level dominance, we investigated McNaughton’s index (the cumulative relative abundance of the two most abundant taxa; McNaughton & Wolf, 1970), the Berger-Parker index (the relative abundance of the single most abundant taxon; Berger & Parker, 1970), and the Simpson dominance index (λ ; Simpson, 1949). Since all three community-level indices produced similar correlations with other variables (Appendix S2), we show only McNaughton’s index in what follows. The natural log-transformed community-weighted mean (CWM) (weighted by VT relative abundance) niche volume was calculated to characterize whether communities on average comprised more generalist or specialist taxa, with respect to the VT niche volume estimates.

Pearson’s correlation was used to measure pairwise associations among (i) the VT-level attributes of dominance (relative abundance and global frequency) and niche volume and (ii) the community-level characteristics of dominance (McNaughton’s index), niche volume (CWM niche volume), and richness. For community-level correlations, the significance of coefficient estimates and confidence intervals were estimated using Dutilleul et al.’s (1993) correction for spatial autocorrelation. The correction was implemented using a version of the modified.ttest function from the R package SpatialPack (Vallejos et al., 2020) that was adapted to incorporate great circle distances, i.e., distances over the surface of a sphere such as the Earth; the modified function is available from Davison (2022). VT for which a niche volume estimate was not available were not included in correlations and calculations of community-level niche volume.

Several studies have shown that VT generally exhibit wide distributions with little evidence of dispersal limitation but that they do respond to environmental gradients (Davison et al., 2015; Davison et al., 2021). We therefore investigated variation in the aforementioned correlations in the different climatic zones and ecosystem types sampled by Davison et al. (2021). We used Holdridge’s (1967) system to describe broad climatic zones: tropical, subtropical, warm temperate, cool temperate, and boreal/polar (we combined polar, subpolar, and boreal because of the low sample sizes in these zones). We defined ecosystems as forest, shrubland, or grassland based on the description of the sampling location. It should be noted that these classifications were not independent—the balance of sampled ecosystems varied between climatic zones (Davison et al., 2021). Differences between climatic zones and ecosystem types in the magnitude of correlation coefficients (measuring association between dominance, niche volume, and richness) was assessed using pairwise z -tests, with false discovery rate correction for multiple comparisons (Benjamini & Hochberg, 1995).

We investigated the turnover of dominant VT in different climatic zones and ecosystem types by calculating accumulation curves (using the function specaccum from the R package vegan; Oksanen et al., 2020) for (i) all VT and (ii) dominant VT (defined as the two most abundant VT in a sample).

RESULTS

Community richness relationships with dominance and niche volume

Richness was consistently negatively related to dominance ($r = -0.80$, $p < 0.001$), i.e., AM fungal communities

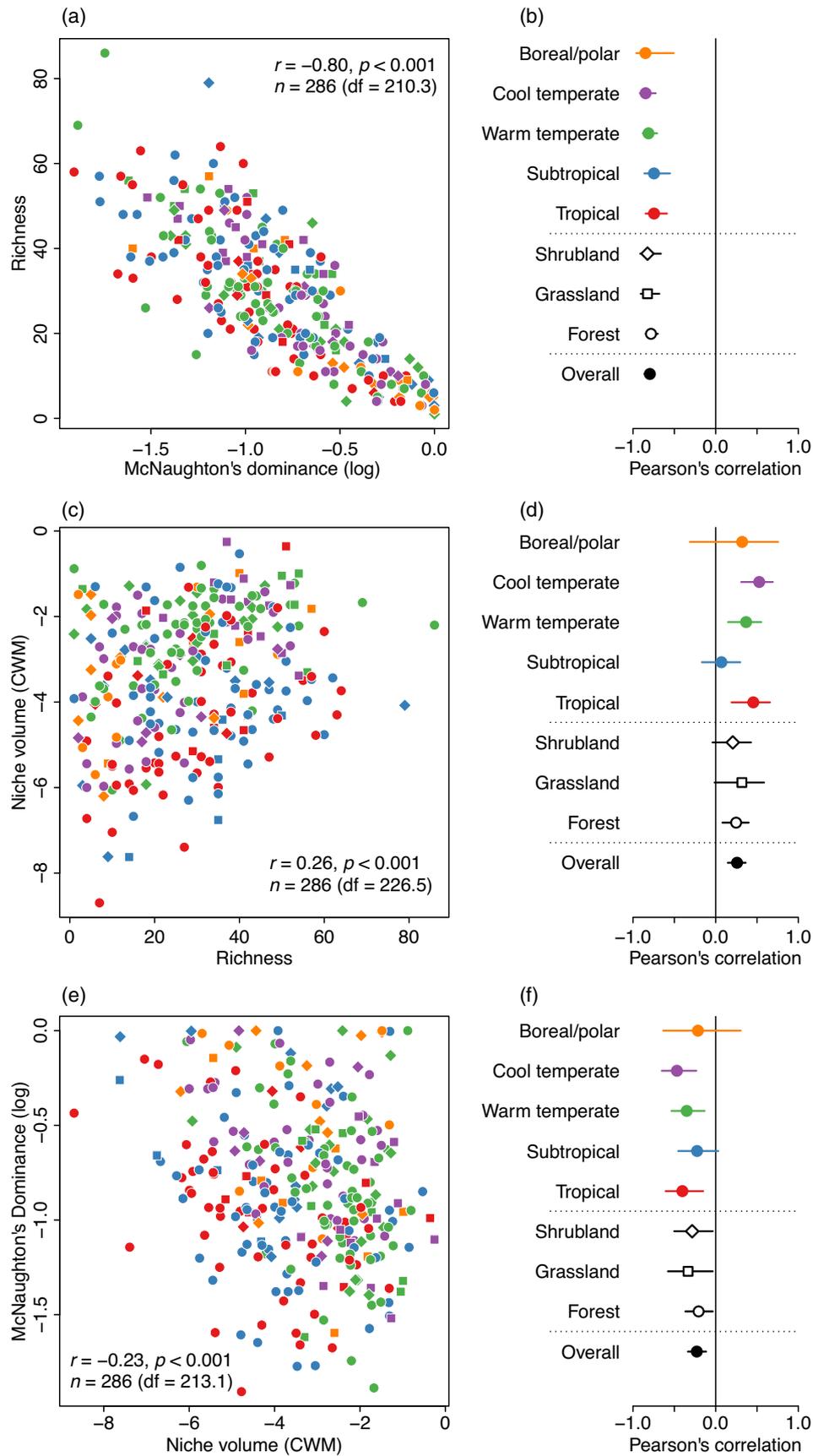


FIGURE 1 Legend on next page.

exhibiting high dominance were taxon poor (Figure 1a). Richness was positively related to community weighted mean (CWM) niche volume ($r = 0.26$, $p < 0.001$), i.e., taxon-rich communities tended to comprise generalist taxa (Figure 1b), though the strength of this relationship varied between climatic zones: correlation was somewhat weaker in the subtropical zone than in the cool temperate (unadjusted $p = 0.005$; adjusted $p = 0.05$), warm temperate (unadjusted $p = 0.06$; adjusted $p = 0.21$), or tropical zones (unadjusted $p = 0.03$, adjusted $p = 0.15$).

Community- and VT-level relationships between dominance and niche volume

There was a negative relationship between McNaughton's dominance and CWM niche volume ($r = -0.23$, $p < 0.001$), i.e., AM fungal communities that comprised on average more generalist VT were characterized by lower dominance—and this relationship was consistent throughout climatic zones and ecosystem types (Figure 1c).

Local VT abundance (mean relative abundance at sites where the VT occurred) was positively correlated with global frequency ($r = 0.61$, $p < 0.001$) (Figure 2a). However, while global frequency was also positively correlated with niche volume ($r = 0.43$, $p < 0.001$) (Figure 2b), local abundance was not ($r = -0.04$, $p = 0.56$) (Figure 2c).

Accumulation of dominants

The pattern of VT accumulation in different climatic zones changed along a latitudinal gradient, with fewest taxa accumulating in high-latitude zones and most in the tropical and subtropical zones (Figure 3a). By contrast, the accumulation of new dominant VT was overall similar in most zones but was notably steepest and least saturated in the high-latitude boreal/polar zone (Figure 3b). The accumulation of VT in different ecosystem types exhibited similar profiles (Figure 3c), but the accumulation of dominant VT differed, being steeper in shrubland and forest than in grassland (Figure 3d).

DISCUSSION

Analysis of a global data set of AM fungal diversity supported our first hypothesis that dominance and community richness are negatively correlated. This relationship was robust to the use of different measures of dominance, as well as across climatic zones and ecosystem types. A negative relationship between dominance and richness is intuitive and is generally (Granot & Belmaker, 2020), though not unanimously (Stirling & Wilsey, 2001), supported by empirical evidence. Future studies should aim to ascertain whether examples of deviation from the theory could reflect methodological issues, such as sample size and scale, or genuinely stem from the specific niche structure of particular communities.

The results did not support our second hypothesis that rich communities comprise taxa with narrow niches. Rather, the opposite relationship emerged: Communities that on average comprised more specialist taxa exhibited higher dominance and lower richness. In principle, different processes may underlie negative, positive, and neutral relationships between species resource use (niche breadth) and community species richness (Carscadden et al., 2020). A negative relationship between niche breadth and richness supports the classical theory of limiting similarity, which implies that extensive niche overlap among species precludes coexistence (MacArthur & Levins, 1967), and thus more species with narrow niche breadths can coexist in a community (“niche packing”). A positive relationship between niche breadth and richness indicates that, on average, narrow niche breadth decreases the likelihood that species can tolerate any given local environment and successfully integrate into an assemblage (i.e., habitat filtering; Cornwell et al., 2006). Alternatively, trait similarity between species with wide niches may minimize competitive differences (Chesson, 2000). The absence of a clear relationship between niche breadth and richness suggests that other factors, such as dispersal limitation and priority effects (Fukami et al., 2015), shape community composition. This analysis of AM fungal community characteristics revealed a weakly positive relationship, suggesting

FIGURE 1 Correlations between arbuscular mycorrhizal (AM) fungal community richness, dominance, and niche volume. Dominance is calculated using McNaughton's index; community niche volume is calculated as the community-weighted mean (CWM) of individual virtual taxon (VT) natural log-transformed niche volume estimates (weighted by read abundance). Pearson's correlation coefficients (whiskers show 95% confidence intervals) are shown separately for climatic zones and ecosystem types. Climatic zones and ecosystems are denoted in the scatterplots (panels a, c, and e) using the same symbol shapes and colors as were used in the correlation plots (panels b, d, and f). Coefficients (r), p -values (p), sample sizes (n), and degrees of freedom (df) are shown (the corresponding parameters for individual climatic zone and ecosystem categories are given in Appendix S2). Degrees of freedom and p -values were estimated using Dutilleul et al.'s (1993) method, which accounts for spatial autocorrelation in the variables to be correlated.

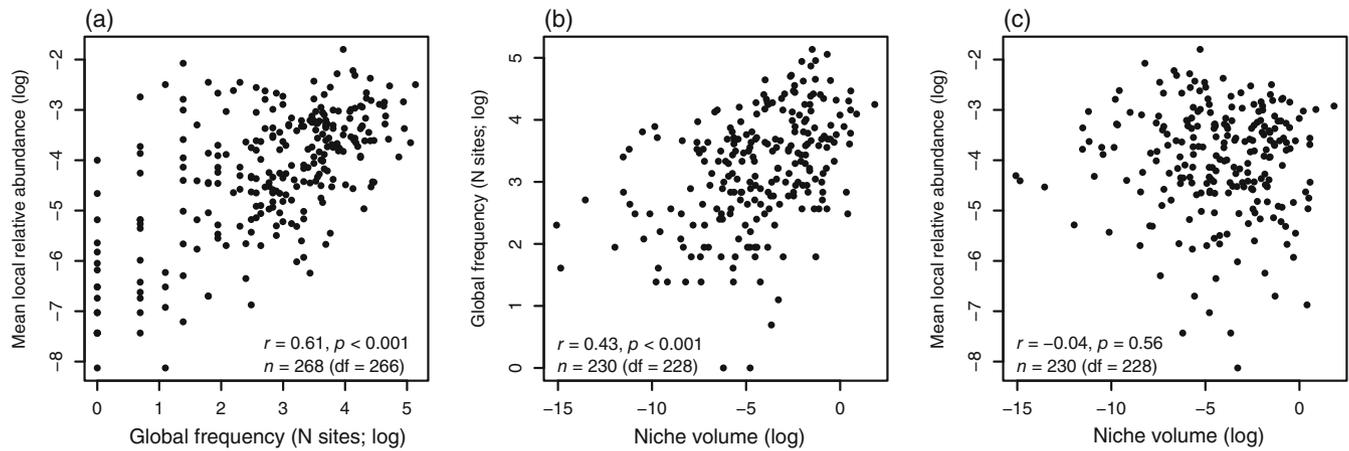


FIGURE 2 Correlations between virtual taxon (VT) local relative abundance, global frequency, and niche volume. Local relative abundance was calculated as the mean relative abundance of VT at sites where they occurred; global frequency reflects the number of sites at which a VT was recorded; niche volume estimates were taken from Davison et al. (2021). Coefficients (r), p -values (p), sample sizes (n), and degrees of freedom (df) are shown. Global frequency, relative abundance, and niche volume were natural log-transformed.

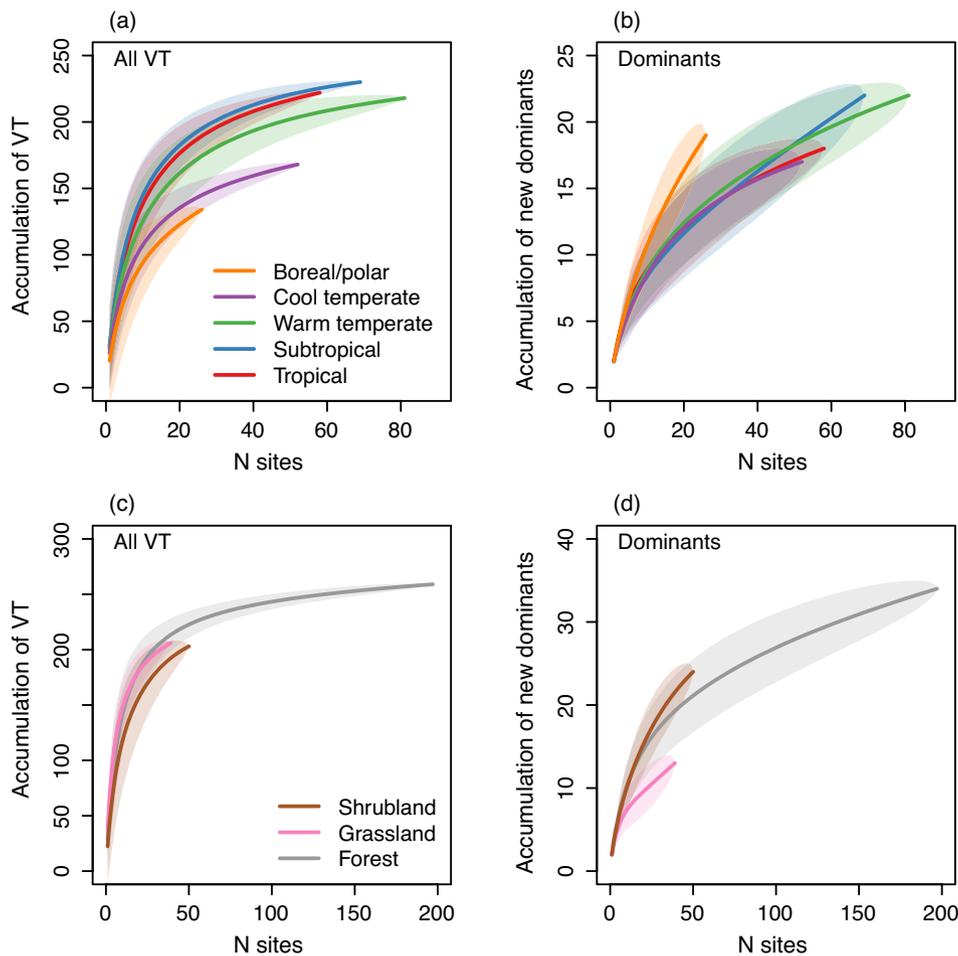


FIGURE 3 Taxon accumulation curves in different (a, b) climatic zones and (c, d) ecosystem types. Panels a and c show the accumulation of all virtual taxa (VT) in communities; panels (b) and (d) show the accumulation of dominant taxa—the two most abundant taxa in each community. Envelopes show 95% confidence intervals around estimated taxon numbers.

that communities are not shaped by niche packing but rather by some or all habitat filtering and dispersal-related and stochastic processes.

Descriptions of niches usually aim to approximate the most important dimensions of real organism–environment relationships. The niche breadth data used here were

calculated on the basis of relationships between AM fungal taxa and a range of abiotic environmental axes, measured in natural conditions. They therefore reflect relationships with many potentially important abiotic gradients as well as the context of biotic interactions. However, they do not directly assess host plant identity or characteristics; nor do they reflect the diversity of fungal functional traits related to symbiosis (e.g., nutrient provision vs stress alleviation). To delve deeper into the relationships described here and potentially generate more accurate niche breadth estimates, it would be informative to include, and distinguish, potential niche axes reflecting biotic versus abiotic environment and those that reflect resources versus local conditions.

Important roles of habitat filtering and stochastic processes are also consistent with the observed turnover of dominant taxa in different ecological conditions: The accumulation of new dominants in different climatic zones and ecosystem types showed little sign of saturating and was particularly steep in high-latitude regions. This pattern of turnover in dominants was previously noted by Dumbrell et al. (2010). Moreover, the particularly rapid turnover of dominants, relative to VT accumulation, in certain conditions (in the boreal/polar zone as well as in shrublands and forests) may indicate the effect of location-specific processes (e.g., frequency of disturbance) on the emergence of community dominants.

The results partially supported the third hypothesis, specifically the expectation, derived from Hanski (1982) and Brown (1984), that local dominance would be positively associated with global frequency. However, a firm mechanistic understanding of this relationship remains somewhat elusive: Gaston et al. (2000) identified several potential mechanisms that could be broadly classified as statistical, range positional, resource-related, and population dynamic explanations. Contrary to expectation, however, we found that niche volume was not systematically related to VT dominance (local abundance), though it was positively related to global frequency. The local abundance–niche breadth relationship should reflect local community assembly processes, and the lack of a systematic relationship may further indicate the limited importance of competition and a more prominent role of stochastic processes. On the other hand, large niche volume presumably allows widely distributed taxa to occur in communities spanning a variety of conditions (Kambach et al., 2019). Further studies could attempt to determine whether widely distributed generalist taxa are also characterized by good dispersal ability (Kivlin, 2020; Paz et al., 2021).

In conclusion, we demonstrate that the structure of AM fungal communities corresponds in part to the predictions of classical theory, with high dominance being associated with low richness and local and global

dominance being positively related. Contrary to the classical theory, there was no association between a taxon's ability to dominate and its niche volume. Moreover, we found that community-level dominance became more evident when component species exhibited greater specialism, and, conversely, higher richness became apparent when coexisting species exhibited greater generalism. The weakly positive relationship between community richness and niche breadth and the high turnover of dominant taxa imply effects of habitat filtering (Cornwell et al., 2006) and stochastic processes, such as priority effects (Fukami, 2015). We suggest that such processes, rather than classical niche-based processes, may underlie the emergence of taxon-rich generalist fungal communities with overlapping realized niches, as well as taxon-poor specialist fungal communities.

AUTHOR CONTRIBUTIONS

John Davison and Martin Zobel conceived the idea. All authors contributed to the collection of the source data set. John Davison, Martti Vasar, and Martin Zobel performed the data analysis. John Davison and Martin Zobel wrote the first manuscript draft. All authors contributed to the final manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sets utilized for this research are freely available as Supporting Information to Davison et al. (2021) at <https://doi.org/10.1111/nph.17240>. Code (Davison, 2022) is available in Figshare at <https://doi.org/10.6084/m9.figshare.19433744.v1>.

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SUPPORTING INFORMATION

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