

Dark diversity at home describes the success of cross-continent tree invasions

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Abstract

Aim: Non-native species threaten ecosystems worldwide, but we poorly know why some species invade more. Functional traits, residence time and native range size have been often used as invasion predictors. Here, we advance in the field by linking invasion success to native range parameters derived from dark diversity – a set of species present in the surrounding region that are absent in a study location even if ecological conditions are suitable. We tested whether those parameters improve the description of species success outside their native range.

Location: North America; Europe and Mediterranean Basin.

Methods: For 170 tree species native in one and non-native in another region, we defined their invasion success as the number of locations occupied at the non-native range. The probabilistic dark diversity was estimated based on the species co-occurrences in their native ranges. It specifies how suitable is a species for a location, even if the species is absent. We calculated two parameters: sum of native location suitabilities (niche breadth proxy) and dark diversity probability (how often a species is absent from suitable locations, indicating niche realization limitations). We explored whether models including the dark diversity parameters performed better than one with a common species range measure, the number of locations occupied. We accomplished our models by adding functional traits, residence time and invasion direction.

Results: Invasion success increased with the sum of native location suitabilities and decreased with dark diversity probability. This model with dark diversity parameters outperformed an alternative using the number of native locations occupied. Our best model included invasion direction, functional traits (including mycorrhizal status) and residence time, but dark diversity parameters remained important predictors.

Main conclusions: The dark diversity parameters can contribute to invasion ecology by linking the species performance in the non-native range to its niches parameters, derived from the native range.

KEYWORDS

alien species, conservation, dark diversity, exotic species, functional traits, invasion, mycorrhiza, native range, non-native species, residence time

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1 | INTRODUCTION

The spread of non-native species is one of the main causes of global biodiversity loss due to their adverse impacts on native species and ecosystem functioning (Bezeng et al., 2020; Sapsford et al., 2020). Identification of the spreadability of invaders in their new range allows to mitigate their impacts or even prevent their introductions (Epanchin-Niell & Hastings, 2010; Fournier et al., 2019; Gallagher et al., 2015; Seebens et al., 2020). Among the drivers influencing plant invasion success, the most noticeable are the native range size, functional traits and residence time (Cassini, 2020; Catford et al., 2019; Gurevitch et al., 2011; Mathakutha et al., 2019; McGregor et al., 2012; Menzel et al., 2017; Pinna et al., 2021). Native range size is a synergistic outcome of dispersal, establishment and persistence, and might efficiently predict invasion success (McGregor et al., 2012). Here, we further widen native range metrics of non-native species, using the dark diversity – the regionally present but locally absent set of ecologically suitable species (Pärtel et al., 2011). For each native species, we can estimate the suitability of locations where the species is absent, i.e., probability of belonging to the dark diversity. Knowing the overall ecological suitability of native range locations and how often species are absent from such locations, we can assess their potential range and its actual realization. This information should describe species' niches and be informative to understand invasion success in the non-native range (Lewis et al., 2017; Ronk et al., 2017).

Widespread species in their native ranges tend to perform better in the new range (Carboni et al., 2016; Fristoe et al., 2021). Such species either display a broad habitat preference, develop persistent populations or are very successful in dispersal (Seliger et al., 2020; Vincent et al., 2020). The species native range size has been frequently characterized as extent (e.g. across latitude, Page & Shanker, 2020) or as a distribution range map drawn by experts (Mainali et al., 2020). Nevertheless, those measures likely overestimate the actual species distribution because many locations within the range extent or area are ecologically unsuitable. A more precise metric can be obtained when the study area is divided into discrete locations, allowing the calculation of the number of locations occupied (NLO). However, this approach likely underestimates the species invasion potential since typically only a fraction of the suitable locations is occupied (Alzate et al., 2020; Castaño-Quintero et al., 2020; Pyšek et al., 2015). The dark diversity approach offers the opportunity to extend the species range description. Specifically, the NLO can be replaced by two contributing metrics – the sum of location suitabilities (SLS) and the dark diversity probability (DDP, Moeslund et al., 2017). SLS is composed of both, locations where the species is present and estimations of ecologically suitable locations where the species is currently absent (i.e. in the dark diversity of that site). DDP is a ratio: the sum of suitabilities in locations not occupied by the species (characterizing how frequently a species is in the dark diversity) divided by the SLS. In theory, SLS provides a characterization of the potential range, a proxy for general niche width, and DDP demonstrates how often a species has failed to realize its potential

range. Thus, SLS should be positively, and DDP negatively related to invasion success, but it remains unknown if both are important and whether these two aspects perform better than NLO.

Native range parameters, dispersal, establishment and persistence are linked to several functional traits (Zambrano et al., 2019). Consequently, plant invasion success has been frequently studied from a functional perspective (Catford et al., 2019; Drenovsky et al., 2012). Non-native species rarely shift their niche when invading a new area (Hierro et al., 2005; Jelbert et al., 2019; Pyšek et al., 2020), suggesting that the same set of attributes can be linked to the likelihood of a given species to occupy suitable locations in both native and non-native ranges (Belinchón et al., 2020; Drenovsky et al., 2012; van Kleunen et al., 2010; Trindade et al., 2020). In their native ranges, plant species are often absent in otherwise suitable habitats if they are adapted to tolerate low nutrient conditions, are dispersal limited, stress intolerant, and exhibit obligately mycorrhizal symbiosis (Moeslund et al., 2017; Riibak et al., 2015). Similar species traits are frequently related to invasion as well. For example, successful non-native plant species tend to be taller, with larger nitrogen-rich leaves and lighter seeds. They often have facultatively mycorrhizal status, leading to higher competition, dispersal ability and metabolic efficiency (Funk & Vitousek, 2007; van Kleunen et al., 2015; Menzel et al., 2017). Nevertheless, native range parameters can be more closely related to plant invasion success than functional traits (e.g. see McGregor et al., 2012). However, native range dark diversity parameters, indicating key niche characteristics, while promising, have not been yet tested.

Regional historical aspects in both, native and non-native ranges are also important determinants of plant invasion success (Ni et al., 2021). Although many species have initially been brought to new areas due to their economic or ornamental attributes, such as tree species in forestry or parks, some of them eventually became ecologically harmful (Brus et al., 2019; Rojas-Sandoval & Ackerman, 2021; Stohlgren et al., 2013; Vítková et al., 2017). Harmful non-native tree species influence the whole ecosystem and cause especially large environmental and economic problems worldwide (Crous et al., 2017). Even in regions that reciprocally exchanged many non-native plant species, such as Europe and North America (Herrando-Moraira et al., 2019; Kalusová et al., 2017), there have been varying reasons for the invasion. After European colonization, North America had plenty of intact forests, and trees were brought from the Old World to create a “home feeling” around settlements (Dyer, 2010; Mack, 2003). In contrast, there was a shortage of forests in Europe and several North-American tree species were then introduced for timber production (Kaplan et al., 2009; Pötzelsberger et al., 2020). Due to such historical differences, these two regions may exhibit distinct ecological forces regulating the spread of non-native trees, which might describe some part of invasion success. In addition to regional history, most species need considerable time to accomplish their potential spread (Essl et al., 2011). A longer residence time also allows a higher propagule pressure from multiple introductions (La Sorte & Pyšek, 2009; Pyšek et al., 2015). However, it remains unknown if the residence time effect is still an important descriptor of invasion

success, even if native range dark diversity parameters have been considered.

Here, we examine the potential of dark diversity parameters to improve the models to predict invasion success by using trees from two regions, North America (NAM) and Europe and the Mediterranean Basin (EMb). We compiled data on species native in one region and non-native in another to test the following hypotheses: (1) the native range dark diversity parameters (SLS and DDP) will describe the invasion success independently to other factors; (2) dark diversity parameters (SLS and DDP) from the native range are more informative to explain the invasion success than the number of locations occupied (NLO); (3) the importance of the dark diversity parameters describing the tree invasion success depends on the invasion direction between study regions; and (4) functional traits and residence time have an additional influence on invasion success, without substituting the effect dark diversity parameters.

2 | METHODS

2.1 | Study area and species selection

Our study area comprises two regions, North America (NAM), and Europe and the Mediterranean Basin (EMb; Figure 1). In both regions, we distinguished discrete locations for species presences and absences. For NAM, we used 64 locations, comprised the Canadian provinces/territories and the mainland USA states, avoiding tropical areas. The latitudes in that region range from 27°N to 70°N, longitudes 135°W to 55°W. For EMb, we used 46 locations (countries from Europe and bordering the Mediterranean Sea, latitudes 24°N to 78°N, longitude 9°W to 44°E).

We compiled the occurrence information of the tree species that are native in one region but non-native in the other, defining a tree according to the GlobalTreeSearch database (BGCI, 2021) as "a woody plant with usually a single stem growing to a height of at

least two meters, or if multi-stemmed, then at least one vertical stem five centimetres in diameter at breast height" (Beech et al., 2017). Tree species occurrences in NAM were extracted from the Plants Database of the United States Department of Agriculture (USDA, 2020). In EMb, we used distribution data from the GlobalTreeSearch database (provides a country scale distribution, Beech et al., 2017). Non-native species in all locations both in NAM and EMb were defined according to the Global Naturalized Alien Flora (GloNAF) dataset, a compendium of more than 200 global data sources at the resolution of our locations (van Kleunen et al., 2019). We excluded species that were marked both native and non-native within the same region: *Alnus incana*, *Juniperus communis* and *Sambucus nigra*. For NAM and EMb we, respectively, obtained 89 and 81 non-native tree species which originated from the other region (Figure 1).

For each species, the invasion success was defined as the number of locations (i.e. provinces/territories/states for NAM and country for EMb) occupied in the non-native range. In their native range, we calculated two variables derived from dark diversity – a set of species that theoretically can inhabit a location but are currently absent (Pärtel et al., 2011). We determined the sum of locations suitabilities (SLS), and the dark diversity probability (DDP, Moeslund et al., 2017). In order to get these measures, the following steps were done (Figure 2). For each native species, we estimated its likelihood to be part of the dark diversity in all locations where they were absent using a probabilistic approach available in the R package DARKDIV (Carmona & Pärtel, 2021). For that, we analysed pairwise co-occurrences of native species and compared the number of observed co-occurrences with the random expectation according to the hypergeometric distribution, which takes into account the frequency of both species and the total number of locations (Carmona & Pärtel, 2021). The standardized difference between observed and expected joint occurrences describes if a pair of species co-occur more or less frequently than expected and can be used as the mutual indication between these two species. If a pair of species share ecological requirements for climate and habitat conditions, they are

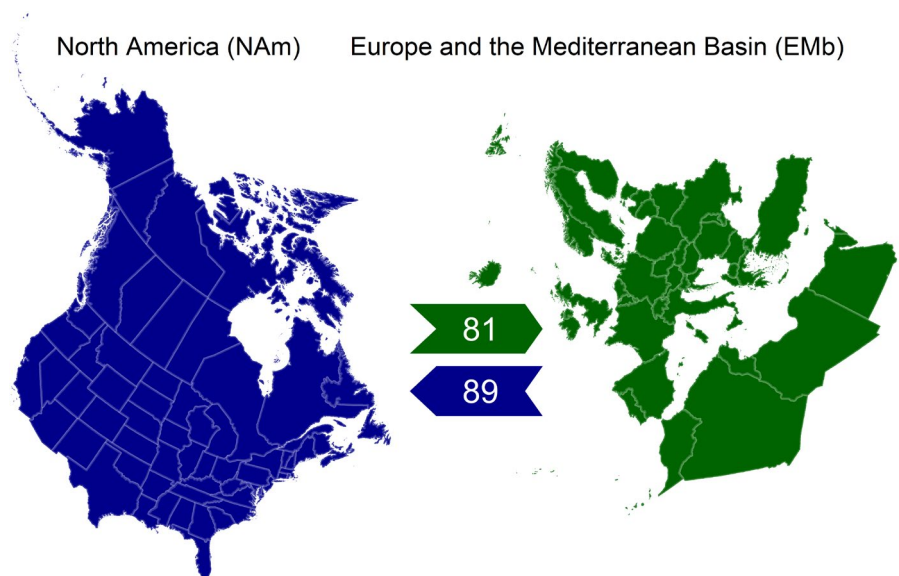


FIGURE 1 Study areas and the number of interchanged tree species. The green arrow shows the number of tree species that are native in NAM and non-native EMb. The blue arrow shows the number of tree species that are native in EMb and non-native in NAM. The map is in the Albers projection where the borders of study locations are shown

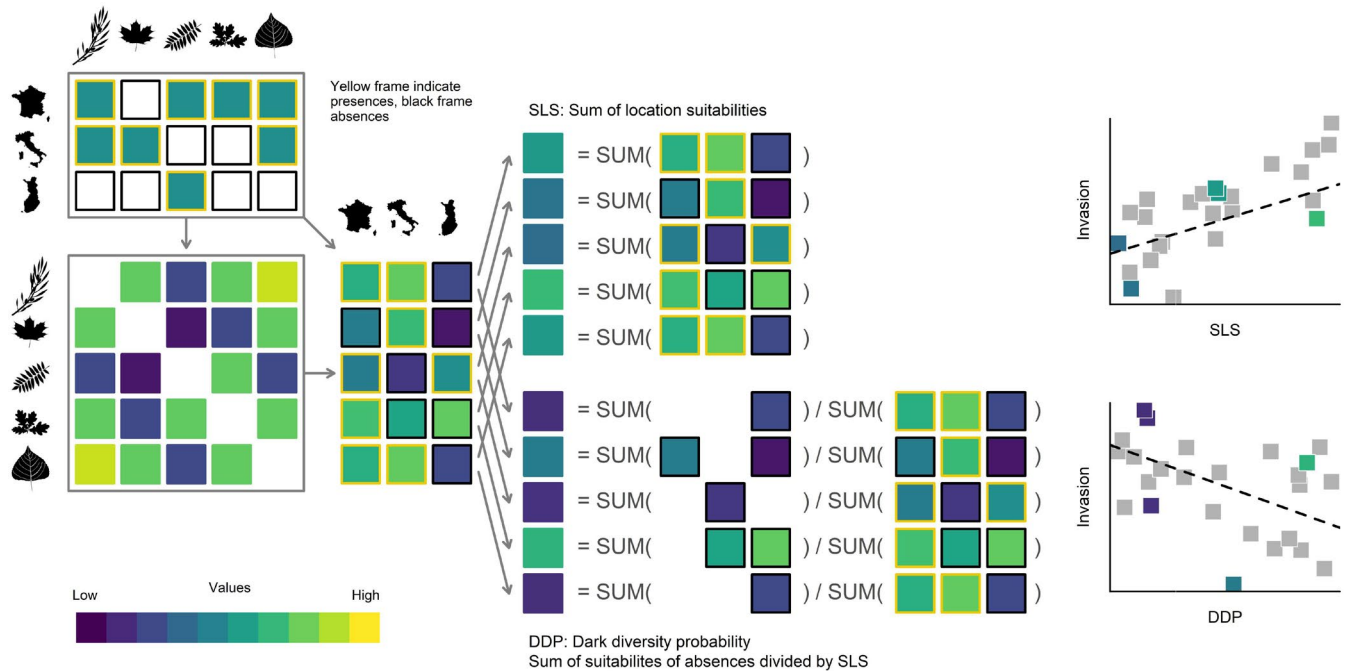


FIGURE 2 A conceptual overview of study variables and expectations. We use species/location occurrence matrix (topeleft, 5 taxa, 3 locations). Based on species co-occurrences, we know which species co-occur more or less likely than expected by random, shown by the indication matrix of 5x5 taxa. Self-indication is not considered (diagonal). Using present species as indicators (columns of the indication matrix), we can average their indication for each location, and each target species (columns). This will results suitability matrix, where the suitability of absent species indicates their membership in the probabilistic dark diversity of a particular location. Suitability for present species is usually large (close to 1). For each species, we calculate two parameters – SLS, sum of location suitabilities; DDP, dark diversity probability, sum of suitabilities when species is absent (membership in dark diversity), divided by SLS. SLS indicates the potential niche width of that species, even if some suitable locations are not occupied. DDP indicates how easily a species can realize its potential niche. In right there are theoretical expectations of how invasion success can be positively related to SLS and negatively to DDP (grey squares indicate other species not shown in previous matrices). All calculations can be done solely from co-occurrence matrix. Silhouettes are for illustration only; species images originate from phylopic.org, countries from R package maps

occurring more likely together. If they need contrasting abiotic and biotic conditions, they co-occur less than expected randomly. To estimate the suitability of a location to an absent species, present native species were used as indicators, and their indications in respect to that absent species were averaged (thus, the number of indicating species does not affect the mean estimate, but more species might give a more precise estimate). A similar suitability calculation was done for all species found in the region, and then transformed to probability to be in dark diversity in that location (a value that varies between 0 and 1). For each species, we defined the SLS as the sum of suitabilities across all locations in the native region (both where the species was observed and not observed). The DDP was calculated as a ratio between the sum of suitabilities in locations where the species was absent divided by SLS (see Figure 2).

Our study is performed at the biogeographic scale where location size is large and variable. This was due to data availability across the whole study region, where we wanted to have as equal sampling effort as possible. Co-occurrence in large sample unit does not mean that studied species can inhabit a same forest, but that general conditions at the used spatial scale are likely favourable for the species (e.g. species in mountain ranges can indicate each other even if they grow at different altitudes).

Thus, the co-occurrence in the native range might still indicate of suitability in the non-native range, if the sampling scale is the same (areas did not differ between NAM and EMb, Wilcoxon test $W = 1739$, $p = .107$). However, co-occurrences from a larger scale might be somehow inaccurate if a smaller location has just a subset of conditions in larger locations. Such effect should be relatively small due to a large number of taxa used to estimate location suitabilities (NAM dataset we had 854 and in EMb 575 native tree species). Nevertheless, to estimate the possible effect of large sampling units, we performed an additional test. We checked how much SLS and DDP change when we gradually eliminate larger locations (up to 25%) from our dataset. We look correlation between metrics calculated from the full dataset vs. dataset without the largest location and tested whether the difference is biased (different from zero). The test indicates a very high correlation (higher than 0.95 when removing up to 25% of the largest locations) and lack of bias, confirming that data from large locations did not invalidate our results. Details on this analysis can be found in Appendix S5: Figure S4. In order to check if our parameters based on the co-occurrences at the countries/states/provinces/territories level provide equivalent outcomes when estimated from smaller scales, we performed one more test using the sPlotOpen

database (Sabatini et al., 2021). This dataset is characterizing co-occurrences at a finer scale (typically between 100 and 1000 m² in forests), and 150 tree species from our 170 species were present in the plots from our study region (total 54963 plots), even if plot distribution is very uneven (in contrast to studied locations in the main analyses). We calculated our study parameters from sPlotOpen for 150 species and correlated these with values from the main analyses. Overall correlations were relatively strong ($45 < r < 64$) and associations linear (Appendix S5: Figures S5–S8). These results suggest that our parameters are not biased by the spatial scale. Thus, further studies aiming to use NSL and DDP estimated from smaller scales should find similar outcomes. These results suggest that species co-occurrences in our dataset likely indicate location suitability.

To compare the performance of dark diversity metrics with that obtained from a traditional native range parameter, we also calculated the number of locations occupied (NLO). In general, the NLO of a species is limited by the overall suitability of locations (characterized by SLS), and how often the species is in dark diversity (characterized by DDP). Thus, NLO is inherently related to both SLS and DDP. Indeed, NLO is highly correlated with both, SLS and DDP (Pearson's correlation 0.62 and -0.93 respectively; Appendix S1: Figure S2). For each of the 170 interchanged species, we retrieved information about functional traits representing their main ecological strategies – plant height (m); leaf area (mm²); leaf nitrogen content per unit of leaf mass (mg/g); seed mass (mg); specific leaf area (mm²/mg); specific stem density in (g/cm³); mycorrhizal type and status (Carmona et al., 2021; Weigelt et al., 2021). The first six traits were extracted from the TRY Plant Trait Database (Kattge et al., 2020). The information about mycorrhizal type and status were collected from multiple sources (Akhmetzhanova et al., 2012; Bueno et al., 2021; Harley & Harley, 1987a, 1987b, 1990; Hempel et al., 2013; Soudzilovskaia et al., 2020; Wang & Qiu, 2006). The mycorrhizal type classification was simplified when complex to three levels: ectomycorrhiza (ECM), arbuscular (ACM) and dual (ECM+AM). Details about how we merged initial mycorrhizal types can be found in Appendix S2: Table S1. Regarding the mycorrhizal status, we classified our species into two levels, facultative (when there are individuals associated with mycorrhizal fungi and others not) or obligate (when all individuals are always associated with mycorrhizal fungi). While plant mycorrhizal types inform about nutrient-specific requirements and demands influencing plant nutrient economy, mycorrhizal status refers to the prevalence of mycorrhizal symbiosis in each studied plant species (Moora, 2014; Smith & Read, 2008).

In our 170 interchanged tree species, 85% had values for all considered traits. To fill the missing trait value gaps, we used a phylogenetically informed trait imputation (missForest R package, Stekhoven & Bühlmann, 2012). Overall, imputation is preferred over omitting species with missing data (Nakagawa & Freckleton, 2008). However, to test the imputation method's potential influence on our results, we repeated all tests using only the subset of data with full trait information, and the results were consistent (Appendix S3: Table S10).

We extracted the approximate residence time from various published and online sources (Data S1). For the species that we did not find information in the previous sources (36 out of 170 species), we used the R package *rgbif* (Chamberlain, 2021) to obtain the earliest record of each non-native species in the Global Biodiversity Information Facility (GBIF). As we found many first records in the year 1600 from gardens, we removed such outliers and used the next record available, which more likely reflects the presence in natural habitats.

In order to make two regions comparable, invasion success, NLO and DDP were expressed as the proportion of the total number of locations in the respective study regions. Leaf area, plant height and seed mass were ln-transformed, and SLS, DDP, NLO and invasion success were logit-transformed (Appendix S1: Figure S1) to meet assumptions of statistical models.

2.2 | Modelling

To test our first hypothesis that native range dark diversity parameters are linked to invasion success, we used linear models to relate invasion success to SLS and DDP. The model also included functional traits, invasion direction and plant residence time. We added an interaction between invasion direction (native species in EMb that are non-native in Nam, non-native trees in EMb native in Nam) and dark diversity parameters (SLS and DDP). We used an information-theoretic approach to compare the different models according to the corrected Akaike Information Criterion (AICc, Burnham & Anderson, 2002). Model selection was made with MuMIn R package (Barton, 2019). We predefined that the highly correlated variables (using ± 0.5 as the threshold) would not be included in the same model (see the correlation matrix in Appendix S1: Figure S2). We examined all models where delta AICc values (hereafter called Δ AIC) were lower than 2 (that can be considered to perform similarly – Burnham & Anderson, 2002) and noticed the overall best model. Assumptions of all examined models were validated graphically. Model significances were tested by using ANOVA type III test (interactions were checked first than their main effects).

To test our second hypothesis that dark diversity parameters (SLS and DDP) from the native range are more informative to explain the invasion success than the number of locations occupied (NLO), we repeated the model selection described above but used NLO instead of the native range dark diversity parameters (i.e. SLS and DDP). We compared the AICc values from the best model using SLS and DDP to these using NLO. Differences in AICc lower than 2 show that models are similar. Differences in AICc > higher than 4 indicate a reasonable likelihood that the model with lower AICc is better (Burnham & Anderson, 2002). In order to estimate the overall importance of native range parameters (i.e. SLS, DDP and NLO), we also examined AICc of the best model without any native range parameter (including invasion direction, traits and residence time).

| Model summary: dAIC = 0.00; $R^2 = .43$; Residuals = 221.145; Df = 160 | | | |
|---|----|---------|----------|
| | Df | F-value | p values |
| Sum of location suitabilities | 1 | 12.27 | .00 |
| Leaf nitrogen | 1 | 10.96 | .00 |
| Mycorrhizal status | 1 | 8.72 | .00 |
| Residence time | 1 | 8.31 | .00 |
| Invasion direction: Sum of location suitabilities | 1 | 6.09 | .01 |
| Dark diversity probability | 1 | 5.09 | .03 |
| Height | 1 | 3.69 | .06 |
| Leaf area | 1 | 3.34 | .07 |
| Seed mass | 1 | 2.74 | .10 |
| Invasion direction | 1 | 2.05 | .15 |

Note: Anova type III table (interactions were checked first than their main effects). Significant variables ($p < .05$) are in bold.

Abbreviation: Df, Degrees of freedom.

To test our third hypothesis that dark diversity parameters depend on regional setting, we examined if our best set of models (dAIC < 2) included the invasion direction, as well the interaction terms with SLS or DDP, and whether these were significant.

To test our fourth hypothesis that functional traits and residence time have an additional effect on invasion, we looked at which of them were included in the best set of models (dAIC < 2), and which were significant. We used all variables present on that set of models to generate effect plots to illustrate their independent influence on the invasion success (effects R package, Fox & Weisberg, 2019). We also averaged residuals from these models and outlined which well-known harmful non-native tree species have over or underestimated invasion success (above or below the predictions respectively), with some implications to conservation (Appendix S4: Figure S3).

3 | RESULTS

We measured the invasion success by the proportion of locations that each non-native species has occupied outside their native range. Most of the non-native tree species showed low invasion success. The median invasion success value was 13% in NAM and 4% in EMb (overall median 9% of locations in the non-native range). The species displaying the highest invasion success occupied 89% and 80% of the NAM locations (*Populus alba*) and EMb (*Robinia pseudoacacia*) respectively.

Using a model selection procedure, we tested whether the invasion success between the two regions is explained by the native range dark diversity parameters – the sum of location suitabilities (SLS), dark diversity probability (DDP). Models also included direction (in interaction to dark diversity parameters), functional traits and residence time. The set of best models always included dark diversity parameters (dAIC = 0.00, $R^2 = .43$; Table 1), supporting our first hypothesis. As expected, SLS was positively, and DDP was negatively related to invasion success (Figure 3; Table 1). The best

TABLE 1 The overall best linear model describing the tree's invasion success between North America (NAM) and Europe and the Mediterranean Basin (EMb)

model with dark diversity parameters had considerably higher support than the best alternative model with NLO (dAIC = 5.39, $R^2 = .39$, Appendix S3: Table S8), supporting our second hypothesis. At the same time, both dark diversity and NLO models were better than the best model without native range distribution parameters, i.e., neither of SLS, DDP, nor NLO (dAIC = 15.55, $R^2 = .36$; Appendix S3: Table S9).

Our third hypothesis was partly supported. The direction itself was not significant in the best set of models (which included dark diversity parameters), but there was a significant interaction with SLS and not with DDP. A strong positive relationship between SLS and invasion success was found for tree species native in EMb and invading in NAM, while SLS did not influence the invasion in the opposite direction. The lack of significant interaction between invasion direction and DDP shows that DDP had a similar negative effect on invasion in both regions. For comparison, invasion direction was the most important variable in the best model using NLO (without significant interaction) and in the best model which did not use the native range distribution variables (Appendix S3: Tables S8 and S9).

Along with our fourth hypothesis, besides the native-range dark diversity parameters and direction, invasion success was additionally related to several functional traits and residence time (Table 1, Figure 3). Invasion success was significantly positively related to leaf nitrogen content (Figure 3), for all dAIC < 2 models. Another significant invasion success descriptor was mycorrhizal status; the non-native species displaying a facultatively mycorrhizal association were more successful than the obligately mycorrhizal ones (Figure 3). The best set of models (dAIC < 2) also included leaf area, plant height, seed mass and mycorrhizal type. However, these variables were not significant in all models (Appendix S3: Tables S2–S8). At least, there is a tendency that more successful non-native trees are characterized by taller height, smaller leaves and seeds and arbuscular or dual (arbuscular and ecto) mycorrhizal types (Figure 3). In contrast, residence time was significantly and positively related to invasion success in all dAIC < 2 models (Table 1 and Tables S2–S7 in Appendix S3).

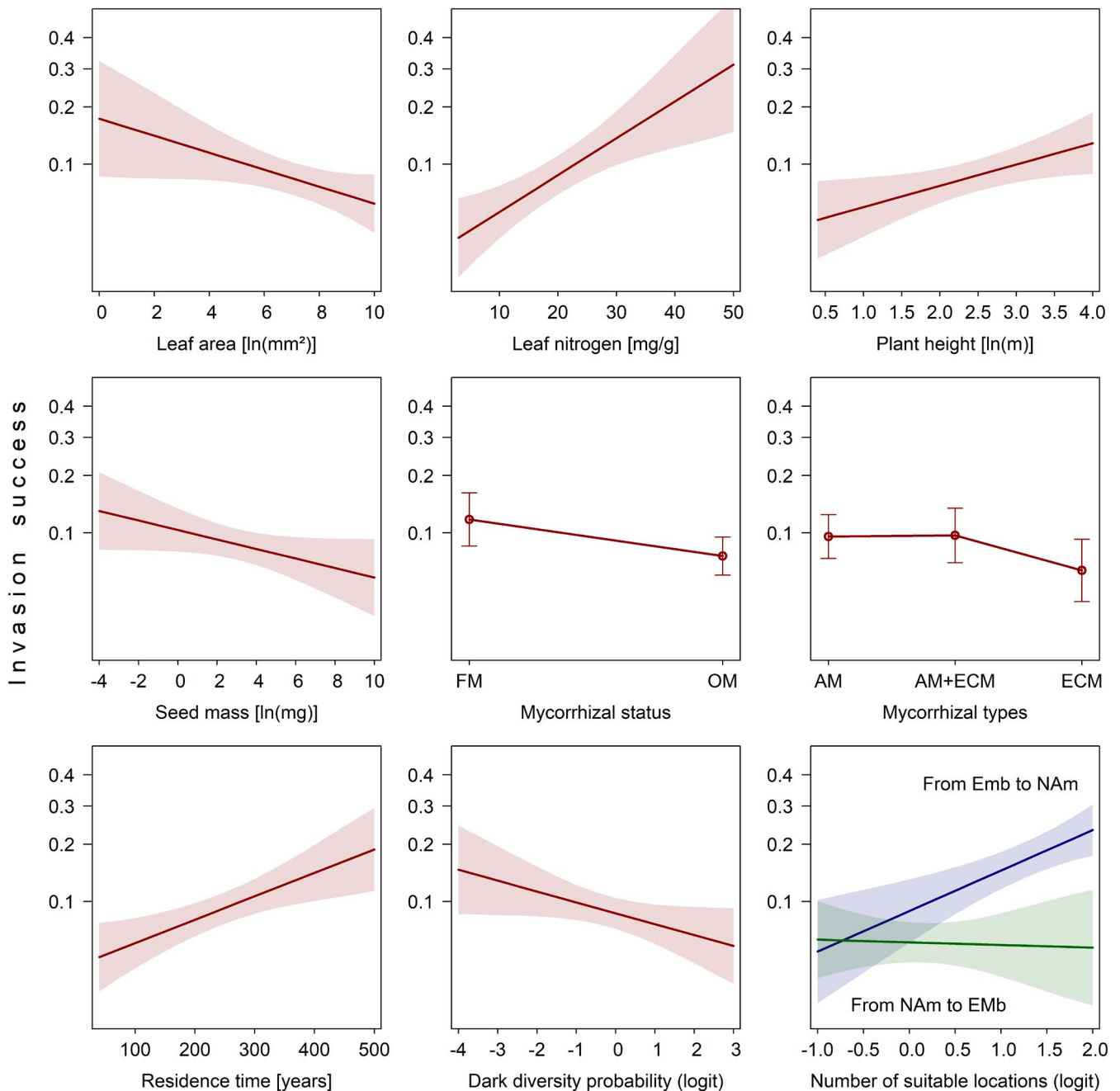


FIGURE 3 Effect plots relating the invasion success to dark diversity parameters (SLS, the sum of location suitabilities; DDP, the dark diversity probability), functional traits and residence time. Panels show independent effects of variables present in the best set of linear models ($\Delta AIC_c < 2$, see Appendix S3: Tables S2–S7). 95% confidence intervals are shown. Invasion success values express proportions of locations invaded, back-transformed from logit used in the model. Interaction with invasion direction is shown if this was present in the best set of models (i.e. with SLS). AM, arbuscular mycorrhizal; AM+ECM, dual mycorrhizal; ECM, ectomycorrhizal; FM, facultative mycorrhiza; OM, obligate mycorrhizal

4 | DISCUSSION

The ongoing biodiversity crisis has been exacerbated with non-native species spread, but we still have a limited understanding of why some species invade more than others (Gallien et al., 2010; Sapsford et al., 2020). Here, we demonstrate that the dark diversity parameters from the native range can considerably improve the model describing invasion success of non-native tree species. By estimating suitable but unoccupied locations, we calculated the sum of location

suitabilities (SLS) and dark diversity probability (DDP, Moeslund et al., 2017), characterizing species niche width and its realization probability respectively. Invasion models using these dark diversity parameters were superior over models with a previously used native range metric – the number of locations occupied (NLO). Functional traits, invasion direction between study regions and the residence time additionally contributed to the models but did not substitute the dark diversity parameters. Our results demonstrate that, besides measured observed diversity, dark diversity estimates contribute to

understanding complex ecological dynamics across different spatial scales (Trindade et al., 2020), including biological invasions.

We found support for our first hypothesis as both considered dark diversity parameters – SLS and DDP – were included in the overall best model (Table 1). As we initially expected, SLS had a positive and DDP a negative relationship with invasion success (Figure 3). Models with NLO performed well but still got considerably less support than dark diversity models, exactly as we predicted in our second hypothesis. Thus, the invasion success is not only defined by the native observed distribution but is even better defined by two metrics, potential distribution and the proportion of how much it is actually realized. These two variables can be readily calculated from co-occurrence data of species (Carmona & Pärtel, 2021), they convey important additional information that were congruent when investigated by both, larger or finer scales (Appendix S5). SLS is directly related to the breadth of species habitat preferences (niche width), while NLO is constrained by many historical and ecological restrictions. For example, many tree species in North America and Europe have not filled their potential range (Camenen et al., 2016; Seliger et al., 2020; Svenning & Skov, 2004) and might have limited distribution due to competitors, pests or land-use changes. Similarly, DDP can facilitate interspecific comparisons since this metric is expressed in a relative scale, independent of the potential range size. So far, DDP has been linked to natural rarity and conservation in native ranges (Moeslund et al., 2017), but our results show that DDP is additionally essential to predict invasion success.

Invasion direction contributed to our best model with dark diversity parameters even if it alone was not significantly related to invasion success (this is in contrast to the models where dark diversity parameters were not used and direction was highly significant – Appendix S3, Tables S8 and S9). Along with our third hypothesis, the SLS interaction with the invasion direction was significant, showing that its effect differed between regions. SLS had a positive relationship with invasion only for tree species originating from EMb and invading NAm, and there was no relationship in the opposite direction. SLS is a proxy of species' niche width, and widespread species are pre-adapted to more habitats in their native and invaded ranges (Carboni et al., 2016; Fristoe et al., 2021; Schlaepfer et al., 2010). According to the abundance–occupancy relationship, widespread species also tend to be more abundant in many locations (Gaston et al., 2002), which, in turn, would facilitate propagule transport to the new range (Buckley & Catford, 2015; Pyšek et al., 2015). In North America, many European tree species were used to make the settlement surroundings more similar to Europe (Dyer, 2010; Mack, 2003). Thus, more common and abundant European tree species were likely selected more often for gardens and parks. In contrast, commercial well-selected tree species were often brought from North America to Europe for forestry, and the regional commonness in their native ranges might have been less important. SLS might have captured some of these regional differences in the two studied regions, but more detailed studies on the modes of introduction would be useful.

Regional invasion differences can also depend on the pre-adaptation of invading species to ecological conditions of hosting ecosystems. Hejda et al. (2015) propose that the predominant forces

underlying invasion have been different in the New and the Old World – especially in Europe. Many Eurasian ecosystems have been shaped by human influence, and they are more resistant to anthropogenic invasions than North American ecosystems (Hejda et al., 2015). Currently, anthropogenic influences are widespread everywhere, and the species pre-adapted to human influence in their native ranges have the advantage in invasions. This has been especially clear with European grassland species (MacDougall et al., 2018), but European woodlands present ample signs of human history as well (Szabó, 2009), and many tree species from Europe might also be pre-adapted to human-modified woodlands.

Several plant traits improved the invasion success models in addition to dark diversity parameters, as was postulated in the fourth hypothesis. Functional attributes that promote efficient growth are usually the same that increase invasion success (Lamarque et al., 2011). Indeed, in forest environments, taller trees with small but nitrogen-rich leaves allow a high metabolic efficiency by sustaining high photosynthetic rates and low water loss (Paganeli & Batalha, 2021; Paganeli et al., 2020). These nitrogen-rich leaves may be connected to the mycorrhizal association (Gorzalak et al., 2015). Following the mycorrhizal-associated nutrient economy hypothesis, in temperate regions, AM trees enhance a fast decomposition of high-quality litter, while the opposite is described for ECM trees (Phillips et al., 2013). This implies that higher amounts of inorganic N can be quickly uptaken by AM plants, leading to nitrogen-rich leaves, also occurring in non-native species (Bialic-Murphy et al., 2021; Phillips et al., 2013). Indeed, our findings show that higher leaf nitrogen content enhances invasion success. Although the higher nitrogen levels favour herbivory, a possible higher phenolic concentration (Funk & Throop, 2009; Kurokawa et al., 2010) or the escape from enemies in the non-native range might decrease this constraint for non-native species (Xu et al., 2020).

To date, there is still contradictory information about whether non-native mycorrhizal plants (especially the facultative ones – FM) are indeed related to high spreadability and wider niche than the non-mycorrhizal (Dai et al., 2020; Gerz et al., 2018; Hempel, 2013; Menzel et al., 2017; Moyano et al., 2019; Pyšek et al., 2019). Our results not only corroborate but expand that tendency to the new range (higher native SLS and invasion success). The FM species present a competitive advantage over the obligatory mycorrhizal (OM) species because even in cases of non-mutualist co-introduction, their establishment is not substantially inhibited (Pringle et al., 2009). Similarly, in unfavourable conditions, FM species may abstain from the high-cost symbiosis, which is not a possible strategy for the OM (Moora, 2014). Ecological and environmental fluctuations definitely change both, how suitable a location is and the probabilities of a given species being part of the dark diversity (Trindade et al., 2020). This interpretation is also supported by native-range studies where a lack of flexibility in the mycorrhizal symbiosis association (OM) is a possible reason for a species to belong more often to the dark diversity, failing to inhabit suitable locations (Moeslund et al., 2017; Riibak et al., 2015).

Another significant factor describing invasion success was the residence time that remained significant even if dark diversity parameters

and functional traits were included. This time effect can have two explanations. First, the residence time can describe the built-up of mutualistic interactions. If there were no symbiont co-introduction, plants might be waiting for the best symbionts to optimize their survival and growth, which might take time; for example, optimal mycorrhizal fungi (Menzel et al., 2017; Pringle et al., 2009; Traveset & Richardson, 2014), efficient pollinators or zoochory vectors (Evstigneev et al., 2017; Pyšek et al., 2011). Second, even if ecological conditions are optimal from the beginning, spreading and establishment will still take some time, and a longer residence time also allows multiple introductions, further enhancing invasion (Pyšek et al., 2015). In addition, temperate forests are usually dominated by species displaying long generation periods, and the range expansion can demand long time delay to succeed (Essl et al., 2011). This time delay can be seen in natural ranges as well after habitat changes, known as colonization credit (Talluto et al., 2017; Trindade et al., 2020).

Similar to any other biodiversity study, scale issues are important also when studying dark diversity. We selected countries/states/provinces/territories as study units to fully cover both study regions with a relatively homogeneous sampling effort – checklists are more common than spatially equal high-resolution sampling. However, the possible effect of the large and varying sample unit size on methods based on species co-occurrence must be examined carefully (Ronk et al., 2017). Our study variables calculated from co-occurrences, SLS and DDP remained relatively similar when we excluded gradually up to 25% of the largest regions ($r > .95$, no significant deviance from the 1:1 line). Similarly, the observed NLO and the dark diversity parameters based on the species co-occurrence were strongly linearly correlated with the same parameters calculated from vegetation plot co-occurrences (usually 10×10 m; Appendix S5: Figures S5–S8). Thus, at least for trees in temperate regions, the co-occurrence approach is applicable in a wide range of spatial scales. Overall, our work demonstrates that the dark diversity concept expands the toolbox for invasion ecology, revealing additional valuable information about species niches breadths and their realization potentials. More informative invasion ecology is urgently needed to slow down the current biodiversity crisis (Banks et al., 2015; Beaury et al., 2019; Seebens et al., 2020). This study used one of the best-known ecological groups in the most documented regions – trees in North America and Europe and the Mediterranean Basin. However, dark diversity parameters should also be applicable in the invasion ecology of other taxa, at other spatial scales, and in other regions.

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CONFLICT OF INTEREST

We declare that there are no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The data used in our study can be found at <https://dx.doi.org/10.15156/BIO/2483904>.

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BIOSKETCH

We are particularly interested in Macroecology using the Dark diversity concept and functional traits (including mycorrhizal ones) to test ecological hypotheses, among other things, those related to invasion ecology. Details of our workgroup lead by Prof. Meelis Pärtel can be found at <https://macroecology.ut.ee/en/>.

Author contribution: BP and MP conceived the ideas. BP made analyses and wrote the first draft of the manuscript, and all authors contributed actively to revisions. Functional traits were retrieved by AT and CGB. The residence time was extracted by ÜR, BP, and MP. JF helped in the modeling part.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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