Non-linear effects of phylogenetic distance on early-stage establishment of experimentally introduced plants in grassland communities

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Abstract

1. The phylogenetic distance of an introduced plant species to a resident native community may play a role in determining its establishment success. While Darwin’s naturalization hypothesis predicts a positive relationship, the preadaptation hypothesis predicts a negative relationship. Rigorous tests of this now so-called Darwin’s naturalization conundrum require not only information on establishment successes but also of failures, which is frequently not available. Such essential information, however, can be provided by experimental introductions.
2. Here, we analysed three datasets from two field experiments in Germany and Switzerland. In the Swiss experiment, alien and native grassland species were introduced as seeds only with and without disturbance (tilling). In the German experiment, alien and native grassland species were introduced both as seeds and as seedlings with and without disturbance (tilling), and with and without fungicide application. For the seedling introduction experiment, there was an additional herbivore-exclusion treatment.
3. Phylogenetic distance affected establishment in the three datasets differently, with success peaking at intermediate distances for the seed datasets, but decreasing with increasing distances in the seedling dataset. Disturbance favoured seedling survival, most likely by weakening the resident community.
4. *Synthesis:* By analysing experimental introductions, we show that the relationship between phylogenetic distance and establishment, at least for seedling emergence, may actually be non-linear with an optimum at intermediate distances. Therefore, Darwin´s naturalization hypothesis and the preadaptation hypothesis need not be in conflict. Rather, the mechanisms underlying them can operate simultaneously or alternately depending on the life stage and on the environmental conditions of the resident community.

Keywords: Darwin’s naturalization hypothesis, introduction experiment, alien plant species, phylogenetic distance, plant colonization, establishment success

Introduction

Invasive alien species – non-native organisms introduced by humans and spreading into a new range (Richardson *et al.*, 2000) – are a major component of global change (Vitousek, D'Antonio and Loope, 1997). While the drivers behind global patterns in plant invasions are beginning to emerge (van Kleunen *et al.* 2015a, Pyšek et al. 2017, Dawson *et al.* 2017), the identification of consistent drivers of invasion success at community scales remains elusive. Most alien, as well as native, plant species enter a resident community as seeds, and thus depend on seed germination and seedling survival for successful establishment (van Kleunen *et al.* 2015b). Identifying what determines plant establishment success at these early stages will provide insight not only into potential drivers of invasion, but also into community assembly in general (Gallien & Carboni, 2016).

Functional traits are thought to be important in determining the success of introduced species (Vilà & Weiner 2004, van Kleunen & Johnson 2007, Dawson *et al.* 2011, Razanajatovo *et al.* 2016). Besides the trait values *per se*, establishment of an introduced species in a resident community might also depend on how functionally similar or different the species is from the resident community (Macdougall *et al.* 2009, Thuiller *et al.* 2010, van Kleunen 2015b). As functional similarity of species may involve numerous traits, which are often not or only partially available for a given set of species, similarity is challenging to measure (Albert *et al.* 2010, Cadotte *et al.* 2010). However, as many traits are phylogenetically conserved, an alternative metric to explain invasion success is the phylogenetic distance between the introduced species and the resident community (Proches *et al.*, 2008). Due to the increasing availability of dated molecular phylogenies for plants (e.g. Durka & Michalski 2012), phylogenetic distance estimates can be readily calculated for most sets of plant species (Cadotte *et al.*, 2010).

Darwin's naturalization hypothesis (DNH) (Darwin 1859, Procheș *et al.* 2008, Thuiller *et al.* 2010) postulates that introduced alien species closely related to the local native species are less likely to become invasive than distantly related alien species. This is because close relatives will have a greater functional similarity, and therefore more similar niche requirements than distant relatives. Such niche overlap is likely to intensify competition and result in exclusion of the alien species by closely related native species, if the latter are stronger competitors (MacDougall *et al.* 2009, van Kleunen *et al.* 2015b). In addition to more intense competition for resources, introduced plants may also be more likely to suffer from pathogens and herbivores that they share with closely related resident plants (Ness *et al.* 2011, Kempel *et al.* 2018).

Studies testing DNH, however, disagree on the strength and direction of the effect of phylogenetic distance. While some studies found evidence in support of DNH (Rejmanek 1996, Ricciardi & Atkinson 2004, Strauss *et al.* 2006), others found the opposite (i.e. that more closely related alien species were more likely to be successful; Duncan & Williams 2002, Diez *et al.* 2009, Daehler 2011), or no relationship between naturalization success and phylogenetic distance (Lambdon & Hulme 2006, Ricciardi & Mottiar 2006, Diez *et al.* 2008). These inconsistent results may partly arise from differences in spatial scale among studies (Thuiller *et al.*, 2010). Contrary to DNH, introduced species more closely related to natives might be more successful due to environmental filtering at larger spatial scales, as due to their similarity to residents they should be preadapted to the new environment (preadaptation hypothesis, Daehler 2011, Schlaepfer *et al.* 2010). The two apparently opposing hypotheses are now referred to as “Darwin’s Naturalization Conundrum” (Thuiller *et al.*, 2010). Preadaptation should operate both at small and large spatial scales, whereas competitive exclusion is likely to act only at the small spatial scales where organisms interact (Carl *et al.*, 2016). Therefore, when preadaptation (environmental filtering) and competitive exclusion both play a role, the highest establishment success may be at intermediate phylogenetic distances (Gallien & Carboni 2014, Gallien *et al.* 2016). To the best of our knowledge, such non-linear relationships have not yet been tested (van Kleunen *et al.* 2018).

Another potential reason for the inconsistent outcomes of studies testing DNH is that most tests are based on observational data. As only established alien species can be observed, these studies have to make assumptions about the potential pool of introduced alien species (i.e. including the ones that failed to establish), and about when and how frequently (i.e. propagule pressure) the species were introduced. Experimental, simultaneous introductions of multiple species with equal propagule pressure, followed by assessment of establishment success, can overcome these limitations. Ideally, such experiments would also manipulate competition with resident plants, and interactions with pathogens and herbivores to test whether these factors mediate relationships between establishment success and phylogenetic distance to the native residents.

Here, we re-analysed three datasets of experimental introductions of alien and native plant species into semi-natural grassland communities. One dataset is from Kempel *et al.* (2013), who introduced equal numbers of seeds of 48 alien and 45 native herbaceous species to eight intact and eight disturbed (tilled) grassland sites. The other two datasets are from Müller *et al.* (2016), who introduced seeds and seedlings of 10 alien and 10 native herbaceous species to a total of five grassland sites that included disturbance and fungicide treatments, and for the introduced seedlings an additional herbivore-exclusion treatment. We used these three datasets to answer the following questions: (1) Does phylogenetic distance between introduced species and resident species affect seedling emergence from seed and survival of planted seedlings of introduced species? (2) Are relationships between seedling emergence or survival and phylogenetic distance affected by alien-native status of the species, disturbance, herbivore exclusion or fungicide application?

Material and Methods

Datasets

The Kempel et al. seed-introduction dataset

Data were obtained from Kempel *et al.* (2013), on early establishment success of 93 forb species introduced as seeds into 16 semi-natural grassland sites in the Canton of Bern, Switzerland (for the full species list, see Table S1 in Supporting Information). A detailed description of the experimental set-up and measurements can be found in Kempel *et al.* (2013). In short, the 93 species were sown into 16 grassland sites in May 2008. Each species was sown into two separate subplots per site. Forty-six of the introduced species are native to Switzerland and the other 47 are alien to Switzerland. Prior to introduction of the species, eight of the 16 grassland sites were disturbed by soil tilling, which largely reduced competition from resident species, and also loosened the soil. Four levels of propagule pressure (2, 10, 100 and 1000 seeds, with one propagule-pressure level per grassland site) were used for each of the 93 species.

Kempel *et al.* (2013) monitored the colonization success of each species in each grassland site over the subsequent three years by counting seedlings and surviving plants each spring and autumn, for a total of six censuses. Here, we only used data from the first census, because we wanted to focus on seedling emergence, and because the data for the later censuses were strongly zero-inflated. As the first census took place within one month after sowing the seeds, we believe that the first census mainly reflects seedling emergence (i.e. germination), although it is possible that some seedlings had died prior to the census. Data on the resident (native) plant composition and coverage in each of the 16 sites were obtained from surveys done in June 2008 using the Braun-Blanquet method (Kempel *et al.*, unpublished data). We converted the Braun-Blanquet coverage classes to percentages, using the *bb2num* function of the “simba” package in R (Jurasinski & Retzer, 2012) (see Table S2 in Supporting Information for details on the conversion).

The Müller et al. seed-introduction dataset

Data were obtained from Müller *et al.* (2016), on the seedling emergence of 20 forb species (see Table S3 in Supporting Information) introduced as seeds into five grassland sites around the University of Konstanz (southern Germany). A detailed description of the experimental set-up can be found in Müller *et al.* (2016). In short, seeds of each of the 20 species were sown in April 2014, and the seedling emergence of each species in each grassland site was monitored over one season. The 20 species belonged to five groups of four confamilials comprising two alien and two native species per family. Two disturbance levels (tilling and no tilling) and two fungicide treatments (fungicide application and no-fungicide application) were applied, yielding a total of four treatment combinations. Each of the five sites contained four plots, each representing one of the four treatment combinations, and there were eight seeds of each species per plot (i.e. 3200 seeds in total).

To assess the composition of the resident vegetation of the plots in the five grassland sites of this experiment, a vegetation survey was carried out using a 12-point frame in September 2014. The frame consisted of a rod with twelve 2-mm diameter pins 5 cm apart. The frame was positioned at random within the plot, and all plants touching the 12 pins were identified and counted as "hits" for those species (Heady & Rader, 1958). This procedure was repeated six times in each plot. Grasses were not considered, as they were difficult to identify in the vegetative state, and because all grasses have the same phylogenetic distance to the 20 introduced forb species. To calculate the relative abundance of each resident species in a plot, the number of hits for each species was divided by the total number of hits across all species.

The Müller et al. seedling-introduction dataset

Data were also obtained from Müller *et al.* (2016) on the survival of 20 forb species (see Table S3 in Supporting Information) introduced as seedlings into five grassland sites around the University of Konstanz. A detailed description of the experimental set-up can be found in Müller *et al.* (2016). In short, seedlings of each of the 20 species were planted in April 2014, and the establishment success of each species in each grassland site was monitored over a one-year period. This was done by assessing seedling survival every two months during the growing season from April to September 2014. The 20 species are the same ones as those used for the seed-introduction experiment of Müller *et al.* (2016). Two disturbance levels (tilling and no tilling), two fungicide treatments (fungicide application and no-fungicide application), and two herbivore-exclusion treatments (closed and open herbivore exclosures, of which the closed ones excluded both large mammal herbivores and arthropod herbivores) were applied, yielding a total of eight treatment combinations. Each of the five sites contained eight plots, each representing one of the eight treatment combinations, and there were eight seedlings of each species per plot (i.e. 6400 seedlings in total). The composition of the resident vegetation of the plots was assessed as described above for the Müller *et al.* seed-introduction dataset.

Phylogenetic trees and distance measures

For each of the datasets separately, we constructed a phylogenetic tree including both the resident and the introduced species. For the Kempel *et al.* seed-introduction dataset, we first created the phylogenetic tree of the resident species by pruning the dated DaPhnE supertree of Central European plant species (Durka & Michalski, 2012). We then merged the resident-species tree with a phylogenetic tree of the 93 introduced species, available from (Kempel *et al.* 2011, 2013). For the Müller *et al.* seed-introduction and seedling-introduction datasets, we pruned the DaPhnE supertree, which contained all introduced and resident species. As the resident species varied among the 16 sites in Kempel *et al.* (2013) and among the 60 plots in Müller *et al.* (2016), the trees were further pruned to the actual species sets for each site and plot, respectively.

Different metrics can be used to quantify the phylogenetic distance between an introduced species and the residents (Thuiller *et al.*, 2010). We chose four frequently used phylogenetic distance measures. First, for each introduced species in a plot or site, we calculated the Mean phylogenetic Distance to the Native resident Species (MDNS). This phylogenetic distance measure assumes that the entire community drives the establishment success of an introduced plant, irrespective of the abundance of the different resident species. Second, we calculated the Weighted Mean phylogenetic distance to the Native Species (WMDNS), which weights the MDNS by the abundances of the native species and assumes that the contribution of each resident species depends on its relative abundance.

Third, we calculated the phylogenetic Distance to the phylogenetically Nearest Native resident Species (DNNS), which assumes that the phylogenetic distance to the phylogenetically closest relative drives the establishment success of an introduced plant. Fourth, we calculated the phylogenetic Distance to the Most Abundant resident Native Species (DMANS), which assumes that the distance to the most abundant resident species drives establishment success of the introduced species. All phylogenetic tree manipulations and phylogenetic distance calculations were performed using the “ape” package (Paradis *et al.* 2004) in R (R-Core-Team, 2016).

Statistical analysis

The Kempel et al. seed-introduction dataset

To test how seedling emergence (i.e. the proportion of seeds that germinated) in the Kempel *et al.* seed-introduction dataset depended on phylogenetic distance measures, we used betabinomial models implemented using the *glmmadmb* function in the “glmmADMB” package (Fournier *et al.*, 2012). We used a betabinomial instead of a binomial distribution to overcome convergence issues caused by the large number of zeroes in the dataset. Because some of the phylogenetic metrics were strongly correlated (in particular MDNS - DNNS, and WMDNS - DMANS, Fig. S1), we ran separate models for each of the four phylogenetic distances measures. The distance measures were standardized to a mean of zero and scaled to a standard deviation of one, to facilitate comparisons of the effects of each explanatory variable (Schielzeth, 2010). To test for linear and non-linear effects, each distance measure was included as a linear and a quadratic term (Gallien & Carboni, 2016). Seed number (2, 10, 100 or 1000 seeds, standardized to a mean of zero and a standard deviation of one), disturbance treatment (no/yes), and status of the introduced species (alien/native) were included as additional explanatory variables. To facilitate interpretation of the model estimates, each of these explanatory variables was also centered to a mean of zero (Schielzeth, 2010). Categorical variables were coded as dummy variables (with values equal to 0 or 1) before centering. To test whether effects of the phylogenetic distance measures depended on the level of the other explanatory variables, we also included interactions of the linear and quadratic components of the distance measure with the other explanatory variables. Site and species were included as random factors. Model validation was performed by comparing data simulated using the *rbetabinom* function (emdbook package, Bolker, 2016) using the model parameters with the real data (see Fig. S8). The four models (i.e. the MDNS, WMDNS, DNNS and DMANS models) were compared, and the one(s) with the lowest AIC value(s) were selected as best fitting. All analyses were done using the statistical software R (R-Core-Team, 2016).

The Müller et al. seed-introduction dataset

To test how seedling emergence (i.e. the proportion of seeds that germinated) in the Müller et al. seed-introduction dataset depended on phylogenetic distance measures, we used binomial generalized linear mixed models implemented in the glmer function of the “lme4” package (Bates *et al.* 2015). Because some of the phylogenetic metrics were strongly correlated (in particular MDNS - DNNS, and WDMS – DMANS; Fig. S2), we again ran separate models for each of the four phylogenetic distance measures. The distance measures were also standardized, and were included both as simple and quadratic terms as before. Disturbance treatment (yes/no) and fungicide treatment (yes/no) were used as fixed factors after converting them to dummy variables (with values equal to 0 or 1) and centering each of them to a mean of zero (Schielzeth 2010). We also included the interactions of the linear and quadratic components of the distance measures with all other explanatory variables, as we did for the Kempel *et al.* (2013) data. To account for non-independence among data points from the same plots and sites, and the same species, plot nested in site and species were included as random factors. The MDNS, WMDNS, DNNS and DMANS models were again compared using AIC values.

The Müller et al. seedling-introduction dataset

To test how seedling survival (yes/no) in the Müller et al. seedling-introduction dataset depended on phylogenetic distance measures, we used binomial generalized linear mixed models implemented in the *glmer* function of the "lme4" package (Bates *et al.*, 2015). The correlations between the different phylogenetic distance measures are shown in Fig. S3. The procedures and models were the same as described for the Müller *et al.* seed-introduction experiment, with the exception that the fixed factors included the additional term herbivore exclusion (yes/no).

Results

The Kempel *et al.* seed-introduction dataset

Averaged across all species, 16% of the seeds emerged as seedlings. Of the four phylogenetic distance measures, mean phylogenetic distance (MDNS) to the entire resident plant community provided the best overall model fit (i.e. lowest AIC; Table 1), closely followed by the weighted mean phylogenetic distance to the resident plant community (WMDNS) and by the phylogenetic distance to the most abundant native resident species (DMANS). The phylogenetic distance to the nearest (most closely related) native resident species (DNNS) provided the worst model fit. The results of the three best models (maximum ΔAIC = 2.46, Table 1) are described below and in Fig. 1.

In the model with the best fit (MDNS), alien species had overall a significantly higher seedling emergence than the native species (Table 1, Fig. 1b). Introduced species with an intermediate MDNS to the resident community had the highest seedling emergence, as indicated by a significant negative MDNS^2 effect (Table 1, Fig. 1a). The strength of the MDNS^2 effect, however, depended on disturbance and the number of seeds sown (Table 1). In the disturbed plots, the curvilinear effect of MDNS on seedling emergence became weaker (Fig. 1c), and at the highest number of sown seeds, the curvilinear relationship changed into a more linear positive MDNS relationship (Fig. 1d).

In the models with the second and third best fits (WMDNS and DMANS, respectively), the difference in emergence of alien and native species remained significant, with a higher emergence for alien species (Table 1, Fig. 1f, j). In addition, in both models, seedling emergence significantly increased with the number of seeds sown (Table 1, Fig. 1h, k). Averaged across all species and treatments, the relationship between seedling emergence and WMDNS was relatively flat (Fig. 1e). However, as indicated by the significant WMDNS^2 × disturbance interaction (Table 1), the relationship between seedling emergence and WMDNS changed from slightly convex in the undisturbed sites to concave in the disturbed sites (Fig. 1g). The average relationship between seedling emergence and DMANS tended to be negative (Fig. 1i), but this effect was not significant (Table 1). However, whereas seedling emergence of the introduced alien species was not or hardly affected by DMANS, seedling emergence of the introduced native species decreased with DMANS (significant DMANS × status interaction in Table 1). For results of DNNS, see Table 1 and Fig. S5 in the Supporting Information.

The Müller *et al.* seed-introduction dataset

Averaged across all species, 43% of the seeds emerged as seedlings. Of the four phylogenetic distance measures, the weighted mean phylogenetic distance to the resident plant community (WMDNS) provided the best overall model fit (i.e. lowest AIC; Table 2), closely followed by the mean phylogenetic distance (MDNS) to the resident plant community. The phylogenetic distance to the most abundant native resident species (DMANS) and the phylogenetic distance to the nearest (most closely related) native resident species (DNNS) provided much worse model fits. The results of the two best models (with $\Delta\text{AIC} = 0.84$, Table 2) are described below and in Fig. 2.

In the two best models (WMDNS and MDNS), native species had overall a significantly higher seedling emergence than the alien species (Table 2, Fig. 2a, d). Moreover, seedling emergence was on average higher in the disturbed plots than in the undisturbed plots (Table 2, Fig. 2c, f). On average, seedling emergence was highest at intermediate values of WMDNS as indicated by a significantly negative WMDNS^2 effect (Table 2, Fig. 2d). However, as indicated by a significant WMDNS^2 × disturbance interaction, this relationship depended on the disturbance treatment (Table 2). In the disturbed plots, seedling emergence was highest at intermediate values, whereas in the undisturbed plots, seedling emergence was highest at the lowest values (Fig. 2f). Seedling emergence was slightly negatively affected by MDNS (Table 2, Fig. 2a). For results of the other phylogenetic distance measure models (DNNS, DMANS), see Table 2 and Fig. S6.

The Müller *et al.* seedling-introduction dataset

Overall, 58.5% of planted seedlings survived until the end of the first season. Among the four phylogenetic distance measures, distance to the nearest native species (DNNS) provided by far the best model fit (i.e. had the lowest AIC; Table 3). Mean phylogenetic distance (MDNS) provided the second best model, followed by phylogenetic distance to the most abundant native species (DMANS). Weighted mean phylogenetic distance (WMDNS) provided the worst model fit. The results of the best model (with ΔAIC > 20 relative to the other models, Table 3) are described below and in Fig. 3.

In the model with the best fit (DNNS), seedling survival was significantly higher in the disturbed plots than in the undisturbed plots, in the closed herbivore exclosures than in the open exclosures, and in the plots not treated with fungicides than in the plots treated with fungicides (Table 3, Fig. 3). On average, the survival probability of seedlings significantly decreased with increasing DNNS (Table 3, Fig. 3). Although alien and native species did not differ in their average survival probability, alien species showed more of a negative convex relationship between survival probability and DNNS, whereas native species showed more of a negative concave relationship with DNNS (significant DNNS × status and DNNS^2 × status interactions in Table 3). The curvilinear component of DNNS also depended on the fungicide and herbivory treatments (significant $DNNS^2$ × fungicide and $DNNS^2$ × herbivory interactions in Table 3). The relationship between seedling survival and DNNS tended to be convex in plots without fungicides and in closed herbivore exclosures, whereas it tended to be concave in plots with fungicides and in open herbivore exclosures. For results of the other three phylogenetic distance measures (MDNS, WMDNS, DMANS), see Table 3 and Fig. S7.

Discussion

Until now, all tests of Darwin's naturalization hypothesis (DNH) or conundrum in (semi-)natural plant communities relied on observational datasets that lacked hard data on species that failed to establish after introduction. Here, we tested DNH for the first time using data from studies in which large numbers of species had been experimentally introduced into grassland sites (Kempel *et al.* 2013, Müller *et al.* 2016). Using four different phylogenetic metrics, we tested whether introduced species' seedling emergence and survival (i.e. the first steps to becoming naturalized) are best explained by phylogenetic distance to all resident species (MDNS), all resident species weighted by their abundance (WMDNS), the closest relative (DNNS) or the most abundant resident (DMANS). We found that the phylogenetic distance measures that provided the best model fits varied among the three introduction datasets that we analysed. In all these best-fitting models, the effects of phylogenetic distance were significant. Overall our results indicate that both environmental filtering and competition determine the establishment success of introduced species into resident communities. However, the direction and shape of these relationships frequently depended on alien-native status of the introduced species, the number of seeds introduced, disturbance, fungicide application or herbivore-exclosure treatments.

Seedling-emergence datasets

For both the Kempel *et al.* and the Müller *et al.* datasets, seedling emergence was best explained by the models that included mean distance of the introduced species to the resident community (MDNS), or the weighted mean distance to the resident community (WMDNS) (Tables 1 and 2). For the Kempel et al. dataset, the model that included the distance to the most abundant resident species (DMANS) was also among the best models (Table 1). These findings suggest that seedling emergence of introduced forb species in native grassland communities is affected by phylogenetic distance to each resident species, but particularly to the most abundant residents.

The best models for both the Kempel *et al.* (MDNS) and the Müller *et al.* (WMDNS) seed-introduction datasets showed that seedling emergence was highest at intermediate phylogenetic distances (Figs. 1a and 2d). In other words, introduced species were less successful if they were either very closely or very distantly related to the residents. This non-linear pattern may result from environmental filtering (reducing establishment of distantly related species) and competitive or other antagonistic biotic interactions (reducing establishment of closely related species) acting simultaneously (Gallien & Carboni, 2016). Direct competitive interactions with resident plant species are unlikely to play a role for seedling emergence (i.e. germination), but other biotic (e.g. herbivores, mycorrhizal fungi, pathogens) and abiotic (e.g. light, moisture, temperature) components of the local environment may be important. These abiotic and biotic factors can also be altered by the resident plant species (Orwin *et al.* 2010, Grigulis *et al.* 2013). For example, the resident plant species may have accumulated pathogens that also affect introduced species, and particularly closely related ones (Cavender-Bares *et al.*, 2009). In line with this, we found in the Müller et al. dataset that fungicide application (which supposedly acted against pathogenic fungi and not against mycorrhiza; Müller *et al.* 2016), increased the seedling emergence of introduced species with abundant, more closely related residents (i.e. with low WMDNS values; Fig. 2g).

The exact direction and shape of the relationship between seedling emergence and phylogenetic distance depended not only on fungicide application but also on several other factors. For example, in the Kempel *et al.* dataset, when many seeds (1000) were introduced, the relationship between seedling emergence and MDNS became linear and positive. This result suggests that higher propagule pressure may overcome the negative effects of environmental filtering, which should act particularly against distantly related species, but does not overcome the effect of competition or other biotic interactions, which should act particularly against closely related species. Furthermore, in both the Kempel *et al.* and Müller *et al.* datasets, soil disturbance by tilling prior to sowing changed the shape of the relationship between seedling emergence and phylogenetic distance (Tables 1 and 2, Figs. 1c and 2f). Soil tilling changes the environment by loosening the soil but also by removing most of the resident plants. The latter should result in a weaker effect of phylogenetic distance, and this is indeed what we found for MDNS in the Kempel *et al.* dataset. However, in the Müller *et al.* dataset, we found that seedling emergence was highest at intermediate WMDNS values in the disturbed plots only, as it was highest at low WMDNS values in the undisturbed plots. This might suggest that environmental filtering played a more important role in the Müller et al. experiment. However, the shape of the fitted relationships might have been strongly determined by a few data points with low WMDNS values that were far away from most of the other WMDNS values (Fig. 2f). Nevertheless, in the second best model, the effect of MDNS was significantly negative (Table 2), though weak (Fig. 2a), which also points to the presence of a role of environmental filtering in the Müller *et al.* dataset.

We found little evidence that the effect of phylogenetic distance on seedling emergence differed between alien and native introduced species. However, in the third best model of the Kempel *et al.* dataset (DMANS), which had an AIC value very similar to those of the top two models, there was a significant DMANS × status interaction (Table 1). The effect of DMANS on seedling emergence was overall negative, indicating the importance of environmental filtering, and although this effect held for both the alien and native introduced species, it was weaker for the latter.

Nevertheless, the overall similar patterns for alien and native introduced species suggest that mechanisms governing seedling emergence of alien species also determine seedling emergence of native species.

Although the effects of phylogenetic distance on seedling emergence were very similar for alien and native introduced species in both datasets, the main effect of status was significant. Interestingly, the direction of this effect differed between the two datasets. In the Kempel *et al.* dataset, alien species had a higher seedling emergence than native species, whereas in the Müller et al. dataset the opposite was true. The original study by Kempel *et al.* (2013) showed that this initial advantage of the aliens over the natives changed into a disadvantage in later years. Unfortunately, we could not analyse those later years, due to the overall low success rate of species in this period. A possible explanation for the higher seedling emergence of the alien species in the Kempel *et al.* (2013) study could be that the alien seeds were all of horticultural origin and have undergone selection for high germination rates. Indeed, Chrobock *et al.* (2011) found that under greenhouse conditions the alien plant species used in Kempel *et al.* (2013) germinated earlier and more profusely than the native species.

Seedling-survival dataset

Our results for seedling survival from Müller *et al.* (2016) (Table 2) differed from our results for seedling emergence from the same study. In the seedling survival analysis, the single best-fitting model was the one that included the phylogenetic distance to the nearest neighbour (DNNS), instead of the mean and weighted mean phylogenetic distance. Moreover, the overall relationship between seedling survival and phylogenetic distance was negative and not hump-shaped (Fig. 3). The shape of the relationship could result from the lack of intermediate DNNS values in this dataset (Fig. 3). Nevertheless, the lower seedling survival at high than at low DNNS values suggests that environmental filtering favours seedling survival of species that have a closely related species present in the resident community (Gallien & Carboni, 2016), and supports the pre-adaptation hypothesis. Alternatively, closely related species may not have similar environmental requirements to resident species *per se*, but instead result in more similar environmental conditions. For example, Li *et al.* (2015) suggested that closely related species tend to create similar soil-nutrient microhabitats, harbouring similar soil enzymes, such as alkaline and acid phosphatases, and therefore favour close relatives preadapted to these conditions. Whatever the exact mechanism, our result indicates that environmental filtering can not only explain large-scale patterns of species occurrence (Thuiller *et al.*, 2010), but also small-scale patterns.

In contrast to seedling emergence, seedling survival in the Müller et al. dataset did not depend on whether the introduced species was native or alien. However, as for seedling emergence, seedling survival was highest when the resident vegetation had been disturbed by soil tilling, and when no fungicides were applied. In addition, seedling survival was highest when herbivore pressure was reduced. This shows that biotic interactions overall play an important role in seedling survival. The negative effect of fungicide application may seem counterintuitive, but probably reflects that it released the native resident vegetation more strongly than the introduced species from fungal pathogens, and that this increased the competitive ability of the residents (Müller *et al.* 2016).

Biotic interactions may differ for native and alien species, and the importance of biotic interactions is likely to be stronger when the introduced species and residents are closely related. Therefore, one would expect status of the introduced species, disturbance, herbivore exclusion and fungicide treatments to change the relationship between seedling survival and phylogenetic distance. This was indeed the case for status, herbivore exclusion and fungicide treatment, but it were mainly only slight effects on the non-linear components of the overall negative relationships. These included changes from convex curves for alien species, fungicide-treated plots and closed herbivore exclosures to more concave curves for native species, plots without fungicide and open herbivore exclosures. As the dataset lacks intermediate DNNS values, we cannot be sure that the apparent changes in curvilinearity are biologically meaningful. The relationships for the different treatments seem to be quite similar (Fig. 3), suggesting that the effects of phylogenetic distance were only slightly mediated by biotic interactions.

Conclusions

Overall, we found that the establishment success of introduced species in grassland communities is significantly related to the phylogenetic distance between the introduced species and residents. However, we found partly different patterns for the three datasets that we analysed, which emphasizes the context specificity of studies on establishment success. Nevertheless, we also found some similarities. For example, in both the seed-introduction experiments, seedling emergence was highest at intermediate phylogenetic distances to the native community, suggesting that preadaptation and biotic interactions both mediate establishment success. A comparison of the seedling emergence and seedling survival data of Müller *et al.* (2016) suggests that factors driving success of an introduced species differ between life stages. Furthermore, we showed that the phylogenetic distance metrics that best explained species success differed among the datasets, but were more similar between the two seedling-emergence datasets than between the seedling-emergence and seedling-survival datasets of Müller *et al.* (2016). Therefore, considering multiple life stages and phylogenetic distance metrics might provide more insights into Darwin’s Naturalization Conundrum. To conclude, Darwin´s naturalization hypothesis and the preadaptation hypothesis need not be in conflict. Rather, the mechanisms underlying them can operate simultaneously or alternately depending on the life stage and on the environmental conditions of the resident community.

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Authors' contributions

MvK and WD developed the idea for the study, EM analysed the data, and wrote the manuscript with the help of MvK and WD. AK and GM collected the original data, and contributed to the writing.

Data accessibility

A part of the data associated with this paper are already available from Dryad Digital Repository, DOI: 10.5061/dryad.k6t16 (Müller et al. 2016) and the remaining data will be archived on Dryad Digital Repository.

Competing interests

The authors declare no competing financial interests.

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Figures and Tables

Table 1 Betabinomial model for seedling emergence (seed-introduction dataset of Kempel *et al.* 2013) for all four phylogenetic distance indices used: Mean phylogenetic Distance to the Native resident Species (MDNS), Weighted Mean phylogenetic Distance to the Native resident Species (WMDNS), phylogenetic Distance to the Nearest Native resident Species (DNNS) and phylogenetic Distance to the Most Abundant Native resident Species (DMANS). The models with the lowest and similar AIC values (MDNS, WMDNS and DMANS; ΔAIC < 4) are highlighted in grey shading. The intercept corresponds to an intermediate disturbance, intermediate status and mean propagule number (208 seeds). The categorical variables status (alien/native) and disturbance (no/yes) were converted to zeros and ones before centering, with the higher value corresponding respectively to native species and disturbed plots.

	MDNS		WMDNS		DNNS		DMANS	
Parameter	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P
Fixed terms								
Intercept	**-5.183 (0.392)**	**<0.001**	**-5.454 (0.380)**	**<0.001**	**-4.946 (0.390)**	**<0.001**	**-5.469 (0.390)**	**<0.001**
Phylogen. Index (PI)	0.115 (0.190)	0.546	-0.111 (0.161)	0.492	0.042 (0.153)	0.784	-0.001 (0.217)	0.998
PI^2	**-0.286 (0.123)**	**0.020**	0.012 (0.056)	0.829	**-0.424 (0.164)**	**0.010**	0.060 (0.064)	0.347
Status (*native*)	**-1.250 (0.580)**	**0.031**	**-1.472 (0.570)**	**0.010**	-0.852 (0.616)	0.167	**-1.384 (0.570)**	**0.015**
Disturbance (*yes*)	-0.447 (0.465)	0.336	-0.621 (0.446)	0.164	-0.407 (0.440)	0.355	-0.464 (0.450)	0.302
Seed number.	0.229 (0.183)	0.209	**0.357 (0.173)**	**0.039**	0.256 (0.179)	0.151	**0.367 (0.181)**	**0.043**
PI × Status	-0.363 (0.264)	0.169	-0.239 (0.254)	0.345	0.268 (0.281)	0.339	**-0.361 (0.157)**	**0.022**
PI × Disturbance	-0.058 (0.145)	0.687	0.053 (0.194)	0.785	0.167 (0.119)	0.161	-0.274 (0.390)	0.482
PI × Seed number	0.059 (0.064)	0.359	0.042 (0.091)	0.642	0.035 (0.055)	0.533	0.039 (0.180)	0.829
PI^2 × Status	-0.174 (0.191)	0.365	-0.011 (0.097)	0.913	**-0.593 (0.414)**	**0.059**	-0.072 (0.070)	0.304
PI^2 × Disturbance	**0.289 (0.117)**	**0.013**	**0.250 (0.092)**	**0.007**	0.065 (0.147)	0.659	0.084 (0.134)	0.531
PI^2 × Seed number	**0.153 (0.059)**	**0.009**	-0.009 (0.042)	0.834	0.078 (0.066)	0.234	-0.025 (0.064)	0.700
Random terms	SD		SD		SD		SD	
Site	0.831		0.798		0.770		0.782	

Species	2.031	2.069	1.975	2.066
AIC	**2889.48**	**2891.36**	2898.1	**2891.94**

Table 2 Binomial model for seedling emergence (seed-introduction dataset of Müller *et al.* 2016) for all the phylogenetic distance indices used: Mean phylogenetic Distance to the Native resident Species (MDNS), Weighted Mean phylogenetic Distance to the Native resident Species (WMDNS), phylogenetic Distance to the Nearest Native resident Species (DNNS) and phylogenetic Distance to the Most Abundant Native resident Species (DMANS). The models with the lowest and similar AIC values (MDNS and WMDNS; ΔAIC < 4) are highlighted in grey shading. The intercept corresponds to an intermediate disturbance, intermediate status and intermediate fungicide treatment. The categorical variables status (alien/native), disturbance (no/yes) and fungicide (no/yes) were converted to zeros and ones before centering, with the higher value corresponding respectively to native species, disturbed and fungicide-treated plots.

	MDNS		WMDNS		DNNS		DMANS	
Parameter	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P
Fixed terms								
Intercept	-0.244	0.338	-0.257	0.314	-0.429	0.142	-0.266	0.330
Phylogen. Index (PI)	**-0.164**	**0.093**	-0.152	0.260	-0.007	0.956	-0.060	0.749
PI^2	-0.078	0.243	**-0.123**	**0.006**	0.076	0.542	-0.407	0.161
Status (*native*)	**0.934**	**0.033**	**0.953**	**0.026**	**1.033**	**0.032**	**0.954**	**0.025**
Disturbance (*yes*)	**1.504**	**<0.001**	**1.565**	**<0.001**	**1.188**	**<0.001**	**1.615**	**<0.001**
Fungicides (*yes*)	-0.141	0.242	-0.200	0.090	-0.328	0.117	-0.209	0.046
PI × Status	-0.022	0.901	0.044	0.822	-0.048	0.847	0.063	0.674
PI × Disturbance	0.086	0.481	0.068	0.576	0.180	0.325	0.120	0.489
PI × Fungicides	-0.034	0.771	0.020	0.872	0.147	0.413	-0.062	0.713
PI^2 × Status	0.027	0.774	0.006	0.886	-0.060	0.798	0.002	0.935
PI^2 × Disturbance	-0.177	0.112	**-0.451**	**0.002**	0.119	0.530	**-1.012**	**0.066**
PI^2 × Fungicides	0.052	0.561	0.269	0.076	0.219	0.243	0.211	0.270
Random terms	SD		SD		SD		SD	
Site	0.277		0.308		0.352		0.342	
Plot within site	<0.001		<0.001		0.108		0.042	
Species	0.940		0.934		0.930		0.933	
AIC	**3600.80**		**3600.16**		3610.10		3608.48	

Table 3 Binomial model for seedling survival (seedling-introduction dataset of Müller *et al.* 2016) for all the phylogenetic distance indices used: Mean phylogenetic Distance to the Native resident Species (MDNS), Weighted Mean phylogenetic Distance to the Native resident Species (WMDNS), phylogenetic Distance to the Nearest Native resident Species (DNNS) and phylogenetic Distance to the Most Abundant Native resident Species (DMANS). The model with the lowest AIC value (DNNS) is highlighted in grey shading (the others have ΔAIC > 4). The intercept corresponds to an intermediate disturbance, intermediate status, intermediate fungicide treatment and intermediate herbivory treatment. The categorical variables status (alien/native), disturbance (no/yes), fungicide (no/yes) and herbivory (no, yes) were converted to zeros and ones before centering, with the higher value corresponding respectively to native species, disturbed, fungicide-treated and open herbivore-exclosure plots.

	MDNS		WMDNS		DNNS		DMANS	
Parameter	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P
Fixed terms								
Intercept	0.397 (0.478)	0.406	0.548	0.234	0.419 (0.429)	0.329	**0.708 (0.393)**	**0.071**
Phylogen. Index (PI)	**-0.531 (0.103)**	**<0.001**	**-0.293**	**0.005**	**-0.366 (0.064)**	**<0.001**	**0.337 (0.094)**	**<0.001**
PI^2	**0.105 (0.054)**	**0.055**	-0.034	0.470	0.088 (0.119)	0.462	**-0.394 (0.122)**	**0.001**
Status (*native*)	0.069 (0.636)	0.914	0.057	0.926	-0.831 (0.665)	0.211	0.047 (0.613)	0.939
Disturbance (*yes*)	**1.055 (0.247)**	**<0.001**	**1.146**	**<0.001**	**0.947 (0.272)**	**0.001**	**1.269 (0.246)**	**<0.001**
Fungicides (*yes*)	-0.250 (0.250)	0.317	-0.080	0.706	**-0.555 (0.266)**	**0.037**	-0.217 (0.244)	0.372
Herbivory (*open excl.*)	**-0.447 (0.247)**	**0.070**	**-0.592**	**0.005**	**-0.690 (0.268)**	**0.010**	-0.300 (0.244)	0.218
PI × Status	0.102 (0.091)	0.265	0.010	0.886	**0.376 (0.109)**	**0.001**	-0.006 (0.076)	0.938
PI × Disturbance	-0.100 (0.127)	0.428	0.040	0.732	-0.066 (0.076)	0.386	**0.729 (0.152)**	**<0.001**
PI × Fungicides	0.110 (0.137)	0.425	0.111	0.331	0.045 (0.073)	0.538	**0.322 (0.149)**	**0.031**
PI × Herbivory	-0.061 (0.123)	0.619	0.188	0.130	-0.059 (0.073)	0.417	0.015 (0.148)	0.919
PI^2 × Status	-0.042 (0.041)	0.310	-0.038	0.151	**0.847 (0.201)**	**<0.001**	-0.019 (0.020)	0.328
PI^2 × Disturbance	**-0.156 (0.093)**	**0.092**	-0.072	0.444	0.065 (0.183)	0.722	-0.052 (0.221)	0.814
PI^2 × Fungicides	0.176 (0.118)	0.136	0.076	0.440	**0.493 (0.171)**	**0.004**	0.372 (0.201)	0.064
PI^2 × Herbivory	0.120 (0.078)	0.122	**0.204**	**0.033**	**0.407 (0.172)**	**0.018**	**-0.399 (0.202)**	**0.048**
Random terms	SD		SD		SD		SD	
Site	0.753		0.7263		0.550		1.362	
Plot within site	0.730		0.6120		0.622		0.648	

Species	1.410	1.3840	1.413	0.470
AIC	6477.93	6525.74	**6457.65**	6486.12

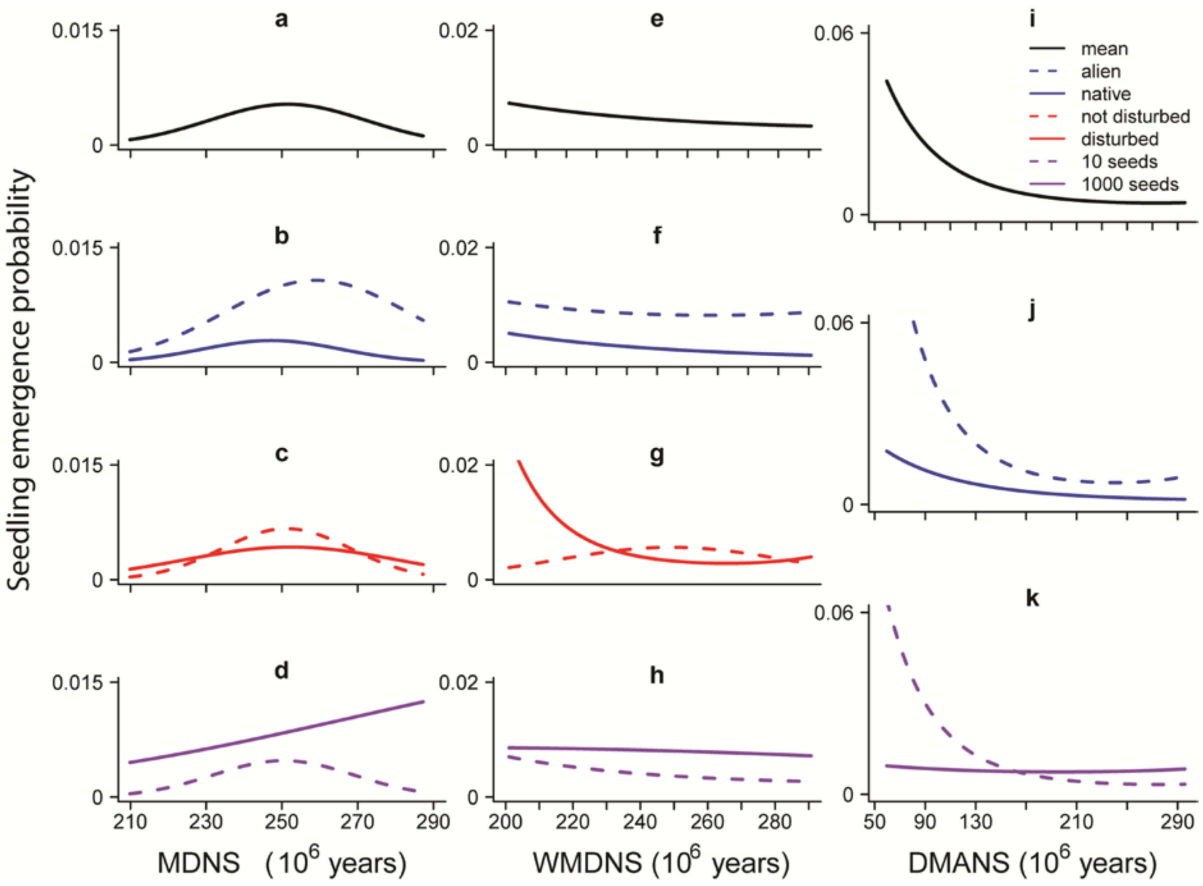

Figure 1 Fitted lines for betabinomial models explaining seedling emergence in the seed-introduction dataset of Kempel *et al.* (2013). The figures show seedling-emergence probability against Mean phylogenetic Distance to the Native resident Species MDNS (a-d), Weighted Mean phylogenetic Distance to the Native resident Species WMDNS (e-h), and phylogenetic Distance to the Most Abundant Native resident Species DMANS (i-k). Black line, a), e) and i): average across all factors; blue, b), f), and j): status (alien/native); red, c) and g): disturbance treatment (no/yes); purple, d), h) and k): seed number (10/1000). Only significant factors were plotted (see Table 1). All other factors are set to an average value within each graph. The raw data are shown in Figure S4.

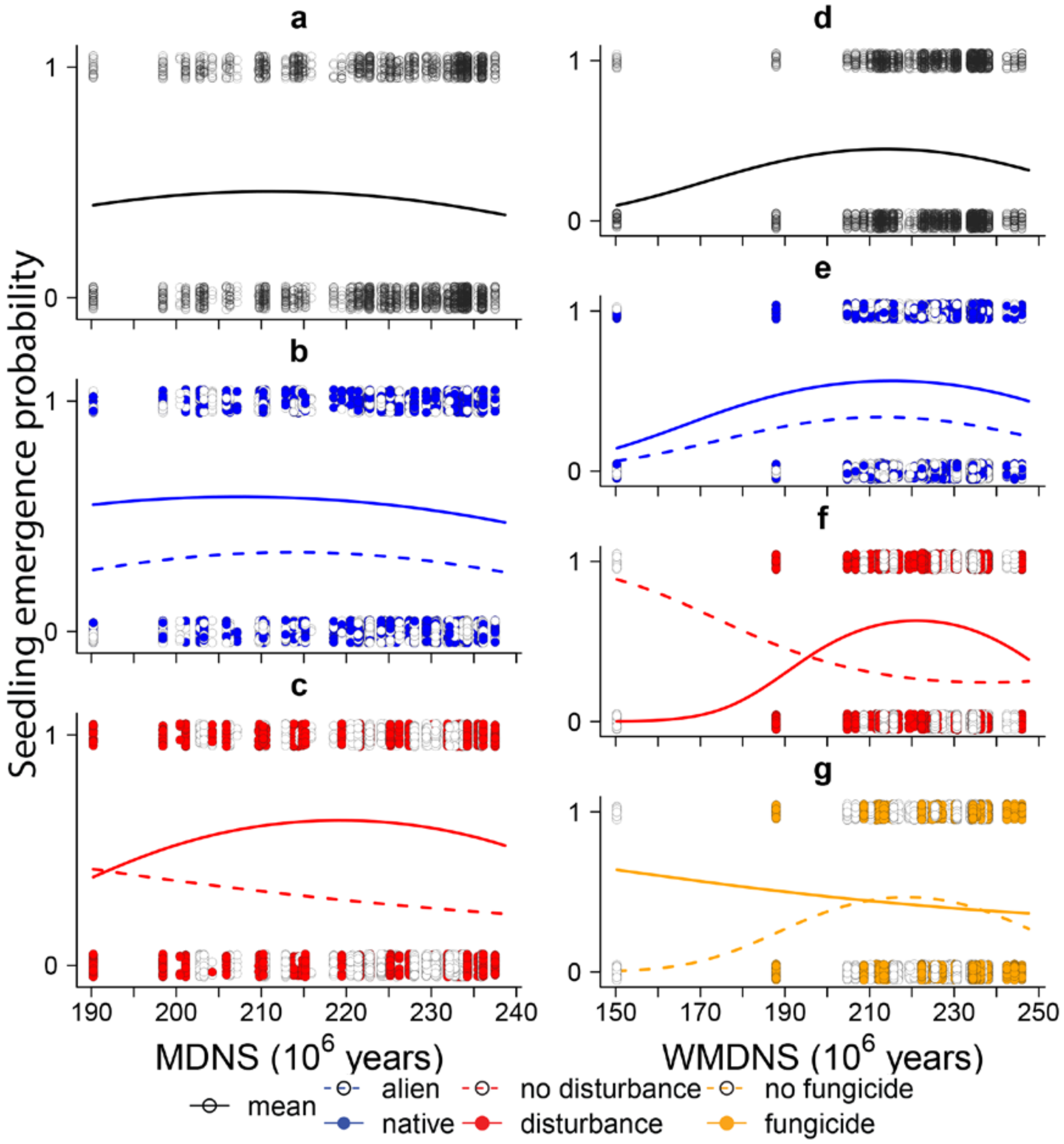

Figure 2 Data points and fitted lines for binomial models explaining seedling emergence in the seed-introduction dataset of Müller *et al.* (2016). The figures show seedling-emergence probability against the Mean phylogenetic Distance to the Native resident Species MDNS (a-c) and the Weighted Mean phylogenetic Distance to the Native resident Species WMDNS (d-g). Black line, a) and d): average among all factors; blue, b) and e): status (alien/native); red, c) and f): disturbance treatment (yes/no); yellow, g): fungicide treatment (yes/no). All other

factors are set to an average value within each graph. Only significant factors were plotted (see Table 2).

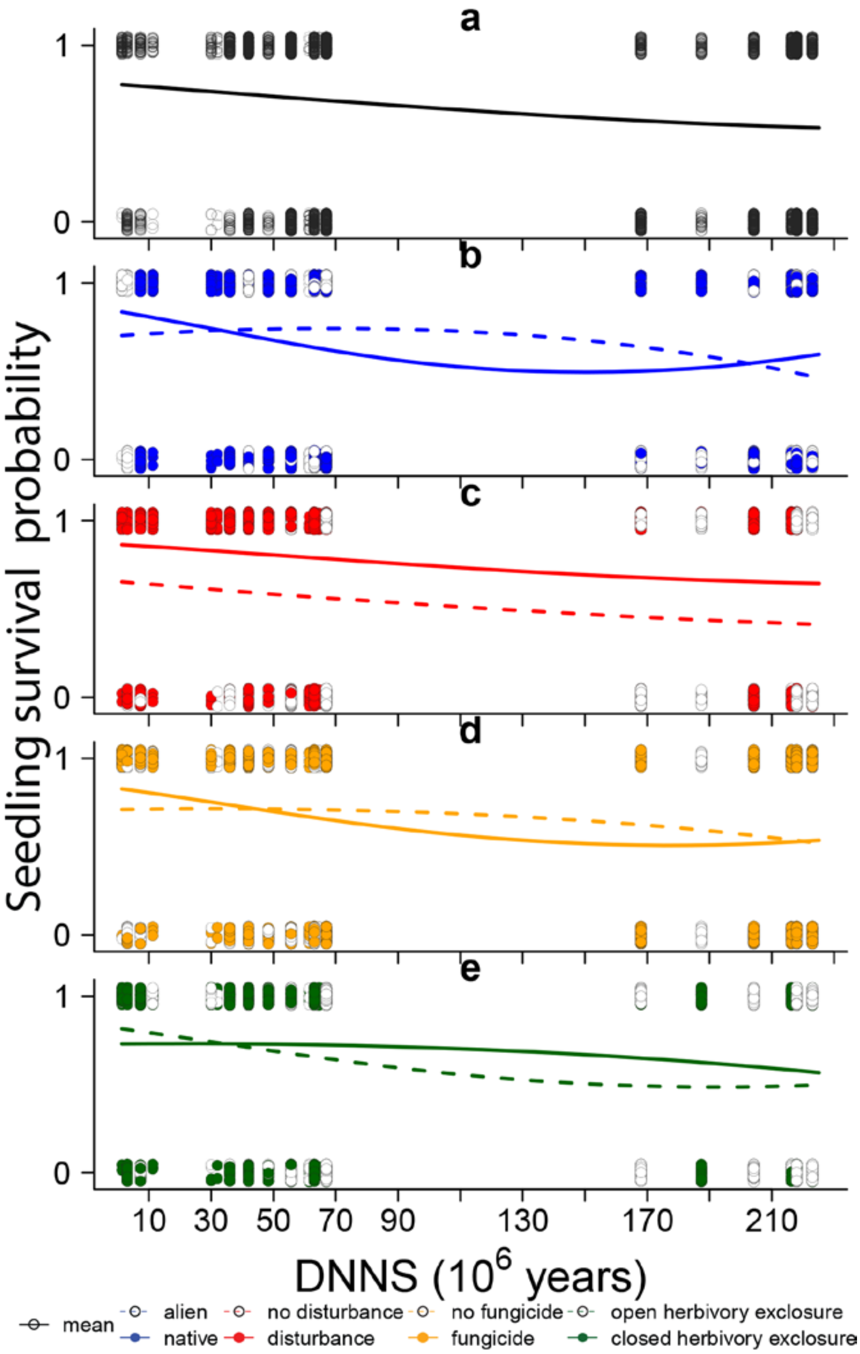

Figure 3 Data points and fitted lines for binomial models explaining seedling survival in the seedling-introduction dataset of Müller *et al.* (2016). The figures show seedling-survival probability against the phylogenetic Distance to the Nearest Native resident Species DNNS (DNNS, Mio years). Black line, a): average among all factors; blue, b): status (alien/native); red, c): disturbance treatment (yes/no); yellow, d): fungicide treatment (yes/no); green, e):

herbivory treatment (closed/open exclosures). All other factors are set to an average value within each graph. Only significant factors were plotted (see Table 3).