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ORIGIN OF PLANT TRAIT DATA MATTERS: SHARED SPECIES OF NORTHWESTERN EUROPE AND THE PANNONIAN ECOREGION HAVE DIFFERENT TRAIT VALUES IN THE TWO REGIONS

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Trait-based research considerably increased our comprehension of various fields related to ecology and evolution. As measuring traits can be time-consuming and costly, analyses regularly use trait data from databases instead of carrying out new measurements. However, intraspecific trait variability can cause substantial differences between trait values of different populations and regions. Here we evaluated whether intraspecific trait variability causes considerable differences in trait values measured in two regions of Europe. We tested whether regionally measured trait values from the Pannonian Ecoregion differ from trait values for the same species originating from northwestern Europe by comparing data from the Pannonian Database of Plant Traits (PADAPT) and the LEDA Traitbase. We evaluated six traits: thousand-seed mass (TSM), seed bank persistence index (SBPI), leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and leaf dry mass. We found that trait data from the two databases significantly differed for TSM, SBPI, SLA, and LDMC. We can assume that the markedly different climates of the two regions can be the reason behind the observed intraspecific trait differences; therefore, the geographical origin of trait data matters in trait-based analyses. The findings support the assumption that regionally measured trait data are essential for reliable regional-scale trait-based studies, and compiling these data into regional databases is the most efficient way to facilitate their use. We conclude that for studies analysing traits in the Pannonian Ecoregion (and possibly in eastern and central Europe in general), it is advisable to use PADAPT instead of databases compiling data from regions with markedly different climatic conditions.

Key words: database, functional trait, intraspecific variability, leaf dry matter content, Pannonian Ecoregion, seed bank persistence, seed mass, specific leaf area

INTRODUCTION

Understanding the growing impacts of anthropogenic habitat destruction and climate change on biodiversity and ecosystem functions is becoming more crucial than ever (Cardinale *et al.* 2012). Functional traits can provide us with tools to reveal and generalise mechanisms related to the formation and maintenance of biodiversity, and to predict how ecosystem functions and services might be affected by changes in biodiversity (Garnier *et al.* 2007, Lavorel *et al.* 2013). This has led to a growing interest in trait-based ecology (Cernansky 2017), which has considerably increased our knowledge and comprehension of various fields related to ecology and evolution (e.g., Cadotte *et al.* 2011, Lavorel and Garnier 2002, McGill *et al.* 2006). However, measuring traits can be time-consuming and costly (Cordlandwehr *et al.* 2013, Kattge *et al.* 2011); therefore, trait data gathered from trait databases is regularly used instead of carrying out new measurements for every single analysis.

As a result of standardised protocols for trait measurements (Cornelissen *et al.* 2003, Pérez-Harguindeguy *et al.* 2016) and the enormous efforts invested in compiling trait data in the last decades, many large plant trait databases have been established to facilitate trait-based analyses. Some global databases compile data for a specific group of traits, for example, SID (Seed Information Database, Royal Botanical Gardens Kew 2023) or D3 (Dispersal and Diaspore Database, Hintze *et al*. 2013). However, most databases gather data for a wide range of traits at regional scales, such as BiolFlor for the German flora (Klotz *et al.* 2002), BROT for the flora of the Mediterranean region (Tavşanoğlu and Pausas 2018), PLADIAS for the flora of the Czech Republic (Chytrý *et al.* 2021), UkrTrait for the Ukrainian flora (Vynokurov *et al.* 2024), or the LEDA Traitbase for the flora of northwestern Europe (Kleyer *et al.* 2008). The largest plant trait database available is TRY (Kattge *et al.* 2020), which provides global coverage for a wide range of traits by integrating several databases and datasets.

Interspecific trait variability is generally considered to be much greater than intraspecific variability, which is a basic tenet of studies using a mean trait value for each species (Cordlandwehr *et al.* 2013, Violle *et al.* 2012), thereby treating intraspecific variability as something that could not conceal broad trends (Shipley *et al.* 2016). The assumption that intraspecific variability is greater than interspecific variability has been corroborated by some studies (Garnier *et al.* 2001, Jung *et al.* 2014). Still, it has also been shown that intraspecific variability is also not necessarily negligible (e.g., Auger and Shipley 2013, Jung *et al.* 2014, Messier *et al.* 2010). Intraspecific trait variability can be a result of genetic differences, phenotypic plasticity, or a mixture of both (Albert *et al.* 2011, Sandquist and Ehleringer 1997), which can cause considerable differences between the trait values of different populations (Albert *et al.* 2012). Some plant traits show more plasticity than others (Shipley *et al.* 2016); for example, traits related to resource acquisition show great variability (e.g., specific leaf area and leaf water potential, Shipley 2000, Violle *et al.* 2009*a*), while reproductive traits such as seed mass show less (Violle *et al.* 2009*b*).

It is well-known that interspecific trait differences correlate with environmental conditions such as climate (Hodkinson *et al.* 1998, Poorter *et al.* 2009, Wright and Westoby 2002) or soil features (Maire *et al.* 2015). However, the effects of environmental conditions on intraspecific trait variability (see e.g., Garnier *et al.* 2001, Hudson *et al.* 2011, Mokany and Ash 2008) are much less considered, although these effects are particularly relevant for studies using data gathered from databases covering large geographical scales (Cordlandwehr *et al.* 2013). Based on the above considerations, if relevant environmental conditions significantly differ between regions, trait data measured in other regions may vary from the trait values representative of the populations in the study area. Methodological decisions such as what database to use and how to clean the available data to have a reliable dataset can substantially change the outcome of the analysis (see Augustine *et al.* 2024). This also means that although data for many traits can be relatively easily gathered from large-scale databases, the fact that they include data from multiple regions and often from markedly different environmental conditions compared to the study region can limit the applicability of large-scale databases for regional-scale studies. Most large databases include metadata which provide information on the locality of the measurements, allowing researchers to filter the dataset and to use only data measured in the region of the study. However, some regions such as eastern Europe are underrepresented in large databases, and a relatively large proportion of species with more eastern distribution areas are entirely missing from them.

We aimed to evaluate whether intraspecific trait variability causes considerable differences in trait values measured in two regions of Europe characterised by markedly different climatic conditions. To this end, we tested whether regionally measured trait data from the Pannonian Ecoregion differ from trait data of the same species originating from northwestern Europe by comparing data on six traits from the Pannonian Database of Plant Traits (PADAPT, Sonkoly *et al.* 2023) with data from the LEDA Traitbase (Kleyer *et al.* 2008).

MATERIAL AND METHODS

We used the checklist of PADAPT, based on which we created paired samples, i.e., we compared trait data from PADAPT and LEDA for the same set of species. We selected those numeric traits for the comparisons for which PADAPT provides a compilation of recent measurements, i.e., thousand-seed mass (TSM), seed bank persistence index (SBPI), leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and leaf dry mass. We calculated the mean value of all records from PADAPT for each species (Appendix 1). SBPI was calculated following the Seed Longevity Index of Bekker et al. (1998): we express the ratio of data indicating a persistent soil seed bank with a value from 0 to 1, where zero means that all available data indicate a transient seed bank and 1 means that all available data indicate a persistent seed bank.

Table 1

Comparison of data from the LEDA Traitbase and the Pannonian Database of Plant Traits (PADAPT), pairwise Wilcoxon signed-rank tests

	LEDA (mean±SE)	PADAPT (mean±SE)	*p* value	n
Thousand-seed mass (TSM, g)	18.79±5.06	16.19±4.60	*<0.001****	1246
Seed bank persistence index (SBPI)	0.35±0.01	0.68±0.02	*<0.001****	468
Leaf area (LA, mm^2)	2,603.01±261.24	2,235.51±220.74	0.101	494
Specific leaf area (SLA, mm^2/mg)	24.92±0.39	24.49±0.47	*<0.001****	960
Leaf dry matter content (LDMC, mg/g)	201.48±3.75	251.580±4.59	*<0.001****	475
Leaf dry mass (LDM, mg)	146.77±18.94	132.59±17.49	0.215	490

Data files for the following traits were obtained from LEDA on 23rd November 2021: (i) Seed mass (corresponding to TSM in PADAPT), (ii) Seed longevity (corresponding to SBPI, we calculated SBPI values for each species based on seed longevity data from LEDA), (iii) Leaf size (corresponding to LA), (iv) SLA, (v) LDMC, and (vi) Leaf mass (corresponding to leaf dry mass after converting mg to g). We extracted data from LEDA data files for the species in our database and calculated the mean value of all records from LEDA for each species (Appendix 1). To maximise comparability, we considered only those records described as 'actual measurement'. In the case of leaf traits, we excluded measurements without petiole and rachis, and in the case of seed mass, we excluded measurements of multi-seeded generative dispersules. We then compared the data using paired Wilcoxon signed-rank tests and calculated the effect size (Cohen's r with 95% CI) for all six traits in R version 4.3.2 (R Core Team 2023). To visualise the agreement or disagreement between the databases, we created scatterplots with PADAPT values on the x axis and LEDA values on the y axis and with a 1:1 line indicating perfect agreement.

RESULTS

PADAPT 1.0 provides thousand-seed mass (TSM) data for 595 species for which LEDA does not provide TSM data, seed bank persistence index (SBPI) for 63 species for which LEDA does not provide seed bank persistence data, leaf area (LA) for 1,087 species for which LEDA does not provide LA data, leaf dry matter content (LDMC) for 1,098 species for which LEDA does not provide LDMC data, specific leaf area (SLA) for 616 species for which LEDA does not provide SLA data, and leaf dry mass (LDM) data for 1,027 species for which LEDA does not provide LDM data. TSM, SBPI, SLA, and LDMC values in PADAPT significantly differed from those in LEDA (Table 1), while LA and LDM values did not differ significantly (Table 1). Effect sizes were rather small generally, but large in case of SBPI and LDMC (Fig. 1). Scatterplots demonstrating the agreement or disagreement between the two databases are found in Appendix 2.

DISCUSSION

We found that shared plant species of northwestern Europe and the Pannonian Ecoregion have significantly different values for several traits based on data originating from northwestern Europe (LEDA Traitbase, Kleyer *et al.* 2008) versus from the Pannonian Ecoregion (PADAPT, Sonkoly *et al.* 2023). The effect sizes were large for seed bank persistence index (SBPI) and leaf dry matter content (LDMC) indicating a pronounced difference, but effect sizes were rather small for some other traits, indicating that although these differences are significant, they probably have limited practical consequences.

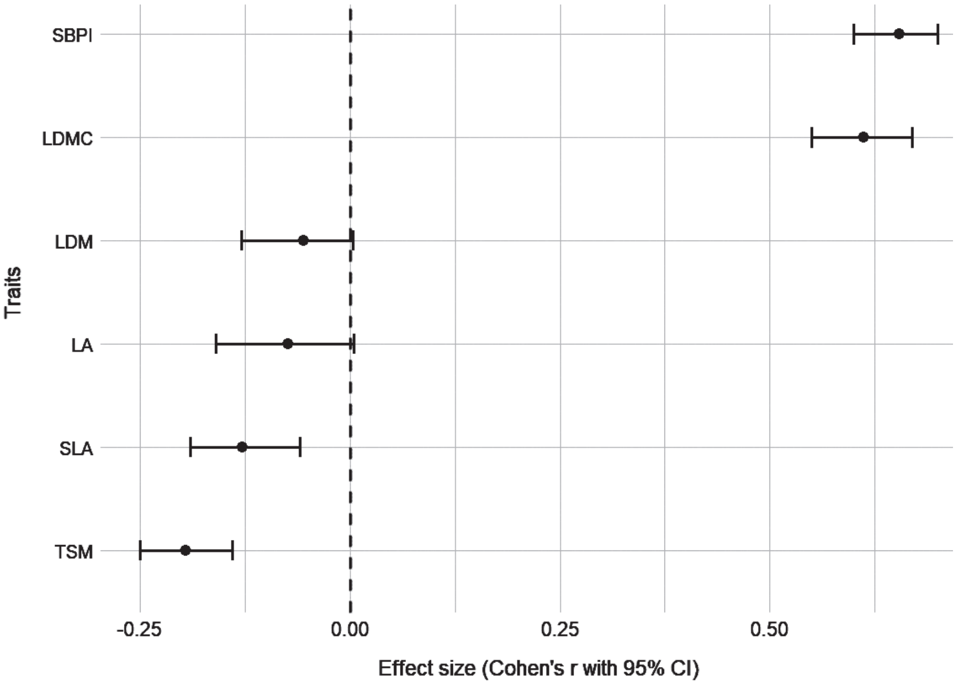

Fig. 1. Forest plot of the effect sizes (Cohen’s r with 95% CI) for the six studied traits. Horizontal lines represent 95% confidence interval (CI) of the effect size. If the confidence interval includes zero, the effect is not considered significant. A positive effect size indicates that PADAPT values are larger, while a negative effect size indicates that LEDA values are larger (SBPI = seed bank persistence index; LDMC = leaf dry matter content; LDM = leaf dry mass; LA = leaf area; SLA = specific leaf area; TSM = thousand-seed mass)

These results underline that intraspecific trait variation between regions can be considerable at least for some traits (Albert *et al.* 2011, 2012), and thus the geographical origin of trait data matters in trait-based analyses.

Our finding that thousand-seed mass (TSM) values from PADAPT are significantly lower than TSM values for the same species from the LEDA Traitbase indicates that species of the Pannonian Ecoregion have lower seed mass in this region than the same species in northwestern Europe (which is the focal region of the LEDA Traitbase). Some results suggest that there is a negative relationship between precipitation and seed mass across species (Baker 1972, Wright and Westoby 1999), more recent studies found that seed mass decreases across species with increasing aridity and precipitation variability (Harel *et al.* 2011, Yu *et al.* 2007). As some previous studies have demonstrated that climatic factors can also cause intraspecific variation in seed mass (e.g., Ge *et al.* 2020, Love *et al.* 2022, Yeşilyurt *et al.* 2017), the difference we observed may be a result of the markedly different climate of northwestern Europe compared to the Pannonian Ecoregion. The Pannonian Ecoregion is characterised by a more continental climate than northwestern Europe, with lower precipitation and higher summer temperatures (New *et al.* 2002, Peel *et al.* 2007), and longer sunshine duration (e.g., Kothe *et al.* 2013), which factors can have various effects on seed size.

In contrast with our finding, some previous studies suggest that dry and hot summers should favour the production of larger seeds. In stressful environments, such as under dry conditions, regeneration success can be increased by producing larger seeds (Muller-Landau 2010). This is in line with some previous findings, for example, *Pinus monophylla* trees growing in drier habitats produced larger seeds than specimens growing in more mesic habitats (Vasey *et al.* 2022), and stressful environments were also associated with larger seeds in the case of *Trichloris crinita* (Marinoni *et al.* 2018). The finding that higher annual minimum temperatures were associated with lower seed mass in *Helianthemum salicifolium* (Yeşilyurt *et al.* 2017) also contrasts with our results. On the other hand, in line with the detected lower seed mass in the Pannonian Ecoregion, Harel *et al.* (2011) found that the seed mass of most of the studied species increased with increasing precipitation of the habitat. Dry conditions experienced by *Desmodium paniculatum* individuals resulted in the production of lighter seeds (Wulff 1986), which is in line with our results. All things considered, climate likely plays a vital role in this difference, but what climatic factor plays the most important role in creating the detected lower seed mass in the Pannonian Ecoregion cannot be determined based on our results, warranting detailed studies of the issue.

The considerable difference detected in the seed bank persistence index (SBPI) is probably at least partly caused by the average number of individual records per species based on which SBPI was calculated being an order of magnitude greater in LEDA than in PADAPT. Results indicating persistent seed banks are easier to obtain than results indicating transient seed banks because if a species is missing from the seed bank, it does not necessarily mean that the species does not have persistent seeds, mainly because seeds of species with low seed production can easily be missed by soil seed bank sampling (Saatkamp *et al.* 2009). This can result in higher SBPI values (indicating more persistent seeds) when the number of data points per species is low, such as in the case of PADAPT.

However, the observed difference may also be caused by climatic factors to some extent. For example, the seed viability of species of dry habitats decreases when they experience moist conditions, mostly due to pathogenic fungi (Blaney and Kotanen 2001, Schafer and Kotanen 2003). Chen *et al.* (2021) also found that the seed persistence of all the 11 studied species decreased with increasing precipitation, which effect could be attributed to the action of soil fungi. These results can at least partly explain our finding that the studied species had drastically lower seed bank persistence based on data from the more humid climate of northwestern Europe than based on data from the Pannonian Ecoregion. On the other hand, some other studies suggest that increased soil temperatures can speed up processes leading to the decline of seed viability (Ooi 2012). Moreover, parent plants experiencing high temperatures produce less dormant seeds (Fenner 1991, Kochanek *et al.* 2010). In contrast with our results, these effects could lead to less persistent seed banks in habitats experiencing high temperatures. Nevertheless, it seems highly likely that soil seed survival, and ultimately the seed bank persistence of a species can vary greatly between sites and regions (Saatkamp *et al.* 2009).

Studies analysing leaf traits across species have generally found that plant species inhabiting regions with drier climates tend to have thicker leaves with low SLA and high LDMC values (e.g., Fonseca *et al.* 2000, Wright *et al.* 2004) because low SLA is linked with improved efficiency of water use in case of drought stress (Wellstein *et al.* 2017). Studies of the effects of climate on the intraspecific variation of SLA and LDMC have found a pattern consistent with the one observed across species: lower SLA values were found in plants exposed to lower water availability (Cornwell and Ackerly 2009, Garnier *et al.* 2001, Wellstein *et al.* 2017), which is consistent with other findings about plastic trait changes allowing plants to withstand drought stress (Chaves *et al.* 2002, Niinemets 2001). However, the fact that we found a low effect size in case of SLA suggests that the ecological relevance and practical consequences of the difference between data originating from the two regions are rather limited.

Although we did not find a significant difference between the leaf area data of the same species originating from northwestern Europe versus the

Pannonian Ecoregion, some previous studies demonstrated that differences in water availability can result in differences in leaf area for some species because leaf size is related to water and energy balance (Cornelissen *et al.* 2003). However, the direction of the effect is not clear; some studies found that plants growing under more arid conditions have higher leaf area values (e.g., Sandquist and Ehleringer 1997), but some other results indicate that leaf area increases with increasing water availability (Cornwell and Ackerly 2009). Nevertheless, the fact that there was no significant difference in leaf area and leaf dry mass between the two databases may reflect that intraspecific variability in leaf size (measured either as area or mass) may be less affected by climatic variables than LDMC and SLA, which are more directly related to the rate of photosynthetic activity (e.g., Reich 2014, Reich *et al.* 1998).

It has to be noted that intraspecific trait variability within the Pannonian Ecoregion is presumably not fully captured by data included in the current version of PADAPT (PADAPT 1.0) due to the limited number of measurements, which might also affect the results of the analyses. In the future, it would be worthwhile to expand the number of measurements per species in PADAPT to increase the captured range of intraspecific trait variability and more adequately characterise trait values within the Pannonian Ecoregion. A more comprehensive representation of intraspecific trait variability within the region would be especially important as it plays a crucial role in determining community functioning and ecosystem properties (Westerband *et al.* 2021) and facilitates more precise estimations of functional diversity (Albert *et al.* 2012). Increasing the coverage of the database would also enable us to directly test the correlation between climatic variables and trait value differences between the regions, helping to clarify mechanisms behind the observed differences.

In conclusion, we observed substantial intraspecific variation in many of the studied traits. It can be reasonably assumed that climatic differences between the two regions can be the reason behind these differences, therefore, the geographical origin of trait data matters in trait-based analyses. These findings corroborate the assumption that regionally measured trait data are essential for reliable regional-scale trait-based studies, and compiling these data into regional databases is the most efficient way to facilitate their use. As the significant differences we found for seed mass, specific leaf area and leaf dry matter content most probably resulted from climatic differences between northwestern Europe and the Pannonian Ecoregion, it is highly advisable that studies analysing these traits in the Pannonian Ecoregion (and possibly in the eastern part of Europe in general) use PADAPT for these traits instead of the LEDA Traitbase or other databases compiling data in regions with markedly different climatic conditions.

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