

Below- and aboveground traits explain success of German grassland plants from plot to global scales

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Abstract

Most plant species are rare and only a few are common, but whether species success is associated with functional traits is debated. We measured five root traits and seed mass on 242 Central European grassland species, and extracted their specific leaf area, height and bud-bank size from databases. Then we tested if trait values are associated with commonness at seven spatial scales from 16m² grassland plots to worldwide naturalization success. At every scale, success was associated with at least four traits, and they explained the highest proportions of variance for naturalization success (41%) and abundance in grassland plots (37%). Low root tissue density characterized successful species at every scale, whereas other traits showed directional changes depending on the scale. Across scales, belowground traits explained overall more variance in species success (18.1%) than aboveground traits (12.5%). So, belowground traits are at least as important as aboveground traits for species success.

INTRODUCTION

Flowering plants are estimated to have diversified into an extant global flora of about 369.000 species . Most of those species have small spatial ranges and maintain low population densities, and are thus considered rare . On the other side, a few species are considered common or dominant, as they achieve high population densities and have colonized large stretches of land . Though this pattern has been recognized as early as the 19th century (Darwin, 1859), the reasons why most species are rare and a few are common or dominant are still unclear .

Plant functional traits have been successfully used to explain species occurrence patterns in relation to environmental conditions . For example, leaf morphology is correlated with climate , and chemical composition of plants is correlated with soil properties . It has also been shown that species with particular trait values increase in abundance when filtered by the environment . Surprisingly, however, a basic description of trait differences between common and rare species, irrespective of changes in environmental conditions, is still missing. A reason for this might be that rarity (or commonness) has multiple dimensions and can apply to different spatial scales. For example, while a species may be locally abundant in a certain habitat type (i.e. be common), it might have a restricted distribution globally (i.e. be rare).

Most studies relating traits to ecological parameters are focussing on aboveground traits, most likely because they are overrepresented in trait databases . Although leaf traits, plant height and seed weight are considered to capture most variation in plant form and function , inclusion of belowground traits can substantially increase predictive power for species distributions . Belowground traits, however, are usually not considered

as their measurement is technically challenging and labour intensive. Moreover, belowground traits are often assumed to be correlated with aboveground trait. However, other studies show that correlations between above and belowground traits vary tremendously among clades and depend on the traits considered.

We tested if plant functional traits explain the success of species across spatial scales from local abundance in grassland plots to their worldwide distribution. To do so, we measured root traits and seed weight on 242 grassland species grown in two large common-environment experiments. In addition, we extracted aboveground and bud-bank traits from databases. We then tested how the traits relate to the abundance and occurrence in grassland plots of the German Biodiversity Exploratories, the occurrence frequency across Germany, the occurrence frequency across the European and Mediterranean region, and their global occurrence as naturalized alien species. We aimed to answer the following questions:

- 1) Do plant functional traits explain species success, i.e. abundance and occurrence frequency across spatial scales?
- 2) Do the contributions of traits to species success vary with the spatial scale considered?
- 3) Do above- and belowground traits contribute differently to explaining species success?

METHODS

Species traits

Species selection, seed material and precultivation

The species used are flowering plants occurring in the grasslands plots of the German “Biodiversity Exploratories”. In each of three regions of Germany, the Schwäbische-Alb (southwestern Germany), Hainich-Dün (central Germany), and Schorfheide-Chorin (northeastern Germany), 50 plots (4×4 m) were selected in grassland habitats covering a wide range of land-use intensities. From 2008 to 2016, the vegetation composition of each of the 150 plots was assessed annually in late spring by estimating the cover of each species. We standardized the species names according to the accepted names in The Plant List 1.1 (<http://www.theplantlist.org>, accessed on 15th June 2019), using the *Taxonstand* package (Cayuela *et al.* 2017), to allow us to align the species names between different distribution and trait datasets (see below). In total, 364 vascular plant species have been identified in the plots. For 312 of those species, we were able to obtain seeds from commercial seed suppliers or botanical gardens for our experiments (see Appendix S1 in Supporting Information).

In two experiments, we measured functional traits on those species. Before the first experiment, we individually weighed 10 randomly chosen seeds of each of the 312 species. Then we did an indoor pot experiment to determine root morphology of the species, and an outdoor pot experiment to determine rooting depth. For both experiments, seeds were sown in plastic pots (7×7×6.5 cm) filled with peat soil. The pots were then placed in a phytochamber for two to three weeks (night/day 9/15 h; 18/21 ± 1.5°C; relative humidity 90 ± 5%) before transplanting the seedlings (for cultivation times, see Appendix S1). We additionally obtained data on aboveground traits (specific leaf area, height) and bud-bank size from several databases.

Experiment on root-system morphology

From May 1 to October 6, 2017, we performed a glasshouse experiment to measure root-system morphological traits of plants grown at either low or high nutrient levels. Because of the large number of species and the time-consuming measurements, we grew the plants in four temporally shifted (4-6 weeks) batches. We aimed to have each species represented in each batch, and to have a total of seven replicates per species and nutrient level across all batches (Appendix S1). The seedlings of the species that had germinated (N=238) were transplanted individually into plastic pots (1.3 L) filled with a mixture of sand and vermiculite (1:1 volume ratio). The pots were then randomly allocated to positions in two glasshouse compartments, and allowed to grow for four weeks (night/day 10/14 h; 22/28 ± 1.5°C; relative humidity 80 ± 15%). Plants

were fertilized three times a week with either a low nutrient solution (40 ml with 1500 μM KNO_3) or a high nutrient solution (40 ml with 12000 μM KNO_3). The fertilizer was a modified version of the Hoagland recipe (see Appendix S2).

After four weeks of growth, plants were harvested. We grew the plants for four weeks to avoid roots becoming pot-bound, and to be able to analyse the entire root systems. After carefully washing off the substrate, the root system was cut below the collar and stored for <1 week in a plastic tube filled with distilled water at 4°C. Then, root systems were spread individually in a thin layer of water in transparent trays (11 cm \times 11 cm) and scanned at 800 dpi with a flatbed scanner modified for root scanning (Epson Expression 10000 XL and 11000 XL). The images were analysed using the software WinRHIZO™ 2017a (Regent Instruments, Quebec, Canada) to obtain the total root length and root volume. Root systems were then oven-dried for >48 hours at 65°C and weighed. We calculated specific root length by dividing the total root length by the belowground dry biomass, and root tissue density by dividing the belowground dry biomass by the sum of the root volumes according to Rose (2017). The diameter of first-order roots (i.e. the most distal roots), thought to be most important for nutrient uptake, was determined by randomly sampling a distal root branch (or a portion of it) for each root system and calculating the mean of the external-internal links diameter obtained with the “Link analysis” function in WinRHIZO. We also dried and weighed the aboveground biomass of each plant, and calculated the root weight ratio (i.e. root biomass divided by total biomass).

Experiment on rooting depth

From the 15th of May to the 10th of October 2018, we performed an outdoor pot experiment to measure the maximum rooting depth of the species. Up to five seedlings of the species that had germinated (n=197; Appendix S1) were transplanted individually into 120 cm high plastic grow tubes (Tubex® Standard Plus, <http://www.tubex.com/products/tree-shelters/tubex-standard-treeshelters/specification.php>) the bottom of which was closed with a thick piece of cotton tissue. The tubes were filled with a mixture of sand and vermiculite (1:1 volume ratio) up to a height of 115 cm. The tubes came in five diameter classes (8.0, 8.4, 10.0, 10.8 and 12.0 cm) stacked in each other. To avoid that tube diameter would be confounded with species identity, each of the five seedlings per species was planted in a different tube-diameter category. We placed the tubes upright in a randomized design in the Botanical Garden of the University of Konstanz (47°41'24.0"N 9°10'48.0"E; see Appendix S10 for pictures).

We planted 734 plants, but due to early mortality we had to replace 126 of them within the next three weeks. The growth period therefore ranged from 16 to 19 weeks. The experiment took place during the summer of 2018 (mean temperature: 19.5 °C, min/max 2.5/37.4°C; relative humidity: mean 74%, min/max 22.7/100%). All the plants were fertilized once a week with 60 ml of a standard nutrient solution (1Universol^(r) Blue, Nordhorn, Germany), and watered regularly from above. We harvested the plants in October. Each tube was carefully sliced open, and we measured the distance from the top of the substrate to the deepest root.

Traits from databases and data imputation

Data on the aboveground traits specific leaf area (236 species) and height (232 species) were obtained from the LEDA database (Kleyer *et al.* 2008; <https://uol.de/en/landeco/research/leda>, accessed on 26th August 2019). In addition, data on bud-bank size (219 species) was obtained from Klimešová *et al.* (2016).

Although for each of the traits we had data for 197 (rooting depth) to 312 (seed weight) species, the number of species with complete trait data was 163. Therefore, we did phylogenetically informed imputation of missing data for the 242 species that were grown in at least one of our two experiments. Imputation was realised for 5.6% of trait values and details about the procedure can be found in Appendix S4. The phylogenetic tree of the species used, their standardized trait values and phylogenetic signal can be found in Appendix S5, S6 and S7.

Species abundance and occurrence frequency

To quantify each species' success from local scale abundance to global distributions, we used four different data sources.

The Biodiversity Exploratories

To obtain information on local abundance and occurrence frequency of our study species in German grasslands, we used data from the Biodiversity Exploratories grassland-composition surveys. In each of the three regions, c. 500 so-called grid plots (GPs) and a subset of those, the 50 so-called experimental plots (EPs), have been monitored for biodiversity measures. The plots are 50 m \times 50 m, and in each of those there is a subplot of 4 m \times 4 m, in which the relative abundance of each plant species has been determined. In the 1494 GPs, vegetation was sampled once from 25 May to 15 August 2007. In May 2009, 138 plots were re-assessed and earlier relevés were discarded because vegetation had been recorded too late in the season of 2007 which led to unreliable data. Of our 242 study species, 213 were present in that census of the GPs (Appendix S1), and, when present in a plot, they covered on average 2.8% of the plot (min: 0.27%; median: 1.44%; max: 17.16%). For the 150 EPs, the vegetation data were collected annually between mid-May and mid-June from 2008 to 2016, and we averaged the data across years. Of our 242 study species, 240 were present in the EPs vegetation survey, and, when present in a plot, they covered on average 1.05% of the plot (min.: 0.09%; median: 0.33%; max.: 13.05%). Two study species, *Spergula arvensis* and *Taraxacum campyloides*, had been selected because their names were included in an earlier version of the vegetation survey due to misidentification. While there are ten times more GPs than EPs, the latter includes data over a longer time period. For both the GPs and EPs, we used two distribution metrics for each species: the occurrence frequency defined as the number of plots in which a species is present divided by the total number of plots, and the local abundance defined as the mean cover of a species across all the plots where it is present.

FloraWeb

For information on the occurrence frequency in all of Germany, irrespective of habitat type, we obtained data from the German plant distribution atlas of NetPhyD and BfN (2013) through the FloraWeb database. For each species, we extracted the number of grid cells in which the species has been reported. Each grid cell is about 130 km², and there are 2995 grid cells in total. Of our 242 study species, 236 had grid-cell data available (Appendix S1).

Euro+Med PlantBase

To obtain information on the extent of the native distribution in all of Europe and its adjacent regions, we used Euro+Med PlantBase (<http://www.emplantbase.org/home.html>, accessed 1st June 2019). This online database provides information on the presence of vascular plant taxa in 117 regions (mostly countries) covering all of Europe and the Mediterranean regions of North Africa and the Near East. Of our 242 study species, 238 species were found in Euro+Med PlantBase, and for those we extracted the total number of regions with native occurrences (Appendix S1). The four remaining species, *Cerastium nutans*, *Erigeron canadensis*, *Matricaria discoidea* and *Medicago \times varia*, are not native to the region.

GloNAF

As 238 of our 242 study species are native to Europe, we also assessed the extent of their global occurrence as naturalized alien species, using the Global Naturalized Alien Flora (GloNAF) database, version 1.2. GloNAF is a compendium of lists of naturalized alien plant species for 1029 regions covering >80% of the terrestrial ice-free surface. Of our 242 study species, 222 species had at least one record in GloNAF. For those species, we extracted the number of regions in which they are naturalized, and for the 20 species without GloNAF records, we set the number of GloNAF regions equal to zero.

Statistical analyses

All statistical analyses were performed in R version 3.6.1 . To test whether more abundant and more widespread species have particular traits values, we used generalized linear models in which the response variables were the different measures of species success and the predictors were a selection of trait mean values. For number of occurrences in GloNAF regions, and in grassland GPs and EPs, we used negative binomial error distributions (with a log-link function). As the number of occurrences in FloraWeb grid cells and Euro+Med regions did not follow negative binomial or Poisson error distributions, we instead analysed the proportion of FloraWeb grid cells and Euro+Med regions in which a species has been recorded, with a binomial error distribution. To account for overdispersion, we used the ‘quasibinomial’ setting, correcting the standard errors. For analyses of the mean local abundance (i.e. the cover proportion) of the species in the GPs and EPs, we used a gamma conditional distribution (with log-link function).

For each success measure, we used a model with nine traits as predictors. We *a priori* chose traits that represent different aspects of plant functioning and that had relatively low correlations between them (all r [?] |0.51|, Appendix S3) to minimize multicollinearity (the maximum generalized variance-inflation factor of a model was 3.55). We used the following traits: individual seed weight (measured on seeds ordered for the experiments), specific root length, root tissue density and first order root diameter (measured in the root-system morphology experiment), maximum rooting depth (measured in the rooting-depth experiment), and bud-bank size, height and specific leaf area (from trait databases). Seed weight was log transformed. To facilitate interpretation of and comparison between model coefficients, each trait was scaled to a mean of zero and a standard deviation of one . To test for potential non-linear effects of traits, orthogonal polynomial terms of second degree (i.e. quadratic terms) were also included for each trait, using the *poly* function. To estimate the proportion of variance explained by the models, we calculated delta R² values, applicable to all distributions and link functions, according to using the package MuMIn . To assess whether belowground traits can explain more than aboveground traits, we also extracted delta R² values for models using only the three aboveground predictors and the three belowground predictors with the highest standardized coefficients overall separately. To account for phylogenetic non-independence of the study species, the models were also run using phylogenetic relatedness of species as a variance-covariance matrix (for details, see Appendix S4). Although the significances of the trait effects differed in some instances between the non-phylogenetic models and the phylogenetic ones, the directions of the effects were largely the same in both types of models (compare Fig. 1 and Appendix S8). Therefore, we only present the results of the non-phylogenetic analyses in the main text.

RESULTS

All of our species success metrics were significantly related to at least four of the nine traits considered, including both above- and belowground traits (Fig. 1). The abundance measures in the grassland GPs and the occurrence in the EPs were associated with the largest number of traits (Fig. 1). The delta R² values ranged from 0.02 for the model on occurrence frequency in the native range (i.e. the proportion of occurrences in Euro+Med) to 0.41 for the model on occurrence frequency outside their native range (i.e. the number of occurrences in GloNAF; Fig. 1; Table 1). When we reduced the models to either include only the three aboveground traits or the three best belowground traits, the variation explained by the belowground-trait models was equal or higher than the variation explained by the aboveground-trait models for all species success metrics, except frequency of occurrence in the grassland EPs (Table 1).

Root-tissue density was a significant predictor in all models (Fig. 1). Species with low root-tissue densities were consistently more successful than species with high root-tissue densities across all spatial scales considered (i.e. all linear coefficients were negative and significant; Fig. 1). For occurrence frequency outside the native range, the coefficient of the quadratic term was also significantly negative (Fig. 1), indicating that this success metric was highest for species with intermediate root-tissue densities (Fig. 1, Appendix S9).

Specific leaf area (SLA) was a significant predictor in most models, but the direction of the effect on species success changed with the spatial scale considered (Fig. 1). Occurrence frequencies outside their native range, in their native range, in Germany, and in the grassland GPs and EPs increased with SLA, and sometimes slightly decreased again at higher SLA values. However, the abundance in the GPs decreased with SLA and the abundance in the EPs was highest at intermediate SLA values, although these effects were only marginally significant (Fig. 1, Appendix S9).

Bud-bank size was also a significant predictor in most models, but its effects on species success varied with spatial scale (Fig. 1). Bud-bank size was negatively associated with occurrence frequency of species outside their native range, whereas occurrence frequencies in their native range and in Germany were lowest at intermediate bud-bank sizes (Fig. 1). However, occurrence frequencies as well as abundances in the grassland GPs and EPs increased linearly or asymptotically with bud-bank size (Fig. 1, Appendix S9).

The other traits were only significant predictors in some of the models of species success (Fig. 1). Seed weight had no significant associations with success at the larger spatial scales, but occurrence in Germany was higher for species with lower seed weights. Occurrence frequency and abundances in the GPs and EPs, on the other hand, were highest at higher seed weights (Fig. 1, Appendix S9). Maximum rooting depth was non-linearly positively associated with occurrence frequency outside the native range, and was positively associated with occurrence frequencies in the native range and Germany, but not in the EPs and GPs (Fig. 1, Appendix S9). Root-weight ratio was marginally negatively associated with occurrence frequency outside the native range, with an optimum in the mid-lower range of the trait, which was also the case for occurrence frequency in GPs and abundance in EPs (Fig. 1, Appendix S9). First-order root diameter had no significant effects on any of the occurrence frequencies, but had significant negative effects on abundance in the GPs and EPs (Fig. 1, Appendix S9). Specific root length only had a weak marginally significant effect for occurrence frequency in Germany (Fig. 1, Appendix S9).

DISCUSSION

This is the first study that tested how above- and belowground functional traits of grassland species relate to their success across multiple spatial scales. Among the 242 study species, low root tissue density was identified as important for all success metrics. However, the effects of the other traits were frequently dependent on the success metric considered. For example, while seed weight was negatively related to the occurrence frequency in Germany, it was positively related to the abundance in German grasslands. This illustrates that some traits may have opposite effects on different dimensions of species rarity and commonness. Moreover, we found that many of the effects had significant non-linear effects, in most cases with the highest success-metric value at intermediate trait values. While most previous studies on relationships between functional traits and species distributions focussed on easy-to-measure aboveground traits, our study shows that belowground traits can also explain a significant amount of variation in species success.

The spatial scale of success ranged from local abundance in 16 m² grassland plots in Germany (GPs and EPs) to the global occurrence outside the native range (number of GloNAF regions). While the local scale abundance data are restricted to a single habitat type, the occurrence at larger spatial scales also covers other habitat types (e.g. 86% of the area in Germany is not used as grassland; BMEL 2017). Each habitat type might select for different values of a trait, resulting in no clear relationship between the trait and the success metric overall. This context specificity could explain why the models of the success metrics at larger spatial scales had overall fewer traits with significant effects than the models on abundance in the grassland plots.

Accordingly, we found varying degrees of consistency in the trait values of successful species across spatial scales. Root-tissue density was the only trait with a consistent effect on all success metrics. Probably, a low root-tissue density, which is indicative of a high resource-acquisition-rate strategy, is beneficial in nutrient-rich habitats, which are locally and globally widespread as a consequences of agriculture. On the other

hand, the effect of specific leaf area, an aboveground trait associated with the resource-acquisition strategy (Onoda & Wright, 2018), depended on the spatial scale of the success metric. Occurrence frequencies at all spatial scales tended to asymptotically increase with specific leaf area, which is in line with the frequent observation that high specific leaf area promotes invasion success. However, abundance in the grassland plots was negatively related to specific leaf area, possibly reflecting that persistence under highly competitive pressures in dense grasslands could require a more conservative growth strategy.

Bud-bank size had significant effects on all success metrics, but the direction and shape of the relationship varied a lot. Species with a large bud-bank had the highest abundance and occurrence frequency in the grassland plots. A large bud-bank is essential for regrowth of long-lived perennials after e.g. grazing or mowing. Species with small bud-banks, on the other hand, had the largest naturalized ranges. This dual effect of bud-bank size on success was also evident from the fact that the highest occurrence frequencies in the native range and in Germany were found for both species with high and low bud-bank sizes. Although buds themselves are not very costly, they require bud-bearing organs and nutrient reserves, which may trade-off with seed production. Thus, species with smaller bud-banks may invest more in seed production, resulting in a higher dispersal ability and larger native and naturalized distributions.

The effect of seed weight on species success metrics ranged from positive at the plot scale to negative or absent at larger spatial scales. The finding that species with heavy seeds tended to be more frequent and abundant in the grassland plots, most likely reflects that large amounts of resources stored in seeds increase seedling survival under the strong competition in grasslands. Species with light seeds, on the other hand, might have a higher reproductive output, could potentially disperse over longer distances, but see Thomson *et al.* (2011), and could persist longer in the seed bank. At the larger spatial scales, this benefit of small seeds could have compensated or overcompensated the reduced seedling survival chances.

Maximum rooting depth was related to success metrics at the largest spatial scales, where it had positive effects. Deep roots allow a plant to take up water with nutrients from deeper soil layers, increasing survival and growth, particularly when the surface soil regularly dries out. As most of the agriculturally used grasslands in Germany are mesic, this could explain why rooting depth was not significantly associated with occurrence frequency and abundance in the grassland plots. At the larger spatial scales, which also cover other habitat types, species with deep roots might be more persistent. For naturalization success, however, there was a significant non-linear effect of rooting depth as both deep-rooting and superficially rooting species were most successful. This could indicate that the alternative strategy of lateral spread to acquire resources and avoid competition with deeper rooting species might also be beneficial at the global scale.

Height of the plants was not related to success of the species at larger spatial scales. This is surprising, particularly for naturalization success, as numerous studies on naturalization and invasion success found that tall species were more successful. Most of those studies, however, considered woody species that are overall much taller than the grassland herbs in our study. Interestingly, while plant height increased abundance in the German grassland plots (at least in the GPs), it decreased the occurrence frequency in those grasslands. On the one hand, tall plants, when they occur somewhere, might be competitively superior and become dominant, whereas, on the other hand, small plants might be less at risk of losing reproductive organs due to mowing or grazing.

We found that species that are abundant in grasslands are typically characterized by thin low-density roots, which promote the uptake of belowground resources. The patterns for success metrics at larger spatial scales, at least those in the native ranges, were less clear. Indeed, plant traits explained large proportions of the variation in local abundance and occurrence frequency in the grasslands (>25%; Table 1), whereas the proportion of variation in occurrence frequency in the native range and in Germany was very low (2% and 11%, respectively; Table 1). This suggests that plant traits could be good predictors of species success if one considers a single habitat type, but that this is less the case for success metrics at large spatial scales that are not habitat specific. However, a notable exception is the global naturalization success of the species, as 41% of the variation in occurrence frequency outside the native range was explained by the plant functional

traits. Possibly, this reflects that most naturalizations happen in anthropogenic environments, and thus largely in a single habitat type.

The plant economics spectrum postulates that the high specific leaf area typical for “acquisitive” plants should be mirrored belowground by a high specific root length, low root-tissue density and a low root diameter. Indeed, specific leaf area was negatively correlated with root-tissue density, but it was not significantly correlated with specific root length and diameter of the first-order roots (Appendix S3). This decoupling from the plant economic spectrum has previously been found for grassland plants as well as tree seedlings. Seed weight and plant height, the other aboveground traits frequently used in studies on functional ecology of plants, were also not very strongly correlated with the belowground traits in our study. These belowground traits explained a considerable proportion of variation in the success metrics, in addition to the variation explained by the three aboveground traits (Table 1). Indeed, for all success metrics, except occurrence frequency in the EPs, the belowground traits explained at least as much of the variation in success metrics as the three aboveground traits did. Therefore, our results show that aboveground traits cannot substitute for belowground traits in studies on plant functional ecology.

CONCLUSIONS

We here showed that functional traits of successful grassland species differed from those of less successful ones, but that the pattern depended on the success metric and the spatial scale it applies to. Low root-tissue density was the only trait that characterized successful species at every spatial scale, from being abundant in German grassland plots to being widely naturalized around the world. We showed that belowground traits are at least as important as the aboveground traits in explaining species success at the different spatial scales. The variation in importance and the sometimes-opposing directions of the effects of traits on species success at different spatial scales can explain why trait variation is maintained. Our study shows that, for Central European grassland species, variation in success is related not only to aboveground traits, but also to belowground traits.

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Figure 1 Estimates of trait effects on different success metrics of German grassland species from generalized linear models. On the y-axis are the nine traits used as predictors, with a linear term (white rows) and a quadratic (non-linear) term (grey rows) for each trait. The errors bars around the estimates are standard errors. Red points and orange points indicate significant ($p < 0.05$) and marginally significant ($p < 0.10$) negative model estimates respectively. Blue points and purple points indicate significant ($p < 0.05$) and marginally significant ($p < 0.10$) positive estimates respectively, and grey points indicate non-significant estimates ($p > 0.10$). The spatial scale of the success metric decreases from left to right. GloNAF: number of regions in which a species is naturalized (number of species, $N=242$); Euro+Med: number of regions in

Europe and the Mediterranean basin in which a species is native (N=238); FloraWeb: number of grid cells in Germany in which a species is present (N=236); GPs Frequency: number of grassland grid plots in which a species is present (N=209); EPs Frequency: number of grassland experimental plots in which a species is present (N=240); GPs Abundance: mean species cover in grassland grid plots in which the species is present (N=209); EPs Abundance: mean species cover in grassland experimental plots in which a species is present (N=240). Delta R² was calculated according to

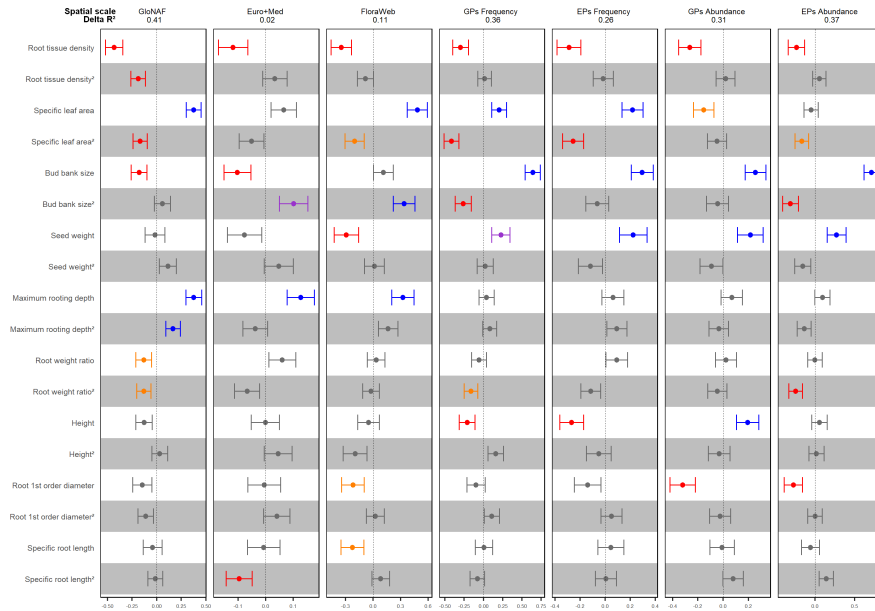


Table 1 Delta R² of models explaining species success using a different set of predictors. On the two first lines are the R² v

Specific leaf area, seed size, height
 Root tissue density, bud-bank size, rooting depth
 All the predictors (9 traits)