Joint Biotic and Abiotic Spatial Turnover: A Basis for Modelling Ecosystem Pattern at Landscape Extents

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Abstract

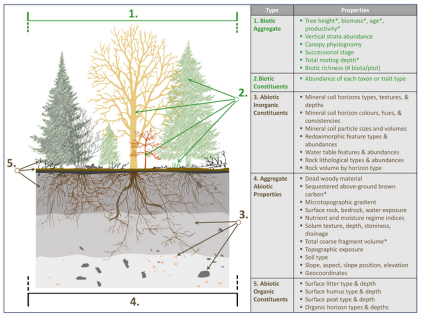
Ecosystem models are typically built to predict patterns of one or more ecosystem properties, and those properties are often biotic. While some ecosystem models incorporate either biotic and abiotic responses, biotic and abiotic variables are rarely applied jointly as responses in ecosystem models. Here we model continuous spatial turnover among 21 biotic and abiotic properties to explore forest ecosystem patterns across landscapes of Nova Scotia, Canada (55 000 km2) at high (10 x 10 m) resolution. To achieve this objective, we fit generalized dissimilarity models to field collected data on biotic and abiotic response variables and geographic and environmental gradients described by remotely sensed predictor variables. We develop three separate models targeting ecosystem, biotic, and abiotic responses to identify relationships among forest ecosystem properties, across levels of ecological organization. Our final ecosystem, abiotic, and biotic models explained 41.4, 29.03, and 50.9 percent of variance. Vegetation-based predictors were the most significant for our ecosystem and biotic response models, while topographic and hydrological predictors were foremost in our abiotic response model. We show how relationships among biotic and abiotic ecosystem properties collectively give rise to predicted patterns of forest ecosystem heterogeneity across Nova Scotia, with the strongest variations occurring along elevational and north-south gradients. Our emphasis on multiple ecosystem properties, and our simultaneous modelling of both biotic and abiotic responses, including ecosystem structural, compositional, and functional variables, differs from the approaches taken in most spatial ecosystem models. This study provides an analytical road map for scientists and conservation practitioners looking to predict continuous variation in ecosystem makeup and to apply those predictions for mapping emergent spatial ecosystem patterns. Such spatial models of ecosystem pattern are crucial for achieving national and sub-national commitments to global ecosystem conservation targets.

Introduction

The **ecosystem** (bolded terms defined in S1, Supplementary Information) is a major focus in several prominent conservation strategies established to curb impacts to biodiversity. For example, the Kunming-Montreal Global Biodiversity Framework (GBF) (CBD 2022a) identifies the maintenance or restoration of ecosystems as a long-term goal. The GBF, and national strategies issued by GBF signatories (e.g., ECCC 2024), includes targets for realizing this goal, and those targets encompass specific **ecosystem properties** including condition (e.g., resilience), type (e.g., terrestrial), functions (e.g., carbon sequestration), and geographic dimensions (e.g., area). To achieve these targets, conservation actions must be informed by relevant spatial information (GBF 2022a, ECCC 2024). This information is needed to ensure decision-makers and practitioners can quantify, and make spatial predictions about, key **ecosystem patterns** , such as where different ecosystems occur and how their properties vary across space. Spatial models are essential for addressing these questions and ensuring targets are based on statistical evidence (Nicholson et al. 2019). Many spatial models will be built at the national or sub-national scale, as regional strategies are the main mechanism for implementing GBF resolutions (Perino et al. 2022, GBF 2022b). Yet spatial models established for predicting ecosystem patterns at regional extents are scarce (Geary et al. 2020, Naas et al. 2024), constraining plans to achieve GBF objectives.

Ecosystems are inherently complex (Riva et al. 2023). To help understand and reduce this complexity, ecologists formulate models to predict ecosystem patterns (Holling and Allen 2002). Spatial ecosystem patterns arise from differing combinations of biotic (e.g., taxa or traits) and abiotic (e.g., soil type) **constituents** , and from**aggregate properties** (e.g., productivity, sequestered carbon) emerging from system development (Holling 1992, Artime and De Domenico 2022) (Figure 1). These patterns are shaped by the varied environmental circumstances within which ecosystems occur (Holling 1992). The rarity of spatial ecosystem models built for predicting these patterns (Geary et al. 2020) may stem from the very complexities that motivate modelling, as they present challenges for model design (Evans et al. 2013). More specific challenges include which ecosystem patterns and**spatial scales** should be selected for modelling, and why (Levin 1998, 2011, Gallagher et al. 2021). We present a general strategy for addressing these challenges with an alternative approach to ecosystem spatial pattern modelling. The patterns we model emerge from spatially structured biotic and abiotic ecosystem properties, predicted as a function of their shared relationships to environmental gradients. Our simultaneous modelling of both biotic and abiotic responses, including ecosystem **structural, compositional, and functional** variables, differs from the approaches taken in most spatial ecosystem models (see Geary et al. 2020).

Spatial ecosystem models are typically built to predict patterns of one or more ecosystem properties and those properties are often biotic (e.g., biomass, dispersal, decomposition) (Geary et al. 2020). In such models, abiotic variables are usually employed as predictors (van der Plas 2019, Hjort et al. 2022). For example, Huxley et al. (2023) show how topographic conditions shape linkages between biotic traits and primary productivity. Abiotic properties have less commonly been incorporated as response variables in spatial ecosystem models (Halvorsen et al. 2020). Here, abiotic properties are frequently limited to those chemical constituents (e.g., nutrients, carbon), with a direct link to biotic processes. Representative models (e.g., Lapierre et al. 2018, Soranno et al. 2019) predict how biotic (productivity) and abiotic (phosphorus, nitrogen) ecosystem properties vary with environmental drivers. Recent formulations (e.g., van der Plas et al. 2020, Gottschall et al. 2022) also predict biotic and abiotic properties, broadening their scope to include physical and chemical abiotic variables (e.g., exposed ground, rain throughfall, and soil temperature, bulk density, and nitrogen). This inclusive approach helps underscore reciprocal relationships between biotic and abiotic properties. It also strengthens recognition of the joint contributions biotic and abiotic properties



Type	Properties
1. Biotic Aggregate	▪ Tree height*, biomass*, age*, productivity* ▪ Vertical strata abundance ▪ Canopy physiognomy ▪ Successional stage ▪ Total rooting depth* ▪ Biotic richness (# biota/plot)
2.Biotic Constituents	▪ Abundance of each taxon or trait type
3. Abiotic Inorganic Constituents	▪ Mineral soil horizons types, textures, & depths ▪ Mineral soil horizon colours, hues, & consistencies ▪ Mineral soil particle sizes and volumes ▪ Redoximorphic feature types & abundances ▪ Water table features & abundances ▪ Rock lithological types & abundances ▪ Rock volume by horizon type
4. Aggregate Abiotic Properties	▪ Dead woody material ▪ Sequestered above-ground brown carbon* ▪ Microtopographic gradient ▪ Surface rock, bedrock, water exposure ▪ Nutrient and moisture regime indices ▪ Solum texture, depth, stoniness, drainage ▪ Total coarse fragment volume* ▪ Topographic exposure ▪ Soil type ▪ Slope, aspect, slope position, elevation ▪ Geocoordinates
5. Abiotic Organic Constituents	▪ Surface litter type & depth ▪ Surface humus type & depth ▪ Surface peat type & depth ▪ Organic horizon types & depths

Figure 1. Range of ecosystem properties available for modelling forest ecosystem patterns in our study. Data encompass constituent and aggregate ecosystem properties occurring across biotic (labels 1 and 2 – green font) and abiotic (labels 3, 4, and 5 – brown font) domains. Properties marked with an asterisk were calculated from field data records. Tree and shrub graphics (Natural Resources Canada 2015).

make to ecosystem patterns. We contend these two premises are key to improving predictions of ecosystem spatial patterns and we have incorporated them into our integrative modelling approach. What is more, our approach is applied at a regional extent which is the extent where many conservation decisions are made (Nicholson et al. 2019).

Our two primary study objectives are to (1) model independent and shared, biotic and abiotic, field-collected response variables to geographic and remotely-sensed environmental predictors; and (2) employ continuous spatial turnover in modelled responses to resolve ecosystem patterns at **landscape** extents. Model outcomes reveal emergent relationships among ecosystem properties, across biotic, abiotic, and ecosystem levels of ecological organization. The approach also provides a basis for partitioning the relative contributions of biotic, abiotic, and geographic predictors to ecosystem spatial patterns.

To quantify variation in ecosystem patterns across space, we predict biotic-abiotic dissimilarities between pairs of ecosystem survey sites using generalized dissimilarity modelling. Generalized dissimilarity modelling (GDM) is an extension of matrix regression developed by Ferrier et al. (2002) for spatial biodiversity modelling. Ferrier and Guisan (2006) highlight GDM as an analytical tool to '*assemble and predict together'* , one of three general strategies they proposed for spatial prediction of community patterns. With this strategy, community constituents (i.e., species, traits) are modelling simultaneously to predict biotic turnover in space or time (Ferrier et al. 2007). Here, we extend this strategy to model ecosystem patterns, arising from simultaneous prediction and mapping of both biotic and abiotic properties. We show how predicted shifts in dissimilarity among combinations of these properties can be used to map spatial ecosystem patterns across landscapes.

Material and Methods

Study Area

We conducted our study across the province of Nova Scotia, Canada. Nova Scotia is a narrow peninsula covering approximately 55,000 square kilometers and extending three degrees of latitude and six degrees of longitude. It is characterized by low to moderate elevation, mostly gentle relief, podzolic soils, and a relatively wide range of local climatic conditions. Much of Nova Scotia is part of the temperate Acadian Forest Zone, except higher montane areas which are outliers of the Eastern Boreal Forest Zone in Canada (Baldwin et al. 2020).

Below, we summarize field-based response data and remotely sensed predictors employed in our models. Those summaries are followed by model overviews and procedures for mapping spatial patterns.

Field-Based Response Data

We obtained ecosystem field data from plot surveys of forested sites following methods detailed in Keys et al. (2023). Surveys involved measuring biotic (e.g., species coverage) and abiotic (e.g., humus depth) forest ecosystem properties (Figure 1) (additional survey information in S1). Following surveys, we calculated several aggregate ecosystem properties from plot data, including biotic (e.g., productivity) and abiotic variables (e.g., brown carbon stocks) (Figure 1; S1). For each of our three models, we employed a response data selection workflow (see S1) to satisfied model assumptions and to account for data errors or survey biases (e.g., missing data attributes).

We generally sought to build parsimonious models incorporating constituent and aggregate ecosystem properties drawn from biotic and abiotic domains. In our ecosystem model (see S1), we strove to ensure the number of biotic and abiotic response variables were relatively similar. For example, representing biota at the species level (664 taxa) would have skewed the ratio of biotic to abiotic response variables in this model, because fewer abiotic variables were available in the plot database. This imbalance would unduly weight the influence of biotic variation on model outcomes. To help address this inequity, we represented biota with ten functional groups (see S1) adapted from the Canadian National Vegetation Classification (Baldwin et al. 2019). Lastly, different measurement units (e.g., percent cover for species, centimeters for humus depth) were employed for quantifying the relative**abundance** of biotic and abiotic properties (see S1). Mixing these variables introduced dissimilar data structures in the response data pool, with a potential bearing on model outcomes. We applied a cube root transformation to a subset of response variables (see S1) (Cox 2011) to help resolve this issue.

Remotely-Sensed Predictor Data

Predictors included gridded environmental data derived from remote sensing. These rasters encompassed topographic, edaphic, hydrological, climatic, and vegetation gradients. We emphasized predictors shaping the distribution of each ecosystem property represented in our independent pool of response data; selections were informed from published models built to predict spatial variations in biodiversity and**geodiversity** (Hjort and Luoto 2012, Mod et al. 2016, Simensen et al. 2020). Where possible, we also sought predictors with a direct influence on the distribution of ecosystem properties, instead of employing proxies (Soley-Guardia et al. 2024).

Following these conditions, we included 22 rasters in our final predictor dataset (see S1). We conducted all raster processing using the terra package (v1.7.29) (Hijmans 2023) in R (v4.3.2) (R Core Team 2023). In addition, we cropped and masked rasters to the extent of Nova Scotia; rescaled them to 10 m using bilinear interpolation, where necessary; and projected them to NAD1983 CSRS v6 UTM Zone 20N. To minimize false accuracies imparted by down scaling (Sillero and Barbosa 2021), we only selected predictor variables with a native spatial grain of [?]10 m (details in S1) to match the finest grain in nested provincial ecosystem surveys. Leaf area index was an exception; data were downscaled from 20 m (see S1).

We extracted predictor values at plot locations using the *simple* method (Hijmans 2023). Afterward, we used correlation (r = 0.7) (Guisan et al. 2017) and variance inflation factor (VIF = 3) analyses (Zuur et al. 2009), to identify correlated environmental predictors, employing the corrplot (v0.92) (Wei and Simko 2021) and usdm (v2.1-6) (Naimi et al. 2014) R packages respectively. To choose between highly correlated predictor pairs, we ran individual models with each predictor, from those pairs, and selected the predictor returning better model fit (see S1). These procedures reduced the number of predictors from 22 to 18. Coupled with geography (i.e., the Euclidian distance between each plot pair), those 18 environmental variables were employed as baseline predictors for modelling (see S1).

Predictive Modelling Strategy

We used generalized dissimilarity modelling (GDM) to predict shifts in combinations of spatial ecosystem response variables. Given this novel application of GDM, we take an exploratory modelling approach (sensu Tredennick et al. 2021) to developing three classes of models with 1) ecosystem, 2) biotic, and 3) abiotic responses. Each model is built with the same combination of predictors and the same model settings, but differing combinations of response variables. GDM formulations predict dissimilarities between pairs of sites as a function of their ecological distance in environmental and or geographic space. Since the modelled response in GDM is a pair-wise distance metric, predictor variables are also represented as pair-wise distances (i.e., difference in predictor values between site pairs). Ferrier et al. (2007) further summarize the statistical underpinnings of GDM, while Mokany et al. (2022) propose a workflow for model fitting. We adapted this workflow (see Figure 2) and employed the GDM package (Fitzpatrick et al. 2024) with default model settings (see S1 for additional detail).

We began the modelling process by selecting ecologically meaningful combinations of response variables informed by patterns summarized in the Nova Scotia Forest Ecosystem Classification (Neily et al. 2023). We built a suite of models to evaluate how varied combinations of these response variables affected model performance (see S1). Performance was assessed using deviance explained, a key GDM performance metric representing the percentage of observed variation (dissimilarity) explained by the model (Mokany et al. 2022). We retained models in all three

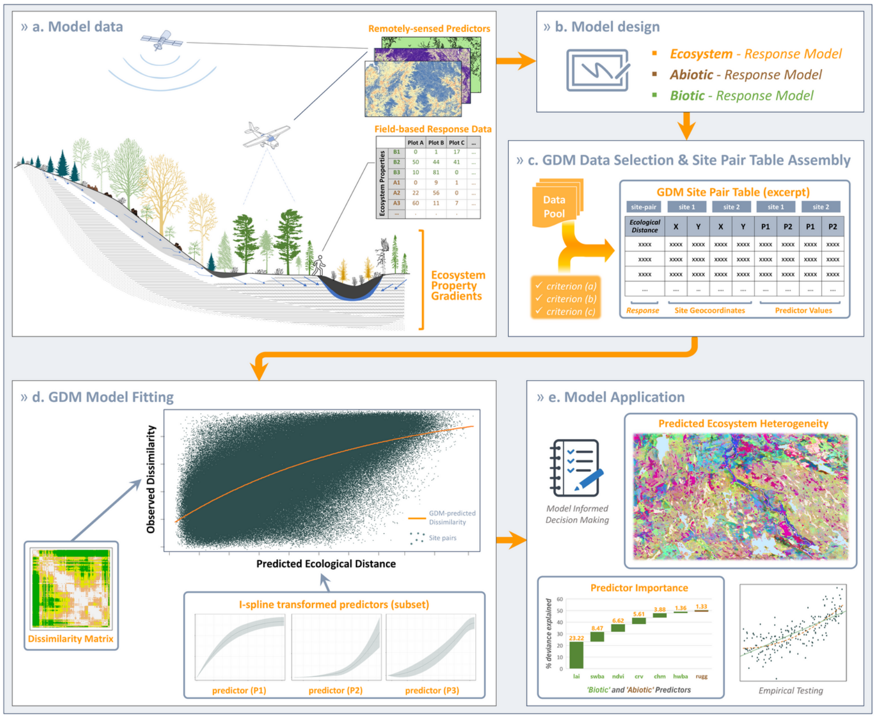


Figure 2. Ecosystem spatial pattern modelling workflow. The sequenced workflow includes steps to: (a) incorporate field-based biotic and abiotic ecosystem response data and remotely-sensed predictors; (b) design and implement independent ecosystem, abiotic, and biotic response models; (c) select model data and assemble a site-pair table for GDM; (d) fit GDM models; (e) apply GDM model outputs to inform decision making and generate follow-up research (e.g., empirical testing). Tree and shrub graphics (Natural Resources Canada 2015); other graphics (Microsoft 365 premium creative content; Creative Commons; or original content).

classes that performed the best and top performing models were subsequently run with matrix permutation (see S1). Matrix permutation was used to cross-validate our models and to assess both model and predictor significance. Here, model significance was determined by comparing the deviance explained between permuted and unpermuted formulations (Fitzpatrick et al. 2024). Matrix permutation was implemented with backward elimination to exclude non-significant (p that included significant predictors, identified through matrix permutation. We report the outputs of the final ecosystem, biotic, and abiotic response models (see S1).

Spatial mapping of ecosystem patterns

To visualize ecosystem patterns, we used GDM transformed predictors to map dissimilarities among modelled combinations of ecosystem properties. Following procedures in Mokany et al. (2022), we used fitted spline functions from our ecosystem model to transform each predictor. Transformed predictors were then used to predict dissimilarity between grid cell pairs, resulting in a multi-dimensional representation of ecological space. To reveal patterns in this space, a principal components analysis was employed to reduce dimensionality. Subsequently, values from the first three principal components were assigned to an RGB palette and plotted simultaneously. The resulting composite map reveals predicted patterns of ecosystem heterogeneity.

Results

Summary of Modelling data

The forest ecosystem dataset assembled for modelling was comprised of field survey records encompassing 16 biotic and 19 abiotic ecosystem properties (see S1). Mean plot separation was 877 m, and elevation ranged from 1 to 506 m above sea level. An average of 7 functional groups were recorded in each plot. Forests in the dataset spanned two biogeoclimatic zones, all ecoregions, and forest soil types recognized in the province (Baldwin et al. 2020, Neily et al. 2017, Keys et al 2023).

Ecosystem, Abiotic, and Biotic Responses – Overview of Models

The final ecosystem, abiotic, and biotic response models explained, 41.4, 29.03, and 50.9 percent of deviance in observed dissimilarity. These values are consistent with those in published generalized dissimilarity models (Mokany et al. 2022) (see S1 for detailed model overviews). Matrix permutation tests, employed to cross-validate model performance, revealed all three formulations were statistically significant, with p-values ranging from 0.04 to < 0.01. The three models were each fit with relatively low numbers of predictors, ranging from 4 to 8 (Table 1).

The final ecosystem response model had six significant predictors (Table 1), including leaf area index, softwood basal area, canopy height, normalized vegetation difference index, hardwood basal area, and terrain ruggedness. The strongest predictors were biotic (jointly explaining 41.31% of deviance), and much of the variation in dissimilarity was accounted for by leaf area index (19.72%) and softwood basal area (11.55%). Terrain ruggedness was the only abiotic predictor making a significant, albeit minor (1.55%), contribution to model fit.

Terrain ruggedness, depth-to-water, canopy height, and geographic distance were significant predictors in the final abiotic model (Table 1). Two of these predictors were abiotic (jointly explaining 23.14% of deviance), with terrain ruggedness making the most important contribution (12.81%). Overall, the most influential biotic predictor was canopy height (5.46%). Among the significant predictors, geographic distance had the lowest strength (<1%).

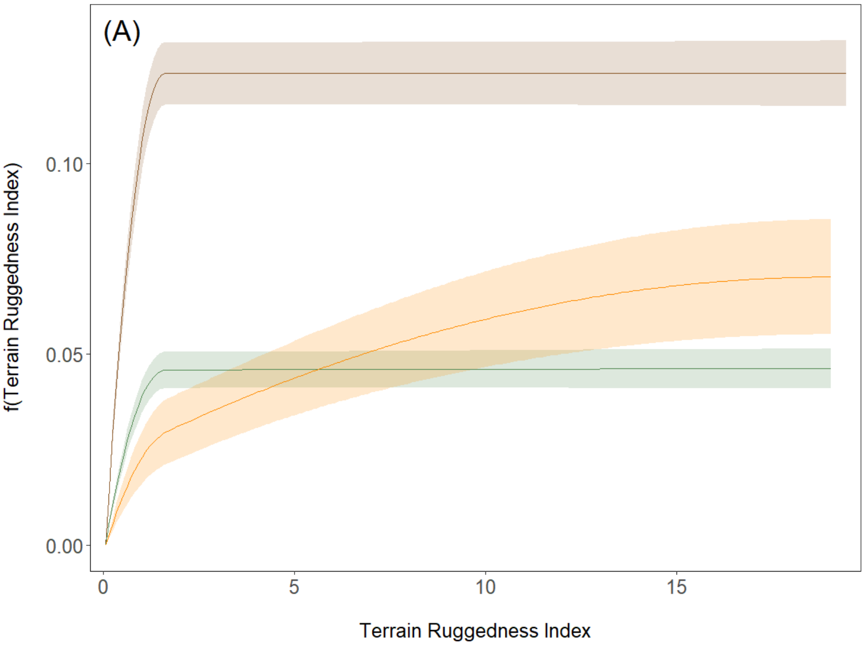
Table 1. Summary of the relative contribution of predictors employed in the ecosystem, abiotic, and biotic response models. For each model, individual predictor coefficient sums are reported, while the proportion of total deviance in dissimilarity, explained by each predictor, is in parentheses. Predictors with higher values, have greater importance, for each given model. The three most important predictors per model are bolded; predictor types are distinguished by font colour: green (biotic), brown (abiotic), and black (geographic distance). Only those significant ($p < 0.05$) predictors retained after matrix permutation with backward elimination (Fitzpatrick et al. 2024) are shown. Predictor data and acronyms are described in S1.

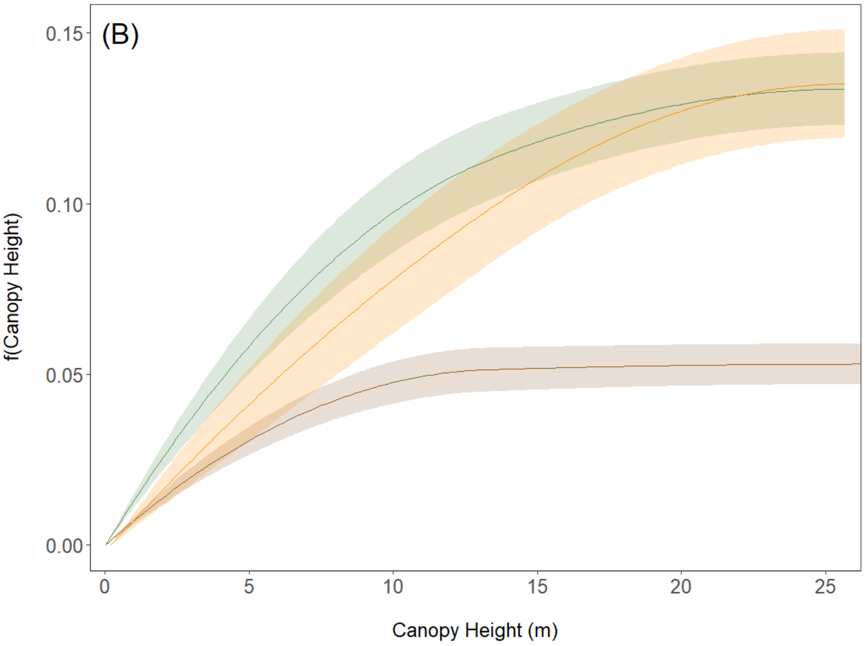
Predictor	**Ecosystem Response Model** coefficient sum (% deviance explained)	**Abiotic Response Mode**
leaf area index	**0.893 (19.72)**	
softwood basal area	**0.523 (11.55)**	
ndvi	**0.177 (3.91)**	
canopy height	0.135 (2.98)	**0.053 (5.48)**
hardwood basal area	0.077 (1.7)	
terrain ruggedness	0.07 (1.55)	**0.124 (12.81)**
depth-to-water		**0.1 (10.33)**
geographic distance		0.004 (0.41)
slope curvature		

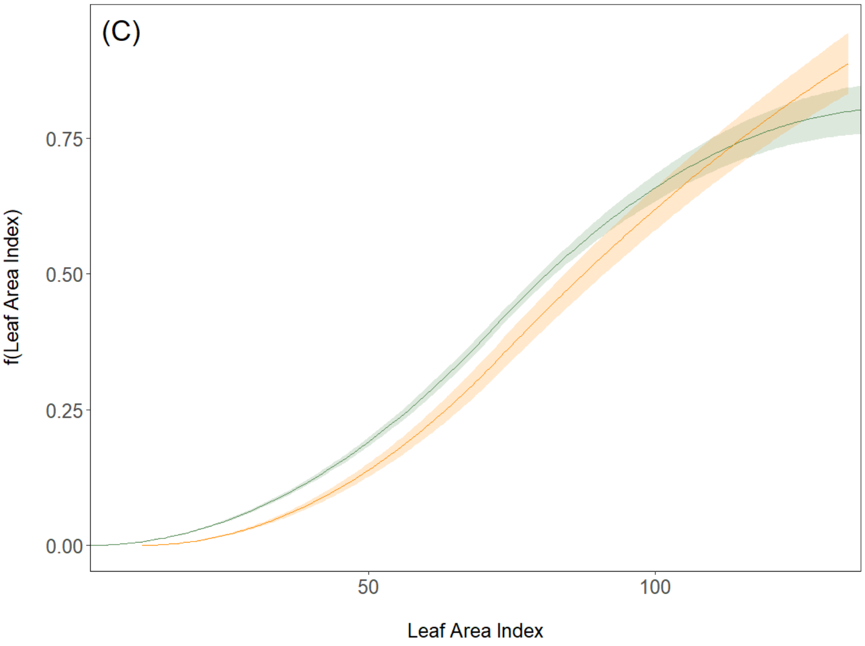
Eight significant predictors were represented in the final biotic response model (Table 1). These included leaf area index, softwood basal area, normalized vegetation difference, slope curvature, canopy height, hardwood basal area, terrain ruggedness, and geographic distance. Just over half of the significant predictors were biotic, together explaining 41.3% of deviance. Of these, leaf area index was the strongest predictor (22.02% of deviance explained), while the most important abiotic predictor was slope curvature (5.32%). Although geographic distance was a significant predictor, it contributed little to model fit (3.02%).

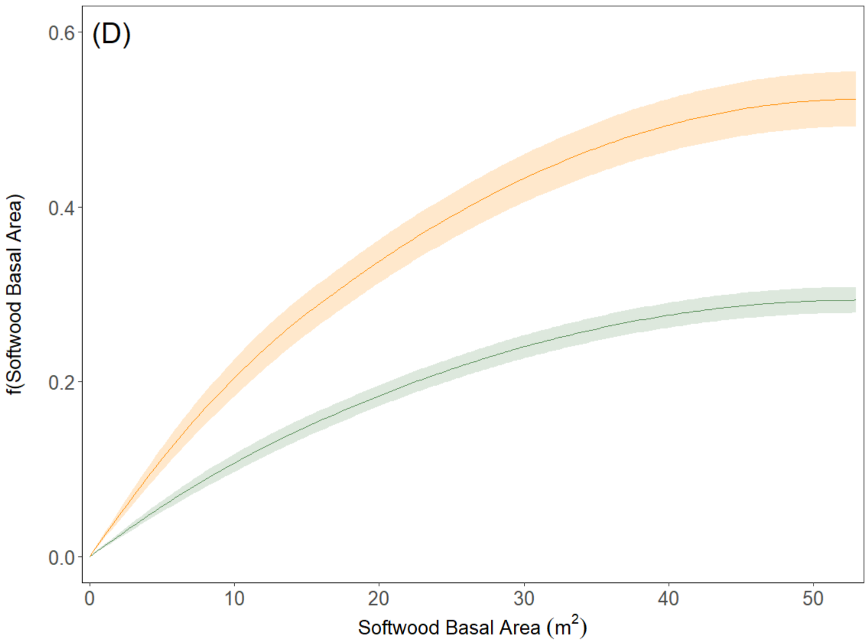
In the ecosystem response model, most fitted I-spline curves increased non-linearly and some were asymptotic (Figure 3). Higher change in model transformed predictor values (y-axis, Figure 3) corresponded directly with higher predictor values (x-axis, Figure 3) for leaf area index, normalized difference vegetation index, and hardwood basal area. Spline curves for softwood basal area, canopy height, and terrain ruggedness plateaued at mid to high predictor values. Geography did not contribute significantly to model fit, suggesting variations in dissimilarity were driven by relationships with biotic and abiotic predictors that did not vary markedly across the study area. In general, steeper changes in I-spline slope (e.g., where canopy height varied between 1 and 15 meters – Figure 3B) indicated greater dissimilarity between site-pairs, while flatter curve segments indicated less change (e.g., Figure 3A – where the terrain ruggedness index exceeds 2). Spline shapes for leaf area and normalized difference vegetation indices were relatively congruent. Here they showed prominent change in dissimilarity, between site-pairs, throughout most of these predictor ranges; parallels in I-splines shape and magnitude indicated their contributions to ecosystem-level responses were quite comparable.

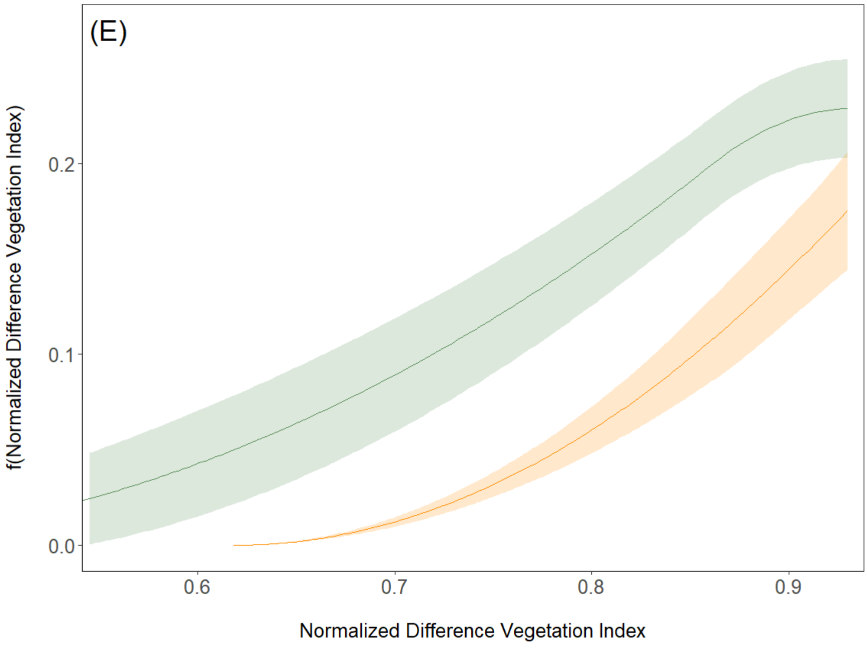
In our biotic response model, fitted I-spline curves for slope curvature and hardwood basal area showed direct correspondence between higher predictor values and higher ecological distance values throughout most of their range (Figure 3). In contrast, spline curves for canopy height, leaf area index, softwood basal area, and normalized difference vegetation index plateaued at mid or higher predictor values. Terrain ruggedness and geographic distance leveled off at lower values.

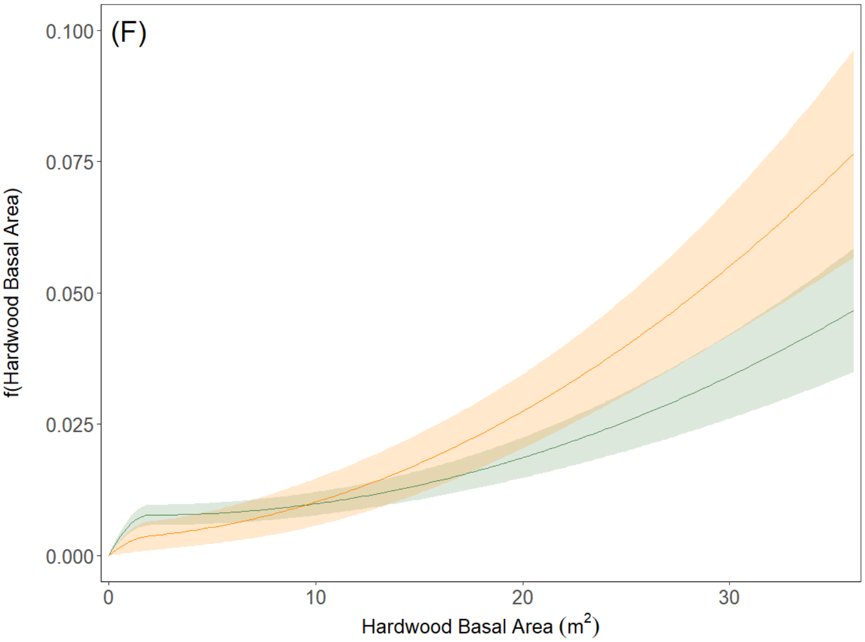


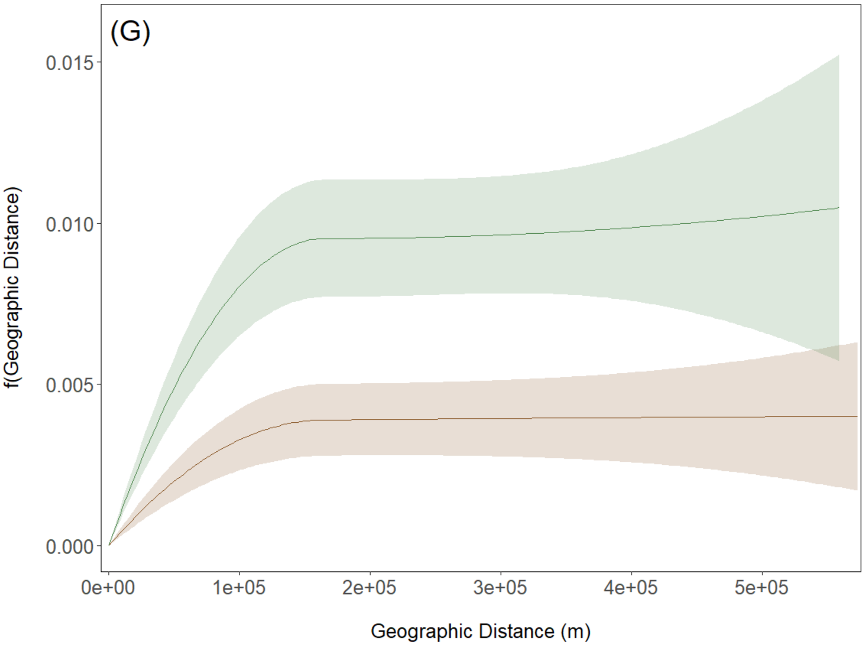

(B)
f(Canopy Height)
0.15
0.10
0.05
0.00
0
5
10
15
20
25
Canopy Height (m)

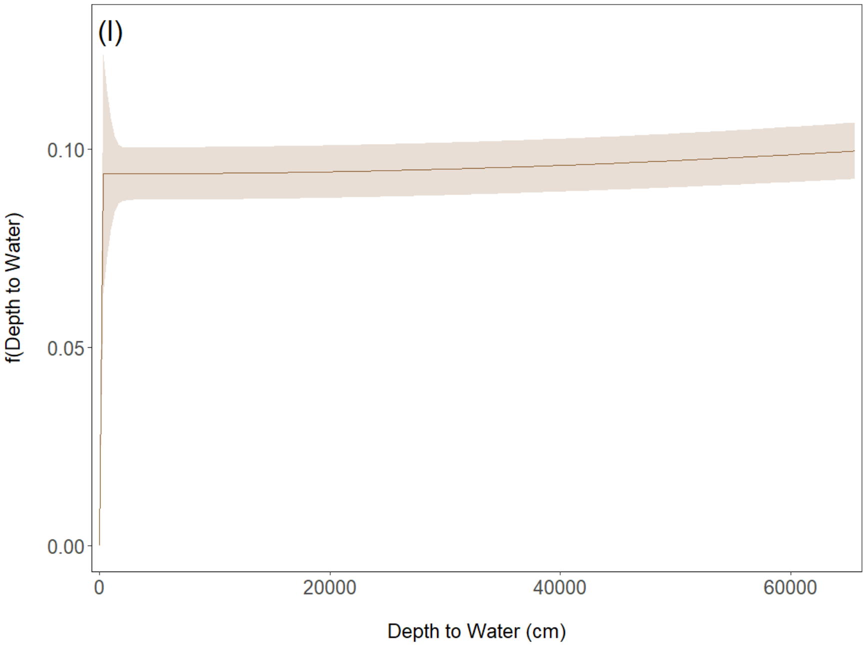

(C)
f(Leaf Area Index)
0.75
0.50
0.25
0.00
50
100
Leaf Area Index


(D)
f(Softwood Basal Area)
0.6
0.4
0.2
0.0
0
10
20
30
40
50
Softwood Basal Area (m^2)


(E)
f(Normalized Difference Vegetation Index)
0.2
0.1
0.0
0.6
0.7
0.8
0.9
Normalized Difference Vegetation Index


(F)
0.100
0.075
0.050
0.025
0.000
f(Hardwood Basal Area)
0
10
20
30
Hardwood Basal Area (m^2)


(G)
0.015
0.010
0.005
0.000
f(Geographic Distance)
0e+00
1e+05
2e+05
3e+05
4e+05
5e+05
Geographic Distance (m)



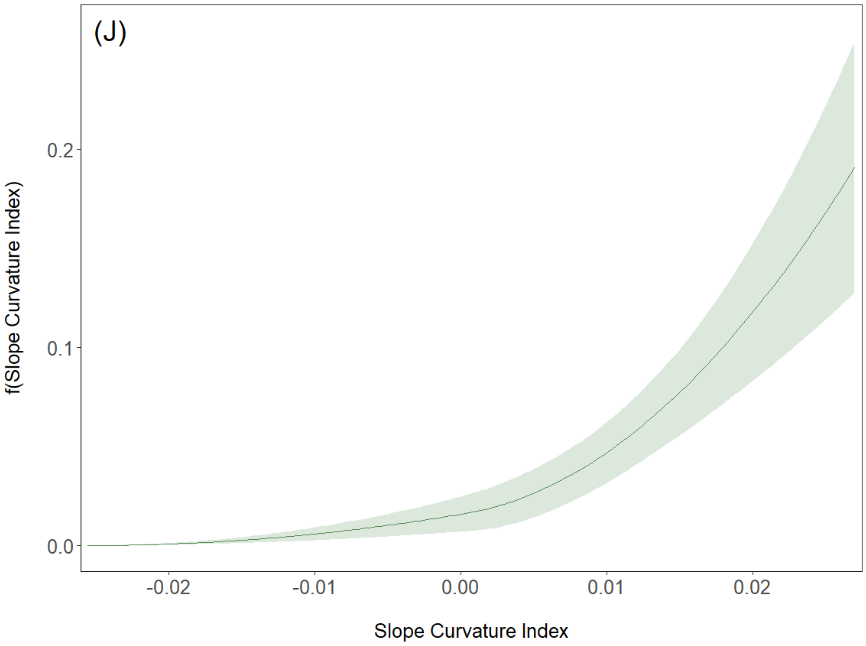


Figure 3. Fitted I-spline functions of significant predictors represented in the ecosystem (coloured orange), abiotic (coloured brown), and biotic (coloured green) response models. Each panel corresponds to an individual predictor with the x-axis (predictor) showing the native unit scale and the y-axis (f(predictor)) corresponding with GDM transformed values. The maximum height of each predictor curve corresponds with the amount of the ecological change along that predictor gradient. It indicates the importance of each predictor, while holding other variables constant (Mokany et al. 2022). Curve slope represents change in dissimilarity and how it shifts with increased predictor values. Error ribbons were created through boot-

strapping and represent +/- one standard deviation of predicted spline functions (Fitzpatrick et al. 2024). Predictor data are described in S1.

Ecosystem, Abiotic, and Biotic Responses – Comparison Among Individual Models

In general, outcomes of the ecosystem and biotic response models were more alike than either was to the abiotic response model. The ecosystem and biotic response models performed similarly, and shared similar sets of significant predictors (Table 1), including the three most important predictors (leaf area index, softwood basal area, and normalized vegetation difference index). The cumulative contribution of abiotic, biotic, and geographic predictors to each model (Figure 4) differed; yet again the ecosystem and biotic response models showed commonalities, particularly with the large relative contribution biotic predictors made to these formulations. I-spline functions for these two latter models also revealed parallels. Comparable curve inflections were apparent between canopy height, leaf area index, softwood basal area, and hardwood basal area I-splines (Figure 3).

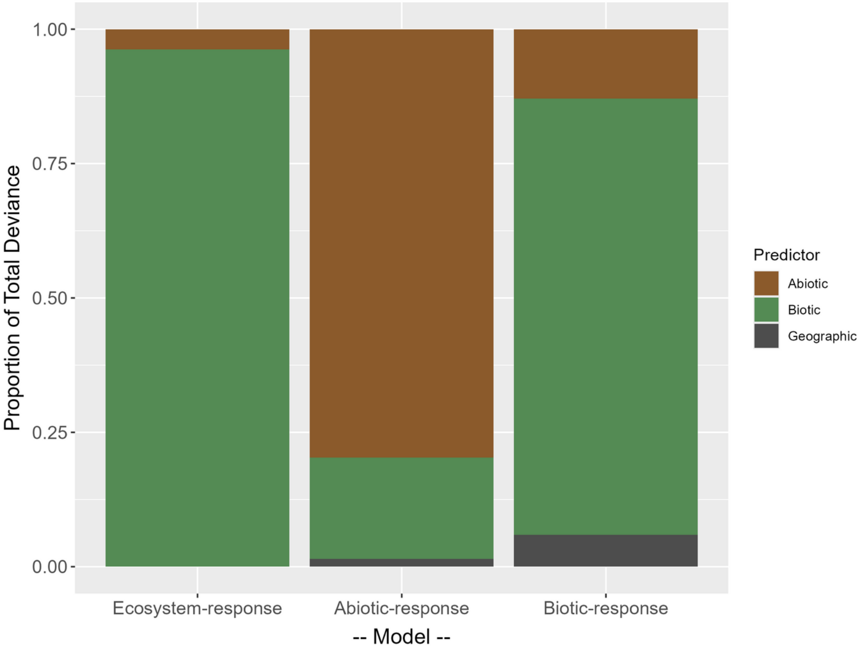


Figure 4 . Stacked bar plot showing proportion of total deviance explained by geographic, abiotic, and biotic predictors for each of the final ecosystem, abiotic, and biotic response models.

Spatial mapping of ecosystem patterns

Spatial GDM predictions, of the final ecosystem response model, revealed ecosystem patterns across Nova Scotia (Figure 5). Higher elevations in northern and central areas (shaded darker green and green-blue) are distinguishable from lower elevations elsewhere in the province. A broad area of the southwest (lighter green and brown shading), which occurs at lower elevation and supports more subdued relief, is also discernible.

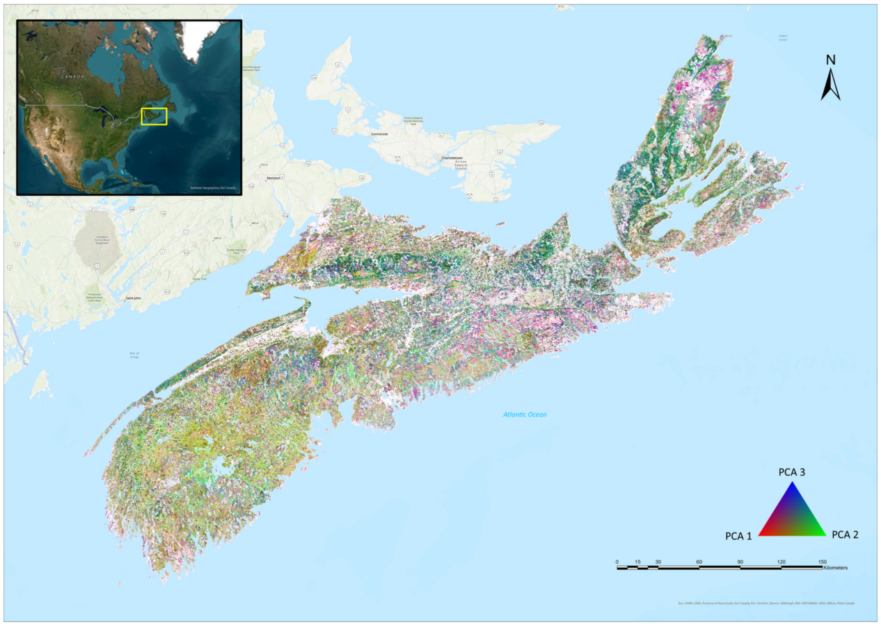


Figure 5. Predicted spatial ecosystem patterns across the study region. The map depicts the first three PCA axes of values from GDM transformed predictors layers for the final ecosystem response model, following procedures outlined in Mokany et al. (2022) and Fitzpatrick et al. (2024). Areas with colours closer on the RGB spectrum are predicted to have more similar ecosystems. Naturally unforested ecosystems, recently harvested forests, plantation forests, and areas completely cleared of trees (e.g., for agriculture, mining, urban development), have been nullified. Water bodies are shown in light blue.

Discussion

Our integrated modelling approach helps fill a gap in ecosystem spatial modelling capacity. We extend Ferrier and Guisan's (2006) well established '*assemble and predict together* ' strategy for community-level distribution modelling to predict ecosystem spatial patterns. Here, we model joint biotic and abiotic responses as a function of environmental gradients. Thereafter, we apply spatial turnover among different combinations of modelled biotic and abiotic responses as a basis for identifying ecosystem patterns. This effort marks one of the first spatial ecosystem models to integrate of biotic and abiotic responses. The novel approach helps illuminate relationships among biotic and abiotic ecosystem properties, and their drivers. It also provides a basis for resolving the collective contributions biotic and abiotic model responses make to ecosystem spatial heterogeneity across landscapes. Our approach can be applied in other regions to provide conservation planners and decision makers with a tool to predict how and where ecosystems vary, and a means to help understand the origins of these patterns. The approach is well suited to regions where the density of survey sites is low relative to the grain of spatial turnover in the targeted ecological entity (e.g., community, ecosystem) (Ferrier et al. 2007). It is also ideal when the objective is to predict continuous spatial variation in ecosystem makeup and to apply those predictions for mapping emergent biodiversity patterns (Basquill and Leroux 2023).

The ecosystem is central to recent global conservation agreements, such the Kunming-Montreal Global Biodiversity Framework, and new scientific guidance is available to implement these and other ecosystem targets across, global, national and sub-national extents (Nicholson et al. 2024, Venegas-Li et al. 2024). A critical impediment is that few sub-global regions have adequate ecosystem mapping (Xiao et al. 2024), and statistical models required to establish those maps are rare (Geary et al. 2020). To address these challenges, previous terrestrial approaches have included modelling the distribution of pre-classified ecosystem types (e.g., Simensen et al. 2020, Naas et al. 2024), or proxies including pre-classified vegetation community types (e.g., Comer et al. 2020, Jiménez-Alfaro et al. 2023) or remotely sensed land cover classes (e.g., Murray et al. 2022). Most examples have been conducted at coarser spatial grains and correspond with Ferrier and Guisan's (2006) '*assemble first, predict later* ' strategy for modelling biodiversity patterns. With this strategy, individual observations – species for example – are assembled (e.g., through numerical classification) into discrete units, such as community types, and those units are modelled in space. Following the '*assemble and predict together* ' strategy, our alternative approach fills a gap for modelling ecosystem patterns at the landscape extent. In addition, we predict at a fine spatial grain. This grain matches the spatial resolution where ecosystem restoration, and much ecosystem-based management and conservation, is implemented (e.g., Makela et al. 2012, Pressey et al. 2013, Aubin et al. 2024).

Different analytical approaches have distinct strengths, and their characteristic applications reflect varied modelling data and intents (Deschamps et al. 2023, Naas et al. 2024). Our adaptation of Ferrier and Guisan's (2006) '*assemble and predict together* ' strategy enabled us to parse the shared and independent components and determinants of ecosystem heterogeneity. More specifically, it allowed us to predict biotic, abiotic, and ecosystem responses to diverse environmental circumstances, which we operationalized in three separate models. Two of our models represent lower levels of ecological organization, which Levins (2011) contends have a controlling influence on ecosystem pattern and process. Predictions from lower ecological levels also allows ecosystem conservation practitioners to represent biotic and abiotic properties in model-informed conservation plans. Here, these distinctions may be necessary for managing or restoring specific groups of ecosystem components or services (e.g., wildlife habitat - Van der Biest et al. 2020; carbon sequestration and storage - Ameray et al. 2021; soil properties - Rader et al. 2022). Our modelling framework provides this functionality, enabling researchers to predict whole ecosystems and their parts, while identifying potential mechanisms.

Our foremost predictors of ecosystem dissimilarity were all vegetation-based, namely leaf area index, softwood basal area, and normalized difference vegetation index (Table 1). Vegetation predictors (e.g., canopy height, normalized vegetation difference index) similarly explained the largest proportion of variation in forest ecosystem distribution models of Norway (Naas et al. 2024). In distribution models of vegetation-based ecosystem proxies (e.g., Ponomarenko et al. 2019, Lee et al. 2021) spectral vegetation indices (e.g., normalized vegetation difference index) and remotely sensed vegetation cover are frequently the primary predictors. These mutual findings suggest the potential effectiveness of employing vegetation canopy features – which represent a fraction of total ecosystem composition and structure – to predict forest ecosystems.

The most influential predictors in our biotic and ecosystem models were identical. This might imply the predominant drivers of biotic properties mirror those shaping whole ecosystems – including constituent facets of abiotic diversity. An alternative interpretation is that the relative influence of abiotic predictors on ecosystem variation has been masked in our ecosystem formulation. Results of our independent biotic and abiotic response models lend relevant evidence. In the abiotic response model, terrain ruggedness and depth to water, both frequent topographic predictors in biodiversity and geodiversity models (Dilts et al 2023, Toivanen et al. 2024), were the top two predictors, accounting for 80% of total deviance explained (Figure 4). Neither of these predictors were important in the biotic or ecosystem response models. One explanation for these disparate findings may lie in our abiotic response model's performance, which was the lowest of the three builds. This model's lower relative performance may indicate new predictors of abiotic variation are warranted. Furthermore, including these same new predictors in an ecosystem response model could shift the ratio of meaningful predictors more evenly among biotic and abiotic predictors. Indeed, commonalities between the biotic and ecosystem response models, and the intermediate performance of the latter model, suggest these two formulations are more strongly favouring biotic properties and their respective predictors.

Generally, our models are exploratory and could benefit from empirical testing with out of sample data from different study areas or time frames (Tredennick et al. 2021). The absence of these data highlights a limitation of our adaptive approach (sensu Holling and Allen 2002). This approach is common in models where relationships between predictors and response variables are poorly understood (Tredennick et al. 2021, Planque et al. 2022), such as they are between ecosystem properties and their determinants (Soranno et al. 2019). Empirical testing could also lead to hypothesis generation and theory development, particularly for mechanisms of ecosystem assembly, which are inadequately substantiated (Levin 1998). Model outcomes could also be employed for making secondary predictions to explicitly link pattern and process (Gallagher et al. 2021). The framework we develop lends itself well to these objectives. It can be rapidly fit to large datasets, allowing for the development and testing of nested models for successive resolution of ecosystem patterns and drivers at various scales and levels of complexity.

One strategy for strengthening our ecosystem build is to draw more explicitly from geodiversity modelling and its potential for improving biodiversity predictions. Recognition of the interplay between biodiversity and geodiversity – the diversity of Earth's abiotic features and processes, including climate – has risen sharply, partly in response to rapidly changing global conditions (Schrodt et al. 2024). Efforts to bridge these two disciplinary foci have emerged from both biodiversity (Vernham et al. 2023) and geodiversity (Alahuhta et al. 2024, Toivanen et al. 2024) research streams. The ecosystem is an apparent focal unit for synthesizing across disciplines, for geodiversity is integral to ecosystems (Richter and Billings 2015, Holling 1992, Ochoa-Hueso et al. 2021). Yet, few ecosystem models jointly incorporate facets of biotic and abiotic diversity as responses (Basquill and Leroux 2023). While we strived to adequately represent abiotic responses in our ecosystem model, the inherent coarse spatial grain of many geodiversity predictors – including geology and climate (e.g., Hjort and Luoto 2012, Read et al. 2020) – precluded their use in our study. We selected predictors to match our survey grain following best practices for biodiversity distribution modelling (Chauvier et al. 2022). Although omitting coarse-grain predictors in our models may seem like a modelling impediment, it raises an opportunity for exploring ecosystem scaling relationships.

Ecosystems occur at all spatial scales (Fritsch et al. 2020) and scales selected for modelling correspond to study objectives (Geary et al. 2020). The fine resolution (10 m) in our models reflects the spatial grain where many topographically controlled terrestrial ecosystem properties (e.g., vegetation – Moeslund et al. 2013; soil – Seibert et al. 2007; water – Detty and McGuire 2010; organic matter – Burton et al. 2011) are strongly expressed. This grain coincides with the fine-grained mapping needed for much natural resource management (Pressey et al. 2013, D'Urban Jackson et al. 2020, Senf 2022) and applied forecasting (Dobrowski 2011). However, ecosystem properties may also be driven by processes occurring at other scales (Holling 1992). For example, climatic processes affect biodiversity from macro to microscales (Coelho et al. 2023, Kemppinen et al. 2024). The paucity of microscale climate data has limited their availability for fine-grained studies (Kling et al. 2024) and resulted in possibly misleading biodiversity predictions (Slavich et al. 2014, Manzoor et al. 2018). Notwithstanding this data deficit, one solution for investigating scaling relationships is to systematically examine the influence of spatial grain on model outcomes (e.g., Guisan et al. 2007). Numerous methods are available for altering grain to advance understanding of scaled relationships across landscapes (Graham et al. 2019, Markham et al. 2023). Our modelling framework would lend itself well to this inquiry, providing a means to test how scaling is affected by grain and level of ecological organization (i.e., biotic, abiotic, and ecosystem levels). Another benefit of our framework is that it could be coupled with separate spatial models to predict assemblages of ecosystem properties.

Our GDM-based framework is a strategy for predicting shifting combinations or turnover of ecosystem properties, analogous to GDM models of community turnover. Working from this premise, we posit the comparable but distinct value of predicting spatially structured assemblages of ecosystem properties. This objective could also be operationalized by extending community-level modelling techniques, such as joint species distribution modelling (jSDM; Basquill and Leroux (2023). jSDM is a community modelling technique (Pollock et al. 2014) which can be applied to predict biotic composition (Franklin 2023). The two adaptations of community-level modelling techniques – GDM in the present study and jSDM – offer complementary approaches for predicting ecosystem patterns. Here, we suggest they could be coupled to predict spatially structured 1) assemblages of ecosystem properties (via jSDM) and 2) continuous shifts in those assemblages (via GDM). Similar pairings of GDM and jSDM were employed for predicting taxonomic and functional composition and turnover of European peat bogs (Robroek et al. 2017), and the assembly and turnover of meiofaunal communities across Denmark (Macher et al. (2024).

Conclusions

Ecosystem spatial pattern modelling – sometime called ecosystem distribution modelling – is in early stages of maturity (Naas et al 2024), and there are few evaluations of suitable approaches. This is expected to change. While species distribution models greatly outnumber models for other levels of biodiversity (Zurell et al. 2022), interest in community and ecosystem spatial modelling is increasing rapidly (Geary et al. 2020, Simpkins et al. 2022). Much of the immediate demand has come from conservation scientists tasked with developing models to identify ecosystems for protection and restoration. This has prompted development of standardized classifications and mapping tools, including those for the red list of ecosystems (Keith et al. 2022, Murray et al. 2022). Yet very few countries presently have suitable models for mapping ecosystems (Xiao et al. 2024) and available models emphasize vegetation proxies. Our framework offers an alternative approach. Our joint emphasis on biotic and abiotic response variables from field surveys contrasts with other approaches. Biotic and abiotic properties are the building blocks of ecosystems (Holling 1992). Predicting regular shifts in groups of these properties is essential for resolving and understanding ecosystem pattern (Levin 1998, Levin et al. 2001). Such patterns express ecosystem assembly outcomes, including the factors shaping lower levels of ecological organization (Keith et al. 2022). Overall, the framework we present is intended to help advance general understanding of ecosystem patterns, which remain poorly understood (Loreau 2020).

References

Alahuhta, J., Garcia-Giron, J., Hjort, J., Salminen, H., Tukiainen, H. and Heino, J., 2024. Quantitative measurement of geodiversity uniqueness: research implications and conservation applications. *Philosophical Transactions of the Royal Society A* , *382* (2269), p.20230056.

Ameray, A., Bergeron, Y., Valeria, O., Montoro Girona, M. and Cavard, X., 2021. Forest carbon management: A review of silvicultural practices and management strategies across boreal, temperate and tropical forests. *Current Forestry Reports* , pp.1-22.

Artime, O. and De Domenico, M., 2022. From the origin of life to pandemics: Emergent phenomena in complex systems. Philosophical Transactions of the Royal Society A, 380(2227), p.20200410.

Aubin, I., Deschenes, E., Santala, K.R., Emilson, E.J., Schoonmaker, A.L., McIntosh, A.C., Bourgeois, B., Cardou, F., Dupuch, A., Handa, I.T. and Lapointe, M., 2024. Restoring forest ecosystem services through trait-based ecology. *Environmental Reviews* .

Balandier, P., Marell, A., Prevosto, B. and Vincenot, L., 2022. Tamm review: Forest understorey and overstorey interactions: So much more than just light interception by trees. *Forest Ecology and Management* , *526* , p.120584.

Baldwin, K., Chapman, K., Meidinger, D., Uhlig, P., Allen, L., Basquill, S., Faber-Langendoen, D., Flynn, N., Kennedy, C., Mackenzie, W. and Major, M., 2019. The Canadian national vegetation classification: principles, methods, and status. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre.

Baldwin, K.; Allen, L.; Basquill, S.; Chapman, K.; Downing, D.; Flynn, N.; MacKenzie, W.; Major, M.; Meades, W.; Meidinger, D.; Morneau, C.; Saucier, J-P.; Thorpe, J.; Uhlig, P. 2020. Vegetation Zones of Canada: a Biogeoclimatic Perspective. Nat. Resour. Can., Info. Rep. Number: GLC-X-25. Can. For. Ser., Sault Ste. Marie, ON.

Basquill, S.P. and Leroux, S.J., 2023. Predicting ecosystem pattern across landscapes. Oikos, 2023(10), p.e09873.

Burton, J.I., Mladenoff, D.J., Clayton, M.K. and Forrester, J.A., 2011. The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. *Journal of Ecology* , *99* (3), pp.764-776.

CBD 2022a. Decision adopted by the conference of the parties to the convention on biological diversity 15/4. Kunming-Montreal global biodiversity framework. https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf.

CBD 2022b. Decision adopted by the conference of the parties to the convention on biological diversity 15/6. Mechanisms for planning, monitoring, reporting and review. https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-06-en.pdf.

Chauvier, Y., Descombes, P., Gueguen, M., Boulangeat, L., Thuiller, W. and Zimmermann, N.E., 2022. Resolution in species distribution models shapes spatial patterns of plant multifaceted diversity. Ecography, 2022(10), p.e05973.

Coelho, M.T.P., Barreto, E., Rangel, T.F., Diniz-Filho, J.A.F., Wuest, R.O., Bach, W., Skeels, A., McFadden, I.R., Roberts, D.W., Pellissier, L. and Zimmermann, N.E., 2023. The geography of climate and the global patterns of species diversity. Nature, 622(7983), pp.537-544.

Comer, P.J., Hak, J.C., Josse, C. and Smyth, R., 2020. Long-term loss in extent and current protection of terrestrial ecosystem diversity in the temperate and tropical Americas. *PLoS One* , *15* (6), p.e0234960.

Cox, N.J., 2011. Stata tip 96: Cube roots. *The stata journal* ,*11* (1), pp.149-154.

D'Urban Jackson, T., Williams, G.J., Walker-Springett, G. and Davies, A.J., 2020. Three-dimensional digital mapping of ecosystems: a new era in spatial ecology. *Proceedings of the Royal Society B* ,*287* (1920), p.20192383.

Deschamps, G., Poggiato, G., Brun, P., Galiez, C. and Thuiller, W., 2023. Predict first–assemble later versus assemble first–predict later: Revisiting the dilemma for functional biogeography. *Methods in Ecology and Evolution* , *14* (10), pp.2680-2696.

Detty, J.M. and McGuire, K.J., 2010. Topographic controls on shallow groundwater dynamics: implications of hydrologic connectivity between hillslopes and riparian zones in a till mantled catchment.*Hydrological Processes* , *24* (16), pp.2222-2236.

Dilts, T.E., Blum, M.E., Shoemaker, K.T., Weisberg, P.J. and Stewart, K.M., 2023. Improved topographic ruggedness indices more accurately model fine-scale ecological patterns. *Landscape Ecology* ,*38* (6), pp.1395-1410.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global change biology* , *17* (2), pp.1022-1035.

ECCC 2024. Canada's 2030 Nature Strategy: Halting and Reversing Biodiversity Loss in Canada. Environment and Climate Change Canada. Gatineau, Quebec. ISBN: 978-0-660-72244-3

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., De Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M. and Wilkinson, D.J., 2013. Do simple models lead to generality in ecology? Trends in ecology & evolution, 28(10), pp.578-583.

Ferrier, S., Drielsma, M., Manion, G. and Watson, G., 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. Biodiversity & Conservation, 11, pp.2309-2338.

Ferrier, S. and Guisan, A., 2006. Spatial modelling of biodiversity at the community level. Journal of applied ecology, 43(3), pp.393-404.

Ferrier, S., Manion, G., Elith, J. and Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and distributions, 13(3), pp.252-264.

Fitzpatrick, M., Mokany, K., Manion, G., Nieto-Lugilde, D., Ferrier, S. 2024. gdm: Generalized Dissimilarity Modeling_. R package version 1.6.0, https://github.com/fitzLab-AL/gdm/, <https://mfitzpatrick.al.umces.edu/gdm/>.

Franklin, J., 2023. Species distribution modelling supports the study of past, present and future biogeographies. *Journal of Biogeography* ,*50* (9), pp.1533-1545.

Fritsch, M., Lischke, H. and Meyer, K.M., 2020. Scaling methods in ecological modelling. *Methods in Ecology and Evolution* ,*11* (11), pp.1368-1378.

Gallagher, C.A., Chudzinska, M., Larsen-Gray, A., Pollock, C.J., Sells, S.N., White, P.J. and Berger, U., 2021. From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. Biological Reviews, 96(5), pp.1868-1888.

Geary, W.L., Bode, M., Doherty, T.S., Fulton, E.A., Nimmo, D.G., Tulloch, A.I., Tulloch, V.J. and Ritchie, E.G., 2020. A guide to ecosystem models and their environmental applications. Nature Ecology & Evolution, 4(11), pp.1459-1471.

Gottschall, F., Cesarz, S., Auge, H., Kovach, K.R., Mori, A.S., Nock, C.A. and Eisenhauer, N., 2022. Spatiotemporal dynamics of abiotic and biotic properties explain biodiversity–ecosystem-functioning relationships. Ecological Monographs, 92(1), p.e01490.

Graham, L.J., Spake, R., Gillings, S., Watts, K. and Eigenbrod, F., 2019. Incorporating fine-scale environmental heterogeneity into broad-extent models. *Methods in Ecology and Evolution* ,*10* (6), pp.767-778.

Guisan, A., Graham, C.H., Elith, J., Huettmann, F. and NCEAS Species Distribution Modelling Group, 2007. Sensitivity of predictive species distribution models to change in grain size. *Diversity and distributions* , *13* (3), pp.332-340.

Guisan, A., Thuiller, W. and Zimmermann, N.E., 2017. Habitat suitability and distribution models: with applications in R. Cambridge University Press.

Halvorsen, R., Skarpaas, O., Bryn, A., Bratli, H., Erikstad, L., Simensen, T. and Lieungh, E., 2020. Towards a systematics of ecodiversity: The EcoSyst framework. *Global Ecology and Biogeography* , *29* (11), pp.1887-1906.

Hijmans, R. 2023. terra: Spatial Data Analysis. R package version 1.7-29, <https://CRAN.R-project.org/package=terra>.

Hjort, J. and Luoto, M., 2012. Can geodiversity be predicted from space? *Geomorphology* , *153* , pp.74-80.

Hjort, J., Tukiainen, H., Salminen, H., Kemppinen, J., Kiilunen, P., Snare, H., Alahuhta, J. and Maliniemi, T., 2022. A methodological guide to observe local-scale geodiversity for biodiversity research and management. *Journal of Applied Ecology* , *59* (7), pp.1756-1768.

Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological monographs* , *62* (4), pp.447-502.

Holling, C.S. and Allen, C.R., 2002. Adaptive inference for distinguishing credible from incredible patterns in nature. Ecosystems, 5, pp.319-328.

Huxley, J.D., White, C.T., Humphries, H.C., Weber, S.E. and Spasojevic, M.J., 2023. Plant functional traits are dynamic predictors of ecosystem functioning in variable environments. Journal of Ecology, 111(12), pp.2597-2613.

Jimenez-Alfaro, B., Aunina, L., Carbognani, M., Ditě, D., Fernández-Pascual, E., Garbolino, E., Hajek, O., Hajkova, P., Ivchenko, T.G., Jandt, U. and Jansen, F., 2023. Habitat-based biodiversity responses to macroclimate and edaphic factors in European fen ecosystems. *Global Change Biology* , *29* (23), pp.6756-6771.

Kemppinen, J., Lembrechts, J.J., Van Meerbeek, K., Carnicer, J., Chardon, N.I., Kardol, P., Lenoir, J., Liu, D., Maclean, I., Pergl, J. and Saccone, P., 2024. Microclimate, an important part of ecology and biogeography. *Global Ecology and Biogeography* , *33* (6), p.e13834.

Keith, D.A., Ferrer-Paris, J.R., Nicholson, E., Bishop, M.J., Polidoro, B.A., Ramirez-Llodra, E., Tozer, M.G., Nel, J.L., Mac Nally, R., Gregr, E.J. and Watermeyer, K.E., 2022. A function-based typology for Earth's ecosystems. Nature, 610(7932), pp.513-518.

Keys, K., Neily, P., Maston, S. Quigley, E., Basquill, S., Stewart, B. 2023. Forest Ecosystem Classification for Nova Scotia (2022): Technical Guide. Nova Scotia Department of Natural Resources, Renewable Resources Branch. NRR Biodiversity Technical Report 2023-003.

Kling, M.M., Baer, K.C. and Ackerly, D.D., 2024. A tree's view of the terrain: downscaling bioclimate variables to high resolution using a novel multi-level species distribution model. *Ecography* ,*2024* (9), p.e07131.

Lapierre, J.F., Collins, S.M., Seekell, D.A., Spence Cheruvelil, K., Tan, P.N., Skaff, N.K., Taranu, Z.E., Fergus, C.E. and Soranno, P.A., 2018. Similarity in spatial structure constrains ecosystem relationships: Building a macroscale understanding of lakes. Global Ecology and Biogeography, 27(10), pp.1251-1263.

Lee, C.K., Nicholson, E., Duncan, C. and Murray, N.J., 2021. Estimating changes and trends in ecosystem extent with dense time-series satellite remote sensing. *Conservation Biology* , *35* (1), pp.325-335.

Levin, S.A., 1998. Ecosystems and the biosphere as complex adaptive systems. Ecosystems, 1, pp.431-436.

Levin, S.A., Dushoff, J. and Keymer, J.E., 2001. Community assembly and the emergence of ecosystem pattern. *Scientia Marina* ,*65* (S2), pp.171-179.

Levin, S.A., 2011. Evolution at the ecosystem level: On the evolution of ecosystem patterns. Contributions to science, 7(1), pp.11-16.

Loreau, M. 2020. Ecosystem. – In: Dobson, A. Tilman, D. and Holt, R. D. (eds), Unsolved problems in ecology. Princeton Univ. Press.

Macher, J.N., Pichler, M., Creer, S., Martinez, A., Fontaneto, D. and Renema, W., 2024. Metacommunity theory and metabarcoding reveal the environmental, spatial, and biotic drivers of meiofaunal communities in sandy beaches. *bioRxiv* , pp.2024-07.

Makela, A., del Rio, M., Hynynen, J., Hawkins, M.J., Reyer, C., Soares, P., van Oijen, M. and Tome, M., 2012. Using stand-scale forest models for estimating indicators of sustainable forest management. *Forest Ecology and Management* , *285* , pp.164-178.

Manzoor, S.A., Griffiths, G. and Lukac, M., 2018. Species distribution model transferability and model grain size–finer may not always be better. *Scientific reports* , *8* (1), p.7168.

Markham, K., Frazier, A.E., Singh, K.K. and Madden, M., 2023. A review of methods for scaling remotely sensed data for spatial pattern analysis. *Landscape Ecology* , *38* (3), pp.619-635.

Mod, H.K., Scherrer, D., Luoto, M. and Guisan, A., 2016. What we use is not what we know: environmental predictors in plant distribution models. Journal of Vegetation Science, 27(6), pp.1308-1322.

Moeslund, J.E., Arge, L., Bocher, P.K., Dalgaard, T., Odgaard, M.V., Nygaard, B. and Svenning, J.C., 2013. Topographically controlled soil moisture is the primary driver of local vegetation patterns across a lowland region. *Ecosphere* , *4* (7), pp.1-26.

Mokany, K., Ware, C., Woolley, S.N., Ferrier, S. and Fitzpatrick, M.C., 2022. A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. *Global Ecology and Biogeography* , *31* (4), pp.802-821.

Murray, N.J., Worthington, T.A., Bunting, P., Duce, S., Hagger, V., Lovelock, C.E., Lucas, R., Saunders, M.I., Sheaves, M., Spalding, M. and Waltham, N.J., 2022. High-resolution mapping of losses and gains of Earth's tidal wetlands. *Science* , *376* (6594), pp.744-749.

Naimi, B., Hamm, Na., Groen, T.A., Skidmore, A.K., Toxopeus, A.G. 2014. Where is positional uncertainty a problem for species distribution modelling. Ecography 37, 191-203. doi:10.1111/j.1600-0587.2013.00205.x <https://doi.org/10.1111/j.1600-0587.2013.00205.x>.

Naas, A.E., Keetz, L.T., Halvorsen, R., Horvath, P., Mienna, I.M., Simensen, T. and Bryn, A., 2024. Choice of predictors and complexity for ecosystem distribution models: effects on performance and transferability. *Ecography* , p.e07269.

Natural Resources Canada 2015. Image data from: trees, insects, and diseases of Canada's Forests. – https://tidcf.nrcan.gc.ca/en/home.

Neily, P.D., Basquill, S., Quigley, E., and Keys, K. 2017. Ecological land classification for Nova Scotia. Nova Scotia. Report FOR 2017-13. Department of Lands and Forestry, Halifax, NS.

Neily, P. Basquill, S. Quigley, E., Keys, K., Maston, S., Stewart, B. 2023. Forest Ecosystem Classification for Nova Scotia 2022: Field Guide. Nova Scotia Department of Natural Resources, Renewable Resources Branch. NRR Biodiversity Technical Report 2023-002.

Nicholson, E., Fulton, E.A., Brooks, T.M., Blanchard, R., Leadley, P., Metzger, J.P., Mokany, K., Stevenson, S., Wintle, B.A., Woolley, S.N. and Barnes, M., 2019. Scenarios and models to support global conservation targets. Trends in ecology & evolution, 34(1), pp.57-68.

Nicholson, E., Andrade, A., Brooks, T.M., Driver, A., Ferrer-Paris, J.R., Grantham, H., Gudka, M., Keith, D.A., Kontula, T., Lindgaard, A. and Londono-Murcia, M.C., 2024. Roles of the Red List of Ecosystems in the Kunming-Montreal Global Biodiversity Framework. *Nature Ecology & Evolution* , *8* (4), pp.614-621.

Ochoa-Hueso, R., Delgado-Baquerizo, M., Risch, A.C., Schrama, M., Morrien, E., Barmentlo, S.H., Geisen, S., Hannula, S.E., Resch, M.C., Snoek, B.L. and van der Putten, W.H., 2021. Ecosystem coupling: A unifying framework to understand the functioning and recovery of ecosystems. *One Earth* , *4* (7), pp.951-966.

Perino, A., Pereira, H.M., Felipe-Lucia, M., Kim, H., Kuhl, H.S., Marselle, M.R., Meya, J.N., Meyer, C., Navarro, L.M., van Klink, R. and Albert, G., 2022. Biodiversity post-2020: Closing the gap between global targets and national-level implementation. *Conservation Letters* ,*15* (2), p.e12848.

Planque, B., Aarflot, J.M., Buttay, L., Carroll, J., Fransner, F., Hansen, C., Husson, B., Langangen, O., Lindstrom, U., Pedersen, T. and Primicerio, R., 2022. A standard protocol for describing the evaluation of ecological models. *Ecological Modelling* , *471* , p.110059.

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A. and McCarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* ,*5* (5), pp.397-406.

Ponomarenko, S., McLennan, D., Pouliot, D. and Wagner, J., 2019. High resolution mapping of tundra ecosystems on Victoria Island, Nunavut–Application of a standardized terrestrial ecosystem classification. *Canadian Journal of Remote Sensing* , *45* (5), pp.551-571.

Pressey, R.L., Mills, M., Weeks, R. and Day, J.C., 2013. The plan of the day: managing the dynamic transition from regional conservation designs to local conservation actions. *Biological Conservation* ,*166* , pp.155-169.

R Core Team 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Rader, A.J., Chiquoine, L.P., Weigand, J.F., Perkins, J.L., Munson, S.M. and Abella, S.R., 2022. Biotic and abiotic treatments as a bet-hedging approach to restoring plant communities and soil functions.*Restoration*

Ecology , *30* (2), p.e13527

Read, Q.D., Zarnetske, P.L., Record, S., Dahlin, K.M., Costanza, J.K., Finley, A.O., Gaddis, K.D., Grady, J.M., Hobi, M.L., Latimer, A.M. and Malone, S.L., 2020. Beyond counts and averages: Relating geodiversity to dimensions of biodiversity. *Global Ecology and Biogeography* ,*29* (4), pp.696-710.

Richter, D.D. and Billings, S.A., 2015. ‘One physical system’: Tansley’s ecosystem as Earth’s critical zone. New Phytologist, 206(3), pp.900-912.

Riva, F., Graco-Roza, C., Daskalova, G.N., Hudgins, E.J., Lewthwaite, J.M., Newman, E.A., Ryo, M. and Mammola, S., 2023. Toward a cohesive understanding of ecological complexity. Science Advances, 9(25), p.eabq4207.

Robroek, B.J., Jassey, V.E., Payne, R.J., Marti, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S.J., Dise, N.B., Kattge, J. and Zając, K., 2017. Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications* , *8* (1), p.1161.

Schrodt, F., Vernham, G., Bailey, J., Field, R., Gordon, J.E., Gray, M., Hjort, J., Hoorn, C., Hunter Jr, M.L., Larwood, J. and Lausch, A., 2024. The status and future of essential geodiversity variables.*Philosophical Transactions of the Royal Society A* ,*382* (2269), p.20230052.

Seibert, J., Stendahl, J. and Sørensen, R., 2007. Topographical influences on soil properties in boreal forests. *Geoderma* ,*141* (1-2), pp.139-148.

Senf, C., 2022. Seeing the system from above: the use and potential of remote sensing for studying ecosystem dynamics. *Ecosystems* ,*25* (8), pp.1719-1737.

Sillero, N. and Barbosa, A.M., 2021. Common mistakes in ecological niche models. International Journal of Geographical Information Science, 35(2), pp.213-226.

Simensen, T., Horvath, P., Vollering, J., Erikstad, L., Halvorsen, R. and Bryn, A., 2020. Composite landscape predictors improve distribution models of ecosystem types. Diversity and Distributions, 26(8), pp.928-943.

Simpkins, C.E., Hanß, S., Spangenberg, M.C., Salecker, J., Hesselbarth, M.H. and Wiegand, K., 2022. spectre: an R package to estimate spatially-explicit community composition using sparse data.*Ecography* , *2022* (12), p.e06272.

Slavich, E., Warton, D.I., Ashcroft, M.B., Gollan, J.R. and Ramp, D., 2014. Topoclimate versus macroclimate: how does climate mapping methodology affect species distribution models and climate change projections? *Diversity and Distributions* , *20* (8), pp.952-963.

Soley-Guardia, M., Alvarado-Serrano, D.F. and Anderson, R.P., 2024. Top ten hazards to avoid when modeling species distributions: a didactic guide of assumptions, problems, and recommendations. Ecography, 2024(4), p.e06852.

Soranno, P.A., Wagner, T., Collins, S.M., Lapierre, J.F., Lottig, N.R. and Oliver, S.K., 2019. Spatial and temporal variation of ecosystem properties at macroscales. Ecology Letters, 22(10), pp.1587-1598.

Wei, T. and Simko, V. 2021. R package 'corrplot': Visualization of a Correlation Matrix (Version 0.92). Available from https://github.com/taiyun/corrplot

Toivanen, M., Maliniemi, T., Hjort, J., Salminen, H., Ala-Hulkko, T., Kemppinen, J., Karjalainen, O., Poturalska, A., Kiilunen, P., Snare, H. and Leppiniemi, O., 2024. Geodiversity data for Europe.*Philosophical Transactions of the Royal Society A* ,*382* (2269), p.20230173.

Tredennick, A.T., Hooker, G., Ellner, S.P. and Adler, P.B., 2021. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology, 102(6), p.e03336.

Van der Biest, K., Meire, P., Schellekens, T., D'hondt, B., Bonte, D., Vanagt, T. and Ysebaert, T., 2020. Aligning biodiversity conservation and ecosystem services in spatial planning: Focus on ecosystem processes. *Science of the Total Environment* , *712* , p.136350.

van der Plas, F., 2019. Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews* ,*94* (4), pp.1220-1245.

van der Plas, F., Schroder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R.L., Buchmann, N., De Kroon, H., Ebeling, A. and Eisenhauer, N., 2020. Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. Nature ecology & evolution, 4(12), pp.1602-1611.

Venegas-Li, R., Grantham, H.S., Rainey, H., Diment, A., Tizard, R. and Watson, J.E., 2023. An operational methodology to identify Critical Ecosystem Areas to help nations achieve the Kunming–Montreal Global Biodiversity Framework. *Conservation Letters* , p.e13037.

Vernham, G., Bailey, J.J., Chase, J.M., Hjort, J., Field, R. and Schrodt, F., 2023. Understanding trait diversity: the role of geodiversity. *Trends in Ecology & Evolution* , *38* (8), pp.736-748.

Xiao, H., Driver, A., Etter, A., Keith, D.A., Obst, C., Traurig, M.J. and Nicholson, E., 2024. Synergies and complementarities between ecosystem accounting and the Red List of Ecosystems. *Nature Ecology & Evolution* , pp.1-10.

Zarnetske, P.L., Read, Q.D., Record, S., Gaddis, K.D., Pau, S., Hobi, M.L., Malone, S.L., Costanza, J., M. Dahlin, K., Latimer, A.M. and Wilson, A.M., 2019. Towards connecting biodiversity and geodiversity across scales with satellite remote sensing. *Global Ecology and Biogeography* , *28* (5), pp.548-556.

Zurell, D., Konig, C., Malchow, A.K., Kapitza, S., Bocedi, G., Travis, J. and Fandos, G., 2022. Spatially explicit models for decision-making in animal conservation and restoration. *Ecography* ,*2022* (4).

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M., 2009. Mixed effects models and extensions in ecology with R (Vol. 574). New York: Springer.