THE ROYAL SOCIETY
PUBLISHING

Community ecology

Integrating plant species contribution to mycorrhizal and seed dispersal mutualistic networks

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Mutualistic interactions like those established between plants and mycorrhizal fungi or seed dispersers are key drivers of plant population dynamics and ecosystem functioning; however, these interactions have rarely been explored together. We assembled a tripartite fungi–plant–disperser network in the Gorongosa National Park—Mozambique, to test (1) if diversity and importance of plant mutualists above- and belowground are correlated, and (2) whether biotically and abiotically dispersed plants are associated with distinct arbuscular mycorrhizal fungi (AMF). We quantified seed dispersal by animals for 1 year and characterized the AMF of 26 common plant species. Sixteen plant species were dispersed by 15 animals and colonized by 48 AMF virtual taxa (VT), while the remaining 10 plant species were not dispersed by animals and associated with 34 AMF VT. We found no evidence for a correlation between the number of plant partners above- and belowground or on plant specialization on both types of partners. We also found no evidence for differentiation of AMF communities between biotically and abiotically dispersed plants. Our results suggest that the establishment of plant interactions with seed dispersers and mycorrhizal fungi is largely independent and that both biotically and abiotically dispersed plants seem to associate with similar communities of AMF.

1. Introduction

Approximately 80% of all vascular plant species form mutualistic associations with arbuscular mycorrhizal fungi (AMF, phylum Glomeromycota), which increase the uptake of water and mineral nutrients, protect against herbivores and pathogens and improve plant overall fitness [1]. These associations also influence plant community composition [2,3] and succession [4,5], thus, being fundamental for the organization of terrestrial ecosystems. The establishment of mycorrhizal associations occurs right after seed germination and depends on the availability of compatible fungal partners at the seed deposition site, which also depends on seed dispersal mode [1,6,7]. Seed dispersal is crucial for plants to avoid intra-specific competition and pathogens and allows them to occupy newly available niches and expand their range [7,8]. However, dispersing seeds far from the mother plant could reduce the availability of compatible mycorrhizal fungi [9,10]. Seeds can be dispersed by biotic vectors, i.e. animals, and abiotic vectors, such as wind or water currents [7,11]. Animal-driven seed dispersal has important advantages over abiotic dispersal in that larger seeds can be transported for long distances and be deposited in particularly suitable germination sites [7,9]. These two mutualisms, mycorrhizas and seed dispersal are therefore crucial for the regeneration of plant
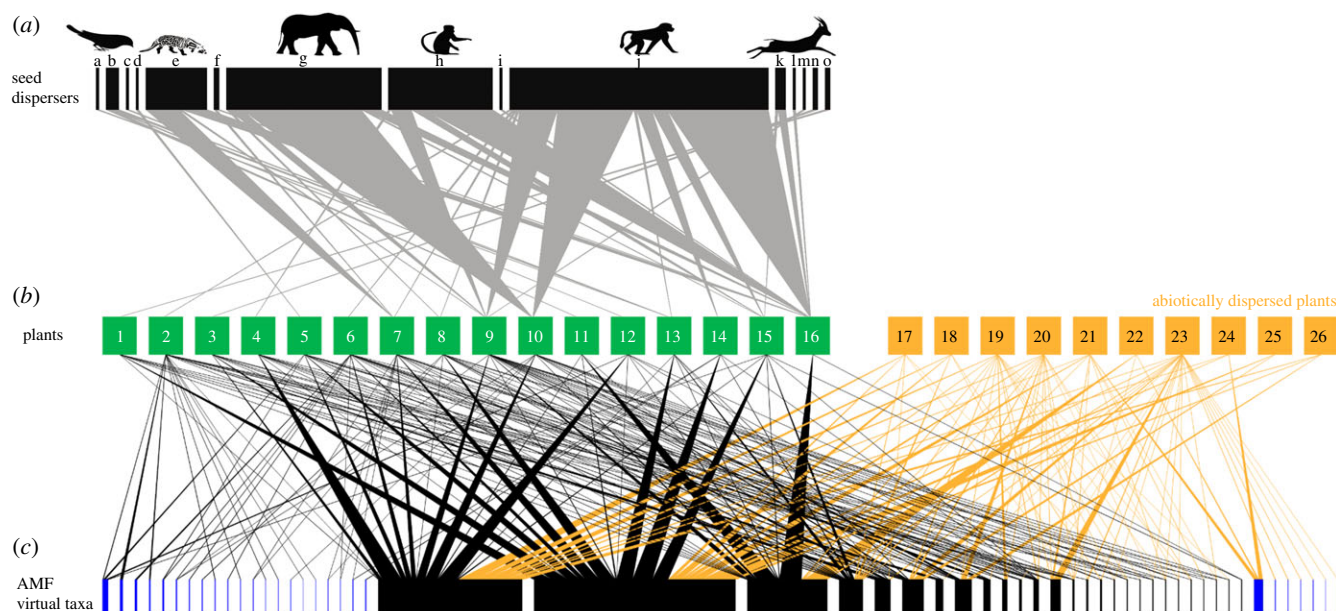
Figure 1. Tripartite network in Gorongosa, representing all detected interactions between mycorrhizal fungi (*c*), plants (*b*) and their seed dispersers (*a*). The width of the top and lower boxes is proportional to the frequency of interactions of each animal species and AMF virtual taxa (VT), respectively. AMF species shared by both plant groups are represented in black and those unique to one of the groups represented in blue. See electronic supplementary material, appendix S6, for common names of dispersers and plant species names.

communities, but the putative trade-offs between them are poorly explored. A correlational analysis using data from approximately 2000 European plant species actually suggests that both processes might be positively associated [12]. However, to date, no study has explored the potential synergies or trade-offs between mycorrhizal and seed dispersal interactions on natural communities.

Species interaction networks have been widely used to explore mostly single type of mutualisms, such as pollination and seed dispersal [13], and more recently, the interaction between plants and AMF [14–18]. However, there is now a growing consensus that, in order to understand the complexity of natural ecosystems, we should integrate knowledge from different types of interactions [19,20]. Thereby, linking above- and belowground interactions is of utmost importance to understand long-term community dynamics [19,21,22].

In this study, we jointly explore seed dispersal and mycorrhizal interactions under the same framework, by focusing on the Gorongosa National Park (GNP), a diversity hotspot, yet relatively poorly studied region, in the tropical climatic zone of Mozambique [23,24]. We use a tripartite interaction network to explore whether the interactions between plant species and seed dispersers are related to their associations with mycorrhizal partners. Specifically, we evaluate: (1) if the number of above and belowground mutualistic partners are correlated across plant species; (2) whether plants are equally selective regarding both types of mutualisms; (3) if biotically dispersed plants tend to be associated with a higher number of AMF than abiotically dispersed plants and (4) if there is any segregation on the species of AMF colonizing biotically and abiotically dispersed plants.

2. Material and methods

This study was conducted at the GNP, a 4067 km^2 protected area in Mozambique. The park is characterized by a mosaic of grasslands, savannahs, mixed dry forests and miombo woodlands [24,25] (electronic supplementary material, appendix S1 and figure S1). Seed dispersal interactions were recorded from June 2014 to May 2015 through complementary protocols used to sample the different guilds of seed dispersers following Timóteo *et al.* [26], and as described in the electronic supplementary material, appendix S2.

Plant–AMF interactions were assessed in the 16 plant species most commonly dispersed by animals in this study and 10 other common plant species but not biotically dispersed (electronic supplementary material, table S2). The AM fungi in plant roots was identified using 454-pyrosequencing following Rodríguez-Echeverría *et al.* [24]. For more details, see electronic supplementary material, appendix S3. The division of plants into the two groups of biotically and abiotically dispersed plants was done using data from 1 year of sampling in GNP. The robustness of the sampling design decreases the chances of missing interactions due to incomplete sampling.

All interactions were assembled into two matrices quantifying the species-specific links between (1) plants and their dispersers and (2) plants and their AMF (figure 1). Seed dispersal interactions were quantified as the proportion of samples containing at least one intact seed of each species (frequency of occurrence), as this is considered a more realistic measure of the potential recruitment probability than the actual number of dispersed seeds [23]. Plant–mycorrhizal interactions were quantified as the proportion of different virtual taxa (VT) reads per plant species [27]. Networks were visualized using Mathematica [28]. To account for plant phylogeny relatedness, we performed a Mantel test to check for a possible correlation between the plant phylogenetic distance and the ecological distance of interactions following Sauve *et al.* [29]. This analysis revealed that there was no significant phylogenetic signal in these networks (electronic supplementary material, appendix S4 and table S1).

In order to contrast plant interaction patterns with both dispersers and AMF, two widely used species-level descriptors were calculated: (1) *normalized degree*, the number of mutualistic partner species (degree) divided by the number of possible interaction partners [30]; and (2) *specialization* (*d'*), quantifying plant selectiveness as a departure from a random (i.e. abundance-based) interaction pattern [31]. Both metrics were
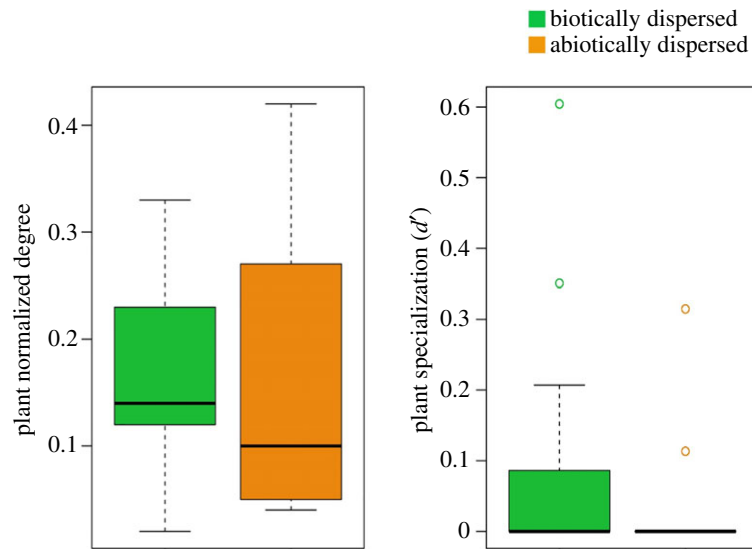
Figure 2. Boxplot of plant normalized degree and plant selectivity (specialization d') from biotically and abiotically dispersed plant species within the mycorrhizal network (outliers depicted as circles). (Online version in colour.)

calculated with the package *bipartite* [32] for R [33]. The potential correlation between plant species role on each sub-network was evaluated with the non-parametric Kendall rank coefficient τ.

Variation in AMF community composition between biotically and abiotically dispersed plants was visualized using non-metric multidimensional scaling (NMDS) with 1000 iterations, using the function *metaMDS()*. Differences on the composition of AMF communities were subsequently analysed with permutational multivariate analysis of variance [34], based on Bray–Curtis distances and using 9999 permutations constrained by site with the function *adonis()*. The diversity of AMF communities in both groups of plants was estimated with the inverse Simpson index [35] and Pielou's evenness [36] using the function *diversity()* from the R package *vegan* [37]. Differences between biotically and abiotically dispersed plants were assessed using linear models (LM) for the estimated indices of diversity. Differences in the normalized degree and specialization (d') of biotically and abiotically dispersed plant species were analysed with an LM and a robust LM, respectively, as the latter did not meet the assumptions of normality and homoscedasticity [38]. Analyses were conducted using the packages *lme4* [39] and *lmerTest* [40], for LM and *robustlmm* package [41] for robust regressions in R [33]. Because network analyses based on binary and weighed matrices might lead to different results [42], we repeated all the analyses based only on binary data (electronic supplementary material, figure S5 and table S6). This did not change any results and below we only present the results for the quantitative networks.

3. Results

Overall, 16 plant species were dispersed by 15 animal species (figure 1), the main dispersers being baboons (*Papio ursinus*), elephants (*Loxodonta africana*) and vervet monkeys (*Cercopithecus pygerythrus*). Together, these three species were responsible for 82% ($n = 205$) of all the dispersal events. Three plant species, *Ziziphus mucronata*, *Hyphaene coriacea* and *Grewia inequilatera* were the most dispersed plant species, representing 79% ($n = 197$) of the dispersal events (electronic supplementary material, table S2). Most biotically dispersed plants were fleshy-fruited trees (56%) while most abiotically dispersed plants had pods (60%). After excluding singletons, a total of 55 AMF VT were identified, of which 21 were exclusive for biotically dispersed plants, seven were exclusive for

abiotically dispersed plants and 27 (c. 50% of all VT) were shared by both plant groups (figure 1; electronic supplementary material, table S3). Most VT belonged to the Glomeraceae, genus *Glomus* (99% of the total number of sequences), whereas the contribution of other families was residual (electronic supplementary material, table S3). Among the shared AMF VT there were three VT from genus *Glomus* that represented 76% of all reads and participated in approximately 26% of all links established (62 out of 238; figure 1).

Overall, plants interacted with a greater number of mycorrhizal fungi species than with disperser species (AMF = 48, dispersers = 15, figure 1). On average, each plant species had approximately two (Min. = 1; Max. = 8) dispersers and 10 AM fungi (Min. = 1; Max. = 18). However, we did not find a correlation between plant normalized degree or specialization between the two mutualisms ($|\tau| = -0.03$; $p = 0.88$; and $|\tau| = -0.30$; $p = 0.14$, respectively; electronic supplementary material, figure S2). To make sure that the lack of significant correlations was not driven by the presence of 'illegitimate seed dispersers', or by merging data from different animal groups, we performed complementary analysis (electronic supplementary material, appendix S5) where we either included only the most likely legitimate seed dispersers or separate animals according to their body size and main habitat. None of these analyses affected the results (electronic supplementary material, figure S3).

The NMDS analysis confirmed the large overlap between the composition of the AMF communities from biotically and abiotically dispersed plants (electronic supplementary material, figure S4), which did not differ significantly (Pseudo-$F = 0.782$, $R^2 = 0.032$, $p = 0.533$). Furthermore, no differences were found on the diversity of AMF VT hosted by both plant groups (inverse Simpson index: biotically dispersed = 2.21 ± 0.29, abiotically dispersed = 2.99 ± 0.48, LM $p = 0.152$; electronic supplementary material, table S4). However, the AMF community of biotically dispersed plants was found to have a lower evenness (Pielou's evenness index: biotically dispersed = 0.46 ± 0.03, abiotically dispersed = 0.66 ± 0.07, LM $p = 0.011$; electronic supplementary material, table S4). Finally, neither plant normalized

degree nor plant specialization for AMF differed consistently between the two plant groups (figure 2; see electronic suplementary material, table S5).

4. Discussion

Overall, our results suggest that plant interaction with seed dispersers and mycorrhizal fungi are largely independent, as neither the number nor the selectiveness for both types of partners is correlated across plant species. We also did not find compelling evidence for differentiation on the composition and diversity of AMF communities associated with biotically and abiotically dispersed plants, although the evenness of the AMF community of the former was lower.

Plants have more mutualists belowground than aboveground (15 dispersers versus 55 AMF), which reflects the greater diversity of AMF than that of vertebrate seed dispersers. In this study, we found no correlation between the number of fungi and dispersers linked to plants. This means that the plants with a greater number of disperser species are not necessarily those with a greater number of AMF partners. Similarly, the level of plant selectivity for both types of mutualistic partners was not correlated, indicating that a greater selectivity for AMF does not give any indication on the level of plant selectivity for dispersers. The pattern of interaction was different for both mutualisms, with most plants (approx. 56%) having only one disperser, while being associated with 10 AMF VT, on average. Nonetheless, some plant species might be pivotal for both types of mutualisms. For example, the abundant fleshy-fruited tree *Ziziphus mucronata* is an important species connecting the two sub-networks by establishing links both with the most dominant AMF VT and the main animal dispersers, i.e. baboons, vervet monkeys and elephants (figure 1). To dispel the possibility of an eventual correlation being blurred by the inclusion of animals with very different 'seed dispersal effectiveness', we repeated the analyses including only animals likely to be legitimate dispersers (i.e. mostly frugivorous species) [43], which did not affect the results, supporting the lack of correlation.

This study also suggests that the AMF communities of woody plants in GNP are dominated by a few generalist fungal species, as it has been shown for other ecosystems [3], and that seed dispersal does not affect the diversity or plant selectivity of AMF communities. Nearly all AMF detected belonged to the Glomeraceae, which is the most widespread family in natural and managed ecosystems [43–45], including the GNP [24]. We hypothesized that biotically dispersed plants would be less specific in terms of their mycorrhizal associations than abiotically dispersed plants, increasing their

chances of finding compatible partners and survive [46]. However, biotically and abiotically dispersed plants share 27 out of 55 AMF partners, which include the most abundant AMF VT, while most fungal partners exclusive to either group were rare and linked only to one plant. Thus, both groups are dominated by a few common fungal species, also revealed by the low species evenness, particularly in biotically dispersed plants. This suggests that they are mainly colonized by abundant and likely ubiquitous fungi, thus ensuring a high probability of finding suitable mutualistic partners.

Our study represents the first attempt to empirically analyse the interactions between mycorrhizal fungi, plants and dispersers by means of a tripartite interaction network. By integrating knowledge on two of the underlying processes structuring plant communities, we can gain a better understanding of how both processes may influence each other [47]. Our results suggest that seed dispersal and AMF colonization are largely independent and not influenced by plant phylogenetic distances, being each of them subject to its own set of physiological constraints and specific selective pressures. We also found a few generalist AMF taxa that are likely to be widely distributed, thus providing suitable mycorrhizal partners for both biotically and abiotically dispersed plant species. Recent work has experimentally shown that seeds and spores of mycorrhizal fungi can both be co-dispersed internally by birds [48], thus providing a new mechanism for the establishment of mycorrhizas after seed dispersal. Although general evolutionary correlations exist between both mutualisms [12], this study shows that plants interact in independent ways with seed dispersers and AMF. More detailed analysis at the community scale and of different types of mycorrhiza are needed to fully understand the potential synergies or trade-offs of these interactions in an ecological context.

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