Tansley review

Codependency between plant and arbuscular mycorrhizal fungal communities: what is the evidence?

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Summary

That arbuscular mycorrhizal (AM) fungi covary with plant communities is clear, and many papers report nonrandom associations between symbiotic partners. However, these studies do not test the causal relationship, or 'codependency', whereby the composition of one guild affects the composition of the other. Here we outline underlying requirements for codependency, compare important drivers for both plant and AM fungal communities, and assess how host preference – a pre-requisite for codependency – changes across spatiotemporal scales and taxonomic resolution for both plants and AM fungi. We find few examples in the literature designed to test for codependency and those that do have been conducted within plots or mesocosms. Also, while plants and AM fungi respond similarly to coarse environmental filters, most variation remains unexplained, with host identity explaining less than 30% of the variation in AM fungal communities. These results combined question the likelihood of predictable co-occurrence, and therefore evolution of codependency, between plant and AM fungal taxa across locations. We argue that codependency is most likely to occur in homogeneous environments where specific plant – AM fungal pairings have functional consequences for the symbiosis. We end by outlining critical aspects to consider moving forward.

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I. What is codependency and why should we care?

Understanding the assembly rules of communities is the foundation of ecological inquiry (Weiher & Keddy, 2001). Despite centuries of probing, our knowledge of assembly rules for most communities and most systems remains at an embryonic stage, or piecemeal, with vast amounts of variation unaccounted for. This is especially true for mutualistic guilds whose community assembly is complicated by not only assembly rules and processes acting on each partner separately, but also on the mutualism itself (Belyea & Lancaster, 1999).

Arbuscular mycorrhizal (AM) fungi form a well-studied microbial mutualism with most plants, due largely to their prevalence in most terrestrial ecosystems (Kivlin *et al.*, 2011; Davison *et al.*, 2015), their effects on plant performance (Hoeksema *et al.*, 2010) and the assumption that they can drive plant community diversity. Speculation on the reciprocal effects of AM fungi and plants on the community assembly of the mutualism itself has driven research over several decades (e.g. van der Heijden *et al.*, 1998; Hart *et al.*, 2001; Johnson, 2004; Hausmann & Hawkes, 2009; Klironomos *et al.*, 2010; Maherali & Klironomos, 2012; Van Geel *et al.*, 2018; Neuenkamp *et al.*, 2018). To understand assembly rules for any given plant community, it is critical to know 'who is there and why', including both plants and their AM fungal symbionts. However, despite advances in our ability to monitor AM fungal communities and increasing global coverage, the answer as to what extent AM fungal and plant community identities are codependent (i.e., causally determine each other) remains ambiguous (Zobel & Öpik, 2014).

Almost two decades ago, the 'driver' and 'passenger' hypotheses proposed that interactions among AM partners may drive their respective community composition (Hart *et al.*, 2001). Recognizing the importance of environmental filtering and dispersal limitation on both partners, two additional hypotheses were put forward. The 'habitat hypothesis' states that the composition of both plant and AM fungal communities is a function of environmental filtering, and the null 'independence hypothesis' states that the communities are uncoupled (Zobel & Öpik, 2014). Twenty years on, we have little empirical evidence to answer whether, and to what extent, any of these hypotheses apply to plant–AM fungal communities (Hempel, 2018). It is not even clear how codependency manifests within the mutualism: abundance, taxonomic richness or composition. All three metrics have been implicated in codependency, yet may not equally represent a causal relationship among partners.

1. Abundance

As obligate biotrophs, AM fungi cannot persist without compatible hosts. Thus, codependency of plant and AM fungal abundance is expected. Covariation (i.e. noncausal relationships between partner abundance) has been shown when plants and fungi colonize new land (Janos, 1980), when invaders of varying host quality replace native plants (Stinson *et al.*, 2006; Lekberg *et al.*, 2013), and when fungicides reduce AM fungal abundance and shift plant communities from more to less AM-dependent hosts

(Hartnett & Wilson, 1999). Likewise, Klironomos *et al.* (2011) estimated that mycorrhizal abundance was similar to competition and herbivory in influencing plant communities and explained between 0 and 57% of the variation in plant composition. Indeed, large-scale distributions of plants are linked to mycorrhizal status, highlighting that the ability to form mycorrhizas may be an important aspect of plant distribution (Hempel *et al.*, 2013). However, both plant and fungal abundance may respond to underlying environmental variation (Steidinger *et al.*, 2019) and thus covary via indirect environmental filtering, without being causally related. Nevertheless, it is clear that covariation, in terms of AM fungal abundance and plant-host quality, occurs and may be functionally important.

2. Taxonomic richness

Noncausal covariation among AM partner taxon richness has been shown in some (Landis *et al.*, 2004; König *et al.*, 2010; Hiiesalu *et al.*, 2014) but not all studies (Johnson *et al.*, 2010; Antoninka *et al.*, 2011; Lekberg *et al.*, 2013; Chaudhary *et al.*, 2018; Toussaint *et al.*, 2020). One may predict that more plant species provide more niches for AM fungi, or vice versa, but carbon availability, fungal competition and priority effects may have an equally strong or even stronger effect on AM fungal species richness than on plant species richness (Waldrop *et al.*, 2006; Antoninka *et al.*, 2011; Werner & Kiers, 2015). If true, it makes the relationship between plant and fungal species richness hard to predict. Both plant and AM fungal species richness may respond to environmental variation (Tedersoo *et al.*, 2014), obscuring underlying biotically driven covariation. Finally, differences in the magnitude of dispersal limitation of plants (high; Ottaviani *et al.*, 2020) and AM fungi (low; Davison *et al.*, 2018; Kivlin, 2020) coupled with variation in evolution and extinction rates may further preclude covarying plant–AM fungal species richness across habitats.

3. Composition

While variation in terms of abundance and species richness of partners is important, it fails to address 'who's there and why?'. For the purpose of this review we restrict our discussion to community compositional changes and define AM fungal–plant community codependency as the species compositional effect of each guild on one another. Furthermore, we pose that, to detect codependency, there must be a quantitative comparison between plant and fungal communities, including experimentation by varying community composition of either guild with the objective of determining the compositional effect on the other. Without this critical qualifier, it is impossible to distinguish between causal effects (codependency) from other, indirect drivers of covariation.

Understanding AM codependency is important not only to understand assembly rules in communities. Knowing whether, where and when codependency occurs is useful for managing plant performance and fitness ranging from systems spanning cropping operations to ecosystem rehabilitation (van der Heijden & Scheublin, 2007). Likewise, it may be useful for managing AM

fungal communities for improved soil health, multitrophic interactions and feedbacks (Antunes & Koyama, 2017). Indeed, AM fungal bioinoculants are increasingly being used in managed landscapes despite the lack of clear evidence to justify their use (Hart *et al.*, 2017). Finally, with the development of ever more sophisticated molecular techniques, the number of publications documenting potential differences in AM fungal community composition among host species is increasing. It is fair to ask when and where this sequencing effort is justified, or if resources should be invested elsewhere. In this review, we describe the criteria required to show codependency in nature and look to the literature for both direct and indirect evidence for codependency. Finally, we provide suggestions for future research efforts.

II. Should we expect codependency among AM communities?

There are several reasons to expect codependency among AM fungal and plant communities:

(**1**) Traits differ among plant as well as AM fungal species (Hart & Reader, 2002), which could result in some degree of species sorting based on complementarity that has functional consequences for the symbiosis.

(**2**) Plants and AM fungi may respond to similar environmental filters and may therefore predictably co-occur (Zobel & Öpik, 2014).

(**3**) Plants and AM fungi can identify and selectively reward better mutualists (Lekberg *et al.*, 2010; Hammer *et al.*, 2011; Kiers *et al.*, 2011; but see Bever *et al.*, 2009).

(**4**) Plants and AM fungi have been in association since plants colonized land more than 400 million years ago, allowing time for selection of beneficial combinations (Lutzoni *et al.*, 2018).

(**5**) Codependency is common in other mutualistic guilds between plants and soil microbes, which require some degree of host preference (Lerouge *et al.*, 1990; Bruns *et al.*, 2002).

Notwithstanding the above, there are reasons why codependency may be counterintuitive:

(**1**) AM fungi are globally distributed (Davison *et al.*, 2015; but see Bruns & Taylor, 2016) and most AM fungi do not appear to suffer dispersal limitations (Correia *et al.*, 2019; Kivlin, 2020). If every fungus has the opportunity to occur in every habitat, regardless of plant community identity, specific associations may be less common.

(**2**) The Glomeromycota have significantly fewer taxa than their hosts (<1000 AMF species vs 391 000 plant species) making it improbable that plants develop strict specificity with fungal partners.

(**3**) AM fungi are obligate biotrophs. Lack of selectivity for hosts and therefore available carbon sources may be selected for, which would reduce or even eliminate codependency (Fitter, 2005).

(**4**) Abiotic factors may be a stronger driver for AM fungal communities than host identity (Schappe *et al.*, 2017) and the factors that drive fungal and plant communities may be very

different (Fitzimmons *et al.*, 2008; Lekberg *et al.*, 2011; Liu *et al.*, 2015, Krüger *et al.*, 2017), resulting in no predictable overlap.

(**5**) The association between plants and AM fungi is dynamic where partners may experience seasonal (Escudero & Mendoza, 2005; Lara-Pérez *et al.*, 2020) or developmental variations (Husband *et al.*, 2002; Hart *et al.*, 2013).

(**6**) Finally, the role of stochasticity in determining AM fungal communities is an emerging field of study, and we have as yet a poor understanding of its relative importance (see Fig. 5).

While there are theoretical reasons to both expect and reject codependency, study after study shows some degree of nonrandom association among plant species and AM fungal communities (Eom *et al.*, 2000; Husband *et al.*, 2002; Helgason *et al.*, 2007; Öpik *et al.*, 2009; Martínez-García & Pugnaire, 2011; Davison *et al.*, 2012; Torrecillas *et al.*, 2012; Hazard *et al.*, 2013; García de León *et al.*, 2016; Sepp *et al.*, 2019). However, this alone is not evidence for codependency as taxa may simply co-occur because they respond to similar environmental filters without any co-dependent functional consequences between symbionts.

III. Requirements for codependency

We created a decision tree outlining important assumptions that are required for codependency at the regional level (Fig. 1). In our model, if plant and AM fungal associations are completely stochastic, codependency is not possible. Likewise, if the symbiotic partners respond to different environmental filters, codependency is impossible because they have no opportunity to predictably co-occur.

If plant and AM fungal compositional associations are not completely stochastic (i.e. involve deterministic processes), then nonrandom associations may result from shared environmental filters (see Fig. 2; Supporting Information Table S2). If observed nonrandom effects result exclusively from shared environmental filters (i.e. the 'Habitat Hypothesis' outlined by Zobel & Öpik, 2014), this is merely co-occurrence because variation is not driven by an interaction among partners.

In our vernacular, codependency is possible only if the partners both pass environmental filters *and* their community composition is dependent on the other's. In practice, this can only be shown through experimental manipulation – by holding AM fungal community constant and varying plant community or vice versa, *sensu* Zobel & Öpik (2014). Simply correlating AM fungal communities and plant communities does not remove the possibility that both partners are responding to an underlying filter. The ultimate test for codependency would be akin to Koch's postulates: 'if components of one community are removed, do we observe changes in the other community? And upon reinstatement of the removed community members, does the other community return to its original state?'

Implicit in our discussion is that for codependency to be possible, partners must 'select' for each other predictably based on specific needs. Underlying this idea is the rather large assumption that variation in fungal and plant traits has consequences for the symbiosis, and, consequently, plant and fungal community assembly (see Box 1).
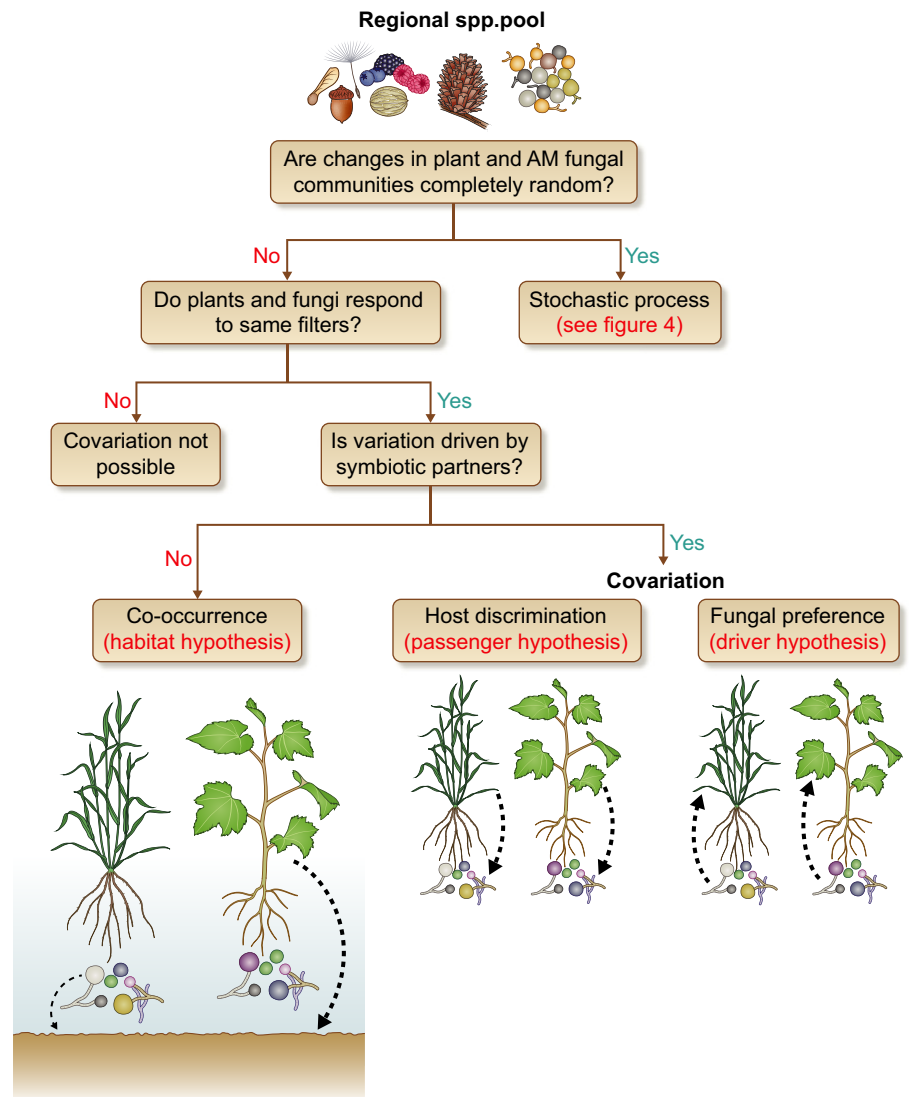
Fig. 1 Unpacking the 'host-effect'. Codependency among AM fungal and plant communities describes the species compositional effect of each guild on one another. It is driven by the *interaction among partners*, rather than simply a shared response to environmental filters, in which case we refer to it as co-occurrence. Whether it is driven by changes in fungal or plant communities (i.e. driver vs passenger hypotheses) requires further examination. Our discussion here concerns the nonrandom distribution of partners at a regional or local scale where dispersal limitations and evolutionary history do not apply and where plants and AM fungi have the potential to interact. This figure was created using BIORENDER (https://biorender.com/).

IV. When and where has codependency been observed?

We surveyed the literature to test for evidence of codependency (see Supplementary Material, Table S1). From an initial list of 397 papers, 158 looked at covariation among AM partners to varying extents. Most papers (84) assessed shifts in AM fungal communities across vegetation types that differed as a result of either succession or environmental gradients. Other papers (64) showed co-occurrence by characterizing the plant community in relationship to the AM fungal community. Only 10 papers qualified as evidence for true 'codependency'; that is, a quantitative comparison between plant and fungal communities, including experimentation by varying community composition of either guild with the objective of determining the compositional effect on the other. Of these, nine showed evidence for codependency. Most of these studied AM fungal community as a dependent factor – effectively testing for the 'passenger' hypothesis. A few studies manipulated AM fungal diversity alone (Stampe & Daehler, 2003; Koziol & Bever, 2017), or both plant and fungal communities (Wagg *et al.*, 2015; Koziol &

Bever, 2019). Regardless of which guild was manipulated, plants and AM fungal communities were codependent. The only study that failed to show codependency (Urcelay *et al.*, 2009) removed plant functional groups from a shrubland but found no effect on AM fungal community composition. However, in this case, AM fungal communities were assessed via the soil spore bank, which does not always reflect contemporary AM fungal communities accurately (Hempel *et al.*, 2007).

The few studies that exist indicate that codependency can occur, but more studies are needed to substantiate these findings. Furthermore, all of the studies that quantified codependency were conducted in single locations or in controlled mesocosm experiments, which prompts the question of whether codependency can also occur *across* spatio-temporal scales?

V. Is codependency scale- and resolution-dependent?

Presumably, studies (our own included) that ask whether AM fungal communities differ among host plant species are conducted because we believe that nonrandom distributions of AM fungi
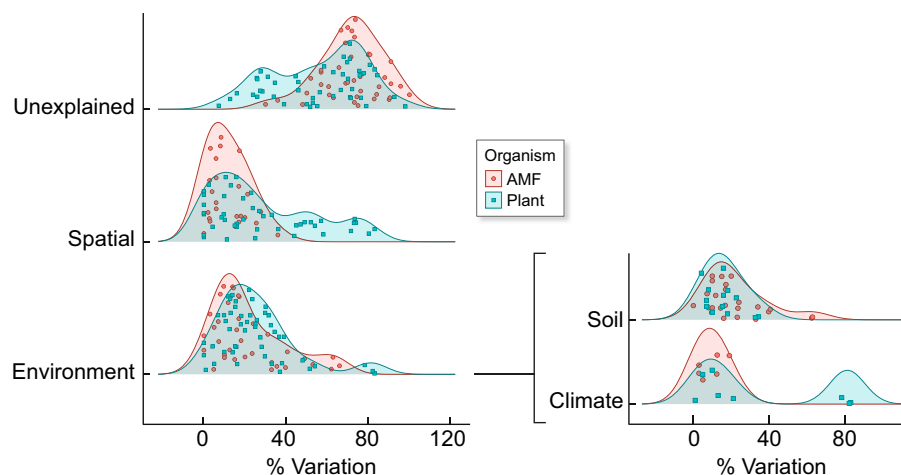
Fig. 2 Comparisons of filters structuring plant and AM fungal communities. To determine if plants and AM fungal communities respond to similar filters, we searched the literature for studies that both quantified beta diversity and used variance partitioning to identify environmental and spatial filters. Our search was not exhaustive, and direct comparisons should be made with caution given that most studies were focused on either AM fungi or plants, but not both. For example, soil abiotic conditions are often highlighted as important for structuring AM fungal communities (e.g. Dumbrell *et al.*, 2010; Lekberg *et al.*, 2011; Davison *et al.*, 2015), whereas competition, herbivory and climate have been focal in plant ecology (e.g. Maron & Crone, 2006; Aschehoug *et al.*, 2016; König *et al.*, 2017). Nonetheless, our attempt illustrates an approach to compare the proportion and identity of potential drivers for both plant (blue) and AM fungal (red) communities. In this figure, the *y*-axis represents the probability of finding an observation reporting different variation values (*x*-axis). Here, each point represents an individual study. Not surprisingly, we find that the total variation (i.e. unique plus shared variation) explained by both environmental and spatial factors varies considerably among studies within both communities but is often quite low, resulting in high unexplained variation within most studies. Our preliminary findings also indicate that plants and AM fungal communities have the potential to respond similarly, albeit using quite coarse filters. Information about which studies were included and the data we extracted is given in Supporting Information Table S2.

among hosts are important; yet few studies proceed to test this importance. Although there is preliminary evidence for codependency among plants and AM fungal species at the local scale, we may be missing the full extent of codependency among partners by failing to consider the various levels at which codependency occurs. Although a few studies have tested for true codependency, studies assessing host preference may provide insight into the likelihood of finding codependency, as nonrandom associations between AM fungal communities and plant species are a prerequisite for codependency. To understand if the likelihood of codependency depends on spatial scale and taxonomic resolution, we asked: Does the relative importance of host identity for structuring AM fungal communities change across scales and when using different taxonomic resolution for plants and AM fungi?

1. Spatial scale

Drivers of community assembly for both plants (Girdler & Connor Barrie, 2008; Legendre *et al.*, 2009) and AM fungi (Fitzsimons *et al.*, 2008) depend on the scale of inquiry. Our ability to detect codependency may therefore be scale-dependent, reflecting both dispersal ability of partners across spatial scales as well as their response to environmental gradients (Figs 2, 3). To quantify the importance of spatial scale, we extracted information from published papers in which the influence of the host for structuring AM fungal communities had been quantified using variance partitioning (Table S2). We considered three levels of scale: Plot (samples came from one field or forest plot); Local (multiple plots within one area (<30 km)); and Regional (hundreds to thousands of kilometers). We did not include Global because the two studies

that have done this (Kivlin *et al.*, 2011; Davison *et al.*, 2015) did not specifically test for plant species or communities, but involved coarser scales of host signal (biomes and shared plant phylogenetic history respectively). We identified 20 papers that fit our criteria (Table S2). Host identity explained on average < 20% of the total variation (including host variation shared with spatial and environmental variation) in AM fungal communities (Fig. 3). The amount of variation explained by host did not differ across scales, suggesting that host effects are independent of spatial scale. While this might seem counterintuitive, because large scales are often associated with high turnover in plant species, small areas can also be environmentally heterogeneous (e.g. Dumbrell *et al.*, 2010) and those environmental filters may outweigh the effect of host identity.

2. Taxonomic resolution

Codependency may be masked by the resolution used to identify interacting plants and AM fungi. The species concept for AM fungi has been challenged (Bruns & Taylor, 2016) and it is increasingly recognized that morphological and functional variation can sometimes be greater within than among AM fungal species (Mulkvold *et al.*, 2004; Koch *et al.*, 2006, 2017). Conversely, studies have shown that plant and fungal responses to each other and environmental factors can occur at coarser levels, including functional groups (Li & Shipley, 2018), life history strategies (Öpik *et al.*, 2009) and plant family (Yang *et al.*, 2017). Recently, AM fungi were shown to differ consistently among plants belonging to different functional groups and life history strategies (Davison *et al.*, 2020). Codependency may be more widespread if the

Box 1 Do AM partners select each other?

If codependency among AM fungi and hosts requires partner selection, then these conditions are necessary:
(**1**) AM fungi are *multifunctional*
(**2**) Fungal *traits are not conserved* in all taxa
(**3**) Fungal *traits have consequences* for the symbiosis
(**4**) *Plants can discriminate* among AM fungi and preferentially associate with fungi whose traits are compatible with their requirements (i.e. nutrient uptake vs pathogen protection). OR
(**5**) *Fungi can discriminate* among hosts and preferentially associate with plants whose traits are most compatible (i.e. seasonality, carbon levels).
 There is evidence for some, but not all, of these assumptions. It is clear that AM fungal taxa differ significantly in traits associated with fungal growth (Hart & Reader, 2002; Koch *et al.*, 2017). However, evidence for specific traits conferring functional attributes to the symbiosis is weak (Aguilar-Trigueros *et al.*, 2015). For instance, there is some evidence that fungi with high levels of sporulation may suppress host growth (Kokkoris & Hart, 2019), and evidence for differential nutrient foraging habits among AM fungi (Smith *et al.*, 2000; Jansa *et al.*, 2008). Maherali & Klironomos (2007) and Sikes *et al.* (2009) showed a phylogenetic signal for the ability of AM fungi to confer disease resistance vs nutrient uptake, but such studies are limited in the breadth of taxa they have examined.
 Trait differentiation is only relevant for codependency if partners have the ability both to discriminate and to choose among partners. Despite indications that selection can occur in simple systems (Kiers *et al.*, 2011), there is no evidence that it occurs in complex root communities which are the norm in natural systems (Bever *et al.*, 2009). Whether it is the fungus 'choosing' a host or hosts based on carbon allocation or the host 'choosing' fungal partners based on fungal functions ('driver' or 'passenger' hypothesis *sensu* Hart *et al.*, 2001) is secondary to our discussion. What matters for codependency is that there is selection on either part. Unless a mechanism for discrimination exists, codependency based on our definition is not possible.
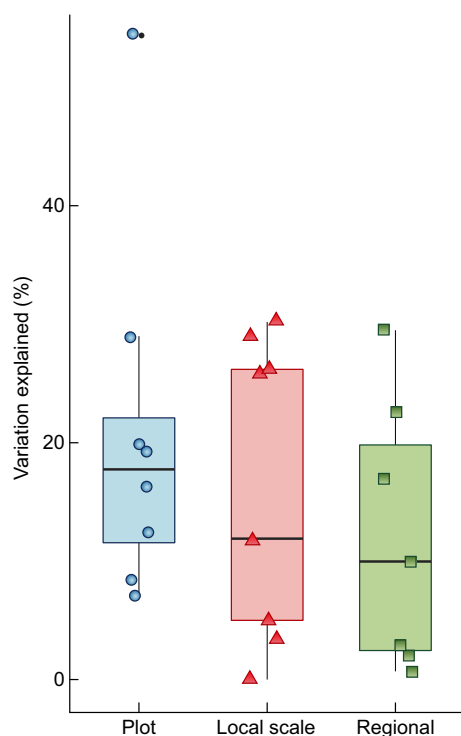

Fig. 3 Host effects across scales. Box plots showing the proportion of the total variance explained by host plants at plot, local and regional scales. Different symbols indicate values from individual studies and information about studies included are given in Supporting Information Table S2, and methods for selecting studies are also given in the Supporting Information. The bold line within each the boxplot represents the median value and whiskers represent standard error. The black dots beyond the whiskers represent outliers.

symbiosis does not require particular species of plants and fungi, but instead respond to specific traits that could be phylogenetically conserved.

To determine if the relative importance of host identity on AM fungal communities depends on the phylogenetic resolution of both partners, we used GenBank AM fungal accessions collected up to 13 January 2020 and associated metadata on host species, environmental conditions and location (see Methods S1, Table S3). We restricted our analyses to host species that occurred in at least two locations, which resulted in a total of 124 plant species, 134 genera and 55 families. We partitioned the proportion of the total variance due to environment (based on climate variables from WORLDCLIM v.2.0), space and host identity using the varpart function in VEGAN v.2.5-6 (Oksanen *et al.*, 2020) in R v.3.6.3 (R Core Team, 2020; see Supporting Information). We then analyzed all pairwise combinations of AM fungal virtual taxa (VT), genus and family by plant species, genus and family. For more detail, see the Supporting Information.

We found that host identity explained the greatest proportion of variation in AM fungal communities at the plant species × VT level (Fig. 4) and declined at coarser taxonomic scales. However, the decline when moving from species to genera to family was much greater for plants than for AM fungi (Fig. 4). These effects were robust even when the overall dataset was down-sampled to account for unequal sampling effort among plant species/genera/families. This makes sense if symbiotic traits are more conserved in AM fungi compared to plants, which seems to be the case (Hart & Reader, 2002; Powell *et al.*, 2009; Salguero-Gomez *et al.*, 2016). Our results agree with Sepp *et al.* (2019) who found that plant species explained substantially more variation in fungal community composition than functional group or mycorrhizal status.

So, does the relative importance of host identity for structuring AM fungal communities change across scales and when using different taxonomic resolution for plants and AM fungi? Overall, spatial scale may be a poor proxy for estimating the likelihood of seeing host effects on AM fungal communities – and thus the
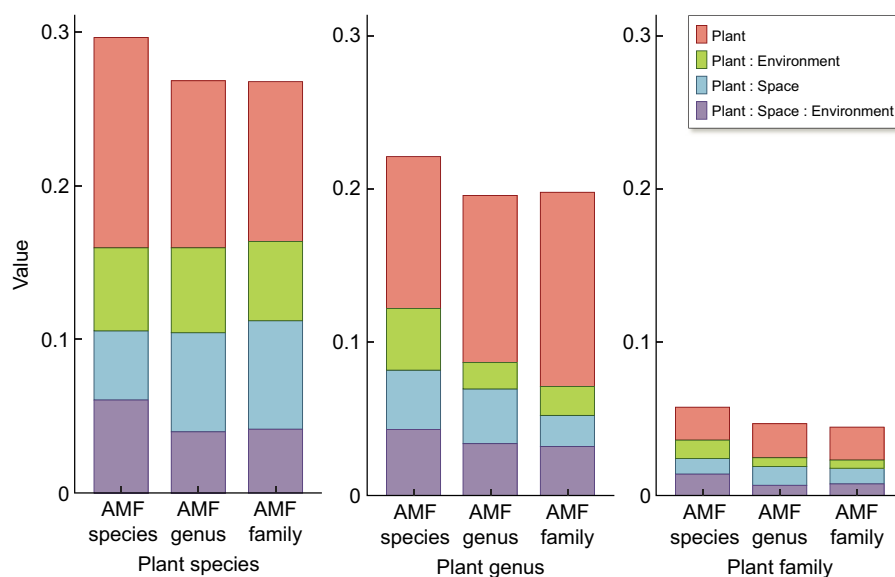
Fig. 4 Variation in AM fungal communities explained by plants. Variation in AM fungal communities (at species, genus and family resolution) explained by plant hosts alone (red) and the covariation of plant host and environment (green), space (blue), or environment and space (violet) when grouped into species, genera and families. Variation was determined by the *varpart* function in VEGAN on plant taxa that occurred in two or more geographic locations.

possibility of codependency – because host effects appear to be independent of spatial scale. This may be because environmental gradients may not correlate with spatial scale: strong gradients can be present at small spatial scale (e.g. Dumbrell *et al.*, 2010) and large scales can be environmentally homogeneous. Thus, the potential for codependency should be evaluated based on the importance of host ID relative to other potential drivers of both plants and AM fungal communities.

Codependency may be most likely to occur in homogeneous, stable environments (irrespective of spatial scale) where plants and AM fungi have co-occurred for a long time. Furthermore, for codependency to occur, the specific plant–AM fungal pairing must have consequences for the symbiosis, and this in turn is most likely if co-occurring plants as well as AM fungi differ in traits. Based on differences in resolution and traits, this may be predictable based on the species or possibly genera richness of plants and family richness of AM fungi.

VI. Unexplained variation: if not codependency then what?

Ultimately, understanding the role of codependency in AM community assembly must include an understanding of deterministic plus stochastic processes. As is true for most communities, AM fungal communities result from stochastic and deterministic processes (Dumbrell *et al.*, 2010; Lekberg *et al.*, 2012). Most research of the factors acting on AM communities, however, concerns deterministic factors. For example, both AM fungal and plant communities are filtered by abiotic conditions such as soil chemistry and climate (Fig. 2; Table S2). Species interactions, including 'host preference', are also deterministic factors. However, after accounting for deterministic processes, more than half of the variation among plant and AM fungal communities remains unexplained (Fig. 2).

Stochastic processes may therefore account for most of the variation for both plant and fungal taxa. In addition, these processes

may act differently on AM partners, contributing to more unexplained variation on the symbiosis. For example, *ecological drift* (changes due to birth and death) (Bencherif *et al.*, 2016) and *priority effects* are stochastic processes that may equally affect plants and AM fungi (Körner *et al.*, 2008; Mummey *et al.*, 2009; Werner & Kiers, 2014). *Dispersal limitations*, however, may be more important for plant community assembly (Chase & Myers, 2011), because AM fungi can disperse more efficiently than plants (García de León *et al.*, 2016).

If codependency is a product of biotic/abiotic selection, then communities dominated by stochastic processes are less likely to exhibit codependency. If we can predict which systems are more likely to be determined by stochastic processes, we can similarly predict where codependency may be more likely. One clue may be stress. In general, more stressful conditions should impose stronger environmental filters on the species pool, leaving fewer taxa to interact. Li & Shipley (2018) observed that with increased stress and/or disturbance, plant communities were progressively driven by deterministic rather than by stochastic processes. A similar trend has been observed for AM fungal communities (Shi *et al.*, 2014). Thus, we may predict stressful environments will exhibit increased codependency as the contribution of stochastic processes decreases (Fig. 5).

VII. Recommendations for future studies

Understanding where and when codependency occurs is currently inhibited by our inability to extract necessary information from existing studies. Changes to experimental approaches and reporting may allow for better comparisons across future studies. We outline the most important ones below:

• Design experiments to test for codependency, not just nonrandom associations: to identify codependency in natural communities, we need first to characterize the plant and fungal communities as well as edaphic properties and relate the three. We must then modify either the plant or the AM fungal community and assess
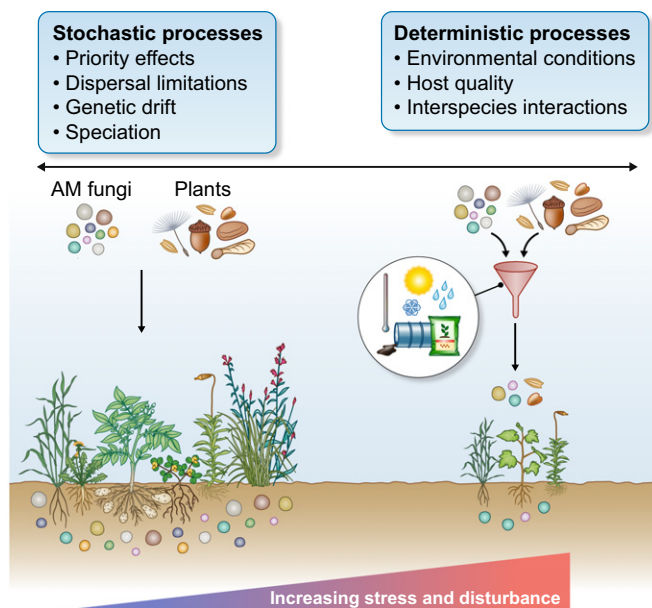
Fig. 5 Deterministic and stochastic processes in shaping of AM fungal and plant communities. Deterministic and stochastic processes represent extremes along a continuum (Caruso *et al.*, 2012). In an AM system the abiotic soil environment is the first filter on nascent AM fungal communities. Similar to AM fungi, plants are also filtered by abiotic conditions upon arrival (Myers *et al.*, 2011). As stress and/or disturbance increase, plant community composition is driven by deterministic processes (Li & Shipley, 2018). Both deterministic and stochastic processes are important for shaping community assembly, while the environment defines which of the two will dominate the process. This figure was created using BioRender (https://biorender.com/).

responses that are independent of environmental shifts. Preferably studies should be designed so we can elucidate the relative importance of taxonomic resolution and scale.

• Relate codependency to both plant and fungal traits wherever possible: this will allow us to detect patterns between particular pairings of plants and fungi, which could allow for predictions and an understanding of underlying mechanisms.

• Quantify and report variation due to factors in addition to *P*-values: given the increased power associated with new sequencing techniques, we are likely to see significant differences among plant and fungal communities, but effect size is as, or perhaps more, important for understanding codependency.

• Statistical analyses are increasingly sophisticated, and choice of analysis may affect results. To avoid any confusion, always provide the raw data, including archived DNA sequences, as well scripts of analyses so that analyses can be repeated.

VIII. Conclusion

The evidence for nonrandom associations between AM fungal and plant communities is undeniable. That they change together is not the question; how and why they change remains to be answered. Despite abundant reports of 'host preference' we cannot yet say that plants and/or fungi are self-selecting, that is that there is codependency in nature.

In addition to determining how and why (and possibly where and when), perhaps the bigger question is does codependency matter?

Given the large proportion of stochasticity observed within both plant and AM fungal communities and relatively weak apparent role of host identity in shaping AM fungal communities, does it make sense to keep looking for codependency? To answer this question, we need to move beyond sequencing roots of plant species to look at nonrandom distributions of AM fungal communities. It will require rigorous manipulations and characterizations of fungal *and* plant communities as well as environmental context as these three tenets are essential for understanding codependency. It also necessitates estimates of what proportion of variance codependency explains rather than simply reporting statistical significance. That is, the fact that host identity significantly affects AM fungal composition is less relevant if it explains little variation.

Ultimately what may matter is that plant and fungal communities need each other irrespective of 'who is there'. We may be interested in what drives AM fungal communities, but if the main goal is to relate this to the distribution, abundance and composition of plant communities, perhaps compositional variation in AM fungal communities represents a kind of 'fine tuning' and we are better off focusing on factors that structure their abundance? Whether it is the AM fungi (driver hypothesis) or the host communities (passenger hypothesis) controlling the dynamic may be less important than originally supposed. Plants and AM fungi probably change each other, although the details about how much and when remain to be seen. As for whether it matters for ecosystems is up for debate.

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References

Aguilar-Trigueros CA, Hempel S, Powell JR, Anderson IC, Antonovics J, Bergmann J, Cavagnaro TR, Chen B, Hart MM, Klironomos J. 2015. Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews* **29**: 34–41.

Antoninka A, Reich PB, Johnson NC. 2011. Seven years of carbon dioxide enrichment, nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland ecosystem. *New Phytologist* **192**: 200–214.

Antunes PM, Koyama A. 2017. Mycorrhizas as nutrient and energy pumps of soil food webs: multitrophic interactions and feedbacks. In: Johnson NC, Gehring C & Jansa J, eds. *Mycorrhizal mediation of soil, fertility, structure, and carbon storage.* Amsterdam, the Netherlands: Elsevier, 149–173.

Aschehoug ET, Brooker R, Atwater DZ, Maron JL, Callaway RM. 2016. The mechanisms and consequences of interspecific competition among plants. *Annual Review of Ecology, Evolution, and Systematics* **47**: 263–281.

Belyea LR, Lancaster J. 2016. Assembly rules within a contingent ecology. *Oikos* 86: 402–416.

Bencherif K, Boutekrabt A, Dalpé Y, Lounès-Hadj SA. 2016. Soil and seasons affect arbuscular mycorrhizal fungi associated with *Tamarix* rhizosphere in arid and semi-arid steppes. *Applied Soil Ecology* 107: 182–190.

Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* 12: 13–21.

Bruns TD, Bidartondo MI, Taylor DL. 2002. Host specificity in ectomycorrhizal communities: what do the exceptions tell us? *Integrative and Comparative Biology* 42: 352–359.

Bruns TD, Taylor JW. 2016. Comment on 'Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism'. *Science* 351: 826.

Caruso T, Powell JR, Rillig MC. 2012. Compositional divergence and convergence in local communities and spatially structured landscapes. *PLoS ONE* 7: 1115–1124.

Chase JM, Myers JA. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351–2363.

Chaudhary VB, Cuenca G, Johnson NC. 2018. Tropical–temperate comparison of landscape-scale arbuscular mycorrhizal fungal species distributions. *Diversity and Distributions* 24: 116–128.

Correia M, Rodríguez-Echeverría S, Timóteo S, Freitas H, Heleno R. 2019. Integrating plant species contribution to mycorrhizal and seed dispersal mutualistic networks. *Biology Letters* 15: 20180770.

Davison J, Ainsaar L, Burla S, Diedhiou AG, Hiiesalu I, Jairus T, Johnson NC, Kane A, Koorem K, Kochar M *et al.* 2015. Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. *Science* 127: 970–973.

Davison J, García de León D, Zobel M, Moora M, Bueno CG, Barceló M, Gerz M, León D, Meng Y, Pillar VD *et al.* 2020. Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. *New Phytologist* 226: 1117–1128.

Davison J, Moora M, Öpik M, Ainsaar L, Ducousso M, Hiiesalu I, Jairus T, Johnson N, Jourand P, Kalamees R *et al.* 2018. Microbial island biogeography: isolation shapes the life history characteristics but not diversity of root-symbiotic fungal communities. *ISME Journal* 12: 2211–2224.

Davison J, Öpik M, Zobel M, Vasar M, Metsis M, Moora M. 2012. Communities of arbuscular mycorrhizal fungi detected in forest soil are spatially heterogeneous but do not vary throughout the growing season. *PLoS ONE* 7: e41938.

Dumbrell AJ, Nelson M, Helgason T, Dytham C, Fitter AH. 2010. Relative roles of niche and neutral processes in structuring a soil microbial community. *ISME Journal* 4: 337–345.

Eom A-H, Hartnett DC, Wilson GWT. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. *Oecologia* 122: 435–444.

Escudero V, Mendoza R. 2005. Seasonal variation of arbuscular mycorrhizal fungi in temperate grasslands along a wide hydrologic gradient. *Mycorrhiza* 15: 291–299.

Fitter AH. 2005. Darkness visible: reflections on underground ecology. *Journal of Ecology* 93: 231–243.

Fitzsimons MS, Miller RM, Jastrow JD. 2008. Scale-dependent niche axes of arbuscular mycorrhizal fungi. *Oecologia* 158: 117–127.

García de León D, Moora M, Öpik M, Jairus T, Neuenkamp L, Vasar M, Bueno CG, Gerz M, Davison J, Zobel M. 2016. Dispersal of arbuscular mycorrhizal fungi and plants during succession. *Acta Oecologica* 77: 128–135.

Girdler EB, Connor Barrie BT. 2008. The scale-dependent importance of habitat factors and dispersal limitation in structuring Great Lakes shoreline plant communities. *Plant Ecology* 198: 211–223.

Hammer EC, Pallon J, Wallander H, Olsson PA. 2011. Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability. *FEMS Microbiology Ecology* 76: 236–244.

Hart MM, Antunes PM, Abbott L. 2017. Unknown risks to soil biodiversity from commercial fungal inoculants. *Nature Ecology and Evolution* 1: 115.

Hart MM, Gorzelak M, Ragone D, Murch SJ. 2014. Arbuscular mycorrhizal fungal succession in a long-lived perennial. *Botany-Botanique* 92: 313–320.

Hart MM, Reader RJ. 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist* 153: 335–344.

Hart MM, Reader RJ, Klironomos JN. 2001. Life-history strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics. *Mycologia* 93: 1186–1194.

Hartnett DC, Wilson GWT. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80: 1187–1195.

Hausmann NT, Hawkes CV. 2009. Plant neighborhood control of arbuscular mycorrhizal community. *New Phytologist* 183: 1188–1200.

Hazard C, Gosling P, van der Gast CJ, Mitchell DT, Doohan FM, Bending GD. 2013. The role of local environment and geographical distance in determining community composition of arbuscular mycorrhizal fungi at the landscape scale. *ISME Journal* 7: 498–508.

der Heijden MGA, Boller T, Wiemken A, Sanders IR. 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79: 2082–2091.

Helgason T, Merryweather JW, Young JPW, Fitter AH. 2007. Specificity and resilience in the arbuscular mycorrhizal fungi of a natural woodland community. *Journal of Ecology* 95: 623–630.

Hempel S. 2018. Passengers and drivers of arbuscular mycorrhizal fungal communities at different scales. *New Phytologist* 220: 952–953.

Hempel S, Götzenberger L, Kühn I, Michalski SG, Rillig MC, Zobel M, Moora M. 2013. Mycorrhizas in the Central European flora – relationships with plant life history traits and ecology. *Ecology* 94: 1389–1399.

Hempel S, Renker C, Buscot F. 2007. Differences in the species composition of arbuscular mycorrhizal fungi in spore, root and soil communities in a grassland ecosystem. *Environmental Microbiology* 9: 1930–1938.

Hiiesalu I, Pärtel M, Davison J, Gerhold P, Metsis M, Moora M, Öpik M, Vasar M, Zobel M, Wilson SD. 2014. Species richness of arbuscular mycorrhizal fungi: associations with grassland plant richness and biomass. *New Phytologist* 203: 233–244.

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC *et al.* 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* 13: 394–407.

Husband R, Herre EA, Turner SL, Gallery R, Young JPW. 2002. Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. *Molecular Ecology* 11: 2669–2678.

Janos DP. 1980. Mycorrhizae influence tropical succession author. *Bioitropica* 12: 56–64.

Jansa J, Smith FA, Smith SE. 2008. Are there benefits of simultaneous root colonization by different arbuscular mycorrhizal fungi? *New Phytologist* 177: 779–789.

Johnson D, Anderson IC, Williams A, Whitlock R, Grime P. 2010. Plant genotypic diversity does not beget root-fungal species diversity. *Plant and Soil* 336: 107–111.

Johnson D, Vandenkoornhuyse PJ, Leake JR, Gilbert L, Booth RE, Grime JP, Young JPW, Read DJ. 2004. Plant communities affect arbuscular mycorrhizal fungal diversity and community composition in grassland microcosms. *New Phytologist* 161: 503–515.

Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A *et al.* 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333: 880–882.

Kivlin SN. 2020. Global mycorrhizal fungal range sizes vary within and among mycorrhizal guilds but are not correlated with dispersal traits. *Journal of Biogeography* doi: 10.1111/jbi.13866.

Kivlin SN, Hawkes CV, Treseder KK. 2011. Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry* 43: 2294–2303.

Klironomos JN, Zobel M, Tibbett M, Stock WD, Rillig MC, Parrent JL, Moora M, Koch AM, Facelli JM, Facelli E *et al.* 2010. Forces that structure plant communities: quantifying the importance of the mycorrhizal symbiosis understanding. *New Phytologist* 189: 366–370.

Koch AM, Antunes PM, Maherali H, Hart MM, Klironomos JN. 2017. Evolutionary asymmetry in the arbuscular mycorrhizal symbiosis: conservatism in fungal morphology does not predict host plant growth. *New Phytologist* 214: 1330–1337.

Koch AM, Croll D, Sanders IR. 2006. Genetic variability in a population of arbuscular mycorrhizal fungi causes variation in plant growth. *Ecology Letters* 9: 103–110.

Kokkoris V, Hart MM. 2019. The role of in vitro cultivation on symbiotic trait and function variation in a single species of arbuscular mycorrhizal fungus. *Fungal Biology* **123**: 732–744.

König C, Weigelt P, Kreft H. 2017. Dissecting global turnover in vascular plants. *Global Ecological Biogeography* **26**: 228–242.

König S, Wubet T, Dormann CF, Hempel S, Renker C, Buscot F. 2010. TaqMan real-time PCR assays to assess arbuscular mycorrhizal responses to field manipulation of grassland biodiversity: effects of soil characteristics, plant species richness, and functional traits. *Applied and Environmental Microbiology* **76**: 3765–3775.

Körner C, Stöcklin J, Reuther-Thiébaud L, Pelaez-Riedl S. 2008. Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist* **177**: 698–705.

Koziol L, Bever JD. 2017. The missing link in grassland restoration: arbuscular mycorrhizal fungi inoculation increases plant diversity and accelerates succession. *Journal of Applied Ecology* **54**: 1301–1309.

Koziol L, Bever JD. 2019. Mycorrhizal feedbacks generate positive frequency dependence accelerating grassland succession. *Journal of Ecology* **107**: 622–632.

Krüger C, Kohout P, Janoušková M, Püschel D, Frouz J, Rydlová J. 2017. Plant communities rather than soil properties structure arbuscular mycorrhizal fungal communities along primary succession on a mine spoil. *Frontiers in Microbiology* **8**: 719.

Landis FC, Gargas A, Givnish TJ. 2005. The influence of arbuscular mycorrhizae and light on Wisconsin (USA) sand savanna understories 2. Plant competition. *Mycorrhiza* **15**: 555–562.

Lara-Pérez LA, Oros-Ortega I, Córdova-Lara I, Estrada-Medina H, O'Connor-Sánchez A, Góngora-Castillo E, Sáenz-Carbonell L. 2020. Seasonal shifts of arbuscular mycorrhizal fungi in *Cocos nucifera* roots in Yucatan, Mexico. *Mycorrhiza* **30**: 269–283.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun I, Hep F. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* **90**: 663–674.

Lekberg Y, Gibbons SM, Rosendahl S, Ramsey PW. 2013. Severe plant invasions can increase mycorrhizal fungal abundance and diversity. *ISME Journal* **7**: 1424–1433.

Lekberg Y, Hammer EC, Olsson PA. 2010. Plants as resource islands and storage units – adopting the mycocentric view of arbuscular mycorrhizal networks. *FEMS Microbiology Ecology* **74**: 336–345.

Lekberg Y, Meadow J, Rohr JR, Redecker D, Zabinski CA. 2011. Importance of dispersal and thermal environment for mycorrhizal communities: lessons from Yellowstone National Park. *Ecology* **92**: 1292–1302.

Lekberg Y, Schnoor T, Kjøller R, Gibbons SM, Hansen LH, Al-Soud WA, Sørensen SJ, Rosendahl S. 2012. 454-sequencing reveals stochastic local reassembly and high disturbance tolerance within arbuscular mycorrhizal fungal communities. *Journal of Ecology* **100**: 151–160.

Lerouge P, Roche P, Faucher C, Maillet F, Truchet G, Promé JC, Dénarié J. 1990. Symbiotic host-specificity of *Rhizobium meliloti* is determined by a sulphated and acylated glucosamine oligosaccharide signal. *Nature* **344**: 781–784.

Li Y, Shipley B. 2018. Community divergence and convergence along experimental gradients of stress and disturbance. *Ecology* **99**: 775–781.

Liu L, Hart MM, Zhang J, Cai X, Gai J, Christie P, Li X, Klironomos JN. 2015. Altitudinal distribution patterns of AM fungal assemblages in a Tibetan alpine grassland. *FEMS Microbiology Ecology* **91**.

Lutzoni F, Nowak MD, Alfaro ME, Reeb V, Miadlikowska J, Krug M et al. 2018. Contemporaneous radiations of fungi and plants linked to symbiosis. *Nature Communications* **9**, 5451.

Maherali H, Klironomos J. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* **316**: 1746–1748.

Maherali H, Klironomos JN. 2012. Phylogenetic and trait-based assembly of arbuscular mycorrhizal fungal communities. *PLoS ONE* **7**: e36695.

Maron JL, Crone E. 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B: Biological Sciences* **273**: 2575–2584.

Martínez-García LB, Pugnaire FI. 2011. Arbuscular mycorrhizal fungi host preference and site effects in two plant species in a semiarid environment. *Applied Soil Ecology* **48**: 313–317.

Mummey DL, Antunes PM, Rillig MC. 2009. Arbuscular mycorrhizal fungi pre-inoculant identity determines community composition in roots. *Soil Biology and Biochemistry* **41**: 1173–1179.

Munkvold L, Kjøller R, Vestberg M, Rosendahl S, Jakobsen I. 2004. High functional diversity within species of arbuscular mycorrhizal fungi. *New Phytologist* **164**: 357–364.

Myers JA, Harms KE, Myers JA, Harms KE. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* **92**: 676–686.

Neuenkamp L, Moora M, Öpik M, Davison J, Gerz M, Männisto M, Jairus T, Vasar M, Zobel M. 2018. The role of plant mycorrhizal type and status in modulating the relationship between plant and arbuscular mycorrhizal fungal communities. *New Phytologist* **220**: 1236–1247.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P et al. 2020. *Vegan: community ecology package.* R package v.2.5-6. https://cran.r-project.org/.

Öpik M, Metsis M, Daniell TJ, Zobel M, Moora M. 2009. Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. *New Phytologist* **184**: 424–437.

Ottaviani G, Keppel G, Götzenberger L, Harrison S, Opedal ØH, Conti L, Liancourt P, Klimešová J, Silveira FAO, Jiménez-Alfaro B et al. 2020. Linking plant functional ecology to island biogeography. *Trends in Plant Science* **25**, 329–339.

Powell JR, Parrent JL, Hart MM, Klironomos JN, Rillig MC, Maherali H. 2009. Phylogenetic trait conservatism and the evolution of functional trade-offs in arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B: Biological Sciences* **276**: 4237–4245.

R Core Team. 2020. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org.

Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, De Kroon H, Buckley YM. 2016. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences, USA* **113**: 230–235.

Schappe T, Albornoz FE, Turner BL, Neat A, Condit R, Jones FA. 2017. The role of soil chemistry and plant neighbourhoods in structuring fungal communities in three Panamanian rainforests. *Journal of Ecology* **105**: 569–579.

Sepp SK, Davison J, Jairus T, Vasar M, Moora M, Zobel M, Öpik M. 2019. Non-random association patterns in a plant–mycorrhizal fungal network reveal host–symbiont specificity. *Molecular Ecology* **28**: 365–378.

Shi G, Liu Y, Mao L, Jiang S, Zhang Q, Cheng G, An L, Du G, Feng H. 2014. Relative importance of deterministic and stochastic processes in driving arbuscular mycorrhizal fungal assemblage during the spreading of a toxic plant. *PLoS ONE* **9**: e95672.

Sikes BA, Cottenie K, Klironomos JN. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *Journal of Ecology* **97**: 1274–1280.

Smith FA, Jakobsen I, Smith SE. 2000. Spatial differences in acquisition of soil phosphate between two arbuscular mycorrhizal fungi in symbiosis with *Medicago truncatula*. *New Phytologist* **147**: 357–366.

Stampe ED, Daehler CC. 2003. Mycorrhizal species identity affects plant community structure and invasion: a microcosm study. *Oikos* **100**: 362–372.

Steidinger BS, Crowther TW, Liang J, Van Nuland ME, Werner GDA, Reich PB, Nabuurs GJ, de Miguel S, Zhou M, Picard N et al. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**: 404–408.

Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology* **4**: 727–731.

Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A et al. 2014. Global diversity and geography of soil fungi. *Science* **346**: 1256688.

Torrecillas E, Del Mar Alguacil M, Roldán A. 2012. Differences in the AMF diversity in soil and roots between two annual and perennial gramineous plants co-occurring in a Mediterranean, semiarid degraded area. *Plant and Soil* **354**: 97–106.

Toussaint A, Bueno G, Davison J, Moora M, Tedersoo L, Zobel M, Öpik M, Pärtel M. 2020. Asymmetric patterns of global diversity among plants and mycorrhizal fungi. *Journal of Vegetation Science* **31**: 355–366.

Urcelay C, Díaz S, Gurvich DE, Chapin FS, Cuevas E, Domínguez LS. 2009. Mycorrhizal community resilience in response to experimental plant functional type removals in a woody ecosystem. *Journal of Ecology* **97**: 1291–1301.

van der Heijden MG, Scheublin TR. 2007. Functional traits in mycorrhizal ecology: the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist* **174**: 244–250.

Van Geel M, Jacquemyn Plue J, SaarKL Peeters G, van Acker K, Honnay O, Ceulemans T. 2018. Abiotic rather than biotic filtering shapes the arbuscular mycorrhizal fungal communities of European seminatural grasslands. *New Phytologist* **220**: 1262–1272.

Wagg C, Barendregt C, Jansa J, van der Heijden MGA. 2015. Complementarity in both plant and mycorrhizal fungal communities are not necessarily increased by diversity in the other. *Journal of Ecology* **103**: 1233–1244.

Waldrop MP, Zak DR, Blackwood CB, Curtis CD, Tilman D. 2006. Resource availability controls fungal diversity across a plant diversity gradient. *Ecology Letters* **9**: 1127–1135.

Weiher E, Keddy P. 2001. *Ecological assembly rules: perspectives, advances, retreats.* Cambridge, UK: Cambridge University Press.

Werner GDA, Kiers ET. 2015. Order of arrival structures arbuscular mycorrhizal colonization of plants. *New Phytologist* **205**: 1515–1524.

Yang H, Zhang Q, Koide RT, Hoeksema JD, Tang J, Bian X, Hu S, Chen X. 2017. Taxonomic resolution is a determinant of biodiversity effects in arbuscular mycorrhizal fungal communities. *Journal of Ecology* **105**: 219–228.

Zobel M, Öpik M. 2014. Plant and arbuscular mycorrhizal fungal (AMF) communities – which drives which? *Journal of Vegetation Science* **25**: 1133–1140.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Methods S1 Assessing the prevalence of covariation in the literature and comparing plant and AM fungal drivers and importance of scale.

Table S1 Assessing the prevalence of covariation in the literature.

Table S2 Comparisons of plant and AM fungal drivers and importance of scale.

Table S3 Assessing the role of taxonomic scale on the importance of host effect.

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