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Inferring ecological selection from multidimensional community trait distributions along environmental gradients

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Abstract

Understanding the drivers of community assembly is critical for predicting the future of biodiversity and ecosystem services. Ecological selection ubiquitously shapes communities by selecting for individuals with the most suitable trait combinations. Detecting selection types on key traits across environmental gradients and over time has the potential to reveal the underlying abiotic and biotic drivers of community dynamics. Here, we present a model-based predictive framework to quantify the multidimensional trait distributions of communities (community trait spaces), which we use to identify ecological selection types shaping communities along environmental gradients. We apply the framework to over 3600 boreal forest understory plant communities with results indicating that directional, stabilizing, and divergent selection all modify community trait distributions and that the selection type acting on individual traits may change over time. Our results provide novel and rare empirical evidence for divergent selection within a natural system. Our approach provides a framework for identifying key traits under selection and facilitates the detection of processes underlying community dynamics.

KEYWORDS

community assembly, disruptive selection, divergent selection, diversity, ecological selection, functional trait, hypervolume, stabilizing selection

INTRODUCTION

Understanding the processes by which natural communities change and their corresponding effects on ecosystem

services is increasingly important under global environmental change. Trait-based approaches have the potential to provide insights on community assembly by offering a taxon-independent approach to characterize organisms responses to a changing environment (McGill et al., 2006; Weiher & Keddy, 1995). Despite well-developed trait-based approaches, predicting community composition and

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disentangling the underlying processes of community assembly remains a challenge (Shipley et al., 2016; Webb et al., 2010). Recent theoretical (Vellend, 2010, 2016), conceptual (Carmona et al., 2016; Webb et al., 2010; Yates et al., 2018) and methodological studies (Gross et al., 2021; Laughlin et al., 2012) collectively suggest that modeling the full trait distributions of communities can facilitate understanding of community assembly.

Communities are composed of individuals with different phenotypic characteristics influencing their performance, that is, their functional traits (McGill et al., 2006; Violle et al., 2007). The abiotic environment and biotic interactions select for individuals conditional on their traits. When selection favors individuals with a certain trait value, regardless of species, we expect a subsequent increase in this trait value in the community (Shipley, 2010; Shipley et al., 2016; Vellend, 2010). Communities and their trait composition are thus aggregate properties stemming from individuals with different trait combinations responding to varying selection pressures. As individuals express multiple traits, selection on one trait inevitably leads to concomitant shifts in other traits and may thus alter the correlation among traits at the community level (Clark, 2016; Dwyer & Laughlin, 2017; Kraft, Godoy, et al., 2015; Laughlin, 2014). Nevertheless, the community assembly literature is dominated by studies which focus on single traits and frequently find evidence of abiotic rather than biotic processes structuring communities (Götzenberger et al., 2012; Münkemüller et al., 2020). Moreover, the commonly used filtering framework, which compares observed variation in single traits to variation produced by random assembly, is often unable to disentangle abiotic and biotic processes, thus providing limited transferable knowledge on how communities are structured (Münkemüller et al., 2020).

Identification of ecological selection types offers a more general view of community assembly (Vellend, 2010, 2016). Ecological selection can appear under three types—directional, stabilizing, and divergent (Rolhauser & Pucheta, 2017; Vellend, 2016) (Figure 1c). Directional selection leads to a shift in the most common, and thereby presumably optimal (Enquist et al., 2015; Violle et al., 2007), trait values in the community (Figure 1d), driven by environmental filtering (Keddy, 1992; Kraft, Adler, et al., 2015) or competitive exclusion (Mayfield & Levine, 2010) (Table 1). Stabilizing selection reduces trait variation and results in trait convergence evidenced by a narrower range of traits (DeMalach et al., 2022; Loranger et al., 2018; Rolhauser & Pucheta, 2017; Vellend, 2010, 2016) (Figure 1e). It can be driven by two opposite environmental filters acting on the same trait (Kraft, Adler, et al., 2015; Rolhauser & Pucheta, 2017), by competitive exclusion (Mayfield & Levine, 2010), or by positive frequency

dependent mechanisms (Vellend, 2016), which benefit species with similar response traits. For example, during succession some plants may influence soil microbial composition so that it facilitates other plant species with similar traits (environmental requirements) to colonize and gain abundance (Fukami, 2015; van der Putten et al., 2013). Stabilizing selection may also stem from stronger trait correlations without a corresponding change in univariate trait means or variances (Arnold et al., 2001; Lande & Arnold, 1983) (Figure 1f). This stronger trait correlation may arise from an environmental filter such as aridity (Dwyer & Laughlin, 2017), or biotic interactions, such as predation (Mikolajewski et al., 2010; Tanaka, 2012). Finally, divergent selection leads to an increase in the number of modes (“peaks”) in trait distributions, or to more even trait distributions (Gross et al., 2021; Kingsolver & Pfennig, 2007; Vellend, 2016) (Figure 1g). Divergent selection may be generated by limiting similarity (MacArthur & Levins, 1967; Meszéná et al., 2006; Weiher & Keddy, 1995) or negative species interactions, such as resource competition via niche differences (Levine & HilleRisLambers, 2009; Mayfield & Levine, 2010) or apparent competition for example via shared pathogens or mutualists (Allan et al., 2010; Devaux & Lande, 2010; Siefert et al., 2018) (Table 1). We note that bimodality or a uniform trait distribution can also emerge from a sudden shift in directional selection, if a new trait optimum has appeared but the individuals representing the past optimum are still present.

Recent studies have explored how selection impacts the distributions of single traits in communities (DeMalach et al., 2022; Gross et al., 2021; Loranger et al., 2018; Rolhauser & Pucheta, 2017). Considering multiple, often correlated, traits is a necessity for more reliable inference on assembly processes (Clark, 2016; Kraft, Godoy, et al., 2015; Pistón et al., 2019; Wüest et al., 2018). To date, few studies have modeled multidimensional trait diversity patterns (Blonder, 2018; Carmona et al., 2016; Clark, 2016), due to challenges associated with modeling trait correlations and comparing multidimensional trait volumes (Blonder, 2018; Carmona et al., 2016; Lu et al., 2021). The Trait Probability Density framework (Carmona et al., 2016) provides a probabilistic framework to quantify multidimensional trait hypervolumes. Here, we transform this conceptual probabilistic framework into a predictive one using a two-stage approach: first modeling species relative abundances along environmental gradients and then translating them to multidimensional trait distributions. Our two-stage approach accounts for trait correlations (or trait syndromes) imposed by species’ phenotypes because we model species’ responses to environment rather than individual traits. At the first stage, we apply a multinomial Bayesian joint species distribution model (JSDM), which accurately predicts observed species relative abundances

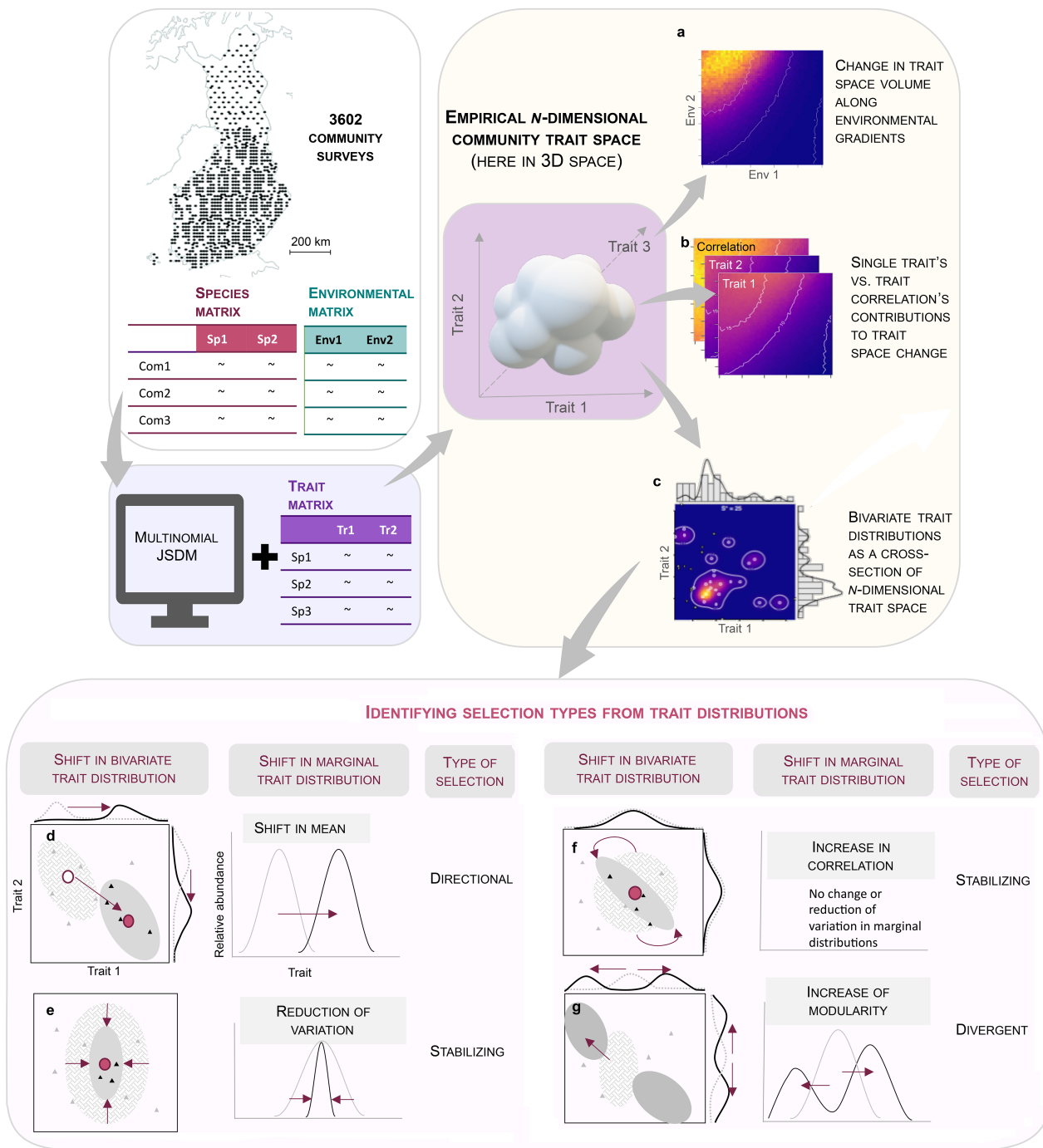


FIGURE 1 Schematic representation of the workflow and hypotheses. Empirical *n*-dimensional community trait spaces were built by transforming species probability estimates (from joint species distribution model [JSDM]) into multivariate trait probability distributions. Using these community trait spaces, we (a) investigated changes in the trait space volume along the modeled environmental gradients (color represents the relative change in volume, contours illustrate richness); (b) partitioned trait space change among individual traits and their correlation along the environmental gradients; and (c) used cross sections of trait spaces (i.e., bivariate trait distributions) to identify different selection types and potential underlying mechanisms (Table 1). Identification of ecological selection types based on shifts in mean, variance, correlation, and number of modes are illustrated both for the marginal distribution of a single trait and for bivariate trait distributions (d–g, see Table 1). The arrows in the subpanels illustrate one possible direction. The weaved and gray ellipsoids represent the trait space occupied by communities in the hypothetical environments A and B, respectively. The red point represents the centroid of the space and triangles are species-specific trait values. Note that species have fixed locations in the trait space, defined by their mean trait values (i.e., trait syndrome; intraspecific trait variation ignored here). Black triangles illustrate species present in environment B; gray triangles illustrate species in the species pool, but absent from the environment B. The gray and black distributions in the margins of panels d and g represent the shifts in single trait distributions when moving from environment A to B.

TABLE 1 Three types of ecological selection, their consequences on trait distributions, examples of underlying low-level mechanisms, classification of the mechanisms into abiotic and biotic filters, and references for mechanisms.

Type of selection	Pattern in trait distribution	Examples of low-level mechanisms	Filter	References
Directional	Shift in mean	Environmental filter	Abiotic	Keddy (1992), Kraft, Adler, et al. (2015)
		Competitive exclusion	Biotic	Mayfield and Levine (2010)
Stabilizing	Reduced variation in a single trait	Competitive exclusion	Biotic	Mayfield and Levine (2010)
		Two opposite environmental filters	Abiotic	Kraft, Adler, et al. (2015), Rolhauser and Pucheta (2017)
		Positively frequency dependent mechanisms: Priority effects	Biotic	Fukami (2015), Vellend (2016)
		Positively frequency dependent mechanisms: Facilitation	Biotic	van der Putten et al. (2013), Vellend (2016)
Stabilizing	Stronger correlation among traits	Trade-offs between traits caused by environmental filter	Abiotic	Dwyer and Laughlin (2017), Kraft, Adler, et al. (2015)
		Trade-offs between traits caused by species interactions	Biotic	Mikolajewski et al. (2010), Tanaka (2012)
Divergent	>1 modes or a more uniform distribution	Negatively frequency dependent mechanisms: Resource competition, apparent competition	Biotic	Allan et al. (2010), Devaux and Lande (2010), Levine and HilleRisLambers (2009), Mayfield and Levine (2010), Siefert et al. (2018), Vellend (2016)
		Limiting similarity	Biotic	Macarthur and Levins (1967), Meszéna et al. (2006), Weiher and Keddy (1995)
		Facilitation	Biotic	Spasojevic and Suding (2012)

(Itter et al., 2024). At the second stage, we use posterior model predictions to construct probabilistic multivariate trait distributions of communities following a modified version of the predictive trait model introduced by Clark (2016). As our JSMD does not account for ecological interactions between species in a causal or mechanistic way, as is true for any JSMD (Blanchet et al., 2020; Poggiato et al., 2021), we do not use this model to separate effects of abiotic versus biotic selection. Instead, we make inferences on ecological selection types and potential low-level processes driving community dynamics by investigating emergent patterns in the predicted multidimensional trait distributions of communities (community trait spaces) along environmental gradients. By modeling species first and applying probabilistic model predictions to construct trait distributions, we can predict entire trait distributions continuously across a range of environmental conditions, not only those conditions observed at sample locations. Further, our model-based approach accounts for uncertainty in underlying community data and species' responses to environmental conditions, which is propagated to predicted trait distributions. Such uncertainty would not be accounted for if we summarized observed multidimensional trait distributions directly.

We apply our framework to species-poor boreal forest understory communities. The data span over 3600 understory communities across a 1200-km latitudinal gradient in Finland, sampled in 1985, 1995, and 2006. At the first stage, we model how vascular plants' relative abundances depend on growing season temperature, habitat fertility, and forest density. At the second stage, we transform the predicted species communities to 4-dimensional community trait distributions (community trait spaces) using specific leaf area (SLA, related to light and nutrient capture), leaf carbon to nitrogen ratio (C:N, describing relative nitrogen acquisition), leaf dry matter content (LDMC, related to nutrient acquisition), and leaf phosphorus (P, related to phosphorus acquisition) as trait axes. Based on leaf economics and plant strategy theories (Laughlin, 2023; Westoby et al., 2002; Wright et al., 2004), these traits are likely to be influential for plant success along with our environmental gradients.

By examining changes in community trait distributions along modeled environmental gradients, we address three objectives. First, we assess how overall functional diversity varies along environmental gradients by quantifying changes in the volume of community trait distribution along growing season temperature and forest density

gradients. We hypothesize that functional diversity will be lowest in the coldest and densest forests, where scarcity of nutrients and light select for resource-conservative strategies in the understory. In contrast, the largest functional diversity is expected in the most resource-rich conditions of warm and fertile habitats with low tree density (Högberg et al., 2017; Merilä et al., 2002). Second, we investigate which traits contribute most to overall changes in the multidimensional trait distribution volume (increase or decrease trait variation) along environmental gradients, that is, identify the traits under selection (Figure 1b). Since nitrogen and light limitation intensifies along the successional gradient in boreal forests (Högberg et al., 2017; Merilä et al., 2002; Vitousek & Reiners, 1975), based on plant strategy theory (Laughlin, 2023), we hypothesize nitrogen acquisition-related traits such as leaf C:N and LDMC, as well as light capture related SLA to be under selection along the forest density gradient, while leaf P will be unaffected by forest density. Because microbial activity and nutrient cycling are strongly controlled by temperature (Chapin et al., 2011), we expect cold growing season temperature to limit nutrient availability and select for resource-conservative traits (high LDMC, high leaf C:N, low leaf P, and low SLA), leading to low trait variation and small trait space volume. Third, we assess how bivariate and marginal trait distributions (i.e., cross sections of the multidimensional trait space) change along modeled environmental gradients to detect signs of ecological selection types (Figure 1c). We expect to find directional or even stabilizing selection as forest density increases given lower soil nitrogen availability selecting for individuals with higher C:N ratios, indicating low nitrogen requirement, and higher LDMC values, indicating resource-conservatism in the form of tough and slow-growing, long-lived leaves (Reich, 2014). This resource-conservatism should be strongest under low habitat fertility in the coldest growing seasons. In contrast, we expect that more nutrient-rich habitats of warmer and younger forests will support a wider range of nutrient use strategies (wider variation in leaf C:N, LDMC, SLA, and leaf P), with potential for divergent selection due to competition for nitrogen or light (Heikkinen & Mäkipää, 2010; Salemaa et al., 2023).

MATERIALS AND METHODS

Understory community and forest stand data

Understory communities were surveyed by National Resources Institute Finland (Luke) in 1985–1986, 1995,

and 2006 on a systematic network of 1700 sites established on mineral-soil in forested land. The systematic sampling network is part of the 8th Finnish National Forest Inventory (Reinikainen et al., 2000) and consists of clusters, which were located 16 km from each other in southern Finland, and 24 and 32 km apart in northern Finland along east–west and north–south axes, respectively. Each cluster includes four linearly located sampling sites 400 m apart from each other in southern Finland and three sampling sites 600 m apart from each other in northern Finland. Data include 1495 sites in 1985–1986, 1673 sites in 1995 and 439 sites in 2006 (3602 unique inventory site-by-year combinations in total). The survey in 2006 was part of the BioSoil project carried out under the Forest Focus scheme, which is a subset of the pan-European International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (UN-ECE ICP Forests) monitoring site network (Level I) (Lorenz & Fischer, 2013). Then the spatial extent of this sampling was comparable to previous surveys covering the whole country (Figure 1), but at maximum one site per cluster was surveyed.

In all three surveys, within each site, vascular plant cover (0.1%–100%) was visually estimated for each species on four permanent square-shaped sampling quadrats of 2 m², located on a transect, 3 m apart from each other. Here, we modeled data at the site level and used the average of species cover across the four sampled quadrats as an estimate of species abundance at each site with percent cover values treated as species-level counts. In total 380 vascular plant species were observed in the surveys. To ensure meaningful estimation of species-specific model parameters, we focused on 39 species, which occurred in at least 5% of sites in each inventory year (a common practice in high-dimensional JSDM settings; Clark et al., 2017). At each site, forest density was estimated as the basal area of the trees (Tomppo et al., 2011). Shrub cover was measured as the projected percent cover of shrubs and 0.5- to 1.5-m tall trees within an 9.8-m radius (11.3 m in 2006) circular plot centered on the permanent vegetation survey sites. Site fertility was determined in the field using six classes based on vegetation (Cajander, 1949; Pohjanmies et al., 2021). Here, we reclassified these into two groups representing “high” and “low” fertility. The growing degree day variable represents the site-level average annual sum of daily mean temperatures exceeding +5°C over the preceding decade calculated based on 10 km²-resolution interpolated daily temperature values modeled by the Finnish Meteorological Institute (Venäläinen et al., 2005).

Trait data

We collected data on 10 traits for each 39 species: height (related to dispersal and ability to compete for light), SLA (related to light and nutrient capture), leaf carbon to nitrogen ratio (C:N, describing relative nitrogen acquisition), LDMC (related to nutrient acquisition), leaf phosphorus (P, related to phosphorus acquisition), leaf N (related to nitrogen acquisition), leaf N:P ratio (describing relative nutrient requirements), mycorrhizal colonization rate (describing association with soil fungi, measured as a proportion of fine root colonized by mycorrhizal fungi), clonality (binary; describing whether species is able to spread clonally or not), and dispersal mode (binary; describing whether species is wind dispersed or not). Species-specific values for height, SLA, and LDMC were obtained as median from the TRY database (Kattge et al., 2011). Leaf C:N were primarily measured from a pooled sample of leaves (ca. 2 g) collected from multiple individuals across several locations in Southern and Eastern Finland, or secondarily obtained as median from TRY database. Leaf N, P, and N:P were primarily measured from the same samples as leaf C:N, or secondarily obtained as median from NP database (Tian et al., 2019). Clonality was extracted from the CLO-PLA database (Klimešová et al., 2017), mycorrhizal colonization as median from the GRooT database (Guerrero-Ramírez et al., 2021), and wind pollination syndrome from TRY (pollination syndrome re-classified here to binary: wind vs. other). The leaf samples were dried at +60°C for 72 h, milled, and analyzed for C and N using flow-injection analyses and for P spectrophotometrically after burning at +550°C and extracting with hydrochloric acid.

Modeling approach

Functional trait prediction under varying environmental conditions occurs as a two-stage process. In the first stage, a multinomial Bayesian JSDM is fit to species relative abundances. In the second stage, the parameterized JSDM is used to predict species' probabilities of success under specified environmental conditions, which are then mapped to traits through a linear transformation. Full description of the multinomial JSDM for predicting species relative abundances along growing season temperature, habitat fertility and forest density gradients can be found in Appendix S1: Section S1, species list in Appendix S1: Table S1 and model selection in Itter et al. (2024). The model applies a multinomial response function, which estimates each species probability of success under local environmental conditions relative to other

species in the community. This means that we model community structure, not only individual species responses. Each species' relative abundance is influenced by other species' responses to the modeled environmental variables as well as to random (i.e., unmeasured environmental) variation between sites. The model assumes finite space and resources: if the probability of one species increases in a community, the total probability of success of all other species must decrease. While this assumption reflects antagonistic interactions among species within the same trophic level—due to shared and limited resources, for example, nutrients, light, and growing space, our model is not mechanistic and does not explicitly account for biotic interactions. Rather, the multinomial response function accounts for the nonindependence of the relative abundances of species within the modeled communities. This statistical dependence is commonly modeled through a residual random effect term in existing JSDMs (Clark et al., 2017; Ovaskainen et al., 2017; see e.g., Poggiato et al., 2021). We explored the inclusion of such residual dependence here but found the multinomial response function alone led to better predictions of observed communities (Itter et al., 2024). Our modeling approach focuses thus on ecological selection (Vellend, 2016) by accounting for several key environmental selection factors and dependence among species within a community.

Functional trait prediction

The fitted multinomial JSDM was applied to predict the expected probability of success of each species under specified environmental conditions. Specifically, posterior predictions of the linear predictor for each species ($j = 1, \dots, m$) are generated as $\tilde{z}_j^{(\delta)} \sim N(\tilde{\mathbf{x}}' \boldsymbol{\beta}_j^{(\delta)}, \boldsymbol{\sigma}_j^{2(\delta)})$, where $\tilde{\mathbf{x}}$ specifies the predictive environmental conditions, $\boldsymbol{\beta}_j$ is a vector of species-specific responses to environmental conditions, $\boldsymbol{\sigma}_j^2$ is a species-specific variance term, and δ indexes the posterior sample ($\delta = 1, \dots, S$). The expected probability of success of a given species under the specified environmental conditions is generated conditional on $\tilde{\mathbf{z}}^{(\delta)} = (\tilde{z}_1^{(\delta)}, \dots, \tilde{z}_m^{(\delta)})$ as

$$\tilde{\pi}_j^{(\delta)} = \frac{\exp \tilde{z}_j^{(\delta)}}{\sum_{j=1}^m \exp \tilde{z}_j^{(\delta)}}.$$

Mapping predicted species probabilities to underlying functional traits is achieved through a linear transformation. The expectation and variance of a local community under the multinomial model are given by

$$E(\mathbf{y}_i|\mathbf{z}_i) = N_i\boldsymbol{\pi}_i,$$

$$V(\mathbf{y}_i|\mathbf{z}_i) = \begin{cases} N_i\pi_{ij}(1 - \pi_{ij'}) & j = j' \\ -N_i\pi_{ij}\pi_{ij'} & \text{o.w.} \end{cases},$$

where $E(\cdot)$ and $V(\cdot)$ denote expectation and variance, respectively, and N_i indicates the total abundance for i th local community. Setting $N_i = 1$, the community-weighted trait mean (CWM) and community-weighted variance (CWV) are calculated as $CWM_i = \mathbf{T}'E(\mathbf{y}_i|\mathbf{z}_i) = \mathbf{T}'\boldsymbol{\pi}_i$ and $CWV_i = \mathbf{T}'V(\mathbf{y}_i|\mathbf{z}_i)\mathbf{T}$, where \mathbf{T} is an $(m \times \ell)$ -dimensional trait matrix defined for m species and ℓ functional traits. Inserting posterior predictions of species probabilities ($\tilde{\boldsymbol{\pi}}$) into the formulas for the CWM and variance allows for the prediction of community-level trait distribution parameters under specified environmental conditions: $CWM_{\tilde{\mathbf{x}}}$ and $CWV_{\tilde{\mathbf{x}}}$. Inherent trait syndromes expressed as nonzero covariance among traits (nonindependence of traits) are captured through the modeled covariance among species possessing specific trait values as quantified by the covariance matrix $\mathbf{T}'V(\mathbf{y}_i|\mathbf{z}_i)\mathbf{T}$.

Baseline community

For reference, we define a fixed baseline community in which all m species have equal probability of occurrence:

$$\pi_j^{(b)} = 1/m,$$

where (b) indicates baseline. This artificial community without any selection (Shipley, 2010) provides a constant reference point against which we measure departures of predicted communities using, for example, CWM, CWV, and trait hypervolume size and dimensions (see below). The baseline community is not to be confused with a null community, which requires decisions on randomization techniques to sample varying numbers of species from the regional pool. Since we expect selection to influence both species richness and trait distributions, it is essential to have a constant comparison community with maximum richness and fixed, equal relative abundances.

Trait goodness of fit

We quantify goodness of fit of our predictive trait model in two ways. First, we calculate Bayesian R -squared values for each functional trait considered in our analysis using a modified approach to that presented in Gelman

et al. (2019). Bayesian R -squared values are calculated as $V_{\text{fit}}/(V_{\text{fit}} + V_{\text{res}})$, where V_{fit} and V_{res} indicate the fitted and residual variance, respectively (Gelman et al., 2019). Fitted variance is calculated as the variance among community-weighted mean prediction:

$$V_{\text{fit}}^\ell = \frac{1}{n-1} \sum_{i=1}^n \left(CWM_i^\ell - \overline{CWM}^\ell \right)^2,$$

where CWM is calculated as described under *Functional trait prediction* and ℓ refers to a specific trait. Residual variance is calculated as the mean of the marginal variance of each trait across sites as calculated within the community-weighted trait covariance matrix:

$$V_{\text{res}}^\ell = \frac{1}{n} \sum_{i=1}^n \sigma_{\ell,i}^2.$$

The Bayesian R -squared provides a measure of the variability in traits among sites explained by the model (Appendix S1: Figure S1). We selected four best predicted continuous traits for further analyses: SLA, LDMC, leaf C:N, and leaf P.

We further quantified the difference in observed versus predicted trait distributions across all sites applying a modified Kolmogorov–Smirnov test. This approach is novel in that it considers the full probability density function of the multivariate trait distribution rather than comparing observed versus predicted summary statistics (e.g., community-weighted means, variances, and coefficient of variation). We generate empirical cumulative density functions, $F_\ell(x)$, for each modeled trait conditional on observed (\mathbf{y}_i) and predicted ($\tilde{\mathbf{y}}_i$) local communities. Specifically, we generate samples of species-level trait means with frequencies matching observed and predicted relative abundances of each species. For the predicted trait distribution, we apply the posterior predictive mean of the relative abundance of species within a local community sampled from a multinomial distribution with size equal to N_i and species probabilities equal to $\tilde{\boldsymbol{\pi}}_i$. We then conduct Kolmogorov–Smirnov (KS) tests for each functional trait of interest across all sites with total observed abundance greater than 20 ($N_i \geq 20$). A total of 3135 out of 3602 met this criterion (the consistency of KS tests is poor for low sample sizes). We applied a Bonferroni-adjusted test level of $\alpha^* = 0.05/3135 = 0.000016$ to control for multiple comparisons. The proportion of the 3135 sites for which there is evidence to reject the null hypothesis is reported for each trait of interest in Appendix S1: Table S2. Across all traits of interest, we find that the null hypothesis that the observed and predicted functional trait distributions are identical is supported at over 90% of sample sites.

Functional trait hypervolumes

We utilize the methodology presented in Lu et al. (2021) to estimate predicted trait hypervolumes (here called community trait spaces) and contribution of each trait and their correlation to changes in hypervolume along environmental gradients. Specifically, functional trait hypervolume is calculated as the determinant of the ℓ -dimensional community-weighted trait covariance matrix: $|\text{CWV}|$. Conditional on posterior predictions of the community-weighted trait covariance matrix (see [Functional trait prediction](#)), we generate predictions of functional trait hypervolumes under specified environmental conditions. For reference, predicted functional trait hypervolumes are presented relative to the hypervolume of the baseline community,

$$\frac{|\text{CWV}_{\tilde{\mathbf{x}}}^{(d)}|}{|\text{CWV}_{(b)}|},$$

and report the posterior median ratio. Note, ratio values larger than one indicate greater hypervolume under specified environmental conditions than in the baseline community, while values less than one indicate reduced hypervolume relative to the baseline community. Given that the community-weighted trait covariance matrix is a positive definite matrix, its determinant is always positive thereby ensuring the hypervolume ratio is also positive.

The determinant of the community-weighted trait covariance matrix is given by, $|\text{CWV}| = \sigma_1^2 \sigma_2^2 \dots \sigma_\ell^2 (1 - \sum_{1 \leq k < k' \leq \ell} \rho_{kk'}^2 + 2 \prod_{1 \leq k < k' \leq \ell} \rho_{kk'})$, where σ_k^2 is the variance of trait k and $\rho_{kk'}$ is the correlation between traits k and k' ($k = 1, \dots, \ell$). As described in Lu et al. (2021), we can use the determinant formula to partition changes in the trait hypervolume to multiplicative terms corresponding to individual trait variances (σ_k^2 for $k = 1, \dots, \ell$) and their correlation. The correlation component is defined by all terms within parentheses, $\psi = 1 - \sum_{1 \leq k < k' \leq \ell} \rho_{kk'}^2 + 2 \prod_{1 \leq k < k' \leq \ell} \rho_{kk'}$, and reaches a maximum value of 1 when all traits are orthogonal such that their correlation is zero. The greater the correlation among traits, the smaller the value of ψ . We calculate relative change in trait-level variance as

$$\frac{(\sigma_{k|\tilde{\mathbf{x}}}^{2(d)} - \sigma_{k|b}^2)}{\sigma_{k|b}^2},$$

where $k|\tilde{\mathbf{x}}$ and $k|b$ indicate the k th trait for the specified environment and baseline community, respectively. Similarly, we calculate the relative change in the correlation component as

$$\frac{(\psi_{\tilde{\mathbf{x}}}^{(d)} - \psi_b)}{\psi_b}.$$

For variance terms, values less than zero indicate a decrease in trait-level variance, while positive values indicate an increase in trait-level variance relative to the baseline community. For the correlation component, values less than zero indicate a decrease in trait independence (i.e., an increase in trait dependence) potentially shrinking the trait hypervolume. Values greater than zero indicate an increase in trait independence (decrease in dependence). We report the posterior median change in individual trait variation and the correlation component.

Empirical trait distributions

Predicted species probabilities under specified environmental conditions ($\tilde{\boldsymbol{\pi}}$) are used to construct empirical trait distributions. Note that these probabilities provide the relative weights of each species' mean trait value within a predicted local community (see [Functional trait prediction](#)). Empirical trait distributions are constructed by specifying a total community abundance (N) and sampling the mean trait values of constituent species with frequencies equal to predicted species probabilities. All empirical trait distributions utilize the median of the posterior predictive species probability vector under specified environmental conditions. We then compute univariate and bivariate Gaussian kernel density estimates of the sampled functional trait values using the minimum and maximum trait values as the density bounds (i.e., density is equal to zero beyond these values). In bivariate plots, ellipsoids are generated illustrating 95% quantiles (i.e., the region spanning 95% of the bivariate probability density) applying linear interpolation to the cumulative sum of the empirical trait density. Baseline empirical trait distributions are estimated by replacing $\tilde{\boldsymbol{\pi}}$ with $\boldsymbol{\pi}^{(b)}$ in the above steps. To quantify tail extremity of the empirical trait distributions, we estimated sample excess kurtosis: positive excess kurtosis describes peaky distributions with more outliers (heavy tails), while negative excess kurtosis refers to flatter distributions with fewer outliers (light tails).

Species richness

To provide context for changes in functional trait distributions along modeled environmental gradients, we estimate species richness under specified environmental

conditions. Specifically, we convert predicted species probabilities to presence/absence as

$$\tilde{\eta}_j = \begin{cases} 1 & \tilde{\pi}_j > 0.005 \\ 0 & \text{o.w.} \end{cases}$$

Species richness (M) is then estimated as $M = \sum_{j=1}^m \tilde{\eta}_j$.

RESULTS AND DISCUSSION

Model validation

We compared our model predictions to observed natural communities at two levels: (1) community composition, and (2) functional trait distribution levels. In-sample and out-of-sample posterior predictive model checks revealed high correlation between predicted and observed relative abundances of species with species-level Bayesian R -squared values exceeding 0.6 for the majority of species (Itter et al., 2024). At the functional trait level, observed and predicted functional trait distributions were not found to differ significantly in over 90% of study sites based on a modified Kolmogorov–Smirnov test (Appendix S1: Table S2). Clonality, SLA and leaf C:N were the best predicted traits, with the model capturing on average 28%, 27%, and 23% of their variation across over 3000 study sites, respectively (Appendix S1: Figure S1). Further, community-level trait predictions (CWM) correlated well with the observed CWM values for the best predicted continuous traits while the model poorly predicted variation in height (Appendix S1: Figure S2).

Community trait space volume along environmental gradients

Community trait space volume describing overall functional diversity (measured by SLA, LDMC, foliar C:N, and foliar P) of understory communities was smallest in the densest and coldest forests (Figure 2), corresponding to our hypothesis. Since forest density correlates positively with stand age especially in the forests under ca. 60 years (Appendix S1: Figure S3), we hereafter use the forest density as a proxy for forest age to infer changes over time in the young forests. In line with our hypothesis, we found that the largest community trait space occurred in the warmest and most open young forests under low habitat fertility (Figure 2a). There, variation of all traits was largest and trait correlation weakest (Figure 3a–e), enlarging the total volume. However, in

contrast to our hypothesis, under high habitat fertility, the largest trait space occurred in the warmest forest with intermediate or high forest density (Figure 2b). This unexpected expansion of trait space toward denser forests in warm and fertile conditions was driven by increasing variation of LDMC and SLA (Figure 3f,g), which overrode the negative influences of declining variation in leaf C:N and leaf P and stronger trait correlation on space volume (Figure 3f–j). This finding is discussed more thoroughly below in Divergent selection section. As hypothesized, our results indicate that cold growing seasons exert selection on all traits in this boreal forest system: variation in SLA, LDMC, and leaf P decreases, while variation in leaf C:N increases toward colder growing seasons in fertile habitats (Figure 3). In the following sections, we describe and discuss specific changes in trait variation linking them to selection types.

Divergent selection

As forests become older and overstory tree density increases, competition for nutrients increases and the resources for understory communities decline. Along the density gradient, in warmer and more fertile habitats, we observed an expansion of the community trait space (Figure 2b). This was driven mainly by increasing variation in LDMC and to lesser degree by SLA (compare Figure 3a,b to 3f,g). Simultaneously, we observed the LDMC distribution shifting from one dominant trait value to a more uniform distribution (Figure 4a–c; Appendix S1: Table S3), corresponding to the pattern predicted to emerge from divergent trait-based selection (Vellend, 2016). LDMC is related to resource-use strategy and leaf lifespan describing species position on the resource use axis (Wilson et al., 1999). Thus, divergent selection for LDMC, as forest density increases, presumably reflects negative interactions among species, potentially intensifying competition for soil nutrients such as nitrogen and favoring species with different resource-use strategies (Högberg et al., 2017; Hyvönen et al., 2008). This finding adds needed evidence to little studied divergent selection in real-world communities (Kingsolver & Pfennig, 2007; Loranger et al., 2018; Rolhauser & Pucheta, 2017). Furthermore, contrary to our expectations, we observed expansion of variation in leaf C:N toward colder forests at low and intermediate density in fertile habitats (Appendix S1: Figure S4j–q, Table S3). Colder temperature limits rates of decomposition and nitrogen cycling (Chapin et al., 2011), reducing nitrogen availability and requiring species to differ in their nitrogen requirements, while in warmer temperatures, species with high nitrogen demand dominate. Interestingly,

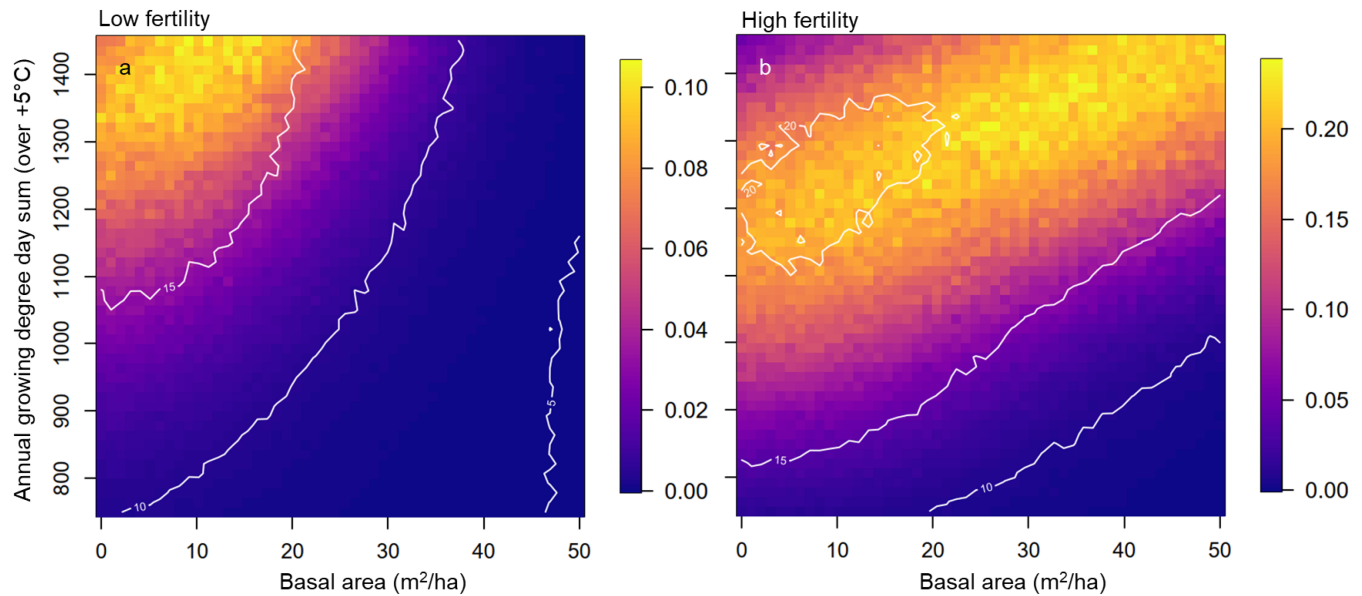


FIGURE 2 Four-dimensional community trait space volume along environmental gradients. Relative change in community trait space volume relative to baseline hypervolume that assumes all species have equal probability of occurrence, along gradients of forest density (basal area of trees, x-axis) and growing season temperature (growing degree days, y-axis) in low (a) and high (b) fertility habitats. Values indicate proportion of the baseline volume (e.g., 0.1 = 10% of baseline volume). Note that colors refer to different values in the two panels. Contour lines represent species richness of predicted communities.

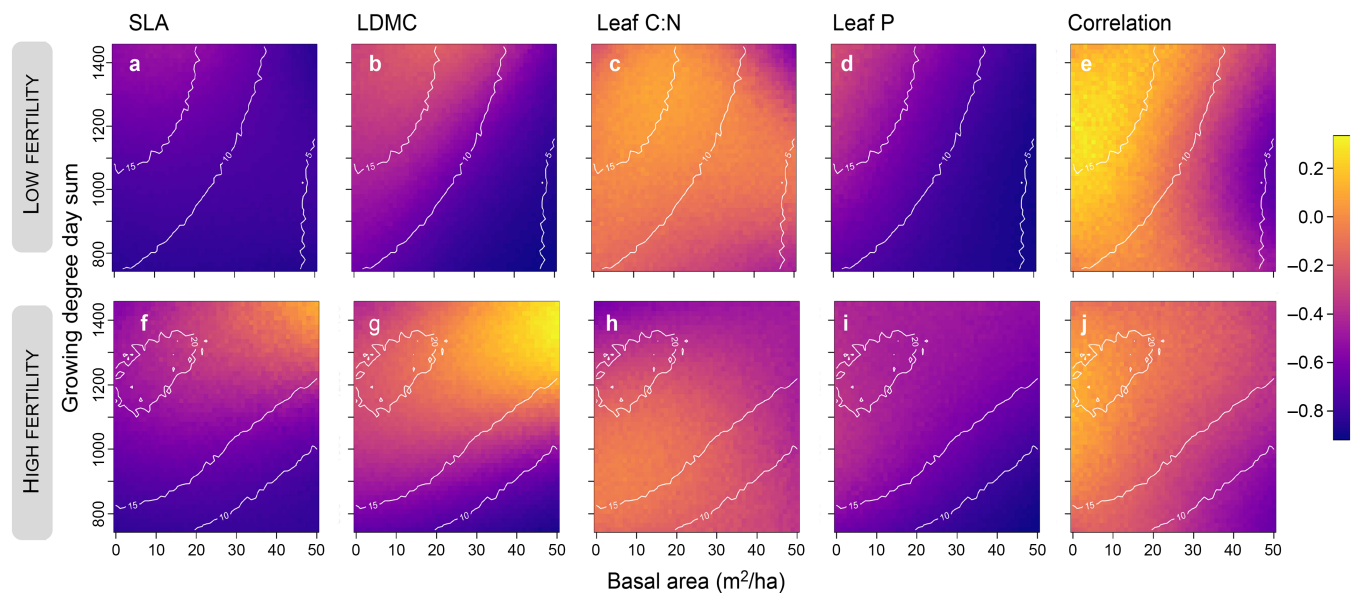


FIGURE 3 Functional trait variance and correlation among all traits along environmental gradients. Relative change in single trait variance and trait correlation along gradients of forest density (basal area, x-axis) and growing season temperature (growing degree days, y-axis) in low (top row) and high (bottom row) fertility habitats. Changes are calculated comparing predicted variance and correlation components to a baseline hypervolume that assumes all species have equal probability of occurrence. Positive values for single trait variances indicate an increase in variance relative to the baseline, while negative values indicate the opposite. For trait correlation, positive values indicate weaker correlation among traits in predicted communities compared with baseline community, while negative values indicate stronger trait correlation. LDMC, leaf dry matter content; SLA, specific leaf area.

under low fertility, nitrogen limitation became so intense toward the coldest forests that it caused a strong directional selection for high leaf C:N (Appendix S1:

Figure S4a–i), as discussed below. Opposite to our expectations, we did not find signs of consistent divergent selection on any traits in the most nutrient-rich habitats

of youngest and warmest forests (Figure 4; Appendix S1: Figures S4 and S5, Table S3). On the contrary, while trait variation was high in these communities, the trait

distribution was typically dominated by one peak suggesting that one trait value or combination of traits was favored.

High fertility

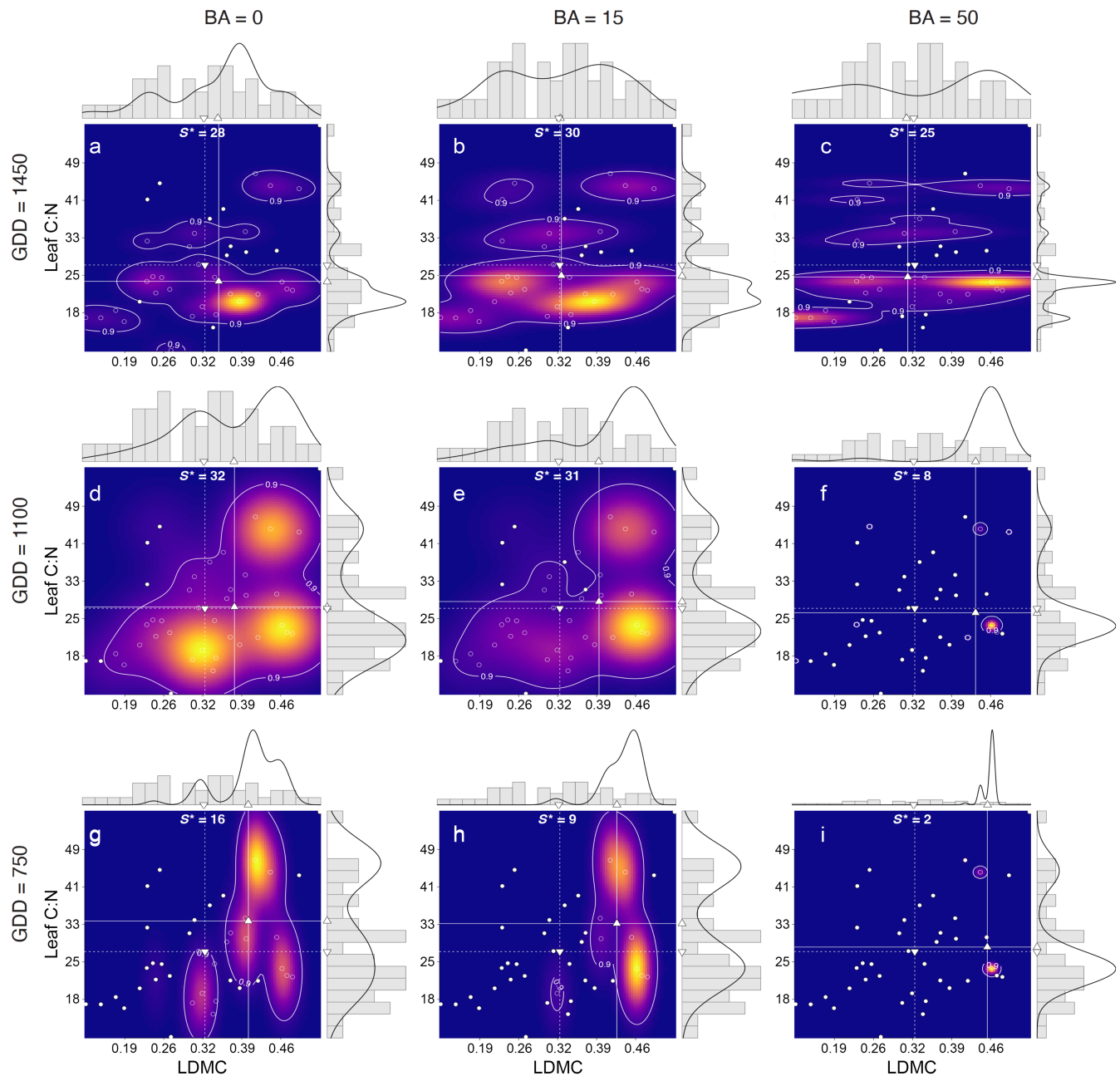


FIGURE 4 Empirical bivariate trait distributions along environmental gradients under high fertility. Predicted empirical distribution of leaf dry matter content (LDMC, x-axis) and leaf C:N ratio (y-axis) under varying basal areas (BAs) (columns) and growing degree days (GDDs) (rows) as predicted by the model in high fertility habitats. In each panel, points indicate the 39 study species in the trait space (species identities in Appendix S1: Figure S6), while the white line indicates the 95% probability density of two traits. Species falling within the 95% area are indicated with solid white symbols and their number with S^* at the top. Modeled marginal community trait distributions are shown as solid black lines. Gray histograms present trait frequency distribution assuming all 39 species have equal probability of occurrence. The downward triangle in the margin and dotted lines denotes community-weighted mean (CWM) for the baseline community, while the predicted CWM is denoted by an upward triangle and dashed lines.

Directional and stabilizing selection

In addition to divergent selection under certain conditions (warm, fertile sites), the predicted trait distributions revealed patterns resembling the hypothesized outcomes

of directional and stabilizing selection (Figure 1). As hypothesized, we found indication of directional selection, as the community-weighted mean of both leaf C:N and LDMC increased when moving from warmer to colder growing seasons (Figures 4 and 5). This pattern

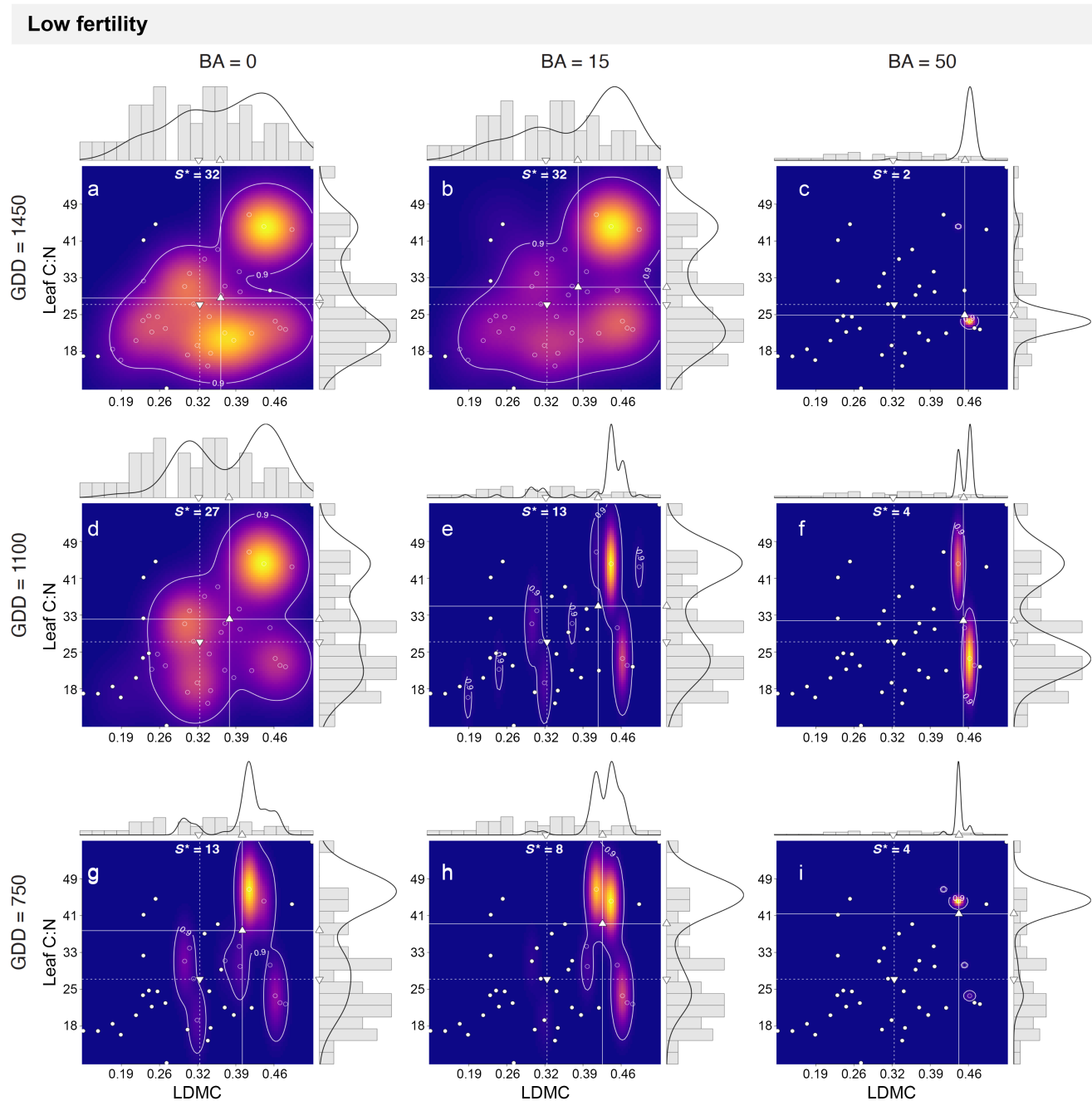


FIGURE 5 Empirical bivariate trait distributions along environmental gradients under low fertility. Predicted empirical distribution of leaf dry matter content (LDMC, x-axis) and leaf C:N ratio (y-axis) under varying basal areas (BAs) (columns) and growing degree days (GDDs) (rows) as predicted by the model in low fertility habitats. In each panel, points indicate the 39 study species in the trait space (species identities in Appendix S1; Figure S6), while the white line indicates the 95% probability density of two traits. Species falling within the 95% area are indicated with solid white symbols and their number with S^* at the top. Modeled marginal community trait distributions are shown as solid black lines. Gray histograms present trait frequency distribution assuming all 39 species have equal probability of occurrence. The downward triangle in the margin and dotted lines denote community-weighted mean (CWM) for the baseline community, while the predicted CWM is denoted by an upward triangle and dashed lines.

was most pronounced for leaf C:N in the densest forest in low fertile habitats (Figure 5c,f,i), suggesting that growing season length (or some correlated but unmeasured variable) acts as a selection agent favoring species with high nitrogen requirement (low leaf C:N) in warm conditions and species requiring less nitrogen in cold conditions. Beyond specific growing season length dependence, N availability may generally act as the proximate selection agent in boreal forests where decomposition rate (Kirschbaum, 1995, 2006) and N mineralization (Liu et al., 2017) are strongly limited by temperature. Pure stabilizing selection, by definition, takes place when there is no change in the mean, but variance decreases, as we observe for LDMC in warm low fertile habitats (Figure 5a–c) as forest density increases (also observed for SLA; Appendix S1: Figure S5a–c).

Stabilizing selection due to trait correlation

Our results also indicated stronger correlation among traits along the forest density gradient across habitat types (Figure 3e,j). The increase in trait correlations in denser (and in fertile habitats also colder) forests implies that the community trait space is smaller than that defined only by variation in single traits, that is, the dependence among traits shrinks the trait space volume. Increasing trait dependence points to multiple concurrent assembly processes inducing trait trade-offs across the modeled gradients. Trade-offs limit the number of species with viable trait combinations especially in the densest and coldest forests. An earlier study reported increasing covariation of two traits, height and seed mass, along an aridity gradient (Dwyer & Laughlin, 2017). In support of this, our results revealed changing dependence among traits along multiple interacting gradients adding to emerging evidence of multiple simultaneous assembly processes along environmental gradients (Cornwell & Ackerly, 2009; Spasojevic & Suding, 2012). Overall, we found clear evidence that functional diversity of understory communities decreases along a forest density gradient in this system characterized by a wide range of growing season temperatures and habitat fertility variation.

Shifts in selection types over time

We found evidence that multiple selection types modify community trait space as the density of study forests increase. First, we observed divergent selection of leaf C:N from the low-density (Figure 5a) to mid-density forests (Figure 5b) in warm low-fertile forests, and later

stabilizing selection on the same trait, when moving to the oldest and densest forests (Figure 5c; Appendix S1: Table S3). Here, the underlying mechanisms behind divergent selection is likely to be competition for nitrogen (Heikkinen & Mäkipää, 2010), while stabilizing selection in the densest forest could be driven by competitive exclusion by the dominant species *Vaccinium myrtillus* (Gundale et al., 2012), although we cannot exclude other possible mechanisms (Table 1). To our knowledge, this is one of the first illustrations that at community level, ecological selection on one trait may change over time, shedding light on one of the open questions regarding phenotypic selection in the natural communities (Kingsolver & Pfennig, 2007).

The advantage of modeling species, not traits, for advancing detection of assembly processes

Because our aim is to investigate how ecological selection shapes communities in natural systems, we need to predict trait distributions continuously across the observed range of environmental gradients. If observed trait values are used directly, we can only assess functional trait distributions under the environmental conditions observed at understory community sample sites providing an incomplete picture of changes to functional trait distributions across broad environmental gradients. By modeling species first and mapping to traits second, we are able to generate probabilistic predictions of the entire multidimensional trait distributions. If we model traits directly, we would be limited to predictions of statistics summarizing the underlying multidimensional trait distribution such as the CWM or CWV (Clark, 2016).

Further, by modeling species first, our approach mirrors our understanding that selection influences success (here joint probability of presence) of species which is reflected in community trait distributions. Species identities contain information on all traits relevant to their spatial distribution and abundance—not only the traits measured in our study. Our species-first modeling approach accounts for the role of unobserved traits in community assembly indirectly through their effect on species' joint responses to the observed local environment, which are mapped to predicted trait distributions under the second stage of our framework. As a result, and perhaps counterintuitively, a species-first approach yields more accurate predictions of community trait means and variation than modeling these community trait statistics directly in response to the environment (Clark, 2016). Overall, our framework yields model-based predictive and transferrable understanding of processes

underlying trait distributions: it provides (1) model-based estimates of community trait space across the full range of observed environmental variables (and importantly can be used to extrapolate trait distributions under novel conditions, that is, transferable applications) and (2) estimates of uncertainty in both model parameters and predictions of trait distributions.

Our approach improves identification of potential community assembly processes by allowing for nonparametric trait-abundance distributions including skewed, peaky, and flat distributions, thus more accurately reflecting real-world communities than commonly used methods (Falster et al., 2021; Rolhauser & Pucheta, 2017). It allows multimodality in trait distributions, which enables detection of divergent selection and shifts in modality, which so far have remained largely undetected (Loranger et al., 2018). Recent research has focused on improving detection of assembly processes by using multiple aspects of community trait distributions (e.g., skewness and kurtosis) as opposed to traditional mean–variance dominated methods (Gross et al., 2021; Laughlin et al., 2015) which implicitly assume Gaussian trait distributions. Our approach advances this field by demonstrating shifts in probabilistic community trait space, and by linking them to ecological selection types, potential underlying low-level mechanisms, and species diversity patterns. Future model developments should integrate intraspecific trait variation into the framework and explore possibilities to include categorical and ordinal traits to quantification of hypervolume.

Conclusions

We introduce a model-based framework to build multidimensional community trait distributions and illustrate how it can be used to detect signs of ecological selection and to identify possible underlying mechanisms. Applying this framework to a large natural community dataset, we find evidence that directional, stabilizing, and divergent selection concurrently shape boreal forest understory communities along environmental gradients. Our results also suggest that the type of selection acting on a trait may change from divergent to stabilizing over time, as succession proceeds. Finding that multiple selection types are possible over time brings novel insights to ecological theory, which often assumes that traits are either under stabilizing or directional selection (Kingsolver & Pfennig, 2007; Vellend, 2016). In these study communities with varying ages, densities and habitat qualities, interacting and alternating selection forces create multiple trait trade-offs selecting for species with specific trait combinations. As a result, we observe a

reduction in the overall functional diversity of boreal forest understory communities along a density gradient. All these findings remain to be validated with experimental data, which allows separation of selection, drift, and dispersal. We encourage researchers with suitable experimental data to test the robustness of this framework in detecting experimentally manipulated selection correctly. Taken together, our results illustrate how interacting selection processes acting on individuals representing multidimensional phenotypes leave distinct imprints on community trait space and functional diversity of communities.

AUTHOR CONTRIBUTIONS

Elina Kaarlejärvi and Malcolm Itter developed the conceptual and theoretical framework and contributed equally. Tiina Tonteri, Leena Hamberg, Maija Salemaa, and Päivi Merilä were responsible for field sampling and data curation. Malcolm Itter and Jarno Vanhatalo developed the model. Malcolm Itter performed data analyses and coding. Elina Kaarlejärvi wrote the first version of the manuscript, and all coauthors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

JSDM models data (Itter et al., 2023a) and code (Itter et al., 2023b) are available on Dryad and Zenodo at <https://doi.org/10.5061/dryad.tmpg4f53g> and <https://doi.org/10.5281/zenodo.7760374>, respectively. Trait hypervolume analyses data (Kaarlejärvi et al., 2024a) and code (Kaarlejärvi

et al., 2024b) are available on Dryad and Zenodo at <https://doi.org/10.5061/dryad.02v6wwq7d> and <https://doi.org/10.5281/zenodo.7837426>, respectively.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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