Preslia 97: 241–260, 2025
doi: 10.23855/preslia.2025.241

Preslia

Disentangling the effects of traits and environmental factors on species' successional optima: a central-European study

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Abstract: Recent data and syntheses in central Europe have led to the development of synthetic variables for describing the successional orderings of species. In particular, the "successional optimum" (SO), developed for describing the vegetation in the Czech Republic, reflects the number of years it takes for a species to reach peak abundance after a disturbance. The aim is to combine data on a species' functional traits and Ellenberg-type indicator values, in order to identify the main plant strategies and environmental factors that predict SO. In this study, linear models with regularization techniques and robust inference methods were used to determine the traits that explain species' SO, and then an analysis of the explained variance was used to assess the relative explanatory power of each trait. In parallel, the effects of Ellenberg-type indicator values, before and after detrending the SO by traits, were determined. This revealed that five traits had the greatest and most consistent effects: therophytic life form, seed mass, flowering duration, bud bank size and leaf dry matter content. The most important Ellenberg-type indicator values predicting SO were moisture and reaction, as light and nutrient concentrations were associated with these traits. The effects of traits were generally consistent and universal in the different environmental conditions, as the interaction of traits and environment did not change inferences or result in better models. This resulted in a robustly defined strategy that relates species to their successional ordering, highlighting the importance of life forms, competitive abilities, and reproductive strategies in succession.

Keywords: succession, functional traits, plant strategies, Ellenberg-type indicator values

Introduction

The study of how and which plants with distinct ecological roles replace one another after a disturbance has always been a major topic of ecological succession (Grime 2001, Laughlin 2023). Ecological succession refers to "the change in species composition or in the three-dimensional cover of a specified place through time" (Pickett et al. 2013), but also as a process of reoccupation of disturbed land by plants (Glenn-Lewin et al. 1992). Within the framework based on taxonomic changes after a disturbance, there has been a proliferation of complementary theories and terminology (Pulsford et al. 2016). More generally, in ecology, the most recent trend points to the need to complement the traditional taxonomic

Received: 6 July 2024; Revised: 8 Nov 2024; Accepted: 21 Dec 2024; Published: 24 Jun 2025

point of view with the functional (i.e. considering species' traits) to better understand ecological processes (Keddy 1992, McGill et al. 2006). However, having a clear understanding of the current dynamics of vegetation is more relevant than ever in a time of great changes in land use and unprecedented disturbance in many natural ecosystems (Cramer et al. 2008). The Czech Republic, a central-European country, has experienced great changes in land use, notably due to the abandonment of agricultural lands (driven by land use intensification) and the expansion of industrial and mining activities, which have had a great effect on the composition of its vegetation (Prach et al. 2007, Chytrý 2017).

Disturbance usually implies the removal of standing biomass and a change in nutrient availability and soil texture and structure (Grime 2001). Primary succession refers to the occupation of a bare substrate from the surroundings by dispersal, while secondary succession is based on seed banks or propagules embedded in the soils of undisturbed sites (Pickett et al. 2013). There are several mechanisms and hypotheses of species replacement, forming a continuum based on how much the successional ordering of species is random vs deterministic (Keever 1983, Wilson et al. 2019). Ecological processes at large spatial and temporal scales tend to be more deterministic than random (Levin 1992, Buma et al. 2019), and in the Czech Republic, in particular, the potential vegetation at the country scale is predominantly forest (Chytrý 2017). Moreover, Tansley's (1935) distinction of allogenic and autogenic factors in succession indicates that mechanisms resulting in changes in vegetation can be due to either the action of plants on their environment (autogenic factors, such as the shading of the forest understory by the canopies of trees, which are modulated by physiological and morphological properties; Horn 1971) or abiotic processes such as soil texture, temperature, or precipitation (allogenic factors). In a series of studies, Karel Prach and his colleagues report that environmental moisture is a strong (allogenic) factor in conditioning the successional trajectory in the composition and diversity of species in the Czech Republic and some eastern-European countries (see Prach et al. 2007 and references therein). Other environmental factors like soil fertility and, to a lesser degree, temperature also alter successional trajectories (Wright & Fridley 2010, Fridley & Wright 2011), and these effects are even more important than the local landscape and topographic conditions (Vítovcová et al. 2021). However, at regional scales, there are consistent, deterministic trends in the successional pathways at the taxonomic level (Prach et al. 2014). Moreover, taxonomic divergence in succession does not imply functional trait divergence (Prach et al. 1997, Fukami et al. 2005), and there is evidence that whether succession is primary or secondary does not have a great effect on the correlation of traits with succession (Latzel et al. 2011). Due to this complexity, succession is generally seen as a process of changes in taxonomic composition that results, from a more or less stochastic composition after a disturbance, to a deterministic dynamic equilibrium (Whittaker 1953). This process is partly due to a change in plant traits. Harsher environmental conditions can slow the rate of reaching this equilibrium (Li et al. 2022), and hence there might be an interaction with the environment with the effects that traits have on the successional ordering of species. Knowing that succession follows directional trends at large scales, that traits are themselves the cause of changes in some of the environmental factors, and that traits tend to follow more converging dynamics than taxonomic identities gives us a means of exploring the relation between the successional arrangement of species and their traits.

Functional traits are measurable qualities of an organism that affect any of the three components of fitness: growth, survival and fecundity (Violle et al. 2007), and life history traits are those inferred at the population scale, such as, demographic elasticity, mean longevity and fecundity (Franco & Silvertown 1996, Adler et al. 2013, Laughlin 2023). Plant ecological strategies are suites of functional or life-history traits that show patterns of covariation ("trade-offs" if such covariation is negative) which allow us to summarize the complexity of traits in a biologically sensible, low-dimensional space of strategies (Laughlin 2013). However, as the fitness component of a trait that makes it "functional" is not easy to prove or measure, this study is simply based on "traits", assuming they can be explanatory for a pattern of interest, without strictly assuming they have a positive effect on fitness. There are well-established relationships between plant traits and environmental variables (Ackerly & Cornwell 2007, Bruelheide et al. 2018, Towers et al. 2023), which have been used to define plant strategies associated with different types of environmental stress (Craine 2009, Laughlin 2023). For the strategies that are particularly associated with succession, there are two complementary hypotheses: Grime's (1977, 2001), based on descriptive research, proposes that there are three types of strategies (ruderal, competitive and stress-tolerant) and Tilman's (1985), based on competition models on a dynamic gradient of light and nutrient availability. However, there is no consensus between these two hypotheses (Craine 2009). Hence, in this study, a data-driven approach is used to find a set of traits forming successional strategies.

Despite the frequent use of extensive databases of traits, such as, TRY (Kattge et al. 2019), most studies on the association of traits with environmental gradients usually focus on above ground traits, especially those associated with leaves, while most belowground traits are overlooked (Laliberté 2017, Ottaviani et al. 2020). In addition, there is a lack of data on the successional ordering of species at large temporal scales that could be summarized, based on many different successional series, in a single value for each species. Fortunately, for many species in the Czech Republic, a database of a wide variety of above and belowground traits has been compiled (Chytrý et al. 2021), and a variable describing the successional ordering of species has been recently devised for the Czech flora (Prach et al. 2017) – the "successional optimum" (SO). Moreover, there is a recent synthesis of Ellenberg-type indicator values for species in the Czech flora that recalibrates and enhances previous lists (Chytrý et al. 2018). This enables the determination of a species' preferred values of environmental factors along different environmental dimensions, and much of vegetation ecology sees these environmental indicator values (EIVs) as representing the optima of a bell-shaped distribution of species' niches along an environmental gradient (Diekmann 2003).

The purpose of this study is to determine the association of traits and EIVs with the successional arrangement of species. Previous studies determine trends in traits along space-for-time substitution gradients (Vile et al. 2006, Navas et al. 2010, Douma et al. 2012, Li et al. 2022), modelling (Huston & Smith 1987, Shipley et al. 2006), ordination-defined successional gradients (Szabó & Prach 2009) or in permanent plots (Kahmen & Poschlod 2004), but little attention has been paid to evaluating the importance of traits in ordering species along a successional gradient. The way in which successional gradients are defined (traditionally either by chronosequences or by permanent plots) has important implications for the results (Johnson & Miyanishi 2008). Here, a new approach that helps to disentangle the relative contribution of each trait and each environmental indicator value to account for the successional arrangement of species is used. The approach is similar to that of Herben et al. (2017) in using a synthetic variable to define the successional gradient as a response variable, but goes further in using a larger spectrum of traits by identifying the relative importance of each trait and EIV and in applying a robust inference methodology. The questions of this research are: (Q1) What are the effects of traits on the successional optima (SO) of species? (Q2) What is the relationship between preferred values of environmental factors expressed as EIVs and SO? (Q3) Does the interaction between traits and preferred values of environmental factors predict SO? (Q4) What is the relative importance of traits and species' preferred values of environmental factors for predicting SO?

Materials and methods

Position of species on the successional gradient

For 961 vascular plant species in the Czech flora, Prach et al. (2017) calculated the median years it takes for each species on the list to reach their optima of abundance during succession after a major disturbance, which here is referred to as the successional optimum (SO). The authors also calculated two other Ellenberg-type variables of colonization potential and colonization success. SO spans from 1 to 95 years and is calculated using the Database of Successional Series (DaSS, Prach et al. 2014; see https://www.restoration-ecology.eu/dass), which contains successional series of phytosociological relevés. It was originally published with a censoring of age values higher than 50 years having an arbitrarily assigned value of 75, as the larger values could be imprecise due to the scarcity of observations. However, this censoring also diminishes the amount of information (the statistical estimators have larger variances) and imposes software limitations and interpretation problems for complex modelling (Ha et al. 2017). Moreover, arbitrary assignations of censored values are known to generate unreliable results (Fox 2015), so the raw estimations provided by Lubomír Tichý, a coauthor in Prach et al. (2017), were relied on before assigning the 75 value to censored observations.

Plant phylogeny

Phylogeny is important for (i) the non-independent nature of species data and (ii) the information on phenotypic properties not included in the selected traits, which might be associated with the environmental gradient if they are phylogenetically conserved. To obtain the phylogenetic tree for our species pool, the species names were standardized based on the Leipzig Catalogue of Vascular Plants (Freiberg et al. 2020) and then pruned the "GBOTB.extended.LCVP" megatree in the V.Phylomaker.2 R package (Jin & Qian 2022) for our species list.

Trait data

The Pladias (PLAnt DIversity Analysis and Synthesis) database (Chytrý et al. 2021) contains information for 120 plant characteristics. Most of these characteristics are traits, including physiological and morphological (both belowground and aboveground), phenological, and reproductive values for plant species in the Czech flora. As many traits as possible were included after correcting for redundancies, such as between life forms and growth forms, and discarding traits that showed no variability for particular species on the list (i.e. having less than 25 "positive" observations for binary variables or having a very small standard deviation), which resulted in a final set of 18 traits (Table 1), defining broad groups: life form (woody, therophyte, geophyte and hemicryptophyte), belowground (bud bank depth, bud bank size, lateral spread, clonality index), size (height, seed mass), leaf quantitative traits (LQTs; leaf area, specific leaf area, leaf dry matter content), reproduction (flowering duration, autogamy, vegetative reproduction) and interactions (parasitism, myrmecochory).

Table 1. List of selected functional traits and their descriptive statistics. The total number of species of vascular plants used for the analyses was 878. The column named Trait includes traits used in analyses. Traits are grouped into broad trait groups based on their phenotypical classification. "N missing" refers to missing values before our imputation. The source of the trait data is the database PLADIAS (Chytrý et al. 2021). Standard deviation/occurrence gives the standard deviation for (semi)quantitative variables and the number of cases for binary variables. Some species have more than one Life Form value, and hence the sum of occurrences is higher than 878. For Autogamy, the descriptive statistics refer to species that are strictly autogamous (i.e. do not share any other fertilization vector). Abbreviations: LA: Leaf area; LDMC: Leaf dry matter content; SLA: Specific leaf area; FloDur: Flowering duration; VegRep: Vegetative reproduction.

Group	Trait	Number of NAs	Mean	Standard deviation (number of occurrences for binary variables)	Min	Max	Unit
Life form	Woody	3	0.16	137	0	1	binary
	Therophyte	3	0.24	206	0	1	binary
	Geophyte	3	0.11	95	0	1	binary
	Hemicryptophyte	3	0.61	535	0	1	binary
Belowground	Bud bank depth	54	4.0	2.7	0	11.7	cm
	Bud bank size	54	17.4	11.2	0	60	count (bud/shoot)
	Lateral spread	63	0.04	0.07	0	0.37	cm
	Clonality index	63	1.76	2.08	0	6	ordinal (2:8)
Size	Height	3	1.69	4.96	0.02	47.5	m
	Seed mass	96	37.3	370.7	0	7,708.7	mg
Leaf quantitative traits (LQTs)	LA	163	3,950	11,678	0.98	142,526	mm^2
	LDMC	159	216.1	77.9	50.0	635.5	mg/g
	SLA	112	24.7	10.4	3.3	94.9	mm^2/mg
Reproduction	FloDur	3	3.2	1.3	1	12	months
	Autogamy	39	0.04	30	0	1	binary
	VegRep	21	0.25	0.25	0	1	ordinal
Interactions	Parasitism	0	0.03	28	0	1	binary
	Myrmecochory	18	0.24	207	0	1	binary

Environmental factors associated with species

Information on the environmental factors associated with species is based on the Ellenberg-type indicator values developed for the Czech flora (Chytrý et al. 2018). These are variables scaled from 1 to 9 (or to 12 for moisture), showing the optimal conditions of species in a gradient of a given indicator value. The used EIVs are: light, nutrients, moisture, reaction, and temperature. The aim of using the EIVs is twofold: (i) to determine how environmental associations relate to successional ordering (Q2), and (ii) to determine the explanatory power in terms of successional ordering that the EIVs have compared to traits (Q4). Hence, light and nutrients are classified as autogenic and moisture, reaction, and temperature as allogenic EIVs. The distinction avoids the circularity in explaining succession in terms of traits and EIVs when, in their turn, EIVs and traits explain each other. Water availability, which is related to moisture, is determined by both evapotranspiration (an autogenic process) and water inflow and outflow, evaporation, and retention (largely allogenic processes, as they depend on climate, topography, and geological properties); this makes it difficult to put it in the same class as light and nutrients (Craine & Dybzinski 2013). Moreover, as the type of information provided by EIVs (i.e. summary of environmental associations of plants in natural communities at equilibrium at large scales), it is sensible to include moisture as allogenic. Disentangling the effect of traits and EIVs on successional optimum reveals what properties of the fundamental niche are being acted upon the traits to generate the successional gradient and which of these properties are strong predictors of successional optimum decoupled from traits. Furthermore, the EIVs were used to remove hydrophytes from the dataset, i.e. species with a value for moisture higher than 9, and avoid conflating hydroseres with more common succession processes on land. In summary, combining the species for which there is data on traits, EIVs, and successional information, resulted in a list of 878 species of vascular plants for the analyses.

Statistical analyses

All analyses were done using the R programming language, version 4.3.2 (R Core Team 2023).

Ordination of plant traits

A principal component analysis (PCA) ordination of traits along with pairwise correlations were used to assess whether it is possible to summarize trait information in a few axes of trait variation.

Phylogenetically informed imputation of missing trait values

Using the phylogenetic tree, a pairwise phylogenetic distance matrix and the eigenvectors of a PCoA ordination of this matrix employing the PVR package (Santos 2018) were obtained. These eigenvectors were incorporated in the missing traits imputation using the method suggested by Debastiani et al. (2021), based on the correlations between both the traits and the phylogenetic relationships, which decrease imputation errors. Imputations were done using the missForest (Stekhoven & Bühlmann 2011) package.

Association of successional optimum with traits

To test the association of traits and phylogeny on the SO variable (Q1), a penalized regression by LASSO (Least Absolute Shrinkage and Selection Operator; Hastie et al. 2009), which alters the traditional ordinary least squares (OLS) estimator of linear models by introducing a penalty based on the sum of the absolute values of the effect sizes and scaled by a λ coefficient, was used. When $\lambda = 0$, the LASSO is a standard linear regression, but as it increases it shrinks the effect sizes of the model continuously and differentially by their predictive power, eventually setting some of them to 0, so "the LASSO does a kind of continuous subset selection" (Hastie et al. 2009); the list of predictors selected by the LASSO is called the "active set". The search for the optimal λ was done by a 20-fold cross-validation (Yates et al. 2023). Although shrinkage methods such as the LASSO are not very popular in ecology due to the prevalence of information-theoretic approaches and multi-model averaging, they avoid some of the latter's shortcomings (Cade 2015, Galipaud et al. 2017) and are useful in many other fields as well as in ecology (Dahlgren 2010, Bolker 2023). The phylogenetic eigenvectors were used, after the traits, to expand the search of important variables by the LASSO.

The LASSO was done using the glmnet package (Friedman et al. 2010). Phylogenetic corrections and selective inference were also used as required for non-independent data and model selection methods.

Association of successional optimum with EIVs

The association of EIVs with SO (Q2) was tested. This was done in two steps: first using a simple linear regression between SO and EIVs, and then by the addition of an offset term made of the predictions of SO by a model using the active set of traits as predictors, which is equivalent to modelling the residuals from the model "SO ~ traits" against the EIVs. This is a way of detrending SO with regards to traits. By comparing the two models of SO vs EIVs, it is possible to determine by which EIVs the traits are being filtered along complex successional gradients.

Interaction of traits and EIVs accounting for their association with successional optimum

For each allogenic EIV (moisture, reaction, and temperature), the model fit and the list of LASSO-selected traits were compared by searching (i) the predictor matrix that includes traits and EIVs; and (ii) a predictor matrix including traits, the EIVs and the interaction between traits and the EIVs. This allowed the assessment of whether it is possible to develop better models from the interaction of traits with the allogenic EIVs, that is, whether the trends in trait values during succession are dependent on environmental preferences, or whether trait trends are invariant with respect to the environment.

Dominance analysis

LASSO is a predictive model tool to include a measure of the relative importance of each variable. For this, a Dominance Analysis (Budescu 1993, Grömping 2007) was used to obtain a decomposition of the adjusted R^2 that each variable adds to a model, which works well in ecology (Murray & Conner 2009). This method was used to determine the amount of variation accounted for by traits, EIVs or their overlap. The analysis was done using the domir package (Luchman 2023).

For the regression of SO against traits, all quantitative predictors were standardized and the binary ones left unchanged, as suggested by Gelman et al. (2021). For the regression of SO against EIVs, they were not standardized as they are all on the same scale. In all regression analyses, SO was normalized by using its cubic root (the Box-Cox algorithm gave an optimal exponent for normalization of 0.337). The variance inflation factor was examined in order to detect possible collinearity.

Results

Relationships between the traits

The pairwise correlation between traits was only substantial (above 0.5 in absolute value) between traits related to belowground properties, between woody and height, and between therophyte life forms and belowground traits (Supplementary Fig. S1). The first three principal components (PCs) of the PCA of traits accounted for almost half of the variance of the whole trait matrix (22.5%, 15%, and 9%, respectively). The first PC was mainly related to plant life forms. Belowground habits and vegetative reproduction were on the first two PCs, and height, seed mass and LQTs were mainly on the second PC (Supplementary Fig. S2). When fitting SO into the ordination space, the first PCs explained 16% of its variance (13% coming just from PC1, 2% from PC2 and almost nothing from PC3; Supplementary Fig. S3).

Associations between successional optima and plant traits

The LASSO algorithm selected the following traits for the active set at $\lambda \approx 0.01$: bud bank size, flowering duration, height, leaf area (LA), leaf dry matter content (LDMC), myrmecochory, parasitism, seed mass, specific leaf area (SLA), therophyte and woody life form. Augmenting the LASSO with the model matrix with the phylogenetic eigenvectors, resulted in none being selected. The non-selected traits were, geophyte and hemicryptophyte life forms, bud bank depth, lateral spread and clonality index in belowground traits, and autogamy and vegetative reproduction in reproductive traits. Autogamy was the only non-selected trait that was not correlated with the rest of the traits (Supplementary Fig. S1).

Using the traits in the active set in the linear regression against SO, the model's adjusted-R^2 was 0.25, and no collinearity was detected. Of the 11 selected traits, seven were statistically significant at the 95% confidence level under standard inference (Fig. 1): therophyte (effect size ± 1.96 × standard error: –0.5 ± 0.14), parasitism (0.54 ± 0.26), seed mass (0.18 ± 0.05), height (–0.1 ± 0.06), LDMC (0.07 ± 0.05), flowering duration (–0.08 ± 0.04) and bud bank size (0.05 ± 0.05). Non-significant traits in the active set were LA (–0.04 ± 0.05), myrmecochory (0.04 ± 0.01), SLA (–0.02 ± 0.06) and woody life form (0.14 ± 0.17). Phylogeny and selection-corrected inferences had little effect on the traits with very small effect sizes, as bud bank size was not significant when corrected for phylogeny and neither bud bank size nor height under selective inference correction (phylogenetic signals are reported in Supplementary Table S1); therophyte life form was marginally significant under selective inference, but robust to phylogenetic corrections. The rest of the traits showed a similar pattern of effect size values and confidence intervals (Fig. 1). All the trait groups contained at least one statistically significant trait on standard inference, although the belowground group was no longer present (bud bank size) in the corrections (Supplementary Data S1, Supplementary Fig. S4).

Relation of successional optimum with environmental indicator values

In contrast to traits, where the effects were generally small, when the EIVs were analysed alone against SO, there was a marked negative effect of EIVs of light (–0.15 ± 0.04) and nutrients (–0.16 ± 0.03) (Fig. 2). Reaction also had a strong positive effect (0.13 ± 0.04), and moisture had a marginally significant negative effect (–0.03 ± 0.04). Temperature had

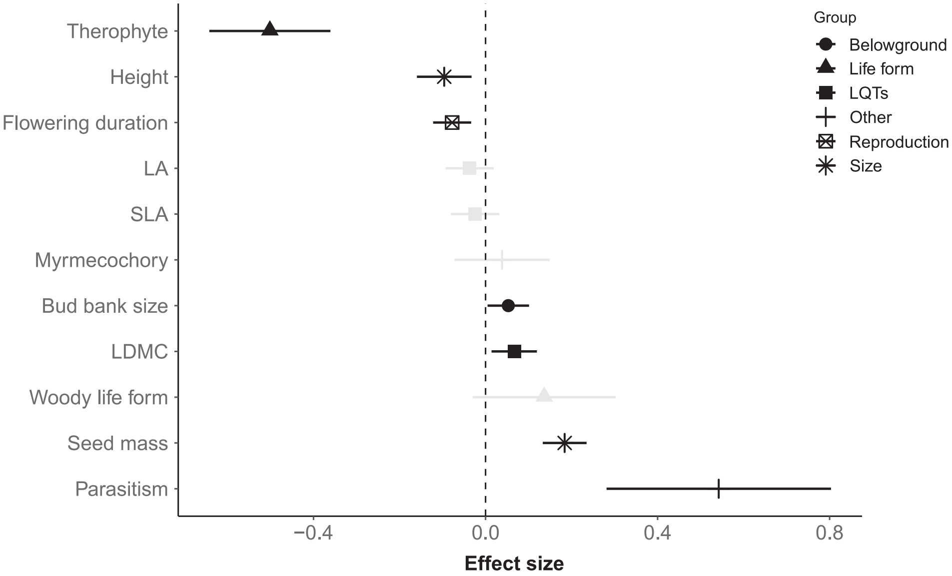

Fig. 1. Effect sizes of the active set of 11 trait predictors selected by the LASSO on the successional optimum (SO). Although not statistically significant, a trait that belongs to the active set has some non-negligible predictive power in defining the response variable. Smaller (i.e. negative) effect sizes indicate a positive association with early stages of succession, whereas large values indicate a positive association with later stages. Point shapes denote the "broad trait group" in Table 1. LQTs: leaf quantitative traits; LA: leaf area, LDMC: leaf dry matter content, SLA: specific leaf area.

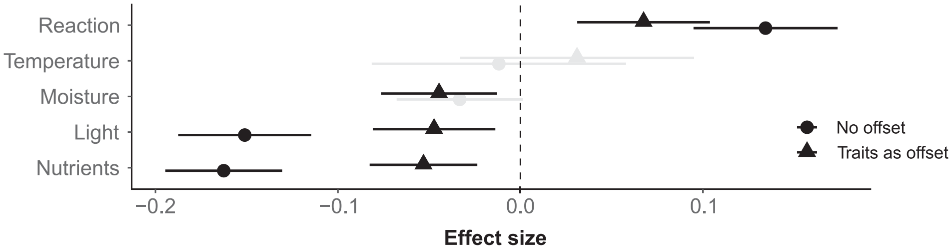

Fig. 2. Effect sizes of the different EIVs on the successional optimum (SO). Triangle effect sizes indicate the effect of EIVs on predictions of SO from traits as an offset (i.e. using traits as covariates with a fixed coefficient), while circle effect sizes indicate the independent effect of EIVs (no offset). Small (i.e. negative) effect sizes indicate a positive association with early stages of succession, while large (positive) values indicate an association with later stages.

a very small negative effect (–0.01 ± 0.07). Global adjusted-R^2 due to EIVs was 0.18. However, once an offset term with the predictions using the traits selected by the LASSO was incorporated, the effects of the dominant EIVs were reduced between 2 and 3-fold (light = –0.05 ± 0.03, nutrients = –0.05 ± 0.03, reaction = 0.07 ± 0.04) while moisture's decreased and became statistically significant (–0.04 ± 0.03). The effect of temperature increased but was still far from being statistically significant (0.03 ± 0.06). Hence, after accounting for traits, there was a more even share of effects between EIVs. Adjusted-R^2 was 0.06. This R^2 is only the part of the variance explained exclusively by EIVs, as that explained by traits that overlap with the EIVs was already included in the offset.

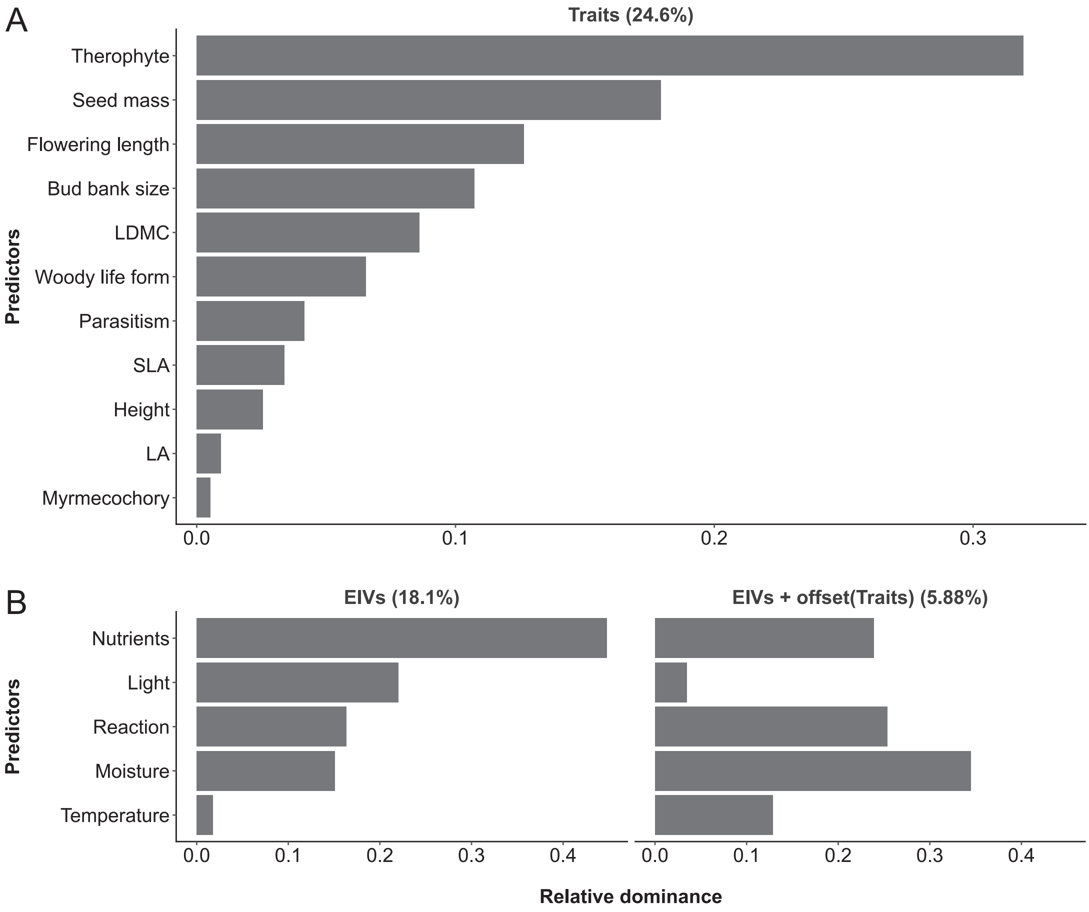

Fig. 3: (A) Relative importance of traits. The five most important traits account for more than 80% of the explained variance. (B) The relative importance of EIVs before (left) and after (right) using predictions of the successional optimum from traits as an offset. There is a decrease in the importance of light and nutrients after accounting for traits, whereas that of moisture and reaction increases. LA: leaf area, LDMC: leaf dry matter content, SLA: specific leaf area.

Interaction between traits and environment

The incorporation of interaction terms between traits and EIVs generally did not provide a better model fit compared to models using traits and each EIV additively. Interactions with reaction increased the adjusted-R^2 by 1.6%, and with moisture and temperature by ~ 1%. This means that by doubling the number of putative predictors, LASSO identified very few better fitting models and they were more complex and difficult to interpret, while almost all the selected traits were the same either with or without interactions (not shown).

Relative importance of traits and EIVs in explaining succession

Relative contribution of traits and EIVs: The proportion of total variance in SO explained by traits and EIVs was $R^2 = 0.3$. Forty percent of this explained variance was exclusively associated with traits, and 19% exclusively with EIVs. The overlap in variance between the two groups of predictors was 41%. Hence, including overlaps, traits accounted for 81% of the explained variance and EIVs for 60%.

The individual contribution of traits: Of the 81% of variance explained by the 11 traits in the active set and their overlap with EIVs, five traits accounted for 83%: therophyte (32%), seed mass (18%), flowering duration (13%), bud bank size (11%), and LDMC (9%). The other six traits only had a minor contribution (Fig. 3).

Individual contribution of EIVs: The relative importance of EIVs in their accounting for 62% of the explained variance when overlap with traits was included, had a very different pattern than the EIV's relative importance in accounting for 19% of the explained variance when only non-overlapping with traits was considered (Fig. 3). Light and nutrients alone accounted for 67% of the total relative importance in the model before using as an offset the predictions of SO by the model trained using only traits in the active set, while they made up slightly above 25% after accounting for traits. This is accompanied by a major increase in the relative importance of moisture (from 15% to 34%) and reaction (from 16% to 25%) after including predictions of SO by traits as an offset. The role of temperature also increased (from 2% to 13%) and became more important than light, which is not in accord with the effect size and significance of the models.

Discussion

This study revealed that the time a species needs to reach its optimal abundance (i.e. successional optimum; SO) is associated with a small number of traits. In particular, life history and life cycle (therophyte), competitive ability (seed mass and LDMC), flowering duration, and regeneration niche (bud bank size) explain more than 80% of the total model fit, while other traits also related to competition (height) and biotic interaction (parasitism) are also significantly associated with succession. Furthermore, traits in general account for the successional ordering of species much better than their values for environmental factors, measured as EIVs and reveal the benefits of using trait-based approaches to describe ecological processes.

Environmental characterization of the successional gradient

The use of EIVs allowed the characterization of successional processes as a complex gradient ranging from nutrient-rich to nutrient-poor, shaded without significant changes in moisture or temperature. The detected changes in soil reaction are attributed to an underlying bias in the species list by which species with high SO values happen to occur in alkaline habitats, as it is unlikely that at the time scales of this study, succession results in a very marked change in the pH of the soil. As some of the EIVs, especially light and nutrients are associated with traits, once the latters' effects are accounted for, there is a marked contrast of relative importance: the autogenic factors light and nutrients (especially the former) became less important than moisture and reaction, and temperature had a minor role. The negative effect of moisture may indicate that the rate of succession in dry habitats (i.e. those harbouring species with low values for moisture) is slower, so the time the species take to reach their abundance optima after disturbance is longer, which results in greater SO values. The greater relative importance of moisture after accounting for traits may help explain the different successional series identified based on taxonomy reported by Prach et al. (2007); associated with different moisture conditions are different species pools, which result in taxonomic differences in successional series. However, the analysis of trait-environment interactions revealed that there is no environmentally determined idiosyncratic pattern in terms of traits, associated with moisture or other allogenic EIVs. The effect of reaction is marked and positive, with species growing on base-rich substrates taking longer to reach their peak abundance. This might seem to contradict what is reported for some mature forests (i.e. those consisting of species with high SO) predominantly growing in acid soils (van der Sande et al. 2022), but in the case of the Czech Republic, it could be that the forests developed in the Carpathian mountain range and basiphilous oak forests or basiphilous submontane pine forests belonging to the class *Erico-Pinetea* class (Chytrý 2013) are driving the positive effect of reaction. Another explanation is that the structure of vegetation with slow dynamics might not necessarily be related to the "potential vegetation" that one might intuitively relate to SO. Dry grasslands, for example, are characterized by slow dynamics, probably due to low availability of water (Weaver & Bruner 1945, Weaver 1954, Fischer et al. 2020).

Interpretation of the effects of traits

The strong negative effect of the size of the therophyte life form found in this study is a very general expectation in succession (Bazzaz 1996), which is consistent with the pattern reported by Prach et al. (1997) and Szabó & Prach (2009). This is due to the early arrival of annual species immediately after a disturbance; coupled with the strong positive effect of seed mass, a trait usually related to competitive ability, this finding validates the hypothesis that there is a competition-colonization trade-off (Bolker & Pacala 1999, Cadotte et al. 2006) and fits well with Grime's CSR framework (Grime 2001). On the other hand, the positive effect of woody life form is also a clear representation of the process of colonization of slow-growing species in stable environments, leading to conservative properties (Franco & Silvertown 1996).

More specifically related to competition is the positive effect of LDMC on SO, which indicates that the first plants are very dependent on the nutrients in the soil, whereas those that occur later invest more and for longer in their photosynthetic organs; the positive relation between LDMC and leaf longevity is part of the leaf economic spectrum (LES; Wright et al. 2004). This finding is in accord with previous results, which show that SLA is negatively correlated with succession (Shipley et al. 2006, Raevel et al. 2012) and supported by the negative correlation between SLA and LDMC in the LES.

In addition, the positive relationship between bud bank size and SO indicates that late-successional species, rather than investing in long-range dispersal, allocate biomass to their "persistence trait" (i.e. a conservative strategy; Latzel et al. 2011). This enables them to resprout after small-scale disturbances and/or display a more active "movement" to search for nutrient-rich microsites, which become scarcer during succession (Eriksson 2023); this is consistent with the findings of Szabó & Prach (2009) and Latzel et al. (2011) on lateral spread. However, patterns of belowground development are related to habitat types in complex ways (Sammul et al. 2004).

The negative effect of flowering duration may indicate an increased niche packing for pollinator availability in more competitive communities in late succession, as in diverse communities species need to exploit the capacity to reproduce sexually more efficiently (i.e. in shorter periods of time) (Parrish & Bazzaz 1979). However, comparative studies of different types of succession indicate that this increase in competition is not universal (Prach & Walker 2020). This is in accord with the positive relationship between succession and species richness at large spatial scales, from disturbed to mature communities (Staude et al. 2023), particularly those based on the DaSS database (Prach et al. 2014). In diverse communities, niche sizes are small and differences in phenology enable coexistence (Blackford et al. 2020). This, together with a higher diversity of pollinators in late succession (Southwood et al. 1979, Steffan-Dewenter & Tscharntke 2001, Penado et al. 2022), may result in more specialized short term plant-pollinator relationships. Kahmen & Poschlod (2004) and Douma et al. (2012) also reported a negative correlation between succession and flowering duration (but not Li et al. 2022).

The relationship between succession and diversity may account for the positive effect of parasitism: parasites (and antagonists in general) typically thrive in stable and high-quality environments (Thrall et al. 2007, Meiners et al. 2015). The rate of taxonomic change is known to decline during succession (Prach et al. 1993, Anderson 2007), so the conditions for the proliferation of antagonists, particularly parasites, in late stages of succession are expected although their degree of specialization declines with increase in diversity (Thrall et al. 2007).

The negative effect of height on SO could be an example of “Simpson’s paradox” or “ecological fallacy”, as the correlation between height and SO is positive, but its effect in the multiple regression including all of the traits in the active set is negative. This could be expected as height is known to have complex allometric relations with other traits, such as seed mass (Rees & Venable 2007); this strong relationship was revealed by the ordination analysis (Supplementary Fig. S2). It is likely that the analysis of relative importance makes the use of specialized statistical tools to avoid Simpson’s fallacy unnecessary. Related to the covariation of height with other traits, Mudrák et al. (2021) report that the relationship of height with SO depends on the life form considered and that the typically unnoticed positive relationship of height with dispersal abilities is favoured in early succession. In addition, Mudrák et al. (2023) report that, at the community level canopy height decreases during grassland restoration. Furthermore, although plant height is a trait usually related to competitive ability, in order to account for its previously documented positive relationships with succession (Grime 2001, Shipley et al. 2006, Vile et al. 2006, Szabó & Prach 2009), it has been shown that in all types of vegetation there is a predominance of small plants and competitive ability is not necessarily only associated with plant height as plants of different sizes interact asymmetrically (Aarssen 2015). Hence, the results for plant height are not considered to be contrary to the interpretations for other traits and reports in the literature but are due to statistical artifacts and biological complexity (i.e. dependence on other traits and types of succession) of the variation in plant height.

It should be noted that the traits are those that LASSO selected and have a higher predictive power, even though some of them are of little importance. Furthermore, many of these relationships remained after controlling for phylogenetic autocorrelations and mathematical artifacts of the model selection algorithm (Supplementary Fig. S4). For the traits not included in the active set, most had clear correlations with other included traits. It is known that LASSO selects only one of the correlated predictors (Friedman et al., 2010). However, it is remarkable that autogamy, which is not strongly correlated with the other traits (Supplementary Fig. S1), was not selected by the LASSO algorithm. Some authors (e.g. Levin 1972, Parrish & Bazzaz 1979) suggest that, due to a lack of pollinators in the early stages of succession (because their colonization lags behind that of plants, or because of more fluctuating populations), plants are mainly self-fertilizing, which increases their chances of reproducing. This hypothesis is not supported by the results of this study.

Finally, as a methodological observation, LASSO selected 11 traits; however, from the principal components from a PCA of the trait matrix, the first 15 PCs to obtain the same goodness of fit would have been needed (Supplementary Fig. S3), calling for a much more difficult interpretation.

Limitations of this study

A limitation of our results is the reliance on SO being an accurate representation of the intricacies of succession. The optimal abundance criterion has a strong effect on which traits will be selected, but other successionally important information may be better represented by other traits. Moreover, SO was only developed for a subset of central-European flora. Therefore, it can exhibit idiosyncratic behavior that is not easily comparable to other geographical regions and/or species pools, both due to the biology of plants and the different types of human geography and disturbances that influence succession in the data sources (Prach et al. 2007). Furthermore, the division between allogenic and autogenic factors can be criticized, as many environmental properties are, to some extent, modified by vegetation (van Andel et al. 1993, Eviner & Stuart Chapin III 2003). Other caveats are the absence of SO data for plant species of the Czech Republic and the uncertainty in the large values of SO due to the scarcity of observations (L. Tichý, personal communication). Furthermore, the focus on linear models might have resulted in more complex relationships being overlooked, such as, unimodal or U-shaped curves of SO against traits, which can be interesting from an ecological standpoint.

Conclusions

This study provides evidence that traits are better predictors of successional optimum than environmental associations at a country-wide scale. Moreover, there are only a few traits that are important, which are related to life form and life cycle, competition, reproduction and regeneration niche, such as the therophytic life form, leaf dry matter content, seed mass, bud bank size and flowering duration. Changes in the successional optimum reflect a coupled gradient of decreasing availability of light and nutrients. However, since plant traits are associated with environmental factors, the underlying factors associated with the successional ordering of species are moisture and soil reaction. These findings not only increase the understanding of successional dynamics at a broad scale but also highlight the resilience and adaptability of plant communities in responding to environmental changes. By recognizing the key traits driving these processes, it may be possible to anticipate and manage ecosystem changes in the face of ongoing environmental challenges.

Supplementary materials

Data S1. Standard vs phylogenetic and selective inference.
Fig. S1. Trait correlations.
Fig. S2. Correlation in ordination space.
Fig. S3. Increase in explained variance.
Fig. S4. Comparison of effect sizes and confidence intervals of the three types of inference methodologies.
Table S1. Phylogenetic signals.

Supplementary materials are available at https://www.preslia.cz

Acknowledgments

We thank Karel Prach and one anonymous reviewer for their valuable comments on a previous version of the manuscript. We also thank Lubomír Tichý for providing the raw data on the successional optima and useful discussions on the use of Ellenberg-type indicator values. We thank Irena Axmanová for the preparation of the trait matrix. This research was funded by the specific research program for PhD students at Masaryk University "Role evolučních a ekologických systémů na ekosystémové úrovni" (The Role of Evolutionary and Ecological Systems at the Ecosystem Level, code: MUNI/A/1489/2023).

References

Aarssen L. W. (2015) Body size and fitness in plants: revisiting the selection consequences of competition. – Perspectives in Plant Ecology, Evolution and Systematics 17: 236–242.

Ackerly D. D. & Cornwell W. K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. – Ecology Letters 10: 135–145.

Adler P. B., Salguero-Gómez R., Compagnoni A., Hsu J. S., Ray-Mukherjee J., Mbeau-Ache C. & Franco M. (2013) Functional traits explain variation in plant life history strategies. – Proceedings of the National Academy of Sciences of the United States of America 111: 740–745.

Anderson K. J. (2007) Temporal patterns in rates of community change during succession. – The American Naturalist 169: 780–793.

Bazzaz F. A. (1996) Plants in changing environments: linking physiological, population and community ecology. – Cambridge University Press, Cambridge.

Blackford C., Germain R. M. & Gilbert B. (2020) Species differences in phenology shape coexistence. – The American Naturalist 196: E168–E180.

Bolker B. M. (2023) Multimodel approaches are not the best way to understand multifactorial systems. – Entropy 26: 506–516.

Bolker B. M. & Pacala S. W. (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. – The American Naturalist 153: 575–602.

Bruelheide H., Dengler J., Purschke O., Lenoir J., Jiménez-Alfaro B., Hennekens S. M., Botta-Dukát Z., Chytrý M., Field R., Jansen F., Kattge J., Pillar V. D., Schrodt F., Mahecha M. D., Peet R. K., Sandel B., van Bodegom P., Altman J., Alvarez-Dávila E., Khan M. A. S. A., Attorre F., Aubin I., Baraloto C., Barroso J. G., Bauters M., Bergmeier E., Biurrun I., Bjorkman A. D., Blonder B., Čarni A., Cayulea L., Černý T., Cornelissen J. H. C., Craven D., Dainese M., Derroire G., De Sanctis M., Diaz S., Doležal J., Farfan-Rios W., Feldpausch T. R., Fenton N. J., Garnier E., Guerin G. R., Gutiérrez A. G., Haider S., Hattab T., Henry G., Hérault B., Higuchi P., Hölzel N., Homeier J., Jentsch A., Jürgens N., Kącki Z., Karger D. N., Kessler M., Kleyer M., Knollová I., Korolyuk A. Y., Kühn I., Laughlin D. C., Lens F., Loos J., Louault F., Lyubenova M. I., Malhi Y., Marcenň C., Mencuccini M., Müller J. V., Munzinger J., Munzinger I. H., Neill D. A., Niinemets U., Orwin K. H., Ozinga W. A., Penuelas J., Pérez-Haase A., Petřík P., Phillips O. L., Pärtel M., Reich P. B., Römermann C., Rodrigues A. V., Sabatini F. M., Sardans J., Schmidt M., Seidler G., Silva Espejo J. E., Silveira M., Smyth A., Sporbert M., Svenning J.-C., Tang Z., Thomas R., Tsiripidis I., Vassilev I., Violle C., Virtanen R., Weiher E., Welk E., Wesche K., Winter M., Wirth C. & Jandt U. (2018) Global trait–environment relationships of plant communities. – Nature Ecology & Evolution 2: 1906–1917.

Budescu D. V. (1993) Dominance analysis: a new approach to the problem of relative importance of predictors in multiple regression. – Psychological Bulletin 114: 542–551.

Buma B., Bisbing S. M., Wiles G. & Bidlack A. L. (2019) 100 yr of primary succession highlights stochasticity and competition driving community establishment and stability. – Ecology 100: e02885.

Cade B. S. (2015) Model averaging and muddled multimodel inferences. – Ecology 96: 2370–2382.

Cadotte M. W., Mai D. V., Jantz S., Collins M. D., Keele M. & Drake J. A. (2006) On testing the competition-colonization trade-off in a multispecies assemblage. – The American Naturalist 168: 704–709.

Chytrý M. (2013) Bazifilní podhorské bory [Basiphilous submontane pine forests]. – In: Chytrý M. (ed.), Vegetace České republiky. 4. Lesní a křovinná vegetace [Vegetation of the Czech Republic. 4. Forest and scrub vegetation], p. 366–379, Academia, Praha.

Chytrý M. (2017) Current vegetation of the Czech Republic. – In: Chytrý M., Danihelka J., Kaplan Z. & Pyšek P. (eds), Flora and vegetation of the Czech Republic, p. 229–337, Springer, Cham.

Chytrý M., Danihelka J., Kaplan Z., Wild J., Holubová D., Novotný P., Řezníčková M., Rohn M., Dřevojan P., Grulich V., Klimešová J., Lepš J., Lososová Z., Pergl J., Sádlo J., Šmarda P., Štěpánková P., Tichý L., Axmanová I., Bartušková A., Blažek P., Chrtek Jr. J., Fischer F. M., Guo W.-Y., Herben T., Janovský Z., Konečná M., Kühn I., Moravcová L., Petřík P., Pierce S., Prach K., Prokešová H., Štech M., Těšitel J., Těšitelová T., Večeřa M., Zelený D. & Pyšek P. (2021) Pladias database of the Czech flora and vegetation. – Preslia 93: 1–87.

Chytrý M., Tichý L., Dřevojan P., Sádlo J. & Zelený D. (2018) Ellenberg-type indicator values for the Czech flora. – Preslia 90: 83–103.

Craine J. M. (2009) Resource strategies of wild plants. – Princeton University Press, Princeton.

Craine J. M. & Dybzinski R. (2013) Mechanisms of plant competition for nutrients, water and light. – Functional Ecology 27: 833–840.

Cramer V., Hobbs R. & Standish R. (2008) What's new about old fields? Land abandonment and ecosystem assembly. – Trends in Ecology & Evolution 23: 104–112.

Dahlgren J. P. (2010) Alternative regression methods are not considered in Murtaugh (2009) or by ecologists in general. – Ecology Letters 13: E7–E9.

Debastiani V. J., Bastazini V. A. & Pillar V. D. (2021) Using phylogenetic information to impute missing functional trait values in ecological databases. – Ecological Informatics 63: 101315.

Diekmann M. (2003) Species indicator values as an important tool in applied plant ecology: a review. – Basic and Applied Ecology 4: 493–506.

Douma J. C., de Haan M. W. A., Aerts R., Witte J.-P. M. & van Bodegom P. M. (2012) Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. – Journal of Ecology 100: 366–380.

Eriksson O. (2023) The power of observation: Eugen Warming (1918) "Om jordudløbere" ('underground runners') and the ecology and evolution of clonal plants. – Nordic Journal of Botany 2023: e04003.

Eviner V. T. & Stuart Chapin III F. (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. – Annual Review of Ecology, Evolution, and Systematics 34: 455–485.

Fischer F. M., Chytrý K., Těšitel J., Danihelka J. & Chytrý M. (2020) Weather fluctuations drive short-term dynamics and long-term stability in plant communities: a 25-year study in a Central European dry grassland. – Journal of Vegetation Science 31: 711–721.

Fox G. A. (2015) What you don't know can hurt you: censored and truncated data in ecological research. – In: Fox G. A., Negrete-Yankelevitch S. & Sosa V. J. (eds), Ecological statistics, p. 106–130, Oxford University Press, New York.

Franco M. & Silvertown J. (1996) Life history variation in plants: an exploration of the fast-slow continuum hypothesis. – Philosophical Transactions of the Royal Society of London B 351: 1341–1348.

Freiberg M., Winter M., Gentile A., Zizka A., Muellner-Riehl A. N., Weigelt A. & Wirth C. (2020) LCVP, the Leipzig Catalogue of Vascular Plants, a new taxonomic reference list for all known vascular plants. – Scientific Data 7: 416.

Fridley J. D. & Wright J. P. (2011) Drivers of secondary succession rates across temperate latitudes of the eastern USA: climate, soils, and species pools. – Oecologia 168: 1069–1077.

Friedman J., Hastie T. & Tibshirani R. (2010) Regularization paths for generalized linear models via coordinate descent. – Journal of Statistical Software 33: 1–22.

Fukami T., Bezemer T. M., Mortimer S. R. & van der Putten W. H. (2005) Species divergence and trait convergence in experimental plant community assembly. – Ecology Letters 8: 1283–1290.

Galipaud M., Gillingham M. A. F. & Dechaume-Moncharmont F.-X. (2017) A farewell to the sum of Akaike weights: the benefits of alternative metrics for variable importance estimations in model selection. – Methods in Ecology and Evolution 8: 1668–1678.

Gelman A., Hill J. & Vehtari A. (2021) Regression and other stories. – Cambridge University Press, Cambridge.

Glenn-Lewin D. C., Peet R. K. & Veblen T. T. (1992): Plant succession. Theory and prediction. – Chapman and Hall, London.

Grime J. P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – The American Naturalist 111: 1169–1194.

Grime J. P. (2001) Plant strategies, vegetation processes, and ecosystem properties. Ed. 2. – John Wiley & Sons, New York.

Grömping U. (2007) Estimators of relative importance in linear regression based on variance decomposition. – The American Statistician 61: 139–147.

Ha I. D., Jeong J.-H. & Lee Y. (2017) Statistical modeling of survival data with random effects. – Springer, Singapore.

Hastie T., Tibshirani R. & Friedman J. (2009) The elements of statistical learning. – Springer, New York.

Herben T., Klimešová J. & Chytrý M. (2017) Effects of disturbance frequency and severity on plant traits: an assessment across a temperate flora. – Functional Ecology 32: 799–808.

Horn H. S. (1971) Adaptive geometry of trees (MPB-3). Vol. 3. – Princeton University Press, Princeton.

Huston M. & Smith T. (1987) Plant succession: life history and competition. – The American Naturalist 130: 168–198.

Jin Y. & Qian H. (2022) V.PhyloMaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants. – Plant Diversity 44: 335–339.

Johnson E. A. & Miyanishi K. (2008) Testing the assumptions of chronosequences in succession. – Ecology Letters 11: 419–431.

Kahmen S. & Poschlod P. (2004) Plant functional trait responses to grassland succession over 25 years. – Journal of Vegetation Science 15: 21–32.

Kattge J., Bönisch G., Díaz S., Lavorel S., Prentice I. C., Leadley P., Tautenhahn S., Werner G. D. A., Aakala T., Abedi M. et al. (2019) TRY plant trait database: enhanced coverage and open access. – Global Change Biology 26: 119–188.

Keddy P. A. (1992) Assembly and response rules: two goals for predictive community ecology. – Journal of Vegetation Science 3: 157–164.

Keever C. (1983) A retrospective view of old-field succession after 35 years. – American Midland Naturalist 110: 397–404.

Laliberté E. (2017) Belowground frontiers in trait-based plant ecology. – New Phytologist 213: 1597–1603.

Latzel V., Klimešová J., Doležal J., Pyšek P., Tackenberg O. & Prach K. (2011) The association of dispersal and persistence traits of plants with different stages of succession in central European man-made habitats. – Folia Geobotanica 46: 289–302.

Laughlin D. C. (2013) The intrinsic dimensionality of plant traits and its relevance to community assembly. – Journal of Ecology 102: 186–193.

Laughlin D. C. (2023) Plant strategies. – Oxford University Press, New York.

Levin D. A. (1972) Competition for pollinator service: a stimulus for the evolution of autogamy. – Evolution 26: 668–674.

Levin S. A. (1992) The problem of pattern and scale in ecology. – Ecology 73: 1943–1967.

Li T., Yang H., Yang X., Guo Z., Fu D., Liu C., Li S., Pan Y., Zhao Y., Xu F., Gao Y. & Duan C. (2022) Community assembly during vegetation succession after metal mining is driven by multiple processes with temporal variation. – Ecology and Evolution 12: e8882

Luchman J. (2023) domir: Tools to support relative importance analysis. R package version 1.1.1. – URL: https://CRAN.R-project.org/package=domir.

McGill B., Enquist B., Weiher E. & Westoby M. (2006) Rebuilding community ecology from functional traits. – Trends in Ecology & Evolution 21: 178–185.

Meiners S. J., Cadotte M. W., Fridley J. D., Pickett S. T. A. & Walker L. R. (2015) Is successional research nearing its climax? New approaches for understanding dynamic communities. – Functional Ecology 29: 154–164.

Mudrák O., Jongepierová I., Řehounková K. & Prach K. (2023) Large-scale restoration of species-rich dry grasslands on arable land: environmental filtering drives successful species establishment over a period of 10 years. – Journal of Applied Ecology 60: 1893–1903.

Mudrák O., Řehounková K., Vítovcová K., Tichý L. & Prach K. (2021) Ability of plant species to colonise human-disturbed habitats: role of phylogeny and functional traits. – Applied Vegetation Science 24: e12528.

Murray K. & Conner M. M. (2009) Methods to quantify variable importance: implications for the analysis of noisy ecological data. – Ecology 90: 348–355.

Navas M.-L., Roumet C., Bellmann A., Laurent G. & Garnier E. (2010) Suites of plant traits in species from different stages of a Mediterranean secondary succession: plant traits and succession. – Plant Biology 12: 183–196.

Ottaviani G., Molina-Venegas R., Charles-Dominique T., Chelli S., Campetella G., Canullo R. & Klimešová J. (2020) The neglected belowground dimension of plant dominance. – Trends in Ecology & Evolution 35: 763–766.

Parrish J. A. D. & Bazzaz F. A. (1979) Difference in pollination niche relationships in early and late successional plant communities. – Ecology 60: 597–610.

Penado A., Rebelo H., Goulson D., Wood T. J., Porto M., Rotheray E. L. & Beja P. (2022) From pastures to forests: changes in Mediterranean wild bee communities after rural land abandonment. – Insect Conservation and Diversity 15: 325–336.

Pickett S. T., Cadenasso M. L. & Meiners S. J. (2013) Vegetation dynamics. – In: van der Maarel E. & Franklin J. (eds), Vegetation ecology, Ed. 2, p. 107–140, John Wiley & Sons, Chichester.

Prach K., Lepš J. & Rejmánek M. (2007) Old field succession in Central Europe: local and regional patterns. – In: Cramer V. A. & Hobbs R. J. (eds), Old fields: dynamics and restoration of abandoned farmland, p. 180–201, Island Press, Washington DC.

Prach K., Pyšek P. & Šmilauer P. (1993) On the rate of succession. – Oikos 66: 343–346.

Prach K., Pyšek P. & Šmilauer P. (1997) Changes in species traits during succession: a search for pattern. – Oikos 79: 201–205.

Prach K., Řehounková K., Lencová K., Jírová A., Konvalinková P., Mudrák O., Študent V., Vaněček Z., Tichý L., Petřík P., Šmilauer P. & Pyšek P. (2014) Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres. – Applied Vegetation Science 17: 193–200.

Prach K., Tichý L., Vítovcová K. & Řehounková K. (2017) Participation of the Czech flora in succession at disturbed sites. – Preslia 89: 87–100.

Prach K. & Walker L. R. (2020) Comparative plant succession among terrestrial biomes of the world. – Cambridge University Press, Cambridge.

Pulsford S. A., Lindenmayer D. B. & Driscoll D. A. (2016) A succession of theories: purging redundancy from disturbance theory. – Biological Reviews 91: 148–167.

R Core Team (2023) R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna. URL: https://www.R-project.org.

Raevel V., Violle C. & Munoz F. (2012) Mechanisms of ecological succession: insights from plant functional strategies. – Oikos 121: 1761–1770.

Rees M. & Venable L. (2007) Why do big plants make big seeds? – Journal of Ecology 95: 926–936.

Sammul M., Kull K., Niitla T. & Möls T. (2004) A comparison of plant communities on the basis of their clonal growth patterns. – Evolutionary Ecology 18: 443–467.

Santos T. (2018) PVR: Phylogenetic eigenvectors regression and phylogenetic signal-representation curve. R package version 0.3. – URL: https://CRAN.R-project.org/package=PVR.

Shipley B., Vile D. & Garnier É. (2006) From plant traits to plant communities: a statistical mechanistic approach to biodiversity. – Science 314: 812–814.

Southwood T. R. E., Brown V. K. & Reader P. M. (1979) The relationships of plant and insect diversities in succession. – Biological Journal of the Linnean Society 12: 327–348.

Staude I. R., Weigelt A. & Wirth C. (2023) Biodiversity change in light of succession theory. – Oikos 2023: e09883

Steffan-Dewenter I. & Tscharntke T. (2001) Succession of bee communities on fallows. – Ecography 24: 83–93.

Stekhoven D. J. & Bühlmann P. (2011) Missforest: non-parametric missing value imputation for mixed-type data. – Bioinformatics 28: 112–118.

Szabó R. & Prach K. (2009) Old-field succession related to soil nitrogen and moisture, and the importance of plant species traits. – Community Ecology 10: 65–73.

Tansley A. G. (1935) The use and abuse of vegetational concepts and terms. – Ecology 16: 284–307.

Thrall P. H., Hochberg M. E., Burdon J. J. & Bever J. D. (2007) Coevolution of symbiotic mutualists and parasites in a community context. – Trends in Ecology & Evolution 22: 120–126.

Tilman D. (1985) The resource-ratio hypothesis of plant succession. – The American Naturalist 125: 827–852.

Towers I. R., Vesk P. A., Wenk E. H., Gallagher R. V., Windecker S. M., Wright I. J. & Falster D. S. (2023) Revisiting the role of mean annual precipitation in shaping functional trait distributions at a continental scale. – New Phytologist 241: 1900–1909.

van Andel J., Bakker J. P. & Grootjans A. P. (1993) Mechanisms of vegetation succession: a review of concepts and perspectives. – Acta Botanica Neerlandica 42: 413–433.

van der Sande M. T., Powers J. S., Kuyper T. W., Norden N., Salgado-Negret B., De Almeida J. S., Bongers F., Delgado D., Dent D. H., Derroire G., Espírito-Santo M. M., Dupuy J. M., Fernandes G. W., Finegan B., Gavito M. E., Hernández-Stefanoni J. L., Jakovac C. C., Jones I. L., Veloso M. D. M., Meave J. A., Mora F., Munoz R., Pérez-Cárdenas N., Piotto D., Álvarez-Dávila E., Caceres-Siani Y., Dalban-Pilon C., Dourdain A., Du D. V., García Villalobos D., Ferreira Nunes Y. R., Sanchez-Azofeifa A. & Poorter L. (2022) Soil resistance and recovery during neotropical forest succession. – Philosophical Transactions of the Royal Society B 378: 20210074.

Vile D., Shipley B. & Garnier E. (2006) A structural equation model to integrate changes in functional strategies during old-field succession. – Ecology 87: 504–517.

Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I. & Garnier E. (2007) Let the concept of trait be functional! – Oikos 116: 882–892.

Vítovcová K., Tichý L., Řehounková K. & Prach K. (2021) Which landscape and abiotic site factors influence vegetation succession across seres at a country scale? – Journal of Vegetation Science 32: e12950.

Weaver J. E. (1954) A seventeen-year study of plant succession in prairie. – American Journal of Botany 41: 31–38.

Weaver J. E. & Bruner W. E. (1945) A seven-year quantitative study of succession in grassland. – Ecological Monographs 15: 297–319.

Whittaker R. H. (1953) A consideration of climax theory: the climax as a population and pattern. – Ecological Monographs 23: 41–78.

Wilson J. B., Agnew A. D. Q. & Roxburgh S. H. (2019) The nature of plant communities. – Cambridge University Press, Cambridge.

Wright I. J., Reich P. B., Westoby M., Ackerly D. D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J. H. C., Diemer M., Flexas J., Garnier E., Groom P. K., Gulias J., Hikosaka K., Lamont B. B., Lee T., Lee W., Lusk C., Midgley J. J., Navas M.-L., Niinemets U., Oleksyn J., Osada N., Poorter H., Poot P., Prior L., Pyankov V. I., Roumet C., Thomas S. C., Tjoelker M. G., Veneklaas E. J. & Villar R. (2004) The worldwide leaf economics spectrum. – Nature 428: 821–827.

Wright J. P. & Fridley J. D. (2010) Biogeographic synthesis of secondary succession rates in Eastern North America. – Journal of Biogeography 37: 1584–1596.

Yates L. A., Aandahl Z., Richards S. A. & Brook B. W. (2023) Cross validation for model selection: a review with examples from ecology. – Ecological Monographs 93: e1557.

Vliv druhových vlastností a environmentálních faktorů na sukcesní optima středoevropských druhů

Současná dostupnost dat a jejich syntéza ve střední Evropě vedly k vytvoření komplexních indexů popisujících pozici druhů v sukcesních řadách. Zejména proměnná „sukcesní optimum“ (SO), vyvinutá pro vegetaci České republiky, odráží počet let po disturbanci, které druh potřebuje k dosažení vrcholu své abundance. V kombinaci s údaji o různorodých funkčních vlastnostech druhů a ellenbergovských indikačních hodnotách, určujícími podmínky prostředí, se snažíme identifikovat hlavní soubor rostlinných vlastností a klíčových environmentálních faktorů, které odpovídají SO druhu. V této studii jsme použili lineární modely s regularizačními technikami a metodami robustního odhadu k nalezení nejrelevantnějších rostlinných vlastností, které vysvětlují hodnotu SO, a následně jsme provedli rozklad vysvětlené variance, abychom posoudili relativní vysvětlovací sílu jednotlivých vlastností. Současně jsme porovnávali vliv ellenbergovských indikačních hodnot před odstraněním trendu SO závislého na vlastnostech rostlin a po něm. Zjistili jsme, že pět vlastností mělo největší a nejkonzistentnější vliv: terofytní životní forma, hmotnost semen, délka kvetení, velikost obnovovací banky pupenů a obsah sušiny v listech, a to napříč různorodým spektrem dalších znaků s menším významem. Hlavními ellenbergovskými indikačními hodnotami, které predikovaly SO, byly vlhkost a reakce půdy, zatímco světlo a nároky na živiny byly samy o sobě spojeny s funkčními vlastnostmi. Vliv vlastností byl obecně konzistentní a univerzální napříč různými podmínkami prostředí, protože interakce mezi vlastnostmi a prostředím neměnila výsledky ani nevedla k lepším modelům. Tímto jsme průkazně definovali strategii, která spojuje druhy s jejich sukcesním uspořádáním, a zdůraznili jsme význam životních forem, konkurenčních schopností a reprodukčních strategií v kontextu sukcesních procesů.

How to cite: Velasco Monés G., Padullés Cubino J. & Lososová Z. (2025) Disentangling the effects of traits and environmental factors on species’ successional optima: a study from central Europe. – Preslia 97: 241–260.

Preslia, a journal of the Czech Botanical Society

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