



The role of long-distance dispersal and mycorrhizas on plant colonisation within mainland Germany

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ABSTRACT

The geographical distribution of species generally reflects their ability to colonise large habitats. Thus, research on species traits affecting the ability of species to colonise (i.e. arrive and establish) new territories is required. Our study investigates whether mycorrhizas and long-distance dispersal (LDD) syndromes play an important role in plant species distribution within mainland Germany, and whether they interact to drive plant distribution at a large scale. **Using a dataset of 1070 vascular plant species** containing information on LDD syndromes, mycorrhizal status, and distribution, we fitted phylogenetic generalised least squares regression models to assess the effects of LDD syndromes and mycorrhizas on plant distribution across Germany. Our study showed that species with LDD syndromes tended to be more widely distributed overall than species without any specialised dispersal structures relevant for LDD (i.e. 'unspecialised' species). In particular, plants with nutritive tissues, which attract frugivores that disperse seeds internally, were more widely distributed than 'unspecialised' species. Moreover, species associated with mycorrhizal fungi, particularly the facultative mycorrhizal species, were more widely distributed than non-mycorrhizal plants. Interestingly, mycorrhizal species with LDD syndromes tended to be more widely distributed than species without any specialised dispersal structures relevant for LDD, whereas the reverse was true for non-mycorrhizal species. Our study suggests that both LDD syndromes and mycorrhizas play an important role in plant distribution within the mainland. More importantly, we show the first evidence that mycorrhizas may interact with LDD syndromes to expand the geographic distribution of plant species within the mainland.

1. Introduction

Why some species are confined to small areas while others span large regions or the globe has interested ecologists for well over a century (Grinnell, 1917; Brown et al., 1996; Liu et al., 2016). Many different factors drive the geographical distribution of species, such as climate change (Theurillat and Guisan, 2001; McKenney et al., 2007), land use change (Dirnböck et al., 2003; Pompe et al., 2008), competition and facilitation between species (Pellissier et al., 2010), and pollination (Pellissier et al., 2012; Duffy and Johnson, 2017). However, geographical distribution of species generally reflects their colonising ability across large habitats. Thus, a mechanistic understanding of the ability of species to colonise new habitats can provide valuable insights into determinants of species distribution. Research on species traits related to arrival and establishment, which are important steps for

species to spread and colonise into new ranges, can aid in understanding plant distribution at large geographical scales.

The ability of plants to spread into unoccupied sites is an essential aspect of plant species survival, commonly referred to as dispersal (Bullock et al., 2002). Plant dispersal is a crucial determinant of the colonisation processes in sessile plant species (MacArthur and Wilson, 1967; Crawley, 1997). Consequently, plant dispersal has been considered a critical feature for understanding species distribution for almost a century (Gleason, 1926). For most plant species, the majority of their seeds are dispersed over relatively short distances from their source location (Willson, 1993), and this generally determines the local distribution of plants rather than the large-scale distribution (Levin et al., 2003; Nathan et al., 2008). However, seeds of some species have traits, such as wings or hooks that can enhance seed dispersal by wind or animals (Heleno and Vargas, 2015). Seeds of such species usually

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disperse over greater distances than other species, although such species usually disperse smaller numbers of seeds (Soons et al., 2004; Soons and Ozinga, 2005). Thus, long-distance dispersal (LDD) events are typically rare, however, these are considered to play a major role in enhancing species range expansion and migration (Clark, 1998; Higgins and Richardson, 1999; Nathan, 2006; Nathan et al., 2008).

In addition to the arrival of species, the establishment of viable populations is another key process affecting plant colonisation of new territories (MacArthur and Wilson, 1967). Therefore, factors affecting the establishment of plants may also influence plant distribution. Biotic interactions (Wisn et al., 2013), particularly mutualistic associations (Pellissier et al., 2012; Hempel et al., 2013; Duffy and Johnson, 2017; Menzel et al., 2018) are receiving greater interest for explaining range expansion of species. Mycorrhizal symbiosis is one such biotic interaction. Mycorrhizal fungi provide plants with increased nutrient foraging ability and tolerance of abiotic and biotic stress, and receive assimilated carbon in return (Smith and Read, 2010; Kim et al., 2015; Gao et al., 2016). Consequently, the mutualistic interaction between mycorrhizal fungi and plants could enhance plant establishment via incorporating seedlings into the common mycorrhizal network (van der Heijden and Horton, 2009; Bennett et al., 2017), thereby driving plant distribution (Hempel et al., 2013). Although LDD and mycorrhizas are the two key processes for determining plant colonisation (i.e. arrival and establishment of plants), no study has tested whether they interact with each other to drive plant distribution within the mainland.

In this study, we investigated whether mycorrhizas and LDD syndromes play an important role in plant species distribution within mainland Germany, and whether they interact to drive plant distribution at a large scale. Using the mycorrhizal status, LDD syndromes, and plant distribution data of 1070 plant species occurring in Germany, we addressed the following questions: (1) does a particular LDD syndrome affect plant species distribution; (2) do mycorrhizas affect plant species distribution; and (3) do mycorrhizas interact with LDD to drive plant species distribution?

2. Materials and methods

2.1. Data source

Long-distance dispersal syndromes and mycorrhizal status were taken from the database published by Correia et al. (2018). This database includes information on 1960 plant species from 685 genera and 124 families. Here, species are assigned to five categories according to diaspore morphological traits related to LDD, which are the following: anemochorous (ANE; structures that favour wind dispersal), thalassochorous (THA; sea dispersal), endozoochorous (END; internal animal dispersal), epizoochorous (EPI; external animal dispersal) syndromes and 'unspecialised' (UNS; species without any specialised dispersal structures relevant for LDD). Species are also classified into three main mycorrhizal statuses: facultative mycorrhizal (FM), obligate mycorrhizal (OM), and non-mycorrhizal plants (NM; for details, see Smith and Read, 2010). This database was compiled using many different published databases. To summarise, the list of LDD syndromes compiled by Heleno and Vargas (2015) for 10,792 species of native European species included in Flora Europaea (Tutin et al., 1980) was used in combination with five databases of plant mycorrhizal status. The five databases were Mycoflor compiled by Hempel et al. (2013), two checklists compiled by Wang and Qiu (2006) and Harley and Harley (1987, 1990), a database compiled by Akhmetzhanova et al. (2012), and a dataset compiled by Bueno et al. (2017).

To test whether seed dispersal and mycorrhizal status play a role in plant distribution within mainland Germany, we combined the database compiled by Correia et al. (2018) with the plant species distribution data obtained from the FLORKART database (<http://www.floraweb.de>). The database records occurrences of 3393 German vascular plant species in grid cells of 10' longitude \times 6' latitude

(arcminutes) in size, which is approximately equal to 130 km² per cell. Therefore, the total area of Germany was divided into 2995 grid cells. In this study, we used a measuring system ranging from 1 to 2995 occupied grid cells per plant species as a proxy of plant distribution. As species names in the database of Correia et al. (2018) were standardised according to The Plant List (<http://www.theplantlist.org>), we first standardised the species names in the FLORKART database via the R package plantlist (<https://github.com/helixcn/plantlist>) before merging the two databases. We then compiled the database for our study according to the following criteria: (i) if species were recorded in both databases; (ii) if species were recorded as native species of Germany in the FLORKART database; and (iii) species were excluded if they were recorded as a THA syndrome, because plant species with sea-dispersal specialisations are often considered important pioneer species in island colonisation (Ridley, 1930; Magnússon et al., 2014; Arjona et al., 2017). Consequently, structures that favour sea dispersal should be important for plant species spreading between islands or between the mainland and islands rather than within the mainland (Fig. S1). Our final database included 1070 native species belonging to 418 genera and 99 families, in which the five categories of LDD syndromes ANE, END, EPI, and UNS included 187, 82, 78, and 723 species, respectively, and the mycorrhizal status FM, OM, and NM included 275, 592, and 203 species, respectively.

2.2. Phylogenetic tree

To account for potential biases due to different degrees of evolutionary relatedness among species in our statistical analyses, a phylogenetic tree of the 1070 species in our dataset was constructed. We constructed the phylogenetic tree by grafting the families, genera, and species to an existing supertree using the R function 'S.PhyloMaker' provided by Qian and Jin (2016). The existing supertree was initially constructed by Zanne et al. (2014), and corrected and extended by Qian and Jin (2016). It included 30,771 seed plants and was time-calibrated for all branches using seven gene regions (i.e., 18S rDNA, 26S rDNA, ITS, matK, rbcL, atpB, and trnL-F) available in GenBank and fossil data (Zanne et al., 2014). For the absent species, we used the Scenario 3 approach of the function 'S.PhyloMaker' to add them to their families or genera in the supertree using the same approach as used in Phylomatic and BLADJ (Webb et al., 2008). The phylogenetic tree was finally visualised using the ggtree package (Fig. S1; Yu et al., 2017).

2.3. Statistical analysis

All analyses in our study were conducted in R 3.4.3 (R Core Team, 2017). To analyse the effects of LDD and mycorrhizas on species distribution and to account for phylogenetic relatedness, we fitted phylogenetic generalised least squares (PGLS) regression models using the ape package in R (Paradis et al., 2004). The number of occupied grid cells per species was the response variable in the models. To test how the different LDD syndromes (i.e. ANE, END, EPI, and UNS) or mycorrhizal status (i.e. FM, OM, NM) affect species distribution, we fitted two models, which only included LDD syndromes or mycorrhizal status as the fixed effect. For both the above models, we also did post-hoc analyses to test for differences between levels of LDD syndromes or mycorrhizal status using the multcomp package in R (Hothorn et al., 2008). To analyse whether the presence of LDD syndromes and mycorrhizas affect species distribution, we fitted the model, including the presence/absence of LDD syndromes, presence/absence of mycorrhizas, and their interactions, as the fixed effects. In this model, we assessed the significance of the fixed effects (i.e. presence/absence of LDD syndromes and mycorrhizas) and their interactions using likelihood ratio tests (Zuur et al., 2009). In all models, phylogeny was included as a phylogenetic correlation structure (Pagel, 1999), which is derived from the Brownian-motion model by multiplying the off-diagonal elements of the phylogenetic variance-covariance matrix by λ ($0 \leq \lambda \leq 1$). The

Table 1

Results of phylogenetic generalised least squares (PGLS) regressions to test how different LDD syndromes (i.e. anemochorous [ANE], endozoochorous. [END], epizoochorous [EPI] and unspecialised [UNS]) or different mycorrhizal status (i.e. facultative mycorrhizal [FM], obligate mycorrhizal [OM], and non-mycorrhizal [NM]) affects plant species distribution in Germany.

Parameter	Estimate (± standard error)	t-value	p-value
LDD syndromes			
Intercept (UNS)	1233.4391 (281.6862)	4.3788	< 0.0001
ANE	97.0994 (102.7149)	0.9453	0.3447
END	379.6745 (139.6041)	2.7197	0.0066
EPI	203.0768 (131.4059)	1.5454	0.1225
Mycorrhizal status			
Intercept (FM)	1954.3903 (382.9642)	5.1033	< 0.0001
NM	−660.8991 (107.9419)	−6.1227	< 0.0001
OM	−684.7758 (81.0213)	−8.4518	< 0.0001

Pagel's λ is often used to measure the “phylogenetic signal” in comparative data. In the present study, a low λ indicates that species distribution was largely phylogenetically independent and close relatives are not more similar than distant relatives; a high λ indicates that species distribution was evolving according to Brownian motion on the given phylogeny, and close relatives are more similar than distant relatives (Pagel, 1999; Freckleton et al., 2002).

3. Results

In the analysis testing for how the different LDD syndromes (i.e. ANE, END, EPI, and UNS) affected species distribution, there was a trend towards species with ANE, END, and EPI syndromes occupying a greater number of grid cells. However, we only found a significantly higher number of occupied grid cells for species with END syndrome than for species without any specialised dispersal structures relevant for LDD (i.e. UNS; Table 1; Fig. 1a). In the analysis testing for how the different mycorrhizal status (i.e. FM, OM, NM) affected species distribution, we found that FM species showed a significantly higher number of occupied grid cells than NM and OM species (Table 1; Fig. 1b).

In the analysis testing for whether the presence of LDD syndromes and mycorrhizas affect species distribution, we found that the presence of LDD syndromes tended to increase ($df = 1$, $\chi^2 = 3.7305$, $p = 0.0534$; Fig. 2) and the presence of mycorrhizas significantly increased ($df = 1$, $\chi^2 = 7.5921$, $p = 0.0059$) the number of occupied grid cells for species (Fig. 2). There was a marginally significant interactive effect

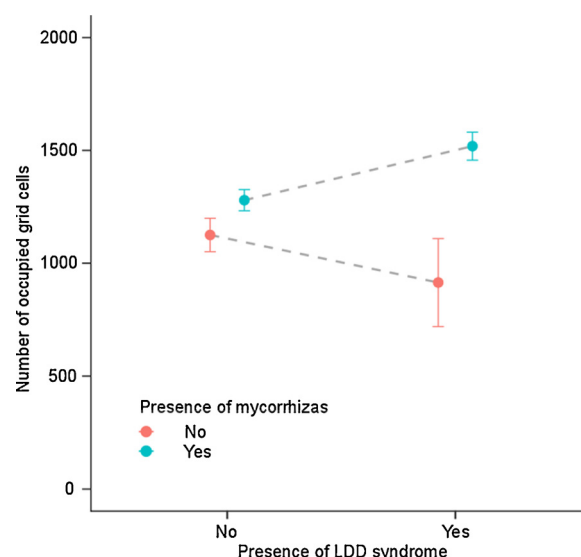


Fig. 2. Distributions for native plants of Germany in the presence/absence of LDD syndromes and mycorrhizas. Distribution is measured as the number of occupied grid cells (each ~130 km² in size) across Germany.

between presence/absence of LDD syndromes and presence/absence of mycorrhizas ($df = 1$, $\chi^2 = 2.7565$, $p = 0.0969$; Fig. 1a) on the number of occupied grid cells for species.

The values of Pagel's λ in the above three PGLS regressions were 0.1673 (in the model testing the effect of LDD syndromes on species distribution), 0.3318 (the model testing the effect of mycorrhizal status on species distribution), and 0.1701 (the model testing whether the presence of LDD syndromes and mycorrhizas affect species distribution). In all analyses, the values of Pagel's λ were low, indicating that the species distribution were largely phylogenetically independent.

4. Discussion

In this study, we found that Central European plant species with LDD syndromes tended to be more widely distributed overall than those without any specialised dispersal structures relevant for LDD (i.e. UNS species). In particular, plants with nutritive tissues, which attract frugivores that disperse seeds internally (i.e. END species), occupied a wider geographic distribution across Germany than UNS species. We found that species associated with mycorrhizal fungi, particularly FM

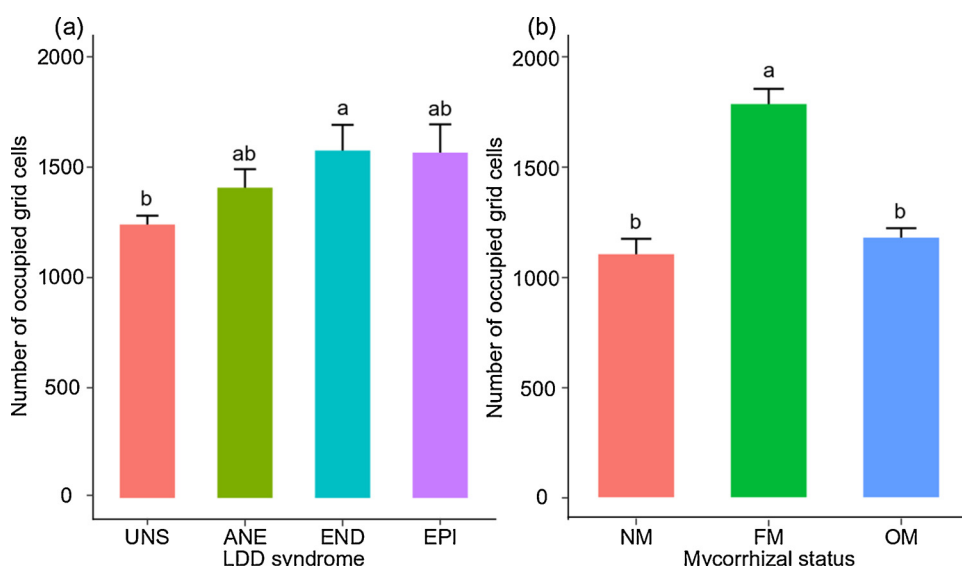


Fig. 1. Distributions for native plants of Germany with (a) different LDD syndromes (anemochorous [ANE], endozoochorous [END], epizoochorous [EPI] and unspecialised [UNS]) and (b) mycorrhizal status (facultative mycorrhizal [FM], obligate mycorrhizal [OM], and non-mycorrhizal [NM]). Distribution is measured as the number of occupied grid cells (each ~130 km² in size) across Germany. For each subfigure, bars sharing the same letters indicate no significant differences between them (i.e. $p > 0.05$).

species, were more widely distributed than non-mycorrhizal plants (i.e. NM species). Interestingly, mycorrhizal species with LDD syndromes tended to be more widely distributed than species without any specialised dispersal structures relevant for LDD, whereas the reverse was true for non-mycorrhizal species.

Long-distance dispersal could enhance species range expansion and migration (Clark, 1998; Higgins and Richardson, 1999; Nathan et al., 2008), and may be a key trait affecting plant distribution at a large scale (Nathan, 2006; Nathan et al., 2008). Previous studies have supported this theory, where the four LDD syndromes (i.e. ANE, END, EPI, THA) were found to play a central role in the colonisation of islands by plants (Heleno and Vargas, 2015; Ridley, 1930; Magnússon et al., 2014; Arjona et al., 2017). Most LDD syndromes except THA are also likely to play an important role in plant colonisation within the mainland because plant seeds dispersed by wind and animals are also common here. Our findings support the idea that these LDD syndromes might also drive the distribution of plant species within the mainland. Furthermore, they indicate that animals, particularly those that disperse seeds internally, are important vectors for carrying propagules to locations far away from the source location, thereby expanding the distribution of plant species within the mainland.

As plant seedling establishment could be promoted by the presence of mycorrhizal fungal symbionts (van der Heijden, 2004; Wurst et al., 2011; Koorem et al., 2012), it is frequently considered that plants with wider niches are predominantly mycorrhizal species. Our findings support this theory, as they show that plant species associated with mycorrhizal fungi inhabit a wider geographical range than non-mycorrhizal species. Our study further corroborates Hempel et al. (2013), who found that FM species had the widest geographic and ecological amplitude compared to OM and NM species. Plant species differ in their ability to regulate the occurrence of mycorrhizal fungi in their roots in relation to the benefits they receive (Grman, 2012). Generally, FM plants have a higher competitive ability, and are successful in habitats where mycorrhizal fungi are abundant (Gerz et al., 2017). On the other hand, FM plants are also mycorrhizal flexible species, in that their mycorrhizal associations are not crucial (Gerz et al., 2017). This flexibility provides FM plants with the ability to occupy a wider range of environmental conditions, such as habitats where mycorrhizal fungi are locally or temporally lacking or limited (Titus and del Moral, 1998; Cázares et al., 2005).

Interestingly, we also found some evidence indicating that LDD syndromes and mycorrhizas interact to drive plant distribution at a large scale (i.e. marginal significant interactive effects were found). For mycorrhizal species, plants tended to have a wider distribution when LDD syndromes were present rather than when they were absent. Long-distance seed dispersal may allow new seedlings to escape specific natural enemies such as pathogens and herbivores (Janzen, 1970; Connell, 1971), and avoid intraspecific competition near the mother plant (Comita et al., 2014). On the other hand, fungi is widely distributed across the earth (Tedersoo et al., 2014; Davison et al., 2015; Vincenot and Selosse, 2017), and some mycorrhizas show a low symbiotic specificity (van der Heijden et al., 2015). As a result, mycorrhizal species are more likely to find mycorrhizal partners enabling them to develop an extensive hyphal network in the soil through which they can supply nutrients to the seedlings and protect them against soil pathogens (van der Heijden et al., 2015). Indeed, Correia et al. (2018) contrasted the mycorrhizal status and LDD syndromes for 1960 European plant species, and suggested that finding mycorrhizal partners is not an important limitation for plant establishment. Therefore, advantages from both LDD and mycorrhizas may help Central European plant species to expand their geographic range.

In contrast to mycorrhizal species, non-mycorrhizal plant species tended to be distributed less widely when LDD syndromes were present rather than when they were absent. A possible explanation for this could be that non-mycorrhizal plants of the European flora are typically annuals, herbaceous, and stress tolerant (Hempel et al., 2013), which

produce small numbers of seed (Peat and Fitter, 1993). Although some of these species lack LDD structures, their lightweight seeds may be dispersed by wind or internally and externally by animals. Alternatively, non-mycorrhizal plants often adapt to environments with extreme nutrient availability (Lambers and Teste, 2013), and thus have smaller realised niches (Gerz et al., 2017). Due to habitat restriction, non-mycorrhizal plants with LDD syndromes may have a lower probability of finding suitable sites for establishment (Correia et al., 2018). In addition, the cost of dispersal structures for small seeds may be disproportionately high (Willson et al., 1990), and thus the fitness of non-mycorrhizal species with LDD syndromes might also be lower than those species without LDD syndromes.

5. Conclusions

Many previous studies have supported the idea that LDD syndromes play a central role in the colonisation of islands by plants (Ridley, 1930; Heleno and Vargas, 2015; Magnússon et al., 2014; Arjona et al., 2017). Our study suggests that plant species with LDD syndromes, particularly those with END syndrome, are also more widely distributed within mainland Germany than species without LDD syndromes. We also corroborate previous findings that mycorrhizas play an important role in plant species distribution. We show the first evidence that mycorrhizas may interact with LDD syndromes to expand the geographic distribution of plant species within the mainland.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.flora.2019.151443>.

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