



Are ecological niche optimum and width of forest plant species related to their functional traits?

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ABSTRACT

The ecological niche is one of the central concepts in plant ecology. Understanding which biological traits influence plant niches remains limited, preventing large-scale generalizations. Using a representative pool of 94 herb-layer species frequently occurring in the Slovenian forest vegetation types and an extensive suite of 28 plant functional traits, we tested whether traits serve as predictors for the optimum and width of plant species ecological niche. Niche optimum (mean) and niche width (standard deviation) of each species were derived from community-level ecological indicator values for six environmental gradients, i.e., light, temperature, continentality, moisture, soil reaction and nutrients. We investigated relationships between niche parameters and functional traits through a random forest analysis to account for relatively high trait correlations. Our results suggest that niche optimum and width of forest plant species are related to their functional traits. The two niche parameters were best explained by similar set of traits; however, the relative importance of traits differed substantially. Traits associated with disturbances (frequency and severity), plant dispersal (seed mass, dispersal syndrome), leaf economics spectrum (specific leaf area) and life strategy (CSR scores) showed the highest overall significance in predicting niche optimum and width. Functional traits were, on average, better predictors for niche optimum (average variance explained across all six environmental factors: 20.2%) than for niche width (average variance explained: 7.7%). Intraspecific trait variability, not considered in this study, likely plays an important role in case of niche width. The analyses suggest that, while not all traits impact niche parameters to the same degree, it is crucial to consider traits representing different ecological dimensions and revealing leading patterns of trait coordination. We recommend that the relative importance of traits for species niche parameters should be tested on a larger spatial scale using broader pool of forest understory plants across Europe.

1. Introduction

The species niche represents a fundamental ecological concept and has been central to community ecology and biogeography. Historical development of ecological niche theory produced the following summarizing formulation: ecological niche subsumes all of the interactions between a species and its abiotic and biotic environment (Chase and Leibold, 2003). First definitions of the ecological niche of species focused on their habitat requirements and accompanying behavioural adaptations (Grinnell, 1917). Elton (1927) understood the species niche as an ecological function of a species within a community, which introduced the idea that species both respond to and affect on their environment (Chase and Leibold, 2003; Polechová and Storch, 2019). All these perspectives tried to simplify the complexity of numerous

factors influencing species performance. One of the most well-known and broadly acceptable approaches to the definition of species ecological niche was that of Hutchinson (1957). Hutchinson proposed that a fundamental niche is a multi-dimensional hypervolume, constrained with many axes that correspond to all possible requirements of the species (e.g., temperature and nutrient supplies). Each dimension in the ecological space represents an environmental condition (of abiotic or biotic nature) or resource that is potentially relevant to the existence of the species. Hutchinson (1957) perceived niches as dynamic systems where the presence of one species inhibits the presence of another due to interspecific competition, leading to realized niche being a subset of fundamental niche. This perspective combines the ecological requirements of a species with its functional role in the local community. The niche concept is often used as a basis for modeling species

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distribution and understanding the shifts of species ranges under environmental change (Treurnicht et al., 2020).

The ecological niche can be described by many parameters but two of its main entities that explain species distribution and abundance have been regularly studied, i.e., niche optimum and niche width (Hutchinson, 1957). The niche optimum or ecological position of a species can be defined as a point along an environmental gradient where the species reaches its global maximum in population growth rate and / or abundance (Treurnicht et al., 2020) and denotes the central tendency of the distribution of a species even in the case of skewed or bimodal ecological niches (Dengler et al., 2023). In this case given environmental conditions largely coincide with species ecological requirements. For example, a plant species with higher light requirements is unlikely to survive in dense forest understory environment with limited light availability at the forest floor (Ottaviani et al., 2019). Such conditions are more favourable for shade-tolerant species. Species are simultaneously constrained by multiple environmental resources; therefore, the niche optimum reflects the combination of conditions under which growth is maximized. On the other hand, niche width or species ecological amplitude (Ter Braak and Gremmen, 1987) describes the range of environmental conditions in which species can thrive and maintain self-sustaining populations (Wasof et al., 2013; Treurnicht et al., 2020). Niche widths are the limits of environmental conditions within which an organism can live and function. Generalists typically exhibit greater niche width than specialist species with a narrow ecological niche. However, the degree of specialization depends on the environmental variable or resource examined. Certain plant species may tolerate a broad range of conditions related to some resources while being highly specialized for other resources. Species with narrow ecological niche are often good indicators of local light, microclimate or soil conditions but may not have the capacity to adapt to anthropogenically induced changing environmental conditions.

Functional traits are measurable physiological and morphological features of an organism that drive fundamental processes of growth, reproduction and survival (McGill et al., 2006; Violle et al., 2007; Kattge et al., 2011; Díaz et al., 2016). These characteristics vary between and within species and act directly as surrogates for the adaptive strategies of plant species under varying living conditions. Plant functional traits allow us to link processes observed in plant individuals to plant population dynamics, species distribution patterns and their coexistence, community assembly rules and ecosystem functioning (Masarovičová et al., 2016; Heilmeier, 2019). Linking plant functional traits to the species ecological niche has become an important aspect in ecology, evolution and biodiversity research as this approach yields important insights into the mechanisms shaping functional biodiversity (Treurnicht et al., 2020). Trait-based studies of species' ecological niches have fundamental and applied importance in ecology (Violle and Jiang, 2009; Schellenberger Costa et al., 2018). Ecological performance of a plant species depends on the simultaneous and coordinated response of multiple functional traits to environmental factors (Masarovičová et al., 2016). Recent advances in the scientific literature reporting trait–environment associations in plant species and communities on a global scale (e.g., Díaz et al., 2016; Bruelheide et al., 2018) have triggered research efforts to quantify trait–niche relationships for specific habitat types (e.g., forest understory vegetation) and to test whether predicted large-scale patterns correspond at more local to regional levels (Kermavnar et al., 2022a). Barring a few exceptions (e.g., Marinšek et al., 2015), studies that integrate plant traits as predictors for niche width are still underrepresented for forest understory species. To this end, functional characterization of plant niche widths will likely be complementary to the recognized links between traits and niche optima, with a potential to provide insights into the responses of functional diversity to ongoing climate-driven range shifts.

Theoretical predictions with supporting evidence from empirical studies suggested that in temperate forests various plant traits are responsible for species establishment and success in different ecological

conditions. Functional traits are shaping the species niche parameters through trait–environment relationship. However, the roles of different traits vary greatly between environmental dimensions. Some traits were shown to be more linked to aboveground resources (light, microclimate) whereas others tend to be decisive in relation to belowground resources (soil properties). One might expect that aboveground resources are key determinants for aboveground traits (e.g., leaf traits, plant height) but this is not always the case. For instance, Chelli et al. (2019) demonstrated that temperature extremes and seasonality are the main drivers of clonal and bud bank traits in Italian forest understories. Trait patterns along environmental gradients can be modified by factors operating at local scale such as management disturbances. While much attention has been given to trait–environment relationship (shifts in mean trait values caused by cross-site environmental variation), an important knowledge gap is how niche widths of forest understory species depend on their traits. Research questions whether forest plant species occurring at ecologically distinctive forest sites are functionally different (and if so, in what way) from species with narrow ecological niche remain poorly studied. Furthermore, a given species can be specialized for one environmental dimension but at the same time may exhibit greater ecological range on other gradient(s) (Marinšek et al., 2015). Species that are widely distributed across the gradient are assumed to also show greater variation in trait values and phenotypic plasticity, i.e., have larger intraspecific trait variability.

An intuitive expectation would be that ecological specialists are positioned on the conservative side of the resource-use strategy spectrum as they usually inhabit sites with more stressful conditions exerting prominent environmental filtering (e.g., deep shade, low soil pH or nutrient availability). Disturbances are also key factor for forest species distribution patterns because changes in environment induced by disturbances might shift ecological boundaries at which plants can survive. Traits associated with frequent and / or severe disturbance are those typical of the r-end of the r–K continuum, namely small and numerous seeds, high growth rate and short generation time (Grime, 1977; Herben et al., 2018). Seeds from temperate forest understory species vary widely in size and shape (Amantangelo et al., 2014). Better dispersers have the ability to spread their seeds over larger distances and thus higher chance of seedling establishment in favourable sites. As many of forest specialist plants are poor dispersers, these species have developed evolutionary adaptations for local persistence linked to clonal and resprouting capacities, which in turn depend on functional traits (Campetella et al., 2020). Niches are generally wider for competitive species with greater seed dispersal or persistence abilities.

Trait-based approaches to quantify various niche parameters of understory plant species in temperate forests are surprisingly rare, probably because such investigations require a sufficient pool of species occurring in a broad spectrum of forest site conditions. Here, we relate 28 plant traits to the niche optimum and width of 94 plant species frequently present in the herb layer of Slovenian forest vegetation types. The relationships between these two niche parameters were tested for each individual environmental gradient represented by ecological indicator values (EIVs) for light, temperature, continentality, moisture, soil reaction and nutrients. All these gradients represent primary resources for plant growth and therefore function as ecologically meaningful determinants of species occurrence patterns in different forest types. By using multiple EIVs we accounted for the multidimensional nature of the ecological niche. Special focus was placed on the relative importance of plant traits in explaining the niche optimum and niche width for different environmental variables.

Average trait expression might change predictably along environmental gradients (Violle et al., 2007) but relationships are not necessarily universal as some traits are highly context dependent. Nevertheless, life-history traits should prove as reliable predictors of species' ecological niches. We hypothesized that traits would generally show stronger associations with niche optima compared to niche widths along environmental gradients because mean traits reflect niche

optimum manifested in trait–environment relationship whereas intra-specific trait variability resulting from phenotypic plasticity or adaptive trait differentiation between populations may be well suited to capture niche width (Violle and Jiang, 2009). We expected that the relative importance of traits would differ between environmental dimensions and between niche parameters. Building upon the established theoretical frameworks and evidence from past studies in temperate forest understories of Europe (e.g., Chelli et al., 2019; Cubino et al., 2021) and North America (e.g., Amatangelo et al., 2014; Rolhauser et al., 2021), we anticipated i) niche optimum of selected forest species relate to plant traits previously identified as important for resource acquisition, retention and use (foliar traits), competitive ability (plant height), reproduction (seed dispersal), local space occupancy and on-spot persistence (clonal traits) and ability to show adaptability to disturbances and recover after disturbance events (bud-bank traits). Furthermore, based on previous findings regarding the disentanglement of different trait–specialization relationships (Marinšek et al., 2015), we also hypothesized that ii) species with wider niches tend to be equipped with traits allowing greater tolerance of abiotic stress, thereby shrinking their degree of ecological specialism. Traits related to plant responses to disturbance frequency / intensity or gradient of stand maturity (Ottaviani et al., 2019; Chelli et al., 2022), were expected to show higher relative importance for niche widths. For example, shade tolerant forest specialists with high affinity to mature and less disturbed stands are thus presumed to exhibit functional profile reflecting trait adaptations to specific and harsh (lack of light) but relatively stable environment (e.g., high specific leaf area, dependence on clonal spread, low dispersal capacity). Conversely, more exploitative strategies that may foster competitive ability for resource acquisition and functional traits suggesting greater dispersal in space and time are thought to extend the potential for occurrence of species along environmental gradients.

2. Materials and methods

2.1. Study dataset construction

Slovenia exhibits a great diversity of forest plant communities covering most of the temperate forest biome in Central and South-Eastern Europe. Due to the large elevational and phytogeographical differentiation, the main forest vegetation types range from oak-hornbeam forests in the lowlands, through beech forests at the intermediate elevations and spruce forests in the mountains. Mountainous and subalpine spruce and mountainous mixed spruce-silver fir forests are of natural origin. On the other end of environmental gradient, forests influenced by Sub-Mediterranean climate importantly add to the broad spectrum of forest vegetation types as well. In some cases, several variants (mostly caused by differences in geology and edaphic conditions) of the same forest vegetation type occur in different phytogeographic regions (Alpine, Pre-alpine, Dinaric, Pre-dinaric, Sub-Mediterranean, Sub-Pannonian).

As a main data source for the selection of forest plant species, we used the recently published monograph describing 78 forest vegetation types in Slovenia (Bončina et al., 2021; hereafter GRTS). A forest vegetation type is here understood as the phytosociological unit within accepted syntaxonomic system, with defined characteristics related to abiotic factors, floristic composition and forest stand structure. This classification largely follows the typology of Slovenian forests according to ecological and vegetation conditions for the purpose of forest management (Kutnar et al., 2012). The two main criteria for this hierarchical classification are geological conditions (carbonate, mixed and silicate bedrock) and vegetation (elevational) belts (lowland forests, colinar-submontane forests, submontane-montane forests, montane-altimontane forests, altimontane-subalpine forests). Five most widespread forest vegetation types in Slovenia are beech-dominated forest associations: *Castaneo-Fagetum sylvaticae*, *Omphalodo-Fagetum*, *Blechno-Fagetum*, *Hacquetio-Fagetum* and *Luzulo-Fagetum sylvaticae*. For

74 forest types, the GRTS work provides a complete list of vascular plant species present in the different vegetation layers, ordered according to their frequency of occurrence. Overall, the vegetation data are based on more than 7500 phytosociological relevés.

In this study, we extracted information from GRTS on herb layer vegetation. From a total pool of almost 600 vascular plant species, we selected species that occur in at least 10 different forest types. We chose a minimum of 10 occurrences as an optimal threshold for having sufficient data per species for estimates of niche parameters and retaining as many species as possible in the analysis. Trees, shrubs and woody lianas were excluded. This resulted in a total of 94 plant species (listed in Appendix A), including forbs, ferns, graminoids and dwarf shrubs. Nomenclature follows the Slovenian National Flora (Martincič et al., 2007).

For each forest vegetation type, a list of plant species is provided, and species are ranked from most common (frequency = 5) to rare species (frequency = 1). These lists thus represent aggregated data derived from numerous phytosociological relevés (Bončina et al., 2021). We first created a species × forest vegetation types matrix and then used presence–absence data to calculate unweighted community-level means for Ellenberg indicator values (Ellenberg et al., 1992; EIVs) for the environmental variables light (L), temperature (T), continentality (K), soil moisture (F), soil reaction (R) and soil nutrients (N). This produced a single EIV for each forest vegetation type and each environmental dimension. These community-level values were then used for the calculation of niche optima and niche widths of selected plant species.

The applicability and usefulness of using EIVs outside their area of origin have been demonstrated by several studies reporting an accurate correlation between mean EIVs and corresponding measurements of environmental variables in the field (Schaffers and Sýkora, 2000; Diekmann, 2003; Wasof et al., 2013; Dengler et al., 2023). Selected environmental factors capture the main resources necessary to enable species to exist and are thus considered as major plant niche dimensions (Dengler et al., 2023) and determinants of plant species and trait diversity and composition in temperate forests (Kermavnar et al., 2021a, 2022b). By using multiple EIVs we accounted for the multidimensionality of the ecological niche. Each variable is defined on an ordinal scale (ranging from 1 to 9, except for moisture which runs from 1 to 12) and expresses species' ecological preferences. Values for light conditions reflect the average amount of light radiation received by forest site. Species with higher L values are most often found on sites with greater light availability, species with lower values, however, most often thrive in shadier conditions and under closed forest stands. The temperature value indicates the average air temperature during the growing season and for the most part matches the elevational gradient. A lower T value means cooler conditions, typical for higher elevations, and a higher value warmer conditions typically found at lower elevations. Values for continentality describe the degree of continentality of the climate, which is determined by e.g., strength of the solar radiation, winter temperatures and air humidity. Values for continentality are higher in sites with less air humidity and large temperature differences (daily and seasonal), in sites with cold winters and long frost periods. Lower K values are characteristic for sites with more humid air, smaller temperature oscillations, i.e., where the climate is more oceanic and the winters are milder. Values for soil moisture indicate the average soil moisture during the growing season in forest sites where the species occurs most often. Small F values indicate drier sites, and larger values indicate wetter soils. The values for the chemical reaction of the soil indicate the content of free hydrogen ions in the soil. Small R values mean sites with acidic soils, and large values with base-rich soils. Soil nutrient values indicate the amount of nutrients, mainly nitrogen and sometimes phosphorus, in the soil. Small N values mean nutrient-poor soil, and large values suggest that soils are rich in nutrients (Ellenberg et al., 1992; Bončina et al., 2021).

For each species, we calculated its niche optimum and niche width. The niche optimum (representing the global maximum density) for a

given environmental factor was calculated as a weighted average of all forest vegetation types in which a species was present. Species frequency was used as a weighting factor in this calculation. The niche width for a given environmental factor was calculated as the standard deviation of all forest vegetation types where species occurred. For detailed information, please see the schematic display with examples of niche parameter computations in the Supplementary materials (Appendix B).

A total of 28 functional traits related to plant habitus, growth form, life strategy, leaf economics, flowering phenology, seed and dispersal characteristics, belowground organs and clonality, bud bank features (size and depth) and response to disturbance severity and frequency were sourced. An overview of all selected plant traits is given in Table 1. The selected traits are well-known to respond to changing environments. Many traits were sourced from the Pladias online platform (Chytrý et al., 2021), which also integrates data from different databases (e.g., BioFlor, CLO-PLA and others). Species-level values for plant height, seed mass, specific leaf area and leaf dry matter content were primarily taken from the LEDA database (Kleyer et al., 2008), while data for plant life form and flowering phenology were used from the Slovenian National Flora (Martinčič et al., 2007). Detailed information on trait definitions, data completeness and sources are provided in Appendix C.

2.2. Data analysis

All statistical analyses and graphic visualisations were performed in R version 4.1.1 (R Core Team, 2021). To study the importance of traits in explaining the niche optima and niche widths, we used random forest algorithm for regression. This nonlinear, nonparametric machine learning technique can be used to calculate the importance of explanatory variables (Breiman, 2001). Random forest analysis is usually implemented with large datasets, but it can work well on data with rather limited number of observations (94 in our case). It has a major advantage over linear regression methods that even strongly inter-correlated variables (in our case functional traits) can be analysed together and it does not hold formal distributional assumptions of the data. By combining bagging (randomly drawing a subset of samples, i.e., species) and random feature subsets (randomly using a subset of features, i.e., traits), a large ensemble of uncorrelated decision trees is created.

For this statistical analysis, we used the R package *randomForest* (Liaw and Wiener, 2022). We used the default of 500 trees (argument “ntree”) as error rate stabilized at 100–150 trees. A random one-third of predictor variables were used to perform data partitioning at each node (argument “mtry”). Seventy-five percent of the overall dataset was randomly selected and used to build the Random Forests model, and the other 25% retained for testing the model. The importance of each explanatory variable averaged over all trees was obtained and described as the change in prediction accuracy, i.e., an increase in the mean squared error (%IncMSE, function “importance”) computed by permuting (value randomly shuffled) the variable with out-of-bag data in the Random Forests validation approach. High values of %IncMSE indicate more important variables in the random forests model whereas negative %IncMSE suggests that a variable does not play a role in the prediction.

Random forest analysis was used to examine how strong traits are related to niche optima and widths of the plant species. We then additionally tested the direction of associations between niche parameters and plant traits, separately for each trait. These tests were performed only for traits with %IncMSE > 0 derived from the random forest analysis because negative %IncMSE values suggest that a variable is insignificant in prediction process. For categorical traits, we used nonparametric Kruskal-Wallis rank sum test with Bonferroni correction for multiple comparisons in the R package *agricolae* (de Mandiburu, 2021). Rank correlations (Spearman’s rho coefficients) were calculated for numerical and semi-quantitative traits.

Table 1

A list of plant functional traits used in this study. For categorical traits, categories are reported whereas for numerical and semi-quantitative variables, basic descriptive statistics (average, minimum, maximum) across selected species ($n = 94$) are provided.

Trait	Variable type	Description
Height (m)	Numerical	Values: avg = 0.47, min = 0.08, max = 2.25
Growth form	Categorical	Categories (4): clonal herb, polycarpic perennial non-clonal herb, annual herb, dwarf shrub
Life form	Categorical	Categories (4): hemicryptophyte, geophyte, chamaephyte, therophyte
Life strategy	Categorical	Categories (5): CSR, CS, C, S, CR
C-score (%)	Numerical	Values: avg = 36.2, min = 0.0, max = 85.8
S-score (%)	Numerical	Values: avg = 23.8, min = 0.0, max = 98.0
R-score (%)	Numerical	Values: avg = 40.1, min = 0.0, max = 79.8
Leaf lifespan	Categorical	Categories (4): summer green, spring green, overwintering green, evergreen
Leaf anatomy	Categorical	Categories (5): hygromorphic, mesomorphic/hygromorphic, mesomorphic, scleromorphic/mesomorphic, scleromorphic
Specific leaf area (mm ² /mg) – SLA	Numerical	Values: avg = 29.8, min = 7.7, max = 66.9
Leaf dry matter content (mg/g) – LDMC	Numerical	Values: avg = 226.7, min = 102.9, max = 388.0
Flowering start (month)	Categorical	Categories (8): January, March, April, May, June, July, August, September
Flowering end (month)	Categorical	Categories (8): March, April, May, June, July, August, September, October
Flowering duration (months)	Ordinal	Values ranging from 1 to 6
Pollination	Categorical	Categories (5): insects, insects and/or other mode (geitonogamy/selfing/ cleistogamy), wind, wind and/or other mode (insect/selfing), selfing
Reproduction type	Categorical	Categories (4): by seed/spores, by seed/spores and vegetatively, mostly by seed/spores and rarely vegetatively, mostly vegetatively and rarely by seed/spores
Dispersal strategy	Categorical	Categories (5): mainly anemochory, mainly anemochory and autochory, mainly autochory, mainly autochory and endozoochory, mainly autochory and epizoochory
Dispersal unit	Categorical	Categories (4): seed, seed/fruit/ infructescence or its part, fruit/ infructescence or its part, spore
Seed mass (mg)	Numerical	Values: avg = 6.3, min = 0.001, max = 133.8
Storage organ	Categorical	Categories (3): rhizome, stolon, other (pleiocorm, bulb, primary storage root)
Clonal growth organ (CGO) type	Categorical	Categories (5): epigeogenous rhizome, hypogeogenous rhizome, stolon, bulb, belowground stem tuber
Clonal growth organ (CGO) persistence (year)	Semi-quantitative	Values: avg = 3.6, min = 1.2, max = 4.0
Lateral spread (m)	Semi-quantitative	Values: avg = 0.08, min = 0.01, max = 0.40
Clonal index	Ordinal	Values from 2 to 6
Bud bank size	Numerical	Values: avg = 18.9, min = 0.0, max = 40.0
Bud bank depth (cm)	Numerical	Values: avg = 4.4, min = 0.0, max = 36.0
Indicator value for disturbance frequency	Numerical	Values: avg = -1.84, min = -1.99, max = -1.20
Indicator value for disturbance severity	Numerical	Values: avg = 0.25, min = 0.14, max = 0.42

3. Results

3.1. Relative importance of plant traits

The niche optimum for light was best explained by disturbance frequency (14.3 %IncMSE). Important variables were also SLA, disturbance severity, R-score, clonal index, flowering start and flowering duration, all with %IncMSE above 2.5 (Fig. 1). In the case of temperature optimum, the most significant traits were seed mass, life form, C-score, dispersal strategy and SLA. These variables showed %IncMSE higher than 5. Disturbance frequency, LDMC and plant height were found to be the best predictors for the continentality niche optimum. However, their %IncMSE was less than 5. The niche optimum for moisture was best explained by seed mass (13.8 %IncMSE), followed by flowering start and dispersal strategy (both with %IncMSE higher than 5). Six different traits had %IncMSE above 5 for the niche optimum related to soil reaction. These were (ranked according to the %IncMSE value): seed mass, SLA, C-score, dispersal strategy, S-score and disturbance severity. Dispersal strategy, S-score, SLA, C-score and bud bank size were recognized as the most valuable explanatory variables for the niche optimum with regards to soil nutrients (Fig. 1).

Overall, studied traits best explained ecological niche optimum for soil reaction (total variation explained: 43.8%). In contrast, the lowest level of predicting power was detected for niche optimum for continentality (total variation explained: 3.1%). In addition to previously mentioned traits, other traits were either less important (lower %IncMSE) or should even be considered as rather unimportant (those with negative %IncMSE values) for predicting the niche optima of forest plant species.

Total variation explained was generally higher for the niche optimum than for the niche width (Fig. 2). Disturbance frequency, disturbance severity, bud bank size and life strategy were the best predictors for species niche width related to light. Niche width for temperature was most strongly associated with bud bank depth and size and S-score. Life strategy, lateral spread, disturbance frequency and dispersal strategy exhibited the strongest connection to continentality niche width. In case of niche width related to moisture, by far the strongest predictor proved to be disturbance frequency. Flowering duration and disturbance severity were also significant for this environmental gradient. Species niche width for soil reaction was best explained by seed mass, dispersal strategy, SLA and disturbance frequency. Traits associated with disturbances were also the most important factors for niche width describing

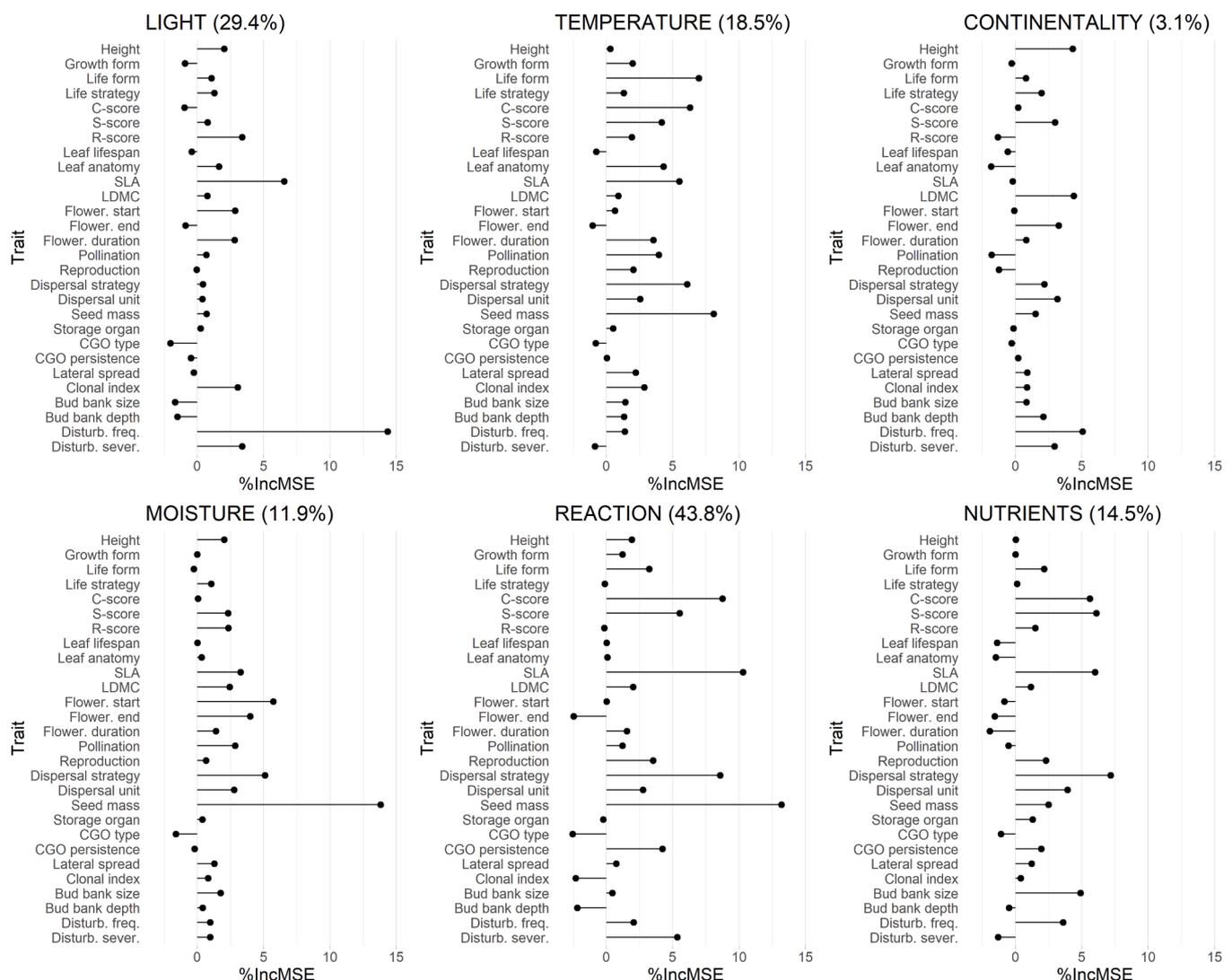


Fig. 1. Results of the random forest analyses showing the importance of functional traits for explaining the species niche optimum, separately for each environmental factor: light, temperature, continentality, soil moisture, soil reaction and soil nutrients. The importance is expressed as percentage increase of the mean standard error (%IncMSE). Negative %IncMSE suggests that a variable does not play a role in the prediction. The percentage in each panel title states the total variation of the dependent variable explained.

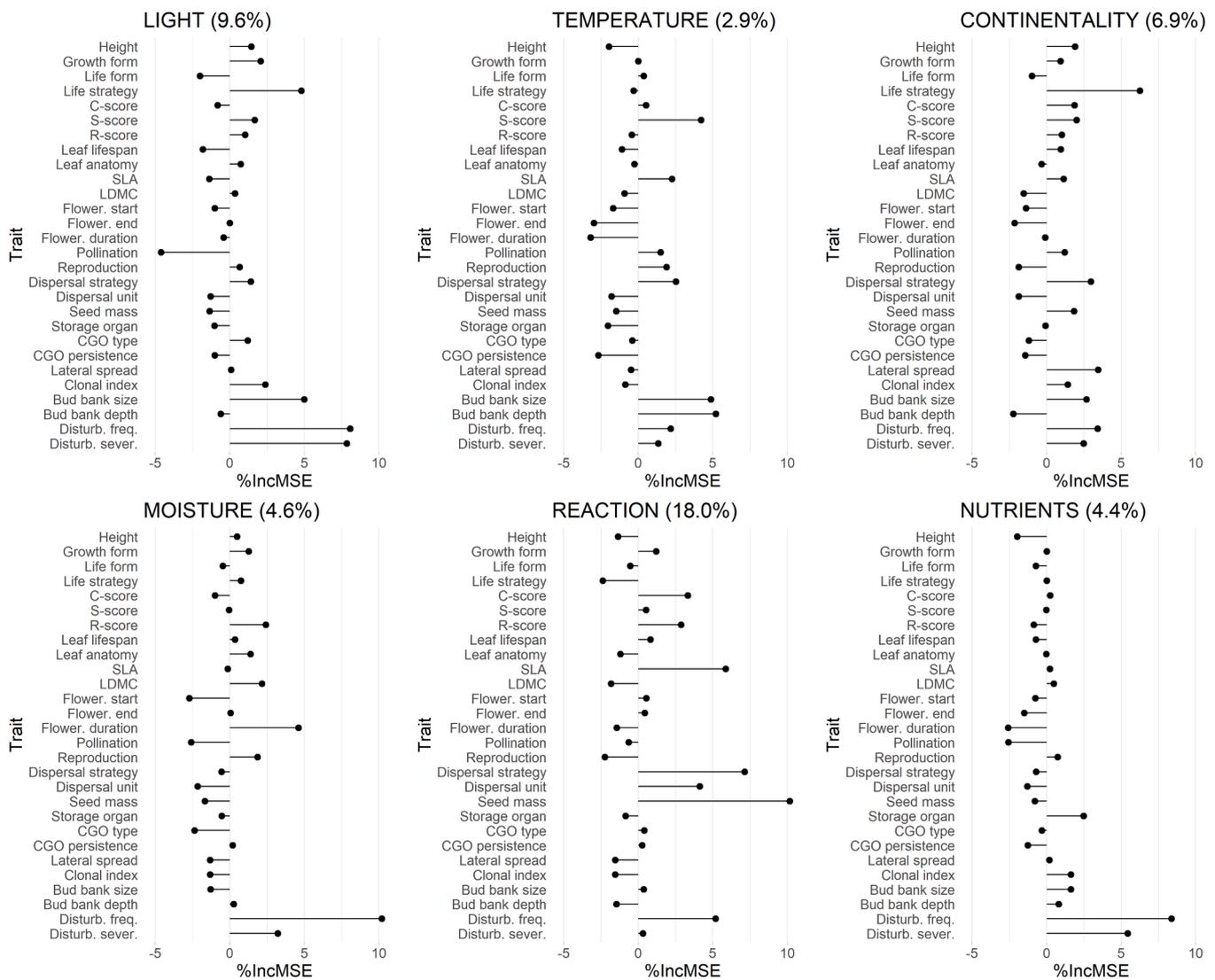


Fig. 2. Results of the random forest analyses showing the importance of functional traits for explaining the species niche width, separately for each environmental factor: light, temperature, continentality, soil moisture, soil reaction and soil nutrients. The importance is expressed as percentage increase of the mean standard error (%IncMSE). Negative %IncMSE suggests that a variable does not play a role in the prediction. The percentage in each panel title states the total variation of the dependent variable explained.

nutrient gradients, for which other traits were found to be largely unimportant, except for some belowground traits, such as type of storage organ, clonal index and bud bank size (Fig. 2).

For each trait, we calculated the average %IncMSE across all six environmental factors (Fig. 3). Taken together, niche optimum was on average most strongly related to seed mass, SLA, dispersal strategy, disturbance frequency, S-score, C-score and dispersal unit. Three out of 28 traits had negative average %IncMSE values, indicating that they were insignificant in explaining ecological niche optima of plant species studied. Both disturbance frequency and severity had the highest average %IncMSE value for niche width, followed by bud bank size, dispersal strategy, life strategy, S-score and SLA. Twelve traits had negative %IncMSE values on average, indicating that their contribution was not significant. When both niche optimum and width were considered together, the following five functional traits were the most significant: disturbance frequency (average %IncMSE: 5.4), seed mass (3.9%), dispersal strategy (3.5%), SLA (3.3%) and disturbance severity (2.6%). In contrast, six traits showed negative %IncMSE values on average: storage organ, persistence of clonal growth organ, pollination mode, leaf lifespan, end of flowering and type of clonal growth organ (Fig. 3).

3.2. Correlations between traits and niche parameters

The niche optimum for light (L_{mean}) was significantly associated with nine different traits (Table 2). We found a positive correlation between L_{mean} and disturbance frequency, LDMC and S-score and a negative correlation with SLA and R-score. Flowering duration correlated positively with L_{mean} , i.e., species that flower longer generally have higher requirements for light. Plants with scleromorphic leaves are also more light-demanding, while stress-tolerators (according to Grime) tend to be more shade tolerant. Chamaephytes exhibited significantly higher L_{mean} values compared to geophytes and therophytes (Table 2; Appendix D).

Species temperature preferences were explained by seed mass (positive correlation), LDMC (negative correlation), C-score and SLA (both with positive correlation). In case of categorical traits, significant differences were found for dispersal strategy, leaf anatomy and pollination mode. Species adapted to warmer climates tend to have autochory dispersal, scleromorphic leaves and self-pollinating form whereas anemochory, mesomorphic leaves and wind-pollination are more common at colder sites. Species affinity for continentality (K_{mean}) showed significant relationships with disturbance severity (negative correlation), disturbance frequency (positive correlation), plant height and C-score

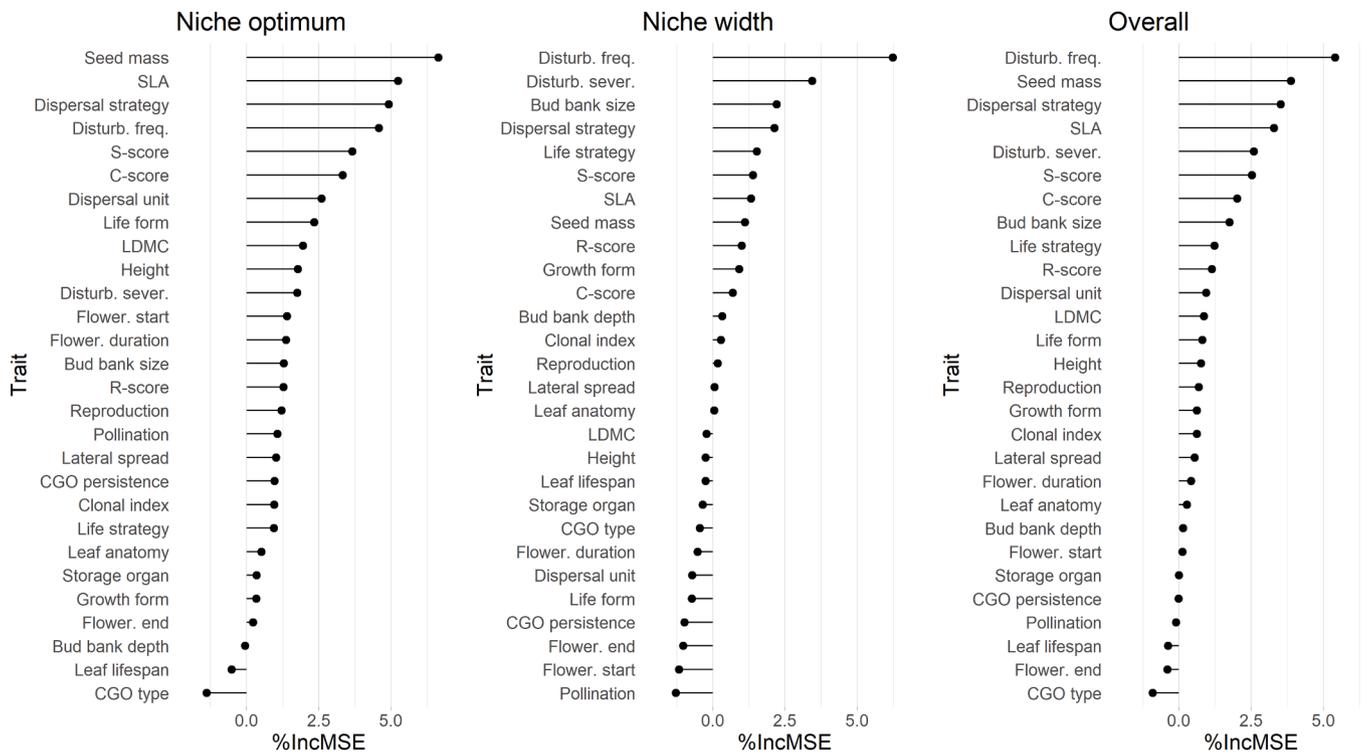


Fig. 3. Ranking of plant functional traits based on average %IncMSE values across all six environmental factors for niche optimum (left), niche width (mid) and both niche parameters together (right).

(both with negative correlation). Chamaephytes were characterized by significantly higher K_{mean} values than geophytes.

Species with higher requirements for soil moisture exhibited higher indicator values for disturbance severity. These species tend to have greater ability for lateral spread, grow taller but have lighter seeds compared to species at drier sites. Plants adapted to lower soil moisture tend to use insects as pollination vector, reproduce mainly by seeds/spores and have scleromorphic leaves. Plant species found in sites with higher soil pH generally have heavier seeds, lower LDMC and S-score and are adapted to lower disturbance severity and frequency. Species from calcareous soils also have higher C-score and SLA values. On the other hand, acidophilous species are mainly anemochorous, disperse with spores and are wind-pollinated. N_{mean} values were found to be positively related to C-score and SLA (e.g., nitrophilous species are stronger competitors) but showed negative correlation with S-score, disturbance frequency, LDMC and persistence of clonal growth organ. Species with higher nutrient requirements tend to be autochorous or epizoochorous. Geophytes tend to be dominant life form at more productive forest sites, while chamaephytes predominate at sites with nutrient-poor soils on silicate bedrock.

We found fewer relationships between plant traits and niche widths (Table 3; Appendix E) compared to species niche optima. Niche width for light (L_{sd}) was most strongly associated with disturbance frequency (positive correlation), R-score (negative correlation), S-score and bud bank size (both with positive correlation). Competitors (according to Grime) can grow in a wider range of light conditions compared to stress-tolerators. Dwarf shrubs exhibited a significantly broader light ecological niche than annual herbs. The same is true for plants with more scleromorphic leaves compared to species with mesomorphic or hygromorphic leaves. There were no significant correlations for T_{sd} values. Niche width for continentality was positively correlated with disturbance frequency and S-score. Forest plant species able to grow on wide gradient of soil moisture are more adapted to disturbance frequency, have longer flowering duration but lower R-score in comparison to species with narrow moisture niche. These species also tend to have

scleromorphic leaves. The niche width for soil reaction (R_{sd}) was positively determined by disturbance frequency and S-score but negatively by SLA, seed mass, C-score and R-score. Species with higher R_{sd} values used anemochory as a dispersal strategy in contrast to autochorous or epizoochorous species, which showed narrower niche for soil reaction. With respect to life forms, dwarf shrubs exhibited a significantly broader soil reaction niche width compared to clonal, annual and non-clonal herbs. Three traits were associated with niche width for soil nutrients (N_{sd}): both disturbance frequency and severity influenced N_{sd} positively. Species with higher SLA had generally narrower niche width for soil nutrients (Table 3; Appendix E).

Density plots depicting ecological niches (optimum and width) of selected plant species are shown in Appendix F. Correlation matrix for both niche parameters and each environmental dimension (used as 12 dependent variables) is given in Appendix G.

4. Discussion

The idea of using plant traits as predictors of species ecological behavior has been present in functional ecology for a long time (Sterck et al., 2011). However, quantified evidence remains sparse. The main added value of this work is the evaluation of functional traits as predictors for both species niche optimum and, in particular, niche width. While correlations between ecological niche optima and traits basically represent trait–environment relationships, the patterns of how species’ ecological range (niche width) is related to plant traits need further investigation. Another advantage of this study is in a broad suite of plant functional traits which were used as predictors for species ecological niche optimum and niche width along multiple environmental gradients. We demonstrated that niche optimum and width of forest plant species were related to interspecific variation in functional traits. Both niche parameters were best explained by a similar suite of traits, but their relative importance varied markedly and varied depending on the niche parameter and environmental factor in question.

Table 2

Relationship between functional traits and species niche optimum for light (L_{mean}), temperature (T_{mean}), continentality (K_{mean}), soil moisture (F_{mean}), soil reaction (R_{mean}) and soil nutrients (N_{mean}). Results are from the Kruskal-Wallis test for categorical traits and the Spearman rank correlations for numerical traits. In the case of categorical traits, p-values are reported. In the case of numerical traits, correlation coefficients are given in italics. Significant results at alpha = 0.05 are in bold (significance levels: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Sign “/” means that the relationship was not tested due to a negative % IncMSE value (see Fig. 1).

Trait	L_{mean}	T_{mean}	K_{mean}	F_{mean}	R_{mean}	N_{mean}
Plant height	<i>0.05</i>	<i>0.05</i>	<i>-0.25</i> *	<i>0.21</i> *	<i>-0.10</i>	<i>0.11</i>
Growth form	/	0.14	/	/	0.54	/
Life form	0.04	0.08	0.04	/	0.29	0.05
Life strategy	0.005	0.46	0.73	0.71	/	0.18
C-score	/	0.22 *	<i>-0.25</i> *	<i>0.12</i>	0.22 *	0.36 ***
S-score	0.33 **	<i>-0.19</i>	<i>0.13</i>	<i>-0.11</i>	<i>-0.21</i> *	<i>-0.32</i> **
R-score	<i>-0.34</i> **	0.13	/	<i>0.01</i>	/	<i>0.18</i>
Leaf lifespan	/	/	/	0.16	0.78	/
Leaf anatomy	<0.001	0.02	/	0.05	0.17	/
SLA	<i>-0.41</i> ***	0.21 *	/	<i>0.13</i>	0.21 *	0.35 ***
LDMC	0.26 *	<i>-0.23</i> *	<i>-0.01</i>	<i>0.06</i>	<i>-0.33</i> **	<i>-0.24</i> *
Flowering start	0.29	0.06	/	0.76	0.12	/
Flowering end	/	/	0.35	0.51	/	/
Flowering duration	0.27 **	<i>-0.02</i>	<i>0.14</i>	<i>-0.03</i>	<i>-0.09</i>	/
Pollination	0.13	0.03	/	0.03	0.004	/
Reproduction type	/	0.74	/	0.04	0.76	0.22
Dispersal strategy	0.22	0.01	0.16	0.40	0.002	0.01
Dispersal unit	0.98	0.32	0.38	0.42	0.03	0.23
Seed mass	<i>-0.02</i>	0.32 **	<i>0.14</i>	<i>-0.19</i> *	0.41 ***	<i>0.18</i>
Storage organ	0.72	0.22	/	0.06	/	0.51
CGO type	/	/	/	/	/	/
CGO persistence	/	<i>0.09</i>	<i>0.11</i>	/	<i>-0.01</i>	<i>-0.21</i> *
Lateral spread	/	<i>-0.11</i>	<i>-0.11</i>	0.22 *	<i>-0.21</i>	<i>0.06</i>
Clonal index	<i>-0.05</i>	<i>-0.01</i>	<i>-0.16</i>	<i>0.19</i>	/	<i>0.15</i>
Bud bank size	/	<i>0.02</i>	<i>0.09</i>	<i>-0.19</i>	<i>-0.01</i>	<i>-0.12</i>
Bud bank depth	/	<i>0.15</i>	<i>-0.04</i>	<i>-0.03</i>	/	/
Disturb. freq.	0.54 ***	<i>-0.13</i>	0.25 *	<i>0.19</i>	<i>-0.24</i> *	<i>-0.30</i> *
Disturb. sever.	<i>0.06</i>	/	<i>-0.29</i> *	0.45 ***	<i>-0.28</i> **	/

4.1. Species niche optimum

Niche position is understood here as the conditions for the best performance of the species (e.g., abundance in the local community) and is represented as the environment where the maximum population growth rate is reached (Treurnicht et al., 2020). The interpretation in this section is focused on the overall top-ranked traits that were important for niche optima (Fig. 1). Seed mass appeared to be important for temperature, soil moisture and soil reaction optima, similarly as documented by Tautenhahn et al. (2008). Plant species growing on warmer, drier and more calcareous soils are characterized by heavier seeds, a pattern demonstrated for forest ecosystems in Slovenia (Kermavnar and Kutnar, 2020; Kermavnar et al., 2022a), German flora (Tautenhahn et al., 2008) and at the European scale (Cubino et al., 2021). Specific leaf area, a functional trait defining worldwide leaf economics spectrum (Wright et al., 2004), has been a significant trait in predicting niche optimum for light, temperature, soil reaction and soil nutrients. The shape of SLA relationship with these environmental factors was similar to that reported in Dalle Fratte et al. (2019). Species

Table 3

Relationship between functional traits and species niche width for light (L_{sd}), temperature (T_{sd}), continentality (K_{sd}), soil moisture (F_{sd}), soil reaction (R_{sd}) and soil nutrients (N_{sd}). Results are from the Kruskal-Wallis test for categorical traits and the Spearman rank correlations for numerical traits. In case of categorical traits, p-values are reported. In case of numerical traits, correlation coefficients are given in italics. Significant results at alpha = 0.05 are in bold (significance levels: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Sign “/” means that the relationship was not tested due to negative %IncMSE value (see Fig. 2).

Trait	L_{sd}	T_{sd}	K_{sd}	F_{sd}	R_{sd}	N_{sd}
Plant height	<i>0.10</i>	/	<i>-0.04</i>	<i>0.02</i>	/	/
Growth form	0.04	/	0.08	0.10	0.03	0.09
Life form	/	0.55	/	/	/	/
Life strategy	0.01	/	0.06	0.10	/	0.20
C-score	/	<i>-0.18</i>	<i>-0.12</i>	/	<i>-0.30</i> **	<i>0.06</i> **
S-score	0.24 *	<i>0.17</i>	0.23 *	/	0.31 **	/
R-score	<i>-0.28</i> **	/	<i>-0.18</i>	<i>-0.28</i> *	<i>-0.24</i> *	/
Leaf lifespan	/	/	0.34	0.64	0.27	/
Leaf anatomy	0.007	/	/	0.04	/	/
SLA	/	/	<i>-0.10</i>	/	<i>-0.33</i> **	<i>-0.20</i> *
LDMC	<i>0.12</i>	/	/	<i>0.08</i>	/	<i>0.09</i>
Flowering start	/	/	/	/	0.21	/
Flowering end	/	/	/	0.08	0.17	/
Flowering duration	/	/	/	0.26 **	/	/
Pollination	/	0.25	0.42	/	/	/
Reproduction type	0.94	/	/	0.86	/	0.72
Dispersal strategy	0.24	0.09	0.26	/	0.004	/
Dispersal unit	/	/	/	/	0.14	/
Seed mass	<i>0.02</i>	/	<i>-0.01</i>	/	<i>-0.32</i> **	/
Storage organ	/	/	/	/	/	0.20
CGO type	0.29	/	/	/	0.28	/
CGO persistence	/	/	/	<i>0.14</i>	<i>0.06</i>	/
Lateral spread	<i>0.00</i>	/	<i>-0.09</i>	/	/	<i>0.02</i>
Clonal index	<i>0.03</i>	/	<i>-0.05</i>	/	/	<i>0.18</i>
Bud bank size	0.20 *	<i>0.12</i>	<i>-0.04</i>	/	<i>0.13</i>	<i>0.05</i>
Bud bank depth	/	<i>0.05</i>	/	<i>0.07</i>	/	<i>0.14</i>
Disturb. freq.	0.41 ***	/	0.26 *	0.46 ***	0.35 **	0.40 ***
Disturb. sever.	<i>0.16</i>	<i>-0.04</i>	<i>-0.11</i>	<i>0.12</i>	<i>0.12</i>	0.34 **

occurring on more productive sites with higher soil reaction and warmer climate show more acquisitive strategy (Kermavnar et al., 2022a). High-SLA plants are also better adapted to low light availability in forest understories (Wilson et al., 1999; Givnish et al., 2004; Chelli et al., 2019). Species with different temperature, soil reaction and nutrients optima differed in terms of dispersal strategy. Autochorous plants were linked to warmer sites with higher soil reaction. Autochory and epizoochory were also more frequent than other dispersal modes at more productive sites. Autochory was the most common dispersal strategy, with more than half of all species studied here belonging to this category. These were mainly dispersal generalists that do not clearly indicate anemochory or zoochory morphologically, also suggesting that those two dispersal modes are less adaptive in forest understory environment. Most myrmecochorous (diaspore dispersal by ants) or probably myrmecochorous species are also assigned to this category (Sádlo et al., 2018). In contrast, the anemochorous dispersal strategy relies on light, very small spores and seeds that are dispersed, besides wind, by a wide variety of vectors. This type of dispersal was more characteristic of species growing in colder and acidic sites and is consistent with the observation that the proportion of fern spores as dispersal unit were negatively related to soil reaction.

Response to disturbance is one of the most important axes of functional differentiation in plant species (Grubb, 1977; Grime, 1979; Westoby, 1998). Forest disturbances such as windthrows result in the

creation of canopy gaps with high light intensities. These conditions are favourable for disturbance-adapted plants but may cause a decline in taxa preferring stable microclimate of closed stands. Our analyses indicated that species adapted to more frequent disturbances have higher light requirements, and are tolerant to more continental climate and acidic, nutrient-poor soils (an example in our dataset is the grass *Deschampsia cespitosa* (L.) P. Beauv.). Acidophilous forest types on nutrient-poor sites usually have tree stands with a low canopy leaf area index and consequently higher light levels at the forest floor. In contrast, species less adapted to disturbances tend to be shade-tolerant plants with higher requirements for soil reaction and nutrients (e.g., *Cyclamen purpurascens* Miller, *Cardamine enneaphylos* (L.) Crantz, *Actaea spicata* L.). This is consistent with Herben et al. (2016) and Herben et al. (2018), who reported that species with high values of disturbance indices (ruderals) tended to have small seeds, to be annual and non-clonal, i.e., traits that are not commonly represented among typical forest plant species. In addition, the disturbance severity was found to serve as a predictor for soil moisture optimum. Species occurring at moist or even wet forest sites (e.g., *Aegopodium podagraria* L.) showed a tendency for greater tolerance to disturbance severity whereas species found at drier sites (e.g., *Vincetoxicum hirsundinaria* Medik.) were less adapted to intense disturbances. Stress-tolerant taxa with high S-scores have higher leaf dry matter content (LDMC; Pierce et al., 2017). Forest vegetation in more extreme habitats is characterized by herb layer composed of species with lower growth rates and higher LDMC, which allows them to survive under stressful conditions, such as low soil pH and lower soil nutrient content (Westoby et al., 2002; Simpson et al., 2016). At the same time, natural forest habitats with more extreme pH values are often more open (less shading of the tree layer), which is favourable for species with higher LDMC values (Cubino et al., 2021). A high LDMC value is an indication that the leaves contain more supporting tissues (e.g., sclerenchyma) that protects the leaves from being eaten by herbivores or from physical damage and therefore have a longer life span (Cornelissen et al., 2003). These plant species have slower metabolism and are adapted to low availability of certain resources.

On the contrary, more competitive taxa with higher C-scores generally exhibit larger leaf areas (Pierce et al., 2017). Similar to our results, Dalle Fratte et al. (2019) also documented increasing leaf area values along temperature and productivity gradients. In terms of life forms, we observed that chamaephytes and geophytes had highly different ecological niches. Chamaephytes are adapted to sites with higher light availability, more continental climates and nutrient-poor soils, while the opposite is true for geophytes. Plant size influences a plant's ability to access above- and below-ground resources, and thus plant height is a key component of species' ecological strategy (Moles, 2018). Our analyses confirmed that plant height increases with increasing moisture availability and that this trait decreases with higher temperature and rainfall seasonality (climatic continentality) (Amatangelo et al., 2014; Moles, 2018). Flowering attributes (start, duration) of herb-layer species are often associated with tree layer characteristics. We found that light-demanding species had longer flowering duration, which is consistent with the results from Kermavnar et al. (2022b), who reported a negative association between flowering duration and tree layer shade-casting ability. In contrast, short and early flowering may be advantageous for shade-avoiding understory plants in the deciduous forests experiencing dense canopy closure (Ottaviani et al., 2019).

4.2. Species niche width

Niche width can be described as a species occurrence range on an environmental gradient (Schellenberger Costa et al., 2018). For plant species in mixed broad-leaved deciduous forests in Slovenia, Marinšek et al. (2015) demonstrated clear relationships between the degree of habitat specialism (realized niche width) and functional traits. In our species dataset, three species with the lowest values for niche width across all six environmental gradients considered were flowering forbs

Actaea spicata L., *Galium odoratum* (L.) Scop. and *Lilium martagon* L. – these can be thus considered habitat specialists. In contrast, the three top-ranked species with the highest niche width across all six environmental factors were the grass *Deschampsia cespitosa* (L.) P. Beauv., the dwarf shrub *Polygala chamaebuxus* L. and the fern *Dryopteris carthusiana* (Vill) Fuchs – these can be considered habitat generalists, mainly in terms of soil reaction and nutrient gradients. The results suggested that compared to the niche optimum of forest plant species, their niche widths are generally less correlated with plant traits. We found 46 significant relationships between species niche optimum and plant traits (Table 2), while there were only 24 significant associations between ecological amplitude and traits (Table 3). For a general understanding of our findings, it is important to emphasize that detected patterns in niche widths were not biased by the occurrence records (number of forest vegetation types in which species was present; correlation analyses not shown). This suggests that even common species present at many forest sites can be ecologically specialized, and vice-versa.

Our analysis showed that the disturbance frequency and intensity act as a strong filtering factor for the assembly of forest plants (Kutnar et al., 2019). Species that are less adapted to disturbances are likely to have more narrow ecological niches, supporting the notion that disturbance may constrain niche widths (Schellenberger Costa et al., 2018). Among the disturbance intolerant species were some species that are considered true or ancient forest species (Hermý et al., 1999) with a high affinity for undisturbed interiors of late-successional forest stands and are commonly found in the herb layer of preserved old-growth forests (e.g., *Actaea spicata* L., *Cardamine enneaphylos* (L.) Crantz, *Cyclamen purpurascens* Miller, *Euphorbia amygdaloides* L., *Hacquetia epipactis* (Scop.) DC., *Lathyrus vernus* (L.) Bernh., *Polygonatum multiflorum* (L.) All., *Sanicula europaea* L.). These shade-tolerant perennials require a stable environment and sudden alterations in ecological variables usually represent an unfavorable change towards more stressful conditions for them. It remains unclear to what extent typical forest species are sensitive to disturbances such as forest management, as some studies suggest their short-term resistance after tree harvesting (Kermavnar et al., 2018, 2021b).

Belowground traits are particularly important as many forest plants rely on vegetative propagation to maintain local populations. We have found that bud bank size is positively correlated with niche width for light. Campetella et al. (2020) showed that clonal and bud bank traits favor fine-scale species persistence in forests more affected by summer drought and more open overstory canopy. Competitors (*sensu* Grime, 1977) were also characterized by wider niches for light compared to stress-tolerators, indicating a trade-off between physiological tolerances at the extremes of environmental gradients and competitive ability. Stress-tolerators are generally species with sufficient adaptations to stressful conditions, which are in forest understory environment manifested in low light availability. S-score (*sensu* Pierce et al., 2017) was also important for light, continentality and reaction niche width of the species studied. Accordingly, a higher S-score (positively correlated with LDMC) is indicative of a wider ecological niche. This is consistent with the findings of Marinšek et al. (2015), reporting that habitat specialists have lower LDMC. In contrast, higher SLA values (in positive correlation with R-score; Pierce et al., 2017) were found to be associated with narrow-ranged species in terms of soil reaction and nutrient, implying that species with an acquisitive resource-use strategy are filtered out on acidic and nutrient-poor forest sites (Kermavnar et al., 2021a). Pattern in seed mass and its relation to soil reaction niche width indicated the influence of forest ferns in our dataset. Ferns have spores of almost negligible weight but are able to grow on a broad spectrum of soil reaction conditions. For instance, two of the most common fern species in our dataset (i.e., *Athyrium filix-femina* (L.) Roth and *Dryopteris filix-mas* (L.) Schott) occur in a variety of forest types on different parent materials (carbonate and silicate) as long as soil moisture availability and relative humidity are sufficient.

Functional traits were, on average, better predictors of niche

optimum (average proportion of variance explained: 20.2%) than of niche width (7.7%), supporting our initial hypothesis. Niche optima and niche widths were explained by similar trait combinations. This may be due to the correlation between optima and widths, but was true only for some of the investigated gradients (light and continentality; Appendix G). The lower degree of trait explanatory power for ecological niche width suggests that additional covariates shape species niches apart from species-mean trait values (interspecific trait differences). Intra-specific trait variability (i.e., variation in trait values among individuals of the same species), which was not considered in this study, likely plays an important role in case of plant niche width (Violle and Jiang, 2009) and how plants will cope with global change (Heilmeier, 2019). Chelli et al. (2022) found that beech forest specialists exhibit high intraspecific variation in leaf traits related to important plant functions (light capture, resource conservation), whereas this was not true for generalist species. Numerous studies provided empirical evidence for the hypothesis that greater intraspecific trait variation allows populations to grow in a broader range of environments, thereby extending species niche widths (Treurnicht et al., 2020). Phenotypic plasticity is the ability of a given genotype to express different phenotypes in different environments (Masarovičová et al., 2016). The intraspecific variability of belowground traits (clonal organs, root depth and morphology) might be of particular relevance for explaining stress resistance and interannual dynamics of forest plant species. Belowground traits are rarely measured and therefore future studies should focus on a better integration of belowground paradigm into the functional traits approach in plant ecology and on an extension of efforts to collect such data (Heilmeier, 2019).

Here we also focused exclusively on abiotic gradients, while we did not consider the effects of biotic interactions (competition at sites with high resource availability vs. mutualism under harsh conditions). From the Hutchinson's (1957) perspective, ecological niches are dynamic as the presence of one species constrains the presence of another species through interspecific competition, which modify the position of species niches within a multidimensional space. Finally, within the pool of species under study, there are some plant species (e.g., diagnostic species for beech-dominated plant communities) with geographically restricted distribution, possibly due to specific evolutionary history or dispersal limitations (Willner et al., 2009). Such potentially confounding effects related to biogeography and historical contingencies are likely to be important in explaining niche parameters, particularly for the niche widths as those species with limited geographic distribution experience limited ability to fully occupy climatically and edaphically suitable habitats.

Our methodological approach of how niche parameters were derived might influence the identified associations between niche optima (position along environmental dimension) and widths (standard deviation around the mean) and plant traits. However, our results in this context cannot be compared to studies dealing with demography-related parameters (e.g., Treurnicht et al., 2020) or deriving niche widths from beta diversity metrics (e.g., Wasof et al., 2013) and co-occurrence patterns (e.g., Marinšek et al., 2015), respectively. While estimates derived from species distribution models based on presence and abundance data could provide more realistic representation of species niches, we conclude that using occurrence patterns across forest vegetation types in the present study is a solid and robust approach. Owing to its simplicity, it can be easily transferred to other systems and in fact, we suggest being tested on broader spatial scales utilizing “big data” from vegetation survey archives, such as recently published by Dengler et al. (2023). These databases can offer comprehensive, range-wide demographic data needed to directly infer ecological niches for multiple species. Instead of using indirect estimates (Ellenberg indicator values), ecological niches of species could be derived from other open-source databases such as large-scale raster layers describing macroclimatic (e.g., WorldClim) and soil conditions (e.g., SoilGrids). In the context of global environmental change, this would also add valuable insights on potential adaptive

responses of individual forest species to shift their realized ecological niches along latitudinal or elevational gradients of temperate forests (Wasof et al., 2013).

5. Conclusions

Our results, even if emerging from a limited dataset, are generally consistent with previous studies of how different species traits are related to niche optima, and that these relationships matched trait–environment associations reported in the literature. Niche widths also showed significant dependence on species traits but to a lesser extent than niche optima. Both niche parameters (optimum and width) were best explained by a few, largely overlapping sets of traits. However, the relative importance of traits differed substantially between niche optimum and width. Trait-based studies of niches provide useful insights into the mechanisms that determine species distributional patterns and functional biodiversity. Moreover, knowledge of the relationships between species ecological niche(s) and functional traits may have important implications for various aspects of community ecology, such as community assembly rules, species coexistence, adaptation to environmental stress, and assessment of species' future responses to global change. Species with narrow niche width are expected to be more vulnerable to alterations in the current environment compared to generalists. We found that niche widths are positively correlated for several environmental factors, suggesting that some forest plant species are specialists on multiple ecological gradients. Habitat specialists, often recognized as priority elements for conservation, or species with low intraspecific trait variability may therefore have limited capacity to respond to simultaneous changes in conditions and resources induced by climate warming and drying, nitrogen depositions and increasing natural and anthropogenic forest disturbances worldwide.

CRedit authorship contribution statement

Janez Kermavnar: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Lado Kutnar:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Aleksander Marinšek:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Valerija Babij:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.flora.2023.152247](https://doi.org/10.1016/j.flora.2023.152247).

Appendix A. List of 94 forest plant species used in analyses.

Appendix B. Calculation schemes for deriving species niche optima and niche widths based on species occurrences in forest vegetation types.

Appendix C. Additional information for selected plant functional traits.

Appendix D. Significant relationships between niche optimum and categorical traits.

Appendix E. Significant relationships between niche width and categorical traits.

Appendix F. Density plots for selected species along different environmental gradients.

Appendix G. Correlation matrix for dependent variables (niche optimum and width) along environmental gradients.

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