

Beyond static species distribution models: temporally dynamic, spatially nested species distribution models reduce extrapolation for future projections

Camila Rocabado^{1*}, Derek Corcoran², Trine Bilde², Samuel J. L. Gascoigne¹, Signe Normand², Marjo Saastamoinen³, Santiago J. E. Velazco^{4,5}, Damaris Zurell⁶, Roslyn Henry^{1,7} & Greta Bocedi¹

*Corresponding author: camilarocabado7@gmail.com

¹School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK.

²Department of Biology, Aarhus University, Aarhus, Denmark

³Department of Biosciences, Metapopulation Research Centre, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland.

⁴Instituto de Biología Subtropical, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Misiones, Puerto Iguazú, Argentina.

⁵Center for Open Geographical Science, Department of Geography, San Diego State University, San Diego, CA, USA.

⁶Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany.

⁷Interdisciplinary Institute, University of Aberdeen, UK.

ORCID IDs:

CR: 0009-0004-5255-8329;

DC: 0000-0002-0248-6230;

TB: 0000-0002-0341-161X;

SN: 0000-0002-8782-4154;

MS: 0000-0001-7009-2527;

SJLG: 0000-0002-2984-1810;

DZ: 0000-0002-4628-3558;

RH: 0000-0003-2942-6753;

GB: 0000-0002-9131-6670.

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Abstract

Species distribution models are widely used to project biodiversity responses to climate change, but geographically restricted training data can truncate species' climatic niches, increasing reliance on extrapolation. Spatially nested models can reduce this truncation by incorporating climatic information from species' wider distributions. However, how accounting for interannual environmental variation rather than temporal averages affects extrapolation remains unclear. Using occurrence records for 28 butterfly species in Denmark, we compared four approaches combining regional *versus* spatially nested training data with static (long-term average) *versus* dynamic (annual) predictors. Regional models used climatic information for Denmark, whereas nested models incorporated European-scale climatic suitability. Static models used temporally averaged predictors, while dynamic models matched observations to year-specific conditions. We assessed climatic niche coverage, model's predictive performance under spatial block cross-validation and a common forward temporal holdout, and future climatic conditions outside the training domain. Regional training excluded ~ 30% of the climatic space occupied across species' European distributions. Temporally averaged predictors captured nearly all climatic space represented by annual conditions across Europe, but only ~ 37% within Denmark. In the forward evaluation for 2010–2018, dynamic models outperformed static models. Under spatial cross-validation, static regional models outperformed dynamic regional models, whereas static and dynamic nested models did not differ significantly. Spatial nesting and temporal matching substantially reduced future extrapolation, with their combination consistently requiring the least extrapolation. Model choice should therefore reflect the intended application. Static models may be adequate for mapping contemporary suitability within well-represented environmental conditions when supported by spatial validation. For projections under environmental change, broadening training domain across space and time reduces extrapolation, even without improving spatial discrimination. Predictive discrimination and environmental support for transfer should be assessed jointly, with temporal validation and extrapolation risk receiving particular attention for climate-change projections.

Introduction

Understanding where species occur and which processes determine their distributions is central to ecology and conservation. Species distribution models (SDMs) relate occurrences to environmental conditions and are widely used to project shifts in suitable habitat under climate and land-use change (Elith and Leathwick 2009, Sillero et al. 2021). Such projections inform protected area design (Penjor et al. 2021), restoration (Strassburg et al. 2020), reintroduction (Miranda et al. 2019, Bellis et al. 2021) and assisted colonization efforts (Casazza et al. 2021).

Correlative SDMs are popular because they have modest data requirements, extensive methodological support and can be projected across space and time (Elith and Franklin 2024). However, SDMs present several well-known limitations (Dormann et al. 2012), including poor transferability when models are projected beyond the environmental conditions represented in the training data (Qiao et al. 2019, Rousseau and Betts 2022, Velazco et al. 2024). Such transferability problems can arise when training data inadequately represent the environmental conditions experienced by a species, either spatially or temporally. Two important sources of this mismatch are niche truncation due to geographically restricted training data (Sánchez-Fernández et al. 2011, Adde et al. 2023, Mateo et al. 2024, Guisan et al. 2025) and temporal mismatch between species observations and environmental predictors (Pang et al. 2022, Zurell et al. 2024).

SDMs trained with regional datasets may omit environmental conditions occupied elsewhere in a species' range if the range is not entirely encompassed in the training data. This omission can lead to truncating the estimated realised niche and biasing projections across space and time, reducing predictive accuracy under extrapolation (Hannemann et al. 2016, Chevalier et al. 2021, 2022, Goicolea et al. 2025, Guisan et al. 2025). Geographically restricted, regional data may reflect only a subset, potentially distinct (e.g., an ecotype), of the environmental space and may not represent the species' full niche and distribution (Scherrer et

al. 2021). The consequent underestimation of niche breadth may increase predicted vulnerability to climate change (Serra-Diaz et al. 2016, Scherrer et al. 2021), while the way response curves are truncated shapes projection biases (Guisan et al. 2025).

Spatially nested SDMs (NSDMs) address niche truncation by combining a coarse range-wide (“global”) climatic model with a fine-resolution “regional” model (Guisan et al. 2025). Beyond capturing the present environmental space the species occupies, these models also account for scale dependency by considering that different drivers of species’ distributions act at different spatial scales, with climate acting at the macroscale to define range limits, and land-use driving habitat suitability at the local scale (Pearson et al. 2004). By explicitly linking range-wide climatic tolerances to local habitat conditions, nested models can reduce niche truncation, stabilise response functions and improve model performance (Goicolea et al. 2025, Guisan et al. 2025).

A second limitation of SDMs, which is less often acknowledged, is the temporal averaging of environmental predictors. Multi-year climatic means and static land-cover snapshots may not adequately represent the conditions associated with occurrence records, potentially biasing niche estimates (Zurell et al. 2024). This is particularly relevant for short-lived and/or mobile taxa, whose populations respond rapidly to interannual temperature variation and extreme events (Srivastava and Carroll 2023). Similarly, local habitat availability can change substantially over the modelled time window. Static (or long-term averaged) land-cover layers may therefore misrepresent the habitat context experienced by populations at the time of observation, and applying land-cover corrections (e.g., masking to restrict models’ projections to intact habitats) can substantially reduce estimated suitable area, highlighting the need to account for non-climatic dynamics as well (Pang et al. 2021, 2024). Models in which observations are spatiotemporally matched to predictors—hereafter termed “dynamic”—can improve ecological realism and, in some studies, predictive performance and temporal transferability (Bateman et al. 2016, Abrahms et al. 2019, Milanese et al. 2020, El-Gabbas et al. 2021, Dobson et al. 2023,

Crispim-Mendes et al. 2024, Pinilla-Buitrago 2025). By capturing ecologically relevant spatiotemporal environmental variability, dynamic SDMs (with temporally matched environmental data) should reduce extrapolation when projecting to future scenarios, while the use of static models (with predictors averaged through time) may underestimate species' persistence and establishment potential because of niche truncation (Serra-Diaz et al. 2016).

Spatially nested and dynamic SDMs address complementary forms of incomplete environmental sampling. Spatial nesting broadens the geographic and climatic space represented during training, whereas temporal matching retains interannual conditions that are lost through temporal averaging. Dynamic models may therefore reduce extrapolation when projected to future scenarios, and their ability to predict occurrences withheld from the training period suggests potential gains in temporal transferability (Pinilla-Buitrago 2025). Yet spatial nesting and temporal matching have largely been studied separately. We address this gap by combining range-wide climatic information with fine-scale, temporally explicit regional models.

We evaluated the spatially nested and dynamic SDMs (dynamic NSDM) framework using butterflies occurring in Denmark, a group that responds rapidly to climate and land-use change and has experienced substantial regional declines (Eskildsen et al. 2015, Warren et al. 2021, Bjerregård et al. 2023). To determine the efficacy of the dynamic NSDM approach, we developed a factorial modelling design that crosses temporal structure, static *versus* dynamic predictors, with spatial structure, regional *versus* nested training. This yields four modelling approaches (Fig. 1) and allows benchmarking dynamic NSDMs (*DynNest*) against static regional (i.e., fitted with a single snapshot of averaged climatic variables, and only for Denmark rather than for the whole species' range; *StatReg*), static nested (*StatNest*), and dynamic regional (*DynReg*) models. We asked whether temporal matching and spatial nesting (i) improve representation of climatic niche space, (ii) alter predictive performance under spatial and temporal validation, (iii) reduce extrapolation under future climates and (iv) change the spatial pattern of future suitability projections.

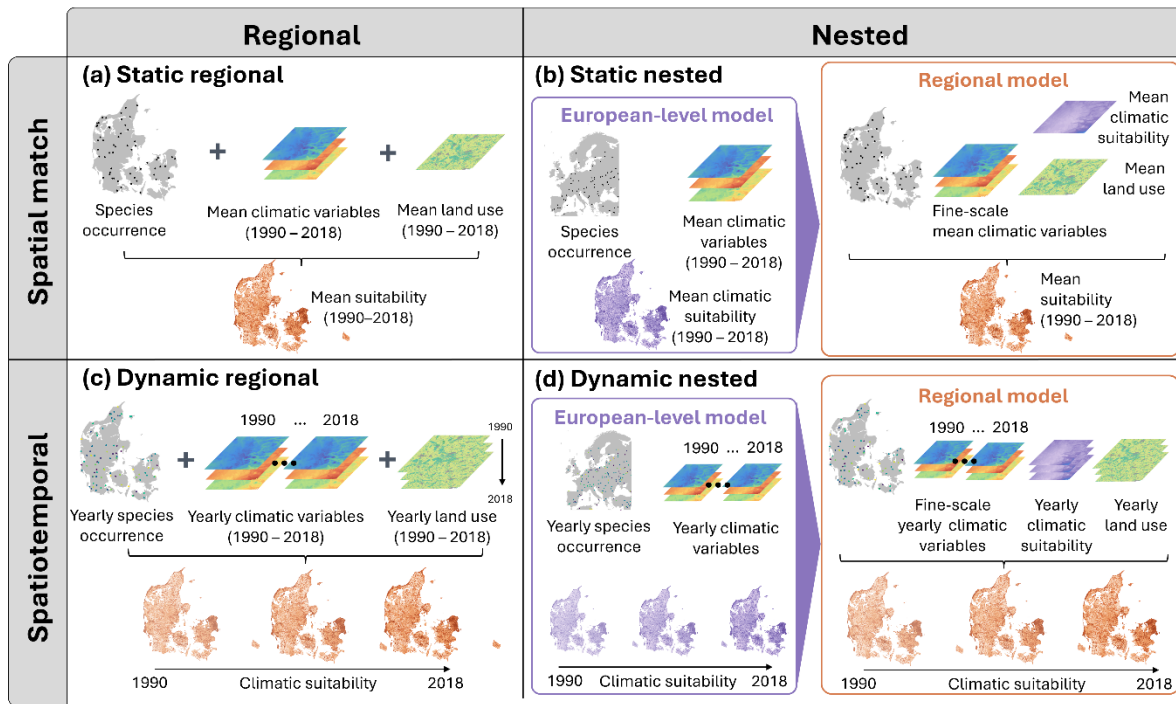


Figure 1. Modelling frameworks. **(a)** The static regional model (*StatReg*) uses temporally averaged climatic and land use variables at the regional level (Denmark) for model training. **(b)** The static nested model (*StatNest*) utilises European-level temporally averaged climatic variables to produce a map of averaged climatic suitability; this is then used as input for a regional model which includes temporally averaged and finer-scale climatic and land use variables. **(c)** The dynamic regional model (*DynReg*) is trained with temporally matched regional climatic and land use data; while **(d)** the dynamic nested model (*DynNest*) is a two-level model where, first, a European-level model is trained with temporally-explicit climatic variables, resulting in yearly climatic suitability projections which are then used in the second level, regional model which incorporates European-level yearly climatic suitability along with yearly finer-scale climatic and land use variables.

Methods

Modelling frameworks

We modelled present and future habitat suitability for 28 butterfly species in Denmark using four SDM frameworks (Fig. 1) that differed in the inclusion of spatial nesting and temporal structure: (i) *StatReg*, fitted to occurrence data from Denmark with climate and land-use averaged across 1990-2018; (ii) *StatNest*, which was spatially nested and included climatic suitability from a Europe-wide model fitted with averaged climate as additional covariate in the regional model; (iii) *DynReg*, fitted for Denmark with climate and land-use temporally matched to each record's year; and (iv) *DynNest*, in which yearly climatic suitability layers derived from Europe-wide models were generated using temporally dynamic climate data and subsequently used as a covariate in a regional model for Denmark that incorporated annually matched land-use and downscaled climate variables. All models were fitted with the Random Forest (RF) algorithm (Breiman 2001), which can accommodate nonlinear relationships and interactions between predictors while being relatively robust to overfitting (Cutler et al. 2007). All details of the model building procedures are summarised in the supplementary S7 following the ODMAP protocol (Zurell et al. 2020).

Regional models covered Denmark (7.88-15.60°E, 54.35-57.81°N) at a 100 m resolution to capture fine-scale land use patterns that may influence butterfly habitat suitability. European components of the nested models covered Europe (-31.28-68.93°E, 18.97-81.85°N) at 1 km resolution to capture range-wide climatic conditions. Analyses were conducted in R 4.4.0 (R Core Team 2024).

Species occurrence data

We compiled a list of butterfly species that are resident in Denmark from Eskildsen et al. (2015), excluding migratory species whose distributions depend strongly on immigration. European and Danish occurrences were obtained from GBIF (GBIF.org 2026a, b). We removed duplicates and

records with dubious coordinates corresponding to country centroids and institutional coordinates using the R package *CoordinateCleaner* (Zizka et al. 2019), restricted records to 1990-2018 to match the temporal coverage of the environmental predictors and retained only coordinates whose uncertainty was below the relevant grid resolution (~1 km in Europe and ~100 m in Denmark).

To reduce spatial and temporal sampling bias, we retained at most one presence per grid cell and year within two-year periods. Static datasets, including presence and pseudoabsence, were thinned further to one record per cell across 1990-2018. We excluded species with < 30 regional records or records that did not span the study period, leaving 28 species (Supplementary Table S1; filtering and thinning details are in S7.2).

Pseudoabsences were generated separately for each species and year and repeated ten times to account for uncertainty associated with selection (Barbet-Massin et al. 2010). Each replicate contained as many pseudoabsences as presences, sampled within a convex hull expanded by 20% of area around presences. By generating yearly pseudoabsences, their temporal resolution matched that of presence records, ensuring that environmental conditions were extracted from temporally matched climate and land-use layers so that both presence and pseudoabsence data reflected the environmental conditions specific to each year.

Environmental predictors

Environmental predictors comprised climate and land-use for 1990-2018 and climate projections for 2071-2100 (Table S2). Historical regional land-use data were obtained from 25 m categorical maps covering Denmark only, compiled from national topographic maps, agricultural registers, habitat monitoring and remotely sensed information (Levin et al. 2014, Levin and Gylden 2022).

Annual climate predictors were derived from monthly minimum and maximum temperature and precipitation in CHELSA v2 at 30 arcseconds (~1 km resolution; Karger et al.

2017). We calculated 19 bioclimatic variables describing means, seasonality and extremes, then excluded variables 8, 9, 18 and 19 because variables combining temperature and precipitation can contain spatial discontinuities (Booth 2022). We generated annual bioclimatic rasters for 1990-2018 with the *dismo* R package (Hijmans et al. 2023) and matched them to occurrence years. European models used the native ~1 km resolution; regional predictors were bilinearly downscaled to 100 m. Static models used the 1990-2018 mean for training and projection.

Future climate represented 2071-2100 under two CMIP6 general circulation models (GFDL-ESM4 and IPSL-CM6A-LR) and low- and high-emissions pathways (SSP1-2.6 and SSP5-8.5). This factorial design sampled contrasting climate sensitivities and emissions futures. Future bioclimatic variables were obtained from CHELSA v2 (Karger et al. 2017).

Land-use predictors represented the proportional cover of grassland, cropland and forest for ten time steps between 1990 and 2018. We aggregated 25 m categorical rasters (Levin et al. 2014, Levin and Gylden 2022) to 100 m resolution and calculated the proportion of each category within each cell using the *terra* R package (Hijmans et al. 2026). This resolution balanced ecological detail against coordinate uncertainty and availability of occurrences.

We reduced multicollinearity separately for each species and spatial extent using variance inflation factors. Variables were removed iteratively with the *vifstep()* function in the *usdm* R package (Naimi et al. 2014), allowing predictor sets to differ between European and regional components.

Species Distribution Models

We fitted Random Forests with 1,000 trees using the *sdm* R package (Breiman 2001, Naimi and Araújo 2016). Bootstrap sampling and default hyperparameters were used (number of input variables randomly sampled as candidates at each split of a tree based on the square root of number of predictors; node size is 1, which is standard for classification). Models were fitted separately for every species, modelling framework and pseudoabsence replicate.

Regional models (*StatReg* and *DynReg*) were trained only with records from Denmark. Nested models (*StatNest* and *DynNest*) were fitted in two steps: a European model was fitted across the species' range, and its predictions were then included as an additional predictor in the regional model. Static frameworks used predictors averaged across 1990–2018, whereas dynamic frameworks used predictors matched to the year of each occurrence record.

Metrics for model comparison

Niche truncation

We quantified climatic niche truncation with the PCA-env unfilling metric from the *ecospat* R package (Di Cola et al. 2017). Unfilling is the proportion of a reference niche absent from a focal niche after both are projected into common environmental space (0 = completely represented; 1 = entirely absent). Here, we interpret unfilling as a measure of niche truncation (Goicolea et al. 2025).

We quantified niche truncation in four complementary comparisons. First, we compared the climatic niche space represented at the European and regional (Danish) scales under (i) static and (ii) dynamic climatic conditions. Second, we assessed the effect of temporal framework by comparing (iii) dynamic and static European climatic niches and (iv) dynamic and static regional climatic niches. For all analyses, 20,000 background points were used to represent the climatic conditions available within each spatial domain. For the static models' training datasets comparison, European and regional background points were sampled once from averaged bioclimatic data. A principal component analysis (PCA) was conducted on the European background, and species presences and regional background points were projected into this PCA-space. This allowed us to quantify the proportion of the European climatic niche that was absent from the regional climatic niche under a static representation of climate.

For the dynamic models' training datasets comparison, occurrences were matched to year-specific climatic layers, and background points were sampled from each year of the study

period to capture interannual climatic variability. Background samples were then pooled across years, together with year-matched species occurrences, to represent the full range of climatic conditions experienced during the study period. A PCA was conducted on the pooled European background, and European and regional presences and backgrounds were projected into this common environmental space. This projection allowed us to quantify the proportion of the dynamically represented European climatic niche that was absent from the corresponding regional niche.

To assess how temporal explicit representation of climate affected estimated niche space, we compared the dynamic and static climatic niches within each spatial domain. At both the European and regional scales, the dynamically characterised niche was treated as the reference and the static niche as the focal niche, such that unfilling quantified the proportion of climatic niche space captured by year-specific climatic conditions that was not represented when climate was characterised using long-term averages. For all PCAs, the proportion of climatic variance explained by the retained axes is reported in Table S3.2.

Model performance

We evaluated model performance with spatial (Valavi et al. 2019) and temporal cross-validation (Roberts et al. 2017) to account for structure in the occurrence data and to estimate transferability more realistically. For spatial cross-validation, records were divided into five spatial blocks. Species-specific block size was based on the estimated spatial autocorrelation range of the response variable using the *cv_spatial_autocor()* function, and blocks were assigned to folds with the *cv_spatial()* function from the *blockCV* R package (Valavi et al. 2019).

We assessed temporal transfer using a forward temporal holdout, fitting regional models with observations from 1990-2009 and evaluating predictions against pooled presence and pseudoabsence records from 2010-2018. Static models used climatic predictors averaged over the training period and were projected using climatic averages for the evaluation period. Dynamic

models used predictors matched to the year of each training observation. At each evaluation location, dynamic models generated predictions using environmental conditions for each year from 2010 to 2018, which were then averaged to obtain a single period-level suitability estimate. This evaluation assessed the ability to predict occurrence patterns pooled across a subsequent period, rather than year-to-year changes in occurrence.

Performance metrics were area under the receiver operating characteristic curve (AUC), True Skill Statistic (TSS), Sorensen similarity index (SSI) and continuous Boyce Index (CBI). AUC measured discrimination across all possible thresholds (Fielding and Bell 1997), whereas TSS quantified threshold-dependent discrimination based on sensitivity and specificity (Allouche et al. 2006). SSI measured agreement between observed and predicted presences after thresholding (Leroy et al. 2018), while CBI assessed whether observed presences occurred increasingly frequently at higher predicted suitability values (Boyce et al. 2002, Hirzel et al. 2006). Only models with $AUC \geq 0.7$ and $TSS \geq 0.4$ were retained for projection.

We tested differences in performance across frameworks separately by validation scheme and metric using linear mixed-effects model (Supplementary S4). Temporal strategy (static or dynamic), spatial strategy (regional or nested) and their interaction were fixed effects; species was a random intercept. Fixed effects were evaluated using type-III F-tests. Where interactions were detected, estimated marginal means were used to compare temporal strategies within each spatial extent and spatial extents within each temporal strategy. Pairwise comparisons were Benjamini-Hochberg-adjusted to control the false discovery rate arising from multiple comparisons. Residual-versus-fitted and quantile-quantile plots were inspected.

Degree of extrapolation

To evaluate the degree of environmental extrapolation associated with future projections, we quantified climatic novelty in Denmark using the Shape metric, implemented in the *flexsdm* R package (Velazco et al. 2024). Shape measures multivariate environmental distance between

projection conditions and the conditions represented in the training data, with larger values indicating greater environmental novelty.

For each species, modelling framework, GCM and SSP, we compared climatic conditions used for model training with those projected for Denmark during 2071-2100. Shape was calculated using the *extra_eval()* function with Mahalanobis distance, producing a continuous raster of environmental novelty per species, modelling framework and scenario. Raster values were summarised using the mean, median and 90th and 95th percentiles (Table S5.2). The mean and sample standard deviation of these values across species and scenarios are reported for each modelling framework in Table S5.1.

Effect of modelling framework on future projections

To test whether the choice of modelling framework influences future projections, we calculated pixel-wise Spearman correlations between continuous suitability maps for every pair of frameworks within each species and GCM-SSP scenario. We asked whether frameworks rank locations similarly while avoiding assumptions introduced by binary thresholds. Correlations were summarised across species and scenarios. We interpreted lower correlation as greater sensitivity to framework choice, not as evidence that either projection is more accurate.

Results

Niche truncation

Across species, mean climatic niche unfilling, or truncation, between Europe and Denmark was 32.28% (SD 15.94) under static climate and 28.36% (SD 9.90) under dynamic climate (Fig. 2). This means that regional models fitted with climatic data only for Denmark, truncated the realised species niche of ca. 30% on average, with greater truncation for static regional models (*StatReg*). Static averages omitted little annual climatic space in Europe (mean 4.17%, SD 2.14) but much more in Denmark (mean 62.61%, SD 11.34). Species-level unfilling values and PCA variance are reported in Tables S3.1 and S3.2.

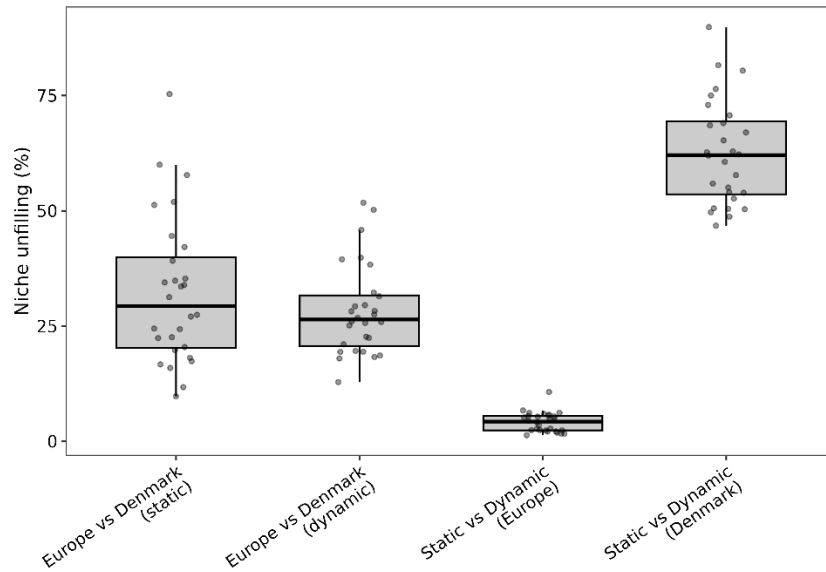


Figure 2. Climatic niche truncation (expressed as niche unfilling, %) across 28 butterfly species under four pairwise comparisons of climatic niche space. Europe vs Denmark (Static) and Europe vs Denmark (Dynamic) compare the proportion of the European climatic niche not represented within Denmark under static and dynamic climate representations, respectively. Static vs Dynamic (Europe) and Static vs Dynamic (Denmark) compare climatic niche space derived from static climate averages versus dynamic annual climate conditions within each spatial extent. Boxes represent the median and interquartile range (IQR), whiskers extend to 1.5 × IQR, and points represent individual species. PCA-axis variance and species-level unfilling values are reported in Tables S3.2 and S3.1, respectively.

Model performance

Model performance differed among frameworks, with *DynReg* generally producing the lowest values under spatial cross-validation (Fig. 3; Tables S4.1–S4.3). Type-III F-tests showed that, under spatial cross-validation, the temporal strategy (static vs dynamic) interacted with the spatial strategy (regional vs nested) for AUC ($F = 20.96$; $p < 0.001$) and TSS ($F = 24.32$; $p < 0.001$), indicating that the effect of the temporal strategy depended on spatial extent. Specifically, static models outperformed dynamic models at the regional extent, whereas performance was similar between temporal strategies at the nested extent. Benjamini-Hochberg-adjusted comparisons

of estimated marginal means showed that *StatReg* models outperformed *DynReg* models by 0.033 AUC and 0.051 TSS (both $p_{adj} < 0.001$), whereas differences between *StatNest* and *DynNest* models were small and not significant ($\Delta AUC = 0.007$, $p_{adj} = 0.094$; $\Delta TSS = 0.011$, $p_{adj} = 0.062$). Interactions were not detected for SSI or CBI, although *DynReg* models generally performed worse than *StatReg* and *StatNest* models.

Under forward temporal evaluation against a common pooled 2010-2018 response dataset, dynamic models achieved higher AUC ($F_{1,81} = 18.36$, $p < 0.001$), TSS ($F_{1,81} = 29.50$, $p < 0.001$) and SSI ($F_{1,81} = 14.31$, $p < 0.001$) overall than static models. No interaction between temporal and spatial extent was detected for any metric (all $p \geq 0.073$). *DynNest* exceeded *StatReg*, *DynReg* and *StatNest* in AUC by 0.040, 0.026 and 0.034, respectively (all $p_{adj} < 0.004$). Both dynamic frameworks exceeded both static frameworks in TSS. For SSI, *DynNest* exceeded both static frameworks, while *DynReg* exceeded *StatNest*. No pairwise differences were detected for CBI.

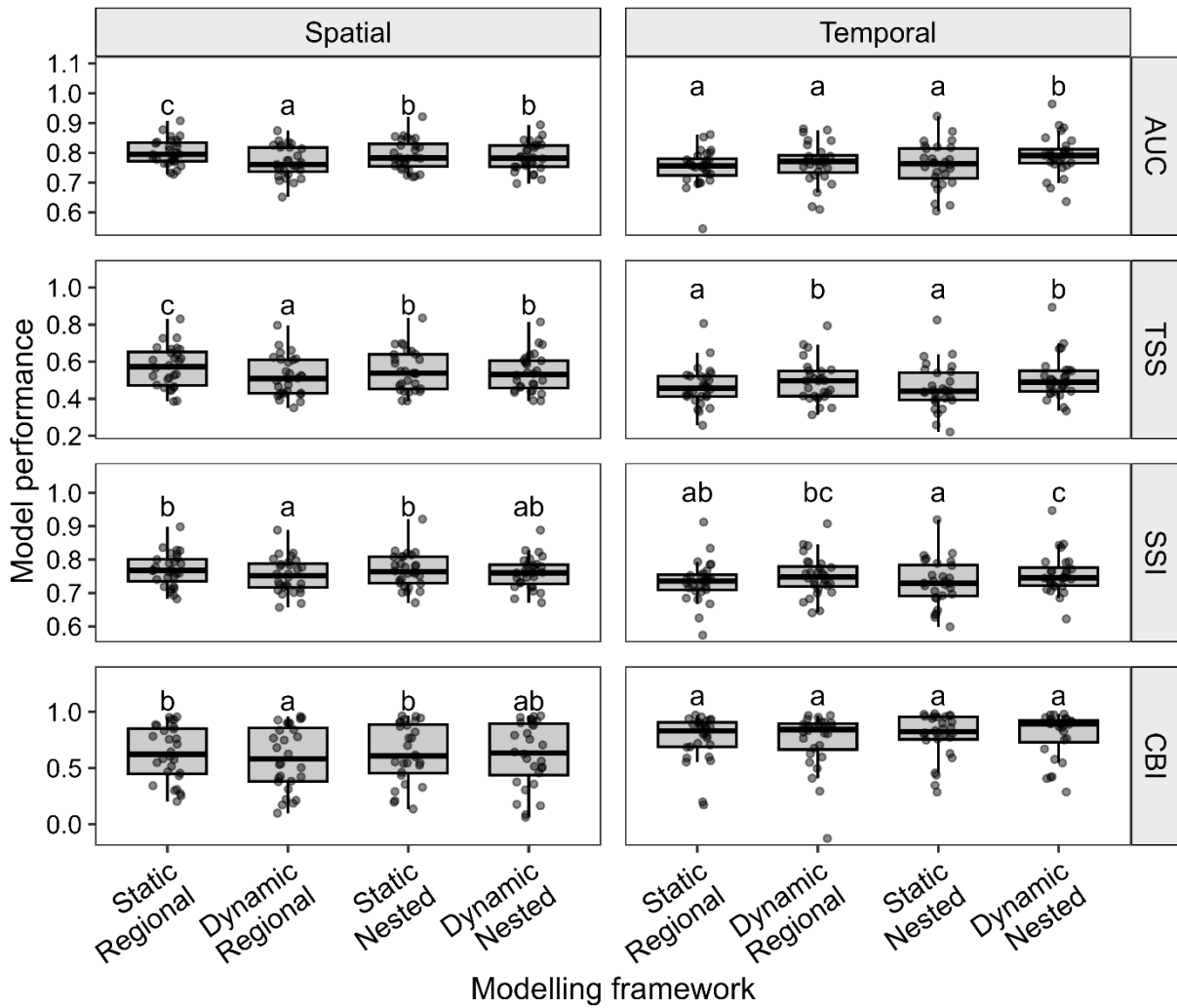


Figure 3. Performance of the four SDM frameworks under spatial and temporal cross-validation across species. Boxplots show the distributions across species of area under receiver operating characteristic curve (AUC), True Skill Statistic (TSS), Sorensen similarity index (SSI) and continuous Boyce index (Boyce) for static regional, dynamic regional, static nested, and dynamic nested frameworks. Boxes represent interquartile ranges, horizontal lines indicate medians, whiskers extend to 1.5 x the interquartile range and points correspond to individual species. Differences among frameworks were assessed separately for each metric and validation scheme using linear mixed-effects models containing temporal strategy, spatial extent and their interaction as fixed effects and species as a random intercept. Letters show compact-letter groupings derived from Benjamini–Hochberg-adjusted pairwise comparisons of estimated marginal means; frameworks sharing a letter did not differ significantly at $p < 0.05$.

Degree of extrapolation

DynNest models consistently produced the lowest environmental extrapolation, whereas *StatReg* produced the highest (Fig. 4). Across species, GCMs and SSPs, mean Shape was highest for *StatReg* (1594.9, SD 624.4), lower for *DynReg* (176.3, SD 103.5) and *StatNest* (142.9, SD 49.4), and lowest for *DynNest* models (34.3, SD 14.5).

Differences among frameworks increased under the higher emissions scenario. Under SSP1-2.6, mean Shape values were 1289.6 (475.7 SD), 132.0 (45.2 SD), 98.1 (19.4 SD) and 26.4 (8.7 SD) for *StatReg*, *StatNest*, *DynReg* and *DynNest* models, respectively. Under SSP5-8.5, these increased to 1900.2 (608.9 SD), 153.8 (51.3 SD), 254.5 (93.7 SD) and 42.2 (14.9 SD), respectively. The emissions-driven increase in extrapolation was therefore greatest for regional frameworks. Differences among GCMs were comparatively small.

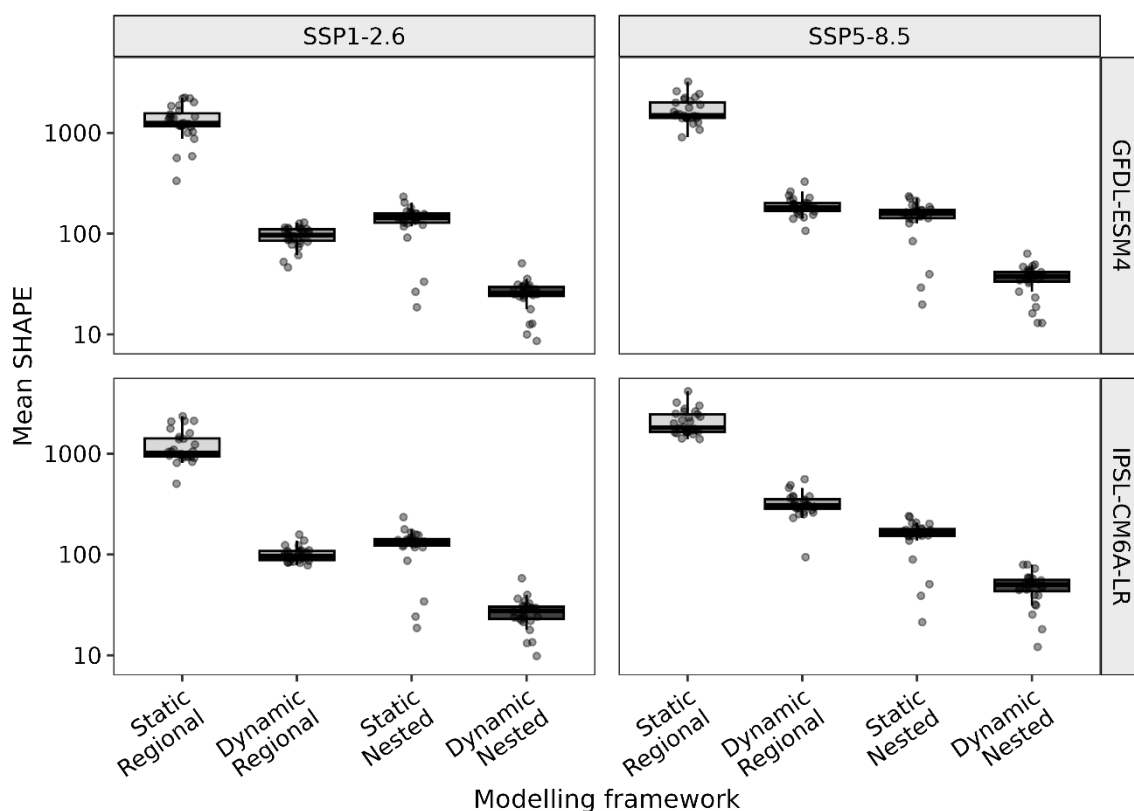


Figure 4. Environmental extrapolation measured by Shape across the four modelling frameworks under two global climate models (GFDL-ESM4 and IPSL-CM6A-LR) and two emissions scenarios

(SSP1-2.6 and SSP5-8.5). Points represent species-specific mean Shape values, while boxplots summarize their distribution. The y-axis is shown on a logarithmic scale. Lower Shape values indicate lower levels of environmental extrapolation relative to training data. See Table S5.2 for species-specific Shape summaries.

Effect of modelling framework on future projections

Across the 28 species, *StatReg* projections correlated less strongly with those from the other frameworks (mean Spearman's $\rho = 0.69\text{--}0.74$; Fig. 5; Table S6). By contrast, correlations among projections from the *DynReg*, *StatNest* and *DynNest* frameworks were consistently higher (mean $\rho = 0.94\text{--}0.97$). This pattern held across all four GCM–SSP combinations, indicating that spatial agreement depended mainly on modelling framework rather than on climate projection.

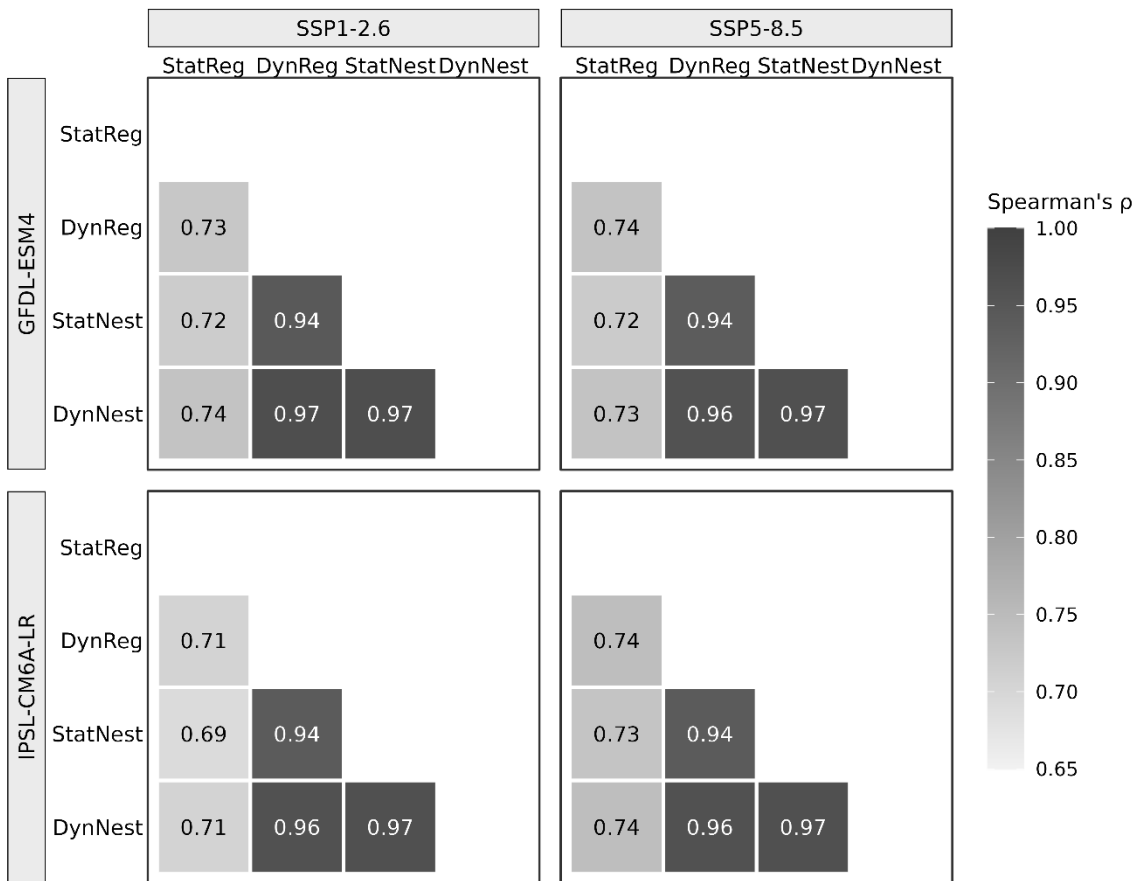


Figure 5. Agreement between continuous future suitability projections generated using alternative modelling frameworks. Cells show mean pairwise pixel-wise Spearman correlations

(ρ) between projections from different modelling frameworks under the same GCM and SSP combination for 2071-2100. Values represent the mean across 28 species. Darker shading indicates greater spatial agreement. Correlations involving the static regional framework were consistently lower than correlations among the dynamic regional, static nested and dynamic nested frameworks. *StatReg*, static regional; *DynReg*, dynamic regional; *StatNest*, static nested; *DynNest*, dynamic nested.

Discussion

Species distribution models are commonly evaluated according to their ability to discriminate occurrences under contemporary conditions, yet models used for climate-change forecasting must also be transferred beyond the environmental conditions on which they were trained (Yates et al. 2018). Our results show that evaluation design can favour different modelling strategies. Static models generally performed better under spatial cross-validation, whereas dynamic models performed better when all frameworks were evaluated against the same pooled 2010-2018 dataset. Broadening the environmental conditions represented during training—through spatial nesting, temporal matching, or both—substantially reduced climatic novelty under future conditions, with the dynamic nested framework producing the least extrapolation. Thus, the framework that best discriminates occurrences depends on the validation target, and strong contemporary discrimination does not necessarily identify the model with the greatest environmental support for future projection.

This contrast arises because spatial nesting and temporal matching address different forms of incomplete environmental sampling. Spatial nesting incorporates climatic conditions occurring beyond the focal region, while temporal matching retains interannual conditions that are lost when predictors are averaged through time. Their importance therefore depends on the environmental variation represented within the training domain. In our case, the consequences of temporal averaging were strongly scale-dependent: long-term climatic averages captured

almost all annual climatic space across Europe but substantially less within Denmark. Together, these results show that spatial and temporal sampling contribute complementary information to model training, with consequences that become particularly apparent when models are transferred to future environments.

Niche truncation and scale-dependent temporal variability

Approximately one-third of the European climatic niche of the modelled butterflies was absent from climatic conditions represented within Denmark. This confirms that geographically restricted training datasets can represent only a subset of the climatic conditions occupied by a species across its wider range, increasing the potential for truncated response functions (Goicolea et al. 2025, Guisan et al. 2025). The extent of such truncation will depend on the relationship between the focal region and the environmental variation represented across the species' wider distribution. Niche unfilling should therefore be interpreted primarily as a diagnostic of environmental coverage rather than evidence that spatial nesting will necessarily improve model discrimination; previous nested species distribution modelling studies have likewise found context-dependent gains in predictive performance (Adde et al. 2023, Mateo et al. 2024, Goicolea et al. 2025).

The effect of temporal averaging was strongly scale dependent. Long-term averages of bioclimatic variables represented nearly all annual climatic space across Europe but omitted much of the annual climatic space within Denmark. At continental extents and coarse resolution, broad spatial climatic gradients may therefore encompass much of the variation observed among years, whereas at regional scales and finer resolution, interannual fluctuations can constitute a proportionally greater component of environmental variation. Climate varies across multiple spatial and temporal scales (Ghil and Lucarini 2020), and spatial climatic gradients are not necessarily equivalent to temporal climatic variation (Metz and Tielbörger 2016). This distinction can be ecologically important because interannual climate variability can influence

ecological patterns and niche estimates in ways that are obscured by long-term climatic averages (Letten et al. 2013, Gardner et al. 2021, Karger et al. 2023). Consequently, static climatic averages may capture much of the climatic space across broad spatial extents while still underrepresenting the magnitude and ecological relevance of interannual variability at regional scales. In the latter case, annual environmental predictors can meaningfully expand the environmental envelope available for model training. Our results therefore suggest that spatial nesting and temporal matching address complementary dimensions of environmental variation.

Environmental representation and predictive performance

Under the common forward temporal evaluation, dynamic models achieved higher AUC, TSS and SSI overall than static models when predictions were evaluated against the same pooled observations from 2010-2018. Dynamic nested models achieved the highest estimated AUC and significantly exceeded each of the other frameworks. Dynamic models also exceeded static models in TSS, while SSI differences were smaller and CBI did not differ among temporal strategies. Because annual dynamic predictions were averaged across 2010-2018 before evaluation, these results support the ability of temporally explicit models to represent pooled period-level occurrence patterns.

In spatial cross-validation, temporal matching reduced AUC and TSS in regional models, whereas no detectable difference occurred between static and dynamic approaches when models were spatially nested. Spatial nesting therefore largely mitigated the poorer discrimination associated with temporal matching in regional models. Previous studies have similarly shown that the effects of spatial nesting on model performance depend on the taxa, predictors and evaluation design (Adde et al. 2023, Mateo et al. 2024, Goicolea et al. 2025, Guisan et al. 2025).

These two evaluation designs address different prediction targets and should not be interpreted as producing a single, universal ranking of the frameworks. The common forward

temporal evaluation assessed whether all frameworks could predict pooled occurrence patterns in a subsequent period using the same 2010–2018 response dataset. In contrast, spatial block cross-validation assessed spatial transferability within the available data structure and showed that temporal matching reduced discrimination in regional models, but not in nested models. The differing results therefore indicate that apparent performance depends on whether the priority is spatial interpolation or transfer across time, rather than showing that either static or dynamic modelling is intrinsically superior.

Model choice should consequently be aligned with the intended application. Where the aim is to map contemporary suitability within environmental conditions that are well represented in the training data, a simpler static framework may be adequate if it performs well under spatial validation. Where the aim is projection into future or otherwise changing environmental conditions, however, broadening the environmental domain through spatial nesting, temporal matching, or both becomes more important because it reduces reliance on extrapolation. Predictive discrimination and environmental support for transfer should therefore be considered jointly, with the relative weight given to each determined by the model's intended use. These findings illustrate that discrimination under spatial cross-validation and temporal transfer to a subsequent period need not coincide (Araújo et al. 2005). AUC and TSS can also be influenced by training extent and pseudoabsence design (Leroy et al. 2018), reinforcing the value of multiple metrics and validation schemes when comparing modelling strategies.

Spatial nesting and temporal matching strongly reduce extrapolation

The clearest benefit of expanding environmental representation emerged when models were projected to future climates. Both spatial nesting and temporal matching sharply reduced environmental novelty relative to static regional models, and combining the two approaches produced the lowest extrapolation under every climate scenario considered. The two strategies operate through different, complementary mechanisms: spatial nesting exposes models to

climatic conditions occurring across a broader geographic range, whereas temporal matching retains interannual conditions that disappear when climatic predictors are averaged through time. Together, they substantially expand the environmental domain represented during model training, making future Danish climatic conditions less novel relative to the training data.

This pattern is consistent with evidence that incomplete sampling of environmental conditions can bias estimated species-environment relationships and inflate apparent climatic risk (Owens et al. 2013, Serra-Diaz et al. 2016, Scherrer et al. 2021, Guisan et al. 2025). By incorporating both range-wide climatic information and temporal variability, the dynamic nested approach provides a broader representation of conditions associated with species' occurrences. Future climatic conditions are consequently less likely to fall far outside the training domain, reducing the need for unsupported extrapolation. The particularly low environmental novelty produced by the combined approach across both emissions scenarios is consistent with this mechanism.

Importantly, lower environmental extrapolation does not demonstrate that future predictions are more accurate. Future species distributions cannot be validated directly, and reduced novelty indicates only that projections are made under environmental conditions more similar to those represented during training. Nevertheless, extrapolation is particularly relevant when models are transferred to future climates because predictions outside the training domain depend on assumptions about species-environment relationships that are not supported directly by the training data (Zurell et al. 2012, Velazco et al. 2024). Reporting environmental novelty alongside conventional performance metrics therefore provides complementary information about the robustness of model transfer (Owens et al. 2013, Velazco et al. 2024). Our results illustrate that a model can perform well within present-day training conditions while nevertheless requiring substantially greater extrapolation when transferred to future environments.

Framework choice can propagate into future projections

Differences in model construction propagated into future suitability projections, especially in comparisons involving StatReg. Projections from DynReg, StatNest and DynNest had highly concordant spatial rankings, whereas StatReg was consistently less similar to the other frameworks. This consistency across climate models and emissions scenarios indicates that modelling choices can be an important source of projection uncertainty. However, the analysis is a sensitivity assessment rather than a comparison of forecast accuracy: Spearman correlations measure spatial rank similarity, not differences in absolute suitability or range size, and species averages may obscure contrasting responses.

Limitations

Some limitations should be considered when interpreting these results. First, GBIF occurrence records reflect heterogeneous sampling effort through space and time despite our filtering and spatiotemporal thinning procedures. Second, all SDMs were fitted using Random Forest; comparisons across additional algorithms or ensemble approaches would be needed to establish whether the model performance patterns reported here generalise across modelling methods (Araújo et al. 2019). Third, as with correlative SDMs generally, future projections assume that fitted species-environment relationships remain applicable through time and do not explicitly account for dispersal constraints, biotic interactions or evolutionary responses (Dormann et al. 2012, Peterson et al. 2015, Sillero et al. 2021). Finally, our analyses of environmental novelty and agreement among future suitability maps evaluate extrapolation and sensitivity to model construction rather than the ecological accuracy of future forecasts.

Conclusions

Taken together, our results show that spatial nesting and temporal matching expand the environmental domain of SDMs in complementary ways. Spatial nesting incorporates climatic conditions represented across a species' wider geographic range, whereas temporal matching

retains interannual environmental variation that is removed by long-term averaging. Their effects on predictive performance depended on validation design: temporal matching reduced discrimination in regional models under spatial cross-validation, while dynamic models achieved higher AUC, TSS and SSI under the common forward 2010-2018 evaluation. Their most consistent benefit emerged under transfer to future climates, where both approaches reduced environmental novelty and their combination produced the lowest extrapolation across all scenarios.

Our results therefore highlight a distinction between predictive performance within the training domain and environmental support for model transfer. High discrimination under contemporary conditions does not ensure that future projections remain within the range of environments represented during model training, while reduced extrapolation does not itself demonstrate greater forecast accuracy. Framework selection should be matched to the intended application: for interpolation of contemporary suitability within well-represented environmental conditions, a simpler static framework may be adequate; for forecasts under environmental change, spatial and temporal scale choices should be treated explicitly as sources of uncertainty and included in sensitivity analyses of future projections. Spatial nesting is likely to be most useful where regional data cover only a restricted part of range-wide climatic variation, whereas temporal matching should matter most where interannual variability is a substantial component of the conditions experienced by populations.

Statement on the use of AI tools

OpenAI's ChatGPT was used to assist with language editing, improving the clarity and structure of selected manuscript sections and organising the R code for sharing. Every AI-assisted suggestion was reviewed and verified by authors.

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Beyond static species distribution models: temporally dynamic, spatially nested models reduce extrapolation for future projections

Supplementary Information

This supplement documents occurrence data, environmental predictors, climatic niche coverage, model evaluation and future projection comparisons for 28 Danish butterfly species. Spatial cross-validation and the common forward temporal holdout are reported separately in Section S4. The modelling workflow is described using the ODMAP protocol (Zurell et al. 2020) in Section S7.

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Framework abbreviations

StatReg – Static Regional; *DynReg* – Dynamic Regional; *StatNest* – Static Nested; *DynNest* – Dynamic nested. Regional calibration uses species occurrence data and environmental predictors for Denmark, while nesting additionally incorporates climatic suitability from a model fitted at the scale of Europe. Static predictors are temporally averaged, whereas dynamic predictors are matched to individual years.

S1. Species occurrence data

European occurrences (1990-2018) were downloaded from GBIF (ref) and filtered to records with coordinates, no flagged geospatial issues and coordinate uncertainty ≤ 1 km. GBIF download DOI: <https://doi.org/10.15468/dl.kqavhr>. Danish occurrences (1990-2018) were filtered using the same criteria, with coordinate uncertainty ≤ 100 m. GBIF download DOI: <https://doi.org/10.15468/dl.79t5mt>. Occurrence filtering, thinning and pseudoabsence generation are described in section S7. The retained species are listed below.

Table S1. The 28 butterfly species retained for analysis.

No.	Species
1	<i>Aglais io</i>
2	<i>Anthocharis cardamines</i>
3	<i>Aphantopus hyperantus</i>
4	<i>Aporia crataegi</i>
5	<i>Argynnis paphia</i>
6	<i>Boloria euphrosyne</i>
7	<i>Brenthis ino</i>
8	<i>Celastrina argiolus</i>
9	<i>Coenonympha tullia</i>
10	<i>Cupido minimus</i>
11	<i>Cyaniris semiargus</i>
12	<i>Euphydryas aurinia</i>
13	<i>Fabriciana adippe</i>

No.	Species
14	<i>Fabriciana niobe</i>
15	<i>Favonius quercus</i>
16	<i>Gonepteryx rhamni</i>
17	<i>Hesperia comma</i>
18	<i>Hipparchia semele</i>
19	<i>Lycaena phlaeas</i>
20	<i>Lycaena virgaureae</i>
21	<i>Maniola jurtina</i>
22	<i>Pararge aegeria</i>
23	<i>Phengaris alcon</i>
24	<i>Pieris napi</i>
25	<i>Plebejus idas</i>
26	<i>Polygonia c-album</i>
27	<i>Polyommatus amandus</i>
28	<i>Speyeria aglaja</i>

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45 S2. Environmental predictors

46 Historical climate covers 1990–2018 and was obtained from CHELSA v2.1 (Karger et al. 2023).
47 European climate layers have an approximately 1 km resolution (30 arcsec); Danish climate
48 predictors were bilinearly downscaled to approximately 100 m. Danish land-cover proportions
49 were aggregated from 25 m maps for ten time steps (1990, 2005, 2011, 2012, 2013, 2014, 2015,
50 2016, 2017, 2018);(Levin and Normander 2008). Future climate represents 2071–2100 for GFDL-
51 ESM4 and IPSL-CM6A-LR under SSP1-2.6 and SSP5-8.5 (Karger et al. 2023).

52 **Table S2.** Candidate environmental predictors and their sources. Bioclimatic variables 8, 9, 18
53 and 19 were excluded before variable selection due to known artifacts (Booth 2022). European
54 climatic suitability was added to regional models in nested frameworks.

Variable	Description	Source
Bio1	Annual Mean Temperature	CHELSA
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	CHELSA

Variable	Description	Source
Bio3	Isothermality (BIO2/BIO7) ($\times 100$)	CHELSA
Bio4	Temperature Seasonality (standard deviation $\times 100$)	CHELSA
Bio5	Max Temperature of Warmest Month	CHELSA
Bio6	Min Temperature of Coldest Month	CHELSA
Bio7	Temperature Annual Range (BIO5-BIO6)	CHELSA
Bio10	Mean Temperature of Warmest Quarter	CHELSA
Bio11	Mean Temperature of Coldest Quarter	CHELSA
Bio12	Annual Precipitation	CHELSA
Bio13	Precipitation of Wettest Month	CHELSA
Bio14	Precipitation of Driest Month	CHELSA
Bio15	Precipitation Seasonality (Coefficient of Variation)	CHELSA
Bio16	Precipitation of Wettest Quarter	CHELSA
Bio17	Precipitation of Driest Quarter	CHELSA
Grassland	Proportion of grassland	Technical Report from DCE – Danish Centre for Environment and Energy (Levin et al. 2014, Levin and Gylden 2022)
Cropland	Proportion of cropland	Technical Report from DCE – Danish Centre for Environment and Energy (Levin et al. 2014, Levin and Gylden 2022)
Forest	Proportion of forest	Technical Report from DCE – Danish Centre for Environment and Energy (Levin et al. 2014, Levin and Gylden 2022)
European climatic suitability	Prediction from the European climatic model	European component of <i>StatNest</i> or <i>DynNest</i>

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S3. Climatic niche unfilling and PCA variance

Unfilling is the percentage of a reference climatic niche absent from a focal niche, measured in common PCA environmental space. In the Europe–Denmark comparisons, Europe is the reference and Denmark is the focal domain. In the dynamic–static comparisons, annual climate is the reference, and averaged climate is the focal representation. Unfilling therefore measures omitted climatic niche space. We used the *ecospat* R package for this analysis (Di Cola et al. 2017).

Mean unfilling within Denmark is 62.61%, corresponding to 37.39% representation by static climate. Within Europe, mean unfilling is 4.17%, corresponding to 95.83% representation.

Table S3.1. Climatic niche unfilling (%). Europe–Denmark columns compare spatial domains under static or dynamic climate. Dynamic–static columns quantify the annual climatic niche omitted by temporal averaging within Europe or Denmark. Standard deviation (SD) is calculated across the 28 listed species from values reported to two decimal places.

Species	Europe–Denmark Static	Europe–Denmark Dynamic	Dynamic–static Europe	Dynamic–static Denmark
<i>Aglais io</i>	20.46	22.45	2.46	48.73
<i>Anthocharis cardamines</i>	24.34	18.31	2.14	50.54
<i>Aphantopus hyperantus</i>	19.79	27.53	6.18	49.67
<i>Aporia crataegi</i>	51.28	39.84	2.71	81.58
<i>Argynnis paphia</i>	31.28	29.30	5.61	75.03
<i>Boloria euphrosyne</i>	60.01	26.80	5.78	89.85
<i>Brenthis ino</i>	44.56	25.15	6.21	62.24
<i>Celastrina argiolus</i>	22.40	32.26	2.40	52.64
<i>Coenonympha tullia</i>	27.08	29.54	3.57	68.54
<i>Cupido minimus</i>	24.48	26.06	5.41	55.05
<i>Cyaniris semiargus</i>	39.17	45.84	2.77	62.91
<i>Euphydryas aurinia</i>	75.31	51.77	1.69	62.70
<i>Fabriciana adippe</i>	33.60	21.05	5.95	70.71

Species	Europe– Denmark Static	Europe– Denmark Dynamic	Dynamic–static Europe	Dynamic–static Denmark
<i>Fabriciana niobe</i>	35.31	50.21	5.22	69.03
<i>Favonius quercus</i>	15.93	22.70	4.66	61.97
<i>Gonepteryx rhamni</i>	9.77	17.99	2.40	60.62
<i>Hesperia comma</i>	51.95	25.69	5.56	80.40
<i>Hipparchia semele</i>	42.17	39.49	4.13	46.79
<i>Lycaena phlaeas</i>	11.76	18.64	1.33	55.93
<i>Lycaena virgaureae</i>	27.46	28.21	6.72	76.42
<i>Maniola jurtina</i>	16.70	19.41	1.90	50.43
<i>Pararge aegeria</i>	22.59	19.45	2.45	54.05
<i>Phengaris alcon</i>	57.74	38.35	10.72	72.95
<i>Pieris napi</i>	17.39	19.63	1.66	50.35
<i>Plebejus idas</i>	33.91	25.90	5.11	66.98
<i>Polygonia c-album</i>	34.86	28.31	4.46	53.92
<i>Polyommatus amandus</i>	18.10	31.48	5.39	65.27
<i>Speyeria aglaja</i>	34.47	12.85	2.16	57.75
Mean	32.28	28.36	4.17	62.61
SD	15.94	9.90	2.14	11.34

71 **Table S3.2.** Cumulative percentage of climatic variance explained by the first two PCA axes.

72 Column definitions follow Table S3.1.

Species	Europe– Denmark Static	Europe– Denmark Dynamic	Dynamic–static Europe	Dynamic–static Denmark
<i>Aglaia io</i>	74.89	66.59	58.25	62.25
<i>Anthocharis cardamines</i>	74.89	57.14	59.49	59.88
<i>Aphantopus hyperantus</i>	74.89	57.80	57.78	64.07
<i>Aporia crataegi</i>	74.89	57.60	64.43	70.96
<i>Argynnis paphia</i>	74.89	58.00	57.91	69.91
<i>Boloria euphrosyne</i>	74.89	57.64	60.39	74.38
<i>Brenthis ino</i>	73.85	56.65	57.20	67.86
<i>Celastrina argiolus</i>	74.89	57.30	61.76	61.63
<i>Coenonympha tullia</i>	74.89	67.16	62.52	65.26
<i>Cupido minimus</i>	74.89	57.44	59.93	61.22
<i>Cyaniris semiargus</i>	74.89	57.65	61.64	62.22
<i>Euphydryas aurinia</i>	74.89	57.48	63.28	53.20
<i>Fabriciana adippe</i>	74.89	57.58	62.36	70.33
<i>Fabriciana niobe</i>	76.25	68.29	59.97	66.50
<i>Favonius quercus</i>	74.89	57.50	62.86	67.76
<i>Gonepteryx rhamni</i>	74.89	57.18	59.61	67.00
<i>Hesperia comma</i>	74.89	57.62	60.12	75.88
<i>Hipparchia semele</i>	74.89	57.09	64.06	64.19
<i>Lycaena phlaeas</i>	76.25	59.03	63.99	64.18
<i>Lycaena virgaureae</i>	73.85	56.98	58.51	71.99
<i>Maniola jurtina</i>	74.89	57.34	62.29	64.33
<i>Pararge aegeria</i>	74.89	57.46	60.87	63.02
<i>Phengaris alcon</i>	74.89	66.72	62.30	62.28
<i>Pieris napi</i>	74.89	57.36	59.13	62.39
<i>Plebejus idas</i>	74.89	57.25	58.24	68.93
<i>Polygonia c-album</i>	74.89	57.32	57.19	61.73
<i>Polyommatus amandus</i>	73.85	56.33	60.20	72.60
<i>Speyeria aglaja</i>	74.89	57.46	57.88	70.91

S4. Model performance

Evaluation design

Spatial cross-validation used five spatial blocks, with species-specific block sizes based on the spatial autocorrelation range. We used the *blockCV* R package for this validation form (Valavi et al. 2019). The forward temporal holdout fitted regional models with 1990–2009 observations and evaluated all four frameworks against a common pooled set of presences and pseudoabsences from 2010–2018. Static climatic predictors were averaged separately for the calibration and evaluation periods. Dynamic predictions were generated for each evaluation year and averaged at each evaluation record before scoring. This evaluates pooled period-level occurrence patterns, not annual changes in occurrence.

Forward-holdout regional refits used the same species-specific VIF-selected predictors list and nested models included the European climatic-suitability covariate. These refits used the same Random Forest settings as in spatial cross-validation.

Model performance was calculated with the *sdm* and *flexsdm* R package (Naimi and Araújo 2016, Velazco et al. 2022); threshold-dependent metrics used the threshold maximising sensitivity plus specificity (*max_sens_spec*). Species–framework metric values were averaged across the ten pseudoabsence replicates before the mixed-effects analyses.

Statistical analysis

Performance was analysed separately for spatial cross-validation and the forward temporal validation, and for AUC, TSS, Sørensen similarity index (SSI) and continuous Boyce index (CBI). Fixed effects were temporal strategy (static or dynamic), spatial strategy (regional or nested) and their interaction; species was a random intercept. Models were fitted by restricted maximum likelihood using *lme4*, with type-III F-tests in *lmerTest*. Estimated marginal means and 95% confidence intervals were obtained with *emmeans*. The six pairwise framework comparisons within each metric and evaluation design were adjusted using the Benjamini–Hochberg

procedure. Tables S4.1–S4.4 report tests, marginal means, pairwise contrasts and model diagnostics, respectively.

Results

Under spatial cross-validation, temporal strategy interacted with spatial extent for AUC ($F_{1,81} = 20.96, p < 0.001$) and TSS ($F_{1,81} = 24.32, p < 0.001$). Mean AUC was 0.802 for *StatReg*, 0.769 for *DynReg*, 0.793 for *StatNest* and 0.786 for *DynNest*. *StatReg* exceeded *DynReg* by 0.033 (SE = 0.004, BH-adjusted $p < 0.001$), whereas *StatNest* exceeded *DynNest* by only 0.007 (SE = 0.004, adjusted $p = 0.094$). Mean TSS was 0.570, 0.520, 0.550 and 0.539 for *StatReg*, *DynReg*, *StatNest* and *DynNest*, respectively. The *StatReg* - *DynReg* difference in TSS was 0.051 (SE = 0.006, adjusted $p < 0.001$), compared with 0.011 between *StatNest* and *DynNest* (SE = 0.006, adjusted $p = 0.062$). For both metrics, the advantage of the static over the dynamic strategy was therefore greater at the regional than at the nested extent.

The interaction between temporal strategy and spatial extent was not supported under spatial cross-validation for SSI was not supported under spatial cross-validation for SSI index ($F_{1,81} = 2.24, p = 0.138$) or CBI ($F_{1,81} = 1.75, p = 0.189$). Nevertheless, *DynReg* had lower SSI than *StatReg* (difference = 0.016, SE = 0.004, adjusted $p = 0.001$) and *StatNest* (difference = 0.015, SE = 0.004, adjusted $p = 0.002$). *DynReg* had lower CBI than *StatReg* (difference = 0.037, SE = 0.013, adjusted $p = 0.014$) and *StatNest* (difference = 0.041, SE = 0.013, adjusted $p = 0.013$), while the other framework comparisons were not significant after correction.

Under forward temporal evaluation against a common pooled 2010-2018 response dataset, dynamic models achieved higher AUC ($F_{1,81} = 18.36, p < 0.001$), TSS ($F_{1,81} = 29.50, p < 0.001$) and SSI ($F_{1,81} = 14.31, p < 0.001$) overall than static models. No interaction between temporal and spatial extent was detected for any metric (all $p \geq 0.073$). *DynNest* exceeded *StatReg*, *DynReg* and *StatNest* in AUC by 0.040, 0.026 and 0.034, respectively (all $p_{adj} < 0.004$). Both dynamic frameworks exceeded both static frameworks in TSS. For SSI, *DynNest* exceeded

both static frameworks, while *DynReg* exceeded *StatNest*. No pairwise differences were detected for CBI.

Residual diagnostics

All eight mixed-effects models included 112 species–framework observations from 28 species and were non-singular. Residual-versus-fitted and normal Q–Q plots are presented in Figures S4.1 and S4.2. Tail departures and variation in residual spread are visible in some metrics.

Fixed effects tests

Table S4.1. Type-III fixed-effects tests. “Spatial” denotes spatial cross-validation; “Forward” denotes the common 2010–2018 temporal holdout. The interaction is temporal strategy × spatial strategy.

Evaluation	Metric	Effect	df1	df2	F	p
Spatial	AUC	Temporal strategy	1	81.0	48.68	<0.001
Spatial	AUC	Spatial strategy	1	81.0	1.82	0.181
Spatial	AUC	Interaction	1	81.0	20.96	<0.001
Spatial	TSS	Temporal strategy	1	81.0	57.85	<0.001
Spatial	TSS	Spatial strategy	1	81.0	0.01	0.923
Spatial	TSS	Interaction	1	81.0	24.32	<0.001
Spatial	SSI	Temporal strategy	1	81.0	16.19	<0.001
Spatial	SSI	Spatial strategy	1	81.0	0.82	0.368
Spatial	SSI	Interaction	1	81.0	2.24	0.138
Spatial	CBI	Temporal strategy	1	81.0	7.89	0.006
Spatial	CBI	Spatial strategy	1	81.0	2.85	0.095
Spatial	CBI	Interaction	1	81.0	1.75	0.189
Forward	AUC	Temporal strategy	1	81.0	18.36	<0.001
Forward	AUC	Spatial strategy	1	81.0	7.86	0.006
Forward	AUC	Interaction	1	81.0	3.30	0.073
Forward	TSS	Temporal strategy	1	81.0	29.50	<0.001
Forward	TSS	Spatial strategy	1	81.0	0.55	0.462
Forward	TSS	Interaction	1	81.0	2.45	0.121
Forward	SSI	Temporal strategy	1	81.0	14.31	<0.001
Forward	SSI	Spatial strategy	1	81.0	0.11	0.736
Forward	SSI	Interaction	1	81.0	0.65	0.424
Forward	CBI	Temporal strategy	1	81.0	0.09	0.759

Evaluation	Metric	Effect	df1	df2	F	p
Forward	CBI	Spatial strategy	1	81.0	5.99	0.017
Forward	CBI	Interaction	1	81.0	0.34	0.561

Estimated marginal means

Table S4.2. Estimated marginal means, standard errors and 95% confidence intervals for each framework. “Spatial” denotes spatial cross-validation; “Forward” denotes the common 2010–2018 temporal holdout.

Evaluation	Metric	Framework	Mean	SE	Lower 95% CI	Upper 95% CI
Spatial	AUC	<i>StatReg</i>	0.802	0.009	0.783	0.821
Spatial	AUC	<i>DynReg</i>	0.769	0.009	0.750	0.788
Spatial	AUC	<i>StatNest</i>	0.793	0.009	0.774	0.812
Spatial	AUC	<i>DynNest</i>	0.786	0.009	0.767	0.805
Spatial	TSS	<i>StatReg</i>	0.570	0.020	0.529	0.612
Spatial	TSS	<i>DynReg</i>	0.520	0.020	0.478	0.562
Spatial	TSS	<i>StatNest</i>	0.550	0.020	0.508	0.592
Spatial	TSS	<i>DynNest</i>	0.539	0.020	0.497	0.581
Spatial	SSI	<i>StatReg</i>	0.769	0.010	0.750	0.789
Spatial	SSI	<i>DynReg</i>	0.753	0.010	0.733	0.772
Spatial	SSI	<i>StatNest</i>	0.767	0.010	0.748	0.787
Spatial	SSI	<i>DynNest</i>	0.760	0.010	0.740	0.779
Spatial	CBI	<i>StatReg</i>	0.628	0.051	0.525	0.732
Spatial	CBI	<i>DynReg</i>	0.591	0.051	0.487	0.695
Spatial	CBI	<i>StatNest</i>	0.632	0.051	0.528	0.736
Spatial	CBI	<i>DynNest</i>	0.618	0.051	0.514	0.722
Forward	AUC	<i>StatReg</i>	0.752	0.013	0.726	0.778
Forward	AUC	<i>DynReg</i>	0.766	0.013	0.740	0.792
Forward	AUC	<i>StatNest</i>	0.757	0.013	0.732	0.783
Forward	AUC	<i>DynNest</i>	0.792	0.013	0.766	0.818
Forward	TSS	<i>StatReg</i>	0.464	0.022	0.420	0.508
Forward	TSS	<i>DynReg</i>	0.493	0.022	0.449	0.537
Forward	TSS	<i>StatNest</i>	0.458	0.022	0.414	0.502
Forward	TSS	<i>DynNest</i>	0.511	0.022	0.467	0.555
Forward	SSI	<i>StatReg</i>	0.734	0.012	0.709	0.758
Forward	SSI	<i>DynReg</i>	0.750	0.012	0.726	0.775
Forward	SSI	<i>StatNest</i>	0.731	0.012	0.707	0.755
Forward	SSI	<i>DynNest</i>	0.757	0.012	0.733	0.781
Forward	CBI	<i>StatReg</i>	0.760	0.040	0.679	0.842

Evaluation	Metric	Framework	Mean	SE	Lower 95% CI	Upper 95% CI
Forward	CBI	<i>DynReg</i>	0.747	0.040	0.665	0.829
Forward	CBI	<i>StatNest</i>	0.788	0.040	0.707	0.870
Forward	CBI	<i>DynNest</i>	0.793	0.040	0.711	0.875

Pairwise framework comparisons

Table S4.3. Pairwise differences between estimated marginal means. Positive values indicate higher performance for the first framework. P-values are Benjamini–Hochberg-adjusted across all six framework comparisons within each metric and evaluation design.

Evaluation	Metric	Contrast	Difference	SE	df	t	Adjusted p
Spatial	AUC	<i>StatReg - DynReg</i>	0.033	0.004	81.0	8.17	<0.001
Spatial	AUC	<i>StatReg - StatNest</i>	0.009	0.004	81.0	2.28	0.030
Spatial	AUC	<i>StatReg - DynNest</i>	0.016	0.004	81.0	3.98	<0.001
Spatial	AUC	<i>DynReg - StatNest</i>	-0.024	0.004	81.0	-5.89	<0.001
Spatial	AUC	<i>DynReg - DynNest</i>	-0.017	0.004	81.0	-4.19	<0.001
Spatial	AUC	<i>StatNest - DynNest</i>	0.007	0.004	81.0	1.70	0.094
Spatial	TSS	<i>StatReg - DynReg</i>	0.051	0.006	81.0	8.87	<0.001
Spatial	TSS	<i>StatReg - StatNest</i>	0.020	0.006	81.0	3.56	<0.001
Spatial	TSS	<i>StatReg - DynNest</i>	0.031	0.006	81.0	5.45	<0.001
Spatial	TSS	<i>DynReg - StatNest</i>	-0.030	0.006	81.0	-5.31	<0.001
Spatial	TSS	<i>DynReg - DynNest</i>	-0.020	0.006	81.0	-3.42	0.001
Spatial	TSS	<i>StatNest - DynNest</i>	0.011	0.006	81.0	1.89	0.062
Spatial	SSI	<i>StatReg - DynReg</i>	0.016	0.004	81.0	3.90	0.001
Spatial	SSI	<i>StatReg - StatNest</i>	0.002	0.004	81.0	0.42	0.676
Spatial	SSI	<i>StatReg - DynNest</i>	0.009	0.004	81.0	2.21	0.061
Spatial	SSI	<i>DynReg - StatNest</i>	-0.015	0.004	81.0	-3.49	0.002
Spatial	SSI	<i>DynReg - DynNest</i>	-0.007	0.004	81.0	-1.70	0.112
Spatial	SSI	<i>StatNest - DynNest</i>	0.007	0.004	81.0	1.79	0.112
Spatial	CBI	<i>StatReg - DynReg</i>	0.037	0.013	81.0	2.92	0.014
Spatial	CBI	<i>StatReg - StatNest</i>	-0.003	0.013	81.0	-0.26	0.797
Spatial	CBI	<i>StatReg - DynNest</i>	0.010	0.013	81.0	0.79	0.517
Spatial	CBI	<i>DynReg - StatNest</i>	-0.041	0.013	81.0	-3.18	0.013
Spatial	CBI	<i>DynReg - DynNest</i>	-0.027	0.013	81.0	-2.13	0.072
Spatial	CBI	<i>StatNest - DynNest</i>	0.013	0.013	81.0	1.05	0.445
Temporal	AUC	<i>StatReg - DynReg</i>	-0.014	0.008	81.0	-1.74	0.127

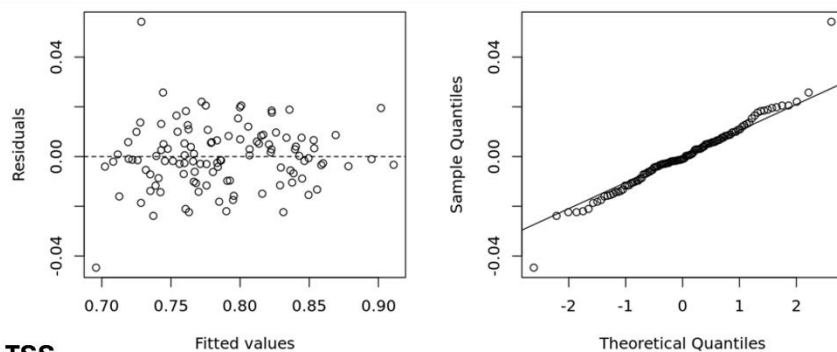
Evaluation	Metric	Contrast	Difference	SE	df	t	Adjusted p
Temporal	AUC	<i>StatReg - StatNest</i>	-0.006	0.008	81.0	-0.70	0.488
Temporal	AUC	<i>StatReg - DynNest</i>	-0.040	0.008	81.0	-5.01	<0.001
Temporal	AUC	<i>DynReg - StatNest</i>	0.008	0.008	81.0	1.05	0.358
Temporal	AUC	<i>DynReg - DynNest</i>	-0.026	0.008	81.0	-3.27	0.003
Temporal	AUC	<i>StatNest - DynNest</i>	-0.034	0.008	81.0	-4.31	<0.001
Temporal	TSS	<i>StatReg - DynReg</i>	-0.029	0.011	81.0	-2.73	0.012
Temporal	TSS	<i>StatReg - StatNest</i>	0.006	0.011	81.0	0.58	0.561
Temporal	TSS	<i>StatReg - DynNest</i>	-0.046	0.011	81.0	-4.36	<0.001
Temporal	TSS	<i>DynReg - StatNest</i>	0.035	0.011	81.0	3.32	0.003
Temporal	TSS	<i>DynReg - DynNest</i>	-0.017	0.011	81.0	-1.63	0.129
Temporal	TSS	<i>StatNest - DynNest</i>	-0.053	0.011	81.0	-4.95	<0.001
Temporal	SSI	<i>StatReg - DynReg</i>	-0.017	0.008	81.0	-2.11	0.057
Temporal	SSI	<i>StatReg - StatNest</i>	0.003	0.008	81.0	0.33	0.743
Temporal	SSI	<i>StatReg - DynNest</i>	-0.023	0.008	81.0	-2.91	0.014
Temporal	SSI	<i>DynReg - StatNest</i>	0.019	0.008	81.0	2.44	0.034
Temporal	SSI	<i>DynReg - DynNest</i>	-0.006	0.008	81.0	-0.81	0.506
Temporal	SSI	<i>StatNest - DynNest</i>	-0.026	0.008	81.0	-3.24	0.010
Temporal	CBI	<i>StatReg - DynReg</i>	0.013	0.021	81.0	0.63	0.636
Temporal	CBI	<i>StatReg - StatNest</i>	-0.028	0.021	81.0	-1.32	0.287
Temporal	CBI	<i>StatReg - DynNest</i>	-0.032	0.021	81.0	-1.51	0.269
Temporal	CBI	<i>DynReg - StatNest</i>	-0.041	0.021	81.0	-1.95	0.165
Temporal	CBI	<i>DynReg - DynNest</i>	-0.046	0.021	81.0	-2.14	0.165
Temporal	CBI	<i>StatNest - DynNest</i>	-0.004	0.021	81.0	-0.19	0.846

142 *Variance components*

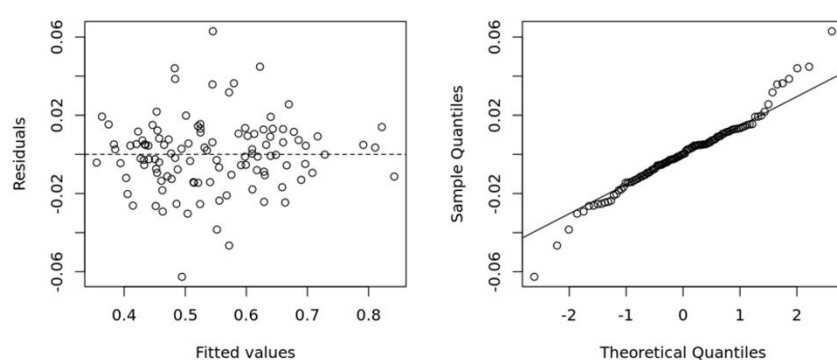
143 **Table S4.4.** Observation counts, species counts, singular-fit flags and variance components for
 144 each fitted model.

Evaluation	Metric	Observations	Species	Singular	Species variance	Residual variance
Spatial	AUC	112	28	FALSE	0.00219	0.00022
Spatial	TSS	112	28	FALSE	0.01130	0.00046
Spatial	SSI	112	28	FALSE	0.00230	0.00024
Spatial	CBI	112	28	FALSE	0.06994	0.00227
Temporal	AUC	112	28	FALSE	0.00366	0.00088
Temporal	TSS	112	28	FALSE	0.01148	0.00159
Temporal	SSI	112	28	FALSE	0.00311	0.00090
Temporal	CBI	112	28	FALSE	0.03912	0.00632

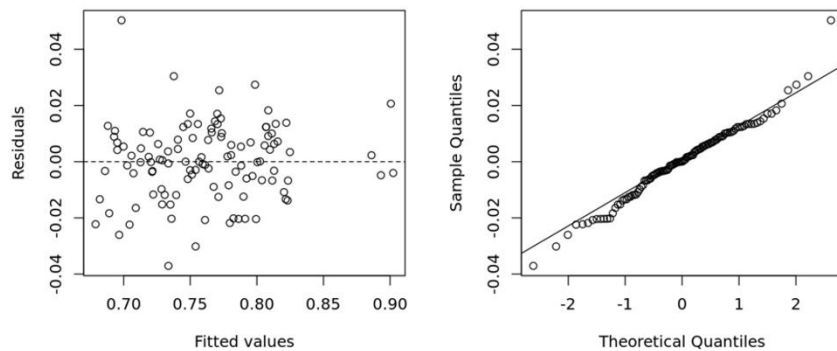
(a) AUC



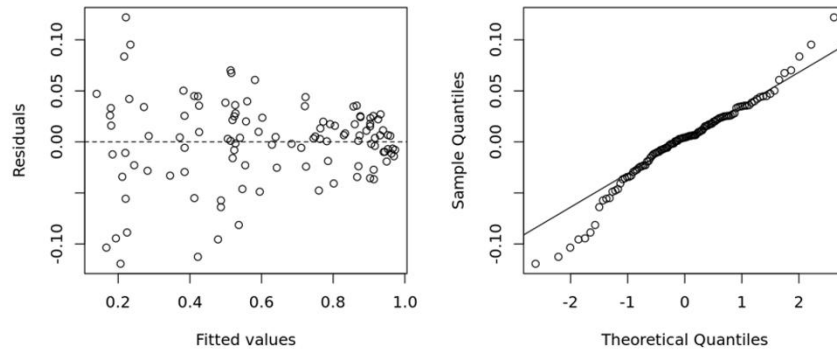
(b) TSS



(c) SSI



(c) CBI



146

147 **Figure S4.1.** Diagnostic plots for the mixed-effects models used to test differences in model

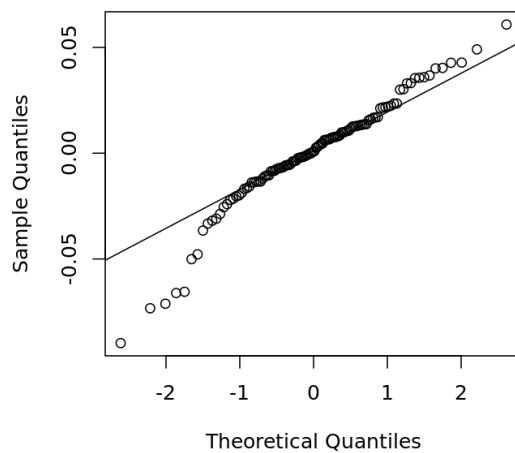
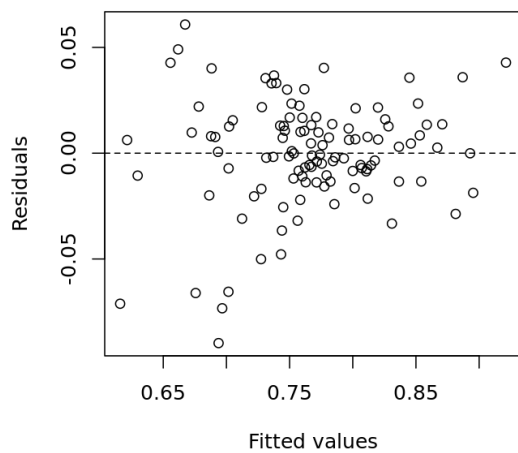
148 performance among the four species distribution modelling frameworks. Residual-versus-fitted

149 plots (left) and normal Q–Q plots (right) for the mixed-effects models. The panels retain the
150 original fitted values, residuals and reference lines.

151

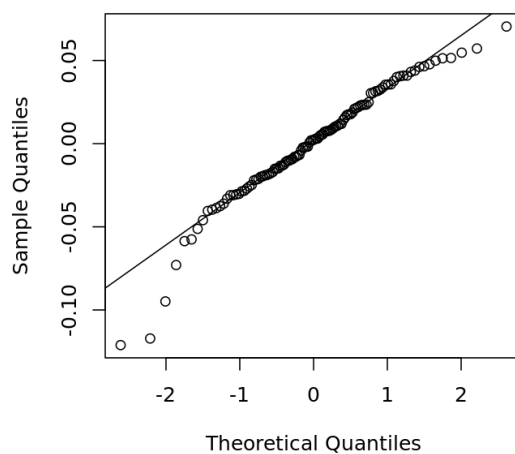
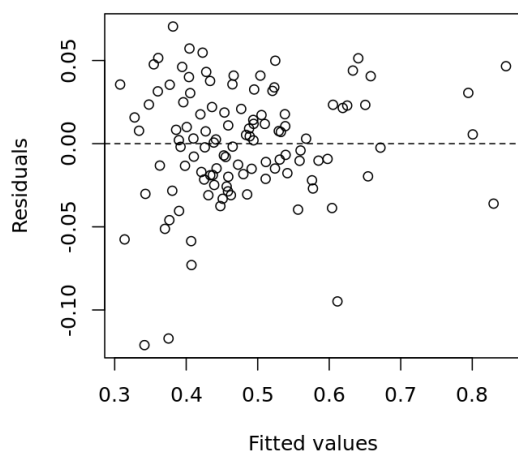
152 *Temporal validation diagnostics*

153 AUC



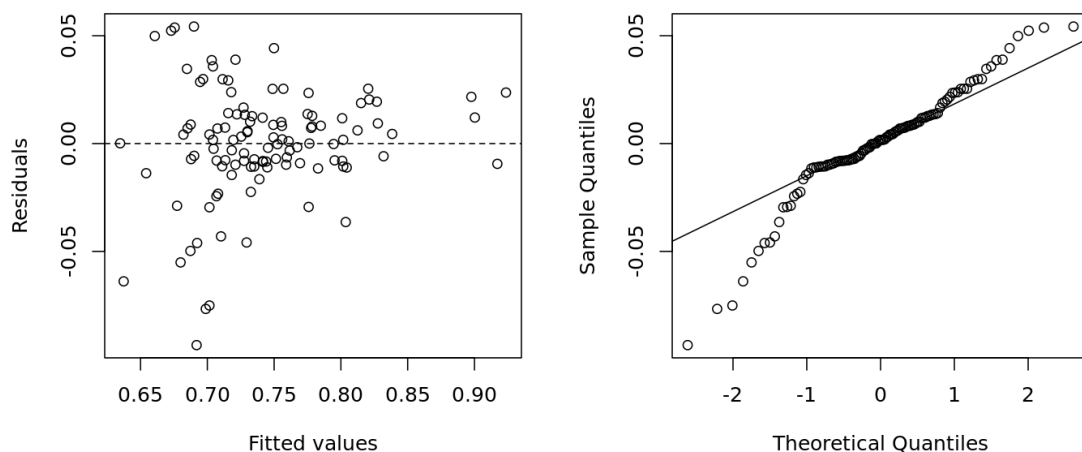
154

155 TSS



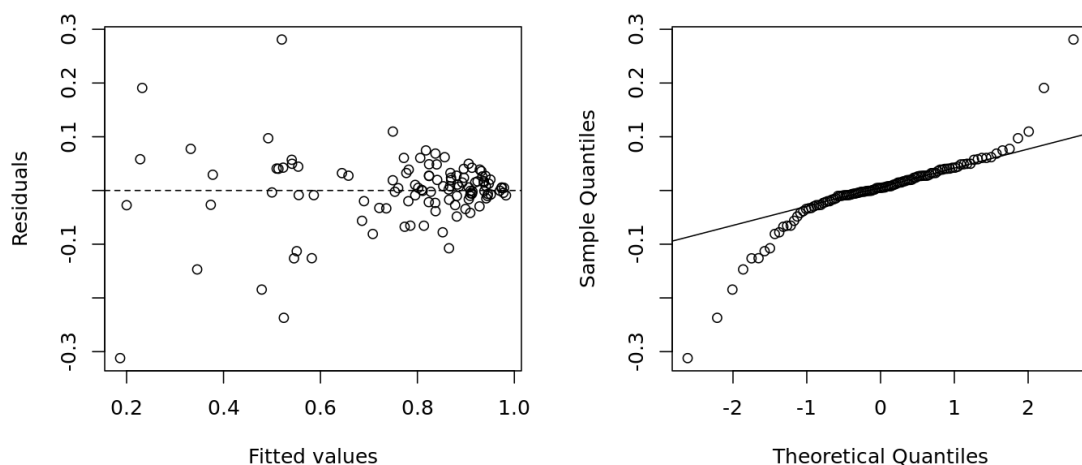
156

157 SSI



158

159 CBI



160

161 Figure S4.2. Diagnostic plots for the mixed-effects models used to test differences in model
162 performance among the four species distribution modelling frameworks. Residual-versus-fitted
163 plots (left) and normal Q–Q plots (right) for the mixed-effects models. The panels retain the
164 original fitted values, residuals and reference lines.

165

166

S5. Environmental novelty

The Shape metric was calculated with Mahalanobis distance using the *flexsdm::extra_eval()* function (Velazco et al. 2022, 2024). Larger values indicate greater multivariate climatic novelty relative to calibration conditions. Table S5.1 summarises the species–scenario mean Shape values. Table S5.2 provides the underlying pixel-level means, medians and upper-tail percentiles for all 448 species–framework–GCM–SSP combinations.

Table S5.1. Mean and sample standard deviation (SD) of Shape across species–scenario combinations for each framework. Each species–scenario combination contributes one mean Shape value. Summaries are based on 112 values per framework when both SSPs are pooled and 56 values per framework within each SSP. SDs quantify variation among these mean values.

Framework	Scenario	n	Mean	SD
<i>StatReg</i>	Both SSPs	112	1594.9	624.4
<i>StatReg</i>	SSP1-2.6	56	1289.6	475.7
<i>StatReg</i>	SSP5-8.5	56	1900.2	608.9
<i>DynReg</i>	Both SSPs	112	176.3	103.5
<i>DynReg</i>	SSP1-2.6	56	98.1	19.4
<i>DynReg</i>	SSP5-8.5	56	254.5	93.7
<i>StatNest</i>	Both SSPs	112	142.9	49.4
<i>StatNest</i>	SSP1-2.6	56	132.0	45.2
<i>StatNest</i>	SSP5-8.5	56	153.8	51.3
<i>DynNest</i>	Both SSPs	112	34.3	14.5
<i>DynNest</i>	SSP1-2.6	56	26.4	8.7
<i>DynNest</i>	SSP5-8.5	56	42.2	14.9

Table S5.2. Species-, framework- and scenario-specific Shape summaries for Denmark in 2071–2100. GFDL denotes GFDL-ESM4 and IPSL denotes IPSL-CM6A-LR. “Low” denotes SSP1-2.6 and “High” denotes SSP5-8.5. P90 and P95 are the 90th and 95th percentiles of raster values. Numerical values are retained at their original precision.

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Aphantopus hyperantus</i>	StatReg	GFDL	Low	1186.2	1172.3	1380.8	1481
<i>Aphantopus hyperantus</i>	StatReg	GFDL	High	1483.5	1471.9	1630.7	1750.5
<i>Aphantopus hyperantus</i>	StatReg	IPSL	Low	978.9	967.5	1111.3	1170.3
<i>Aphantopus hyperantus</i>	StatReg	IPSL	High	1834.9	1825.6	1992.7	2033.5
<i>Aporia crataegi</i>	StatReg	GFDL	Low	1533.4	1554.5	1717.1	1758.1
<i>Aporia crataegi</i>	StatReg	GFDL	High	1994.7	2001.5	2271	2330.5
<i>Aporia crataegi</i>	StatReg	IPSL	Low	1779.7	1781.6	1971.3	2012.5
<i>Aporia crataegi</i>	StatReg	IPSL	High	2494.3	2493.5	2664.6	2706.7
<i>Argynnis paphia</i>	StatReg	GFDL	Low	1206.3	1188.5	1426.6	1519.2
<i>Argynnis paphia</i>	StatReg	GFDL	High	1407.8	1390.6	1571.8	1687.2
<i>Argynnis paphia</i>	StatReg	IPSL	Low	946	937.1	1088.1	1144.5
<i>Argynnis paphia</i>	StatReg	IPSL	High	1689.9	1679.2	1857.8	1907.3
<i>Boloria euphrosyne</i>	StatReg	GFDL	Low	2235.3	2196	2851.9	2938.5
<i>Boloria euphrosyne</i>	StatReg	GFDL	High	2063.5	2155.5	2448.6	2584
<i>Boloria euphrosyne</i>	StatReg	IPSL	Low	2120.2	2191.7	2420.8	2486.1
<i>Boloria euphrosyne</i>	StatReg	IPSL	High	2087.8	2112.4	2380.9	2468.8
<i>Brenthis ino</i>	StatReg	GFDL	Low	2207.5	2181.8	2617.9	2769.5
<i>Brenthis ino</i>	StatReg	GFDL	High	2263.3	2237.6	2601.6	2827.4
<i>Brenthis ino</i>	StatReg	IPSL	Low	1598.2	1591.9	1910.7	2018.6
<i>Brenthis ino</i>	StatReg	IPSL	High	2623.1	2608.3	2963.1	3073.2
<i>Celastrina argiolus</i>	StatReg	GFDL	Low	1238	1227	1454.3	1543.2
<i>Celastrina argiolus</i>	StatReg	GFDL	High	1414.3	1397.7	1594.6	1698.7
<i>Celastrina argiolus</i>	StatReg	IPSL	Low	994.1	981	1153.9	1198
<i>Celastrina argiolus</i>	StatReg	IPSL	High	1620.1	1608.6	1797.8	1851.1
<i>Coenonympha tullia</i>	StatReg	GFDL	Low	1252.4	1260.1	1415	1447.8
<i>Coenonympha tullia</i>	StatReg	GFDL	High	1777.1	1780.9	2028.4	2075.1
<i>Coenonympha tullia</i>	StatReg	IPSL	Low	1404.9	1405	1574.8	1612.6
<i>Coenonympha tullia</i>	StatReg	IPSL	High	2281.6	2281.6	2472.3	2509
<i>Cupido minimus</i>	StatReg	GFDL	Low	1349.2	1328.6	1593.3	1709.9

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Cupido minimus</i>	StatReg	GFDL	High	1616.4	1593.8	1806.4	1948
<i>Cupido minimus</i>	StatReg	IPSL	Low	1042.5	1026.2	1223.1	1293.1
<i>Cupido minimus</i>	StatReg	IPSL	High	2003.6	1992.9	2214.3	2268.6
<i>Cyaniris semiargus</i>	StatReg	GFDL	Low	1647	1620.6	1929.1	2056.7
<i>Cyaniris semiargus</i>	StatReg	GFDL	High	2145.2	2106.6	2459.4	2561.1
<i>Cyaniris semiargus</i>	StatReg	IPSL	Low	1394.9	1378.7	1592.9	1641.1
<i>Cyaniris semiargus</i>	StatReg	IPSL	High	2617.1	2595	2926.8	2996.6
<i>Euphydryas aurinia</i>	StatReg	GFDL	Low	1848	1847.7	2066.6	2143.8
<i>Euphydryas aurinia</i>	StatReg	GFDL	High	2590.2	2559.3	2903.8	2972.9
<i>Euphydryas aurinia</i>	StatReg	IPSL	Low	2088.7	2014.7	2624.9	2713.8
<i>Euphydryas aurinia</i>	StatReg	IPSL	High	3222.4	3183	3577.8	3654.2
<i>Fabriciana adippe</i>	StatReg	GFDL	Low	1882.2	1862.9	2188.9	2352.7
<i>Fabriciana adippe</i>	StatReg	GFDL	High	2222.2	2192.9	2488.3	2702
<i>Fabriciana adippe</i>	StatReg	IPSL	Low	1464.8	1443	1728.1	1810.6
<i>Fabriciana adippe</i>	StatReg	IPSL	High	2787.9	2774.5	3091.7	3170.7
<i>Fabriciana niobe</i>	StatReg	GFDL	Low	2017.4	2044.5	2280	2353
<i>Fabriciana niobe</i>	StatReg	GFDL	High	2434.2	2424.9	2891	2975.3
<i>Fabriciana niobe</i>	StatReg	IPSL	Low	2123	2116	2457.1	2534.5
<i>Fabriciana niobe</i>	StatReg	IPSL	High	2997.8	2985.9	3302.2	3354.2
<i>Gonepteryx rhamni</i>	StatReg	GFDL	Low	998.1	1003.6	1124.7	1188.9
<i>Gonepteryx rhamni</i>	StatReg	GFDL	High	1233.3	1225.2	1408.1	1451.2
<i>Gonepteryx rhamni</i>	StatReg	IPSL	Low	924.2	913.9	1068.2	1126.3
<i>Gonepteryx rhamni</i>	StatReg	IPSL	High	1558.8	1548	1667.6	1696.5
<i>Hesperia comma</i>	StatReg	GFDL	Low	586.6	588.9	693.7	721.2
<i>Hesperia comma</i>	StatReg	GFDL	High	1453	1449.8	1595	1638.4
<i>Hesperia comma</i>	StatReg	IPSL	Low	832.1	849	972.3	998.6
<i>Hesperia comma</i>	StatReg	IPSL	High	2461.9	2455.2	2638.2	2699.4
<i>Hipparchia semele</i>	StatReg	GFDL	Low	1410.7	1376.1	1727.5	1801.4
<i>Hipparchia semele</i>	StatReg	GFDL	High	1515.2	1477.9	1796.3	1857.6
<i>Hipparchia semele</i>	StatReg	IPSL	Low	1051.6	1045.5	1183.9	1233.9
<i>Hipparchia semele</i>	StatReg	IPSL	High	1597.8	1581.3	1774.3	1825
<i>Maniola jurtina</i>	StatReg	GFDL	Low	873.7	882.5	1014.2	1050.7
<i>Maniola jurtina</i>	StatReg	GFDL	High	1074.1	1058.3	1289.4	1344.2
<i>Maniola jurtina</i>	StatReg	IPSL	Low	909.3	897.2	1070.7	1123
<i>Maniola jurtina</i>	StatReg	IPSL	High	1397.1	1386.1	1533.7	1560.4

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Aglaia io</i>	StatReg	GFDL	Low	1150.3	1137.5	1342.4	1439.8
<i>Aglaia io</i>	StatReg	GFDL	High	1403.9	1392.5	1547	1666.6
<i>Aglaia io</i>	StatReg	IPSL	Low	930.4	918.3	1065.2	1120.2
<i>Aglaia io</i>	StatReg	IPSL	High	1712.9	1702.5	1868.5	1911
<i>Anthocharis cardamines</i>	StatReg	GFDL	Low	1172.1	1161.9	1366.8	1452.5
<i>Anthocharis cardamines</i>	StatReg	GFDL	High	1407.1	1393.2	1566.9	1662.4
<i>Anthocharis cardamines</i>	StatReg	IPSL	Low	983.1	970.3	1121.7	1160.3
<i>Anthocharis cardamines</i>	StatReg	IPSL	High	1642	1631.4	1796.3	1838.5
<i>Lycaena phlaeas</i>	StatReg	GFDL	Low	1226	1212.8	1427.7	1532.9
<i>Lycaena phlaeas</i>	StatReg	GFDL	High	1476.6	1463.9	1632.6	1759.5
<i>Lycaena phlaeas</i>	StatReg	IPSL	Low	984	971.1	1132.9	1189.9
<i>Lycaena phlaeas</i>	StatReg	IPSL	High	1776.7	1765.6	1950.2	1999.6
<i>Lycaena virgaureae</i>	StatReg	GFDL	Low	1451.5	1438.6	1672.7	1800.5
<i>Lycaena virgaureae</i>	StatReg	GFDL	High	1900.7	1892.1	2070	2224.2
<i>Lycaena virgaureae</i>	StatReg	IPSL	Low	1234.9	1219.7	1403.6	1472.9
<i>Lycaena virgaureae</i>	StatReg	IPSL	High	2333.6	2323	2520	2565.7
<i>Pararge aegeria</i>	StatReg	GFDL	Low	1174	1158.8	1362.4	1457.6
<i>Pararge aegeria</i>	StatReg	GFDL	High	1408.6	1384.9	1615.1	1683.4
<i>Pararge aegeria</i>	StatReg	IPSL	Low	902	890.3	1041.5	1087.7
<i>Pararge aegeria</i>	StatReg	IPSL	High	1652.6	1639.4	1838.2	1890.6
<i>Phengaris alcon</i>	StatReg	GFDL	Low	2198	2223	2389.7	2475.6
<i>Phengaris alcon</i>	StatReg	GFDL	High	3223.1	3241.2	3531.3	3607.7
<i>Phengaris alcon</i>	StatReg	IPSL	Low	2358.7	2341.4	2658.4	2732.4
<i>Phengaris alcon</i>	StatReg	IPSL	High	4169.2	4137.7	4468.2	4562.7
<i>Plebejus idas</i>	StatReg	GFDL	Low	1026	1031.8	1191.3	1240.8
<i>Plebejus idas</i>	StatReg	GFDL	High	1274.2	1257.4	1533.6	1608.6
<i>Plebejus idas</i>	StatReg	IPSL	Low	1056.1	1041.3	1259.8	1339.3
<i>Plebejus idas</i>	StatReg	IPSL	High	1661.2	1643.9	1838.5	1879.3
<i>Polygonia c-album</i>	StatReg	GFDL	Low	1424.1	1396.1	1705.8	1806.1
<i>Polygonia c-album</i>	StatReg	GFDL	High	1492.5	1466.1	1718	1822.9
<i>Polygonia c-album</i>	StatReg	IPSL	Low	958.3	945.8	1107	1162.9
<i>Polygonia c-album</i>	StatReg	IPSL	High	1629	1624.7	1786.7	1830.4
<i>Polyommatus amandus</i>	StatReg	GFDL	Low	563.3	567.9	649.7	673.7
<i>Polyommatus amandus</i>	StatReg	GFDL	High	1396.4	1399.4	1487.3	1508.6
<i>Polyommatus amandus</i>	StatReg	IPSL	Low	811.6	810.2	937.9	966.3

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Polyommatus amandus</i>	StatReg	IPSL	High	2160.5	2160.4	2291.3	2329.1
<i>Speyeria aglaja</i>	StatReg	GFDL	Low	333.9	334.8	396.3	413.9
<i>Speyeria aglaja</i>	StatReg	GFDL	High	903.3	907	967.4	987.6
<i>Speyeria aglaja</i>	StatReg	IPSL	Low	504.1	505.2	588.4	607.2
<i>Speyeria aglaja</i>	StatReg	IPSL	High	1416.1	1417.5	1501.8	1529.6
<i>Pieris napi</i>	StatReg	GFDL	Low	1171	1159.5	1368.4	1454.8
<i>Pieris napi</i>	StatReg	GFDL	High	1411.5	1396.6	1574.1	1672.1
<i>Pieris napi</i>	StatReg	IPSL	Low	975.4	962.2	1116.2	1153
<i>Pieris napi</i>	StatReg	IPSL	High	1662.5	1650.8	1820	1863.3
<i>Favonius quercus</i>	StatReg	GFDL	Low	1403.9	1387.8	1648.6	1738
<i>Favonius quercus</i>	StatReg	GFDL	High	1542.6	1528.2	1730.6	1847.8
<i>Favonius quercus</i>	StatReg	IPSL	Low	1097.1	1090.1	1258.3	1318.6
<i>Favonius quercus</i>	StatReg	IPSL	High	1791.9	1781.6	1972.7	2025.4
<i>Aphantopus hyperantus</i>	DynReg	GFDL	Low	79.8	78.8	98.6	103.8
<i>Aphantopus hyperantus</i>	DynReg	GFDL	High	178.9	173.7	210.2	220.2
<i>Aphantopus hyperantus</i>	DynReg	IPSL	Low	82.5	80	105.5	121.5
<i>Aphantopus hyperantus</i>	DynReg	IPSL	High	305.1	303.3	332.6	340.6
<i>Aporia crataegi</i>	DynReg	GFDL	Low	73.2	71.7	94.6	97.3
<i>Aporia crataegi</i>	DynReg	GFDL	High	145	143.5	179.1	184.3
<i>Aporia crataegi</i>	DynReg	IPSL	Low	107.4	106	127.6	132.9
<i>Aporia crataegi</i>	DynReg	IPSL	High	250.9	251.6	275.9	281.7
<i>Argynnis paphia</i>	DynReg	GFDL	Low	105.2	101.5	138.4	145.7
<i>Argynnis paphia</i>	DynReg	GFDL	High	181.3	179.2	197.8	206
<i>Argynnis paphia</i>	DynReg	IPSL	Low	95.7	93.8	110.2	113.9
<i>Argynnis paphia</i>	DynReg	IPSL	High	308.1	307.6	329.2	335.3
<i>Boloria euphrosyne</i>	DynReg	GFDL	Low	111.3	109.2	148.1	155.8
<i>Boloria euphrosyne</i>	DynReg	GFDL	High	106.7	109.6	132.9	139.4
<i>Boloria euphrosyne</i>	DynReg	IPSL	Low	109.2	111.7	131.2	136.7
<i>Boloria euphrosyne</i>	DynReg	IPSL	High	94.1	95.7	111.7	115.7
<i>Brenthis ino</i>	DynReg	GFDL	Low	114	112.9	148.4	155.1
<i>Brenthis ino</i>	DynReg	GFDL	High	190.5	188.2	212.6	219.9
<i>Brenthis ino</i>	DynReg	IPSL	Low	103.5	100.2	130.9	143.5
<i>Brenthis ino</i>	DynReg	IPSL	High	308.4	306.7	336.2	347.1
<i>Celastrina argiolus</i>	DynReg	GFDL	Low	94.9	95.2	112.7	119
<i>Celastrina argiolus</i>	DynReg	GFDL	High	167.8	164.8	188.1	194.7

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Celastrina argiolus</i>	<i>DynReg</i>	IPSL	Low	96.2	94.8	109.1	115
<i>Celastrina argiolus</i>	<i>DynReg</i>	IPSL	High	289.3	289.4	310.5	317.7
<i>Coenonympha tullia</i>	<i>DynReg</i>	GFDL	Low	106.1	107.7	128.2	131.4
<i>Coenonympha tullia</i>	<i>DynReg</i>	GFDL	High	166.8	162.9	200.7	218.3
<i>Coenonympha tullia</i>	<i>DynReg</i>	IPSL	Low	110	107	135.9	148.5
<i>Coenonympha tullia</i>	<i>DynReg</i>	IPSL	High	293.8	291.6	325.6	337.5
<i>Cupido minimus</i>	<i>DynReg</i>	GFDL	Low	94.5	91.6	119.2	128.4
<i>Cupido minimus</i>	<i>DynReg</i>	GFDL	High	180.1	178.2	199.9	207.8
<i>Cupido minimus</i>	<i>DynReg</i>	IPSL	Low	92.1	90.1	108.7	112.6
<i>Cupido minimus</i>	<i>DynReg</i>	IPSL	High	298.8	297.7	321.5	331.3
<i>Cyaniris semiargus</i>	<i>DynReg</i>	GFDL	Low	111.6	107.7	144.6	150.3
<i>Cyaniris semiargus</i>	<i>DynReg</i>	GFDL	High	176.7	174.6	196.9	206.3
<i>Cyaniris semiargus</i>	<i>DynReg</i>	IPSL	Low	104.9	103.4	120.3	124.2
<i>Cyaniris semiargus</i>	<i>DynReg</i>	IPSL	High	276.3	275.1	291.6	297
<i>Euphydryas aurinia</i>	<i>DynReg</i>	GFDL	Low	125.9	124.8	157.5	169.1
<i>Euphydryas aurinia</i>	<i>DynReg</i>	GFDL	High	328	325.5	387	408.9
<i>Euphydryas aurinia</i>	<i>DynReg</i>	IPSL	Low	157.8	155.4	202.6	220.3
<i>Euphydryas aurinia</i>	<i>DynReg</i>	IPSL	High	559.1	557.2	622.6	642
<i>Fabriciana adippe</i>	<i>DynReg</i>	GFDL	Low	110.7	104.4	152.6	161.5
<i>Fabriciana adippe</i>	<i>DynReg</i>	GFDL	High	181.3	177.9	210.3	220.1
<i>Fabriciana adippe</i>	<i>DynReg</i>	IPSL	Low	95.2	91.6	115.4	121.9
<i>Fabriciana adippe</i>	<i>DynReg</i>	IPSL	High	309.9	307.8	341.3	352.4
<i>Fabriciana niobe</i>	<i>DynReg</i>	GFDL	Low	129.1	134.9	160.3	166.8
<i>Fabriciana niobe</i>	<i>DynReg</i>	GFDL	High	227.3	219.2	287.7	301.7
<i>Fabriciana niobe</i>	<i>DynReg</i>	IPSL	Low	138	131	184.5	192.3
<i>Fabriciana niobe</i>	<i>DynReg</i>	IPSL	High	377.6	372.3	428.4	441.7
<i>Gonepteryx rhamni</i>	<i>DynReg</i>	GFDL	Low	98.4	96.7	123	128.1
<i>Gonepteryx rhamni</i>	<i>DynReg</i>	GFDL	High	221.1	214.5	255.5	265.4
<i>Gonepteryx rhamni</i>	<i>DynReg</i>	IPSL	Low	108.2	104.3	142.9	152.7
<i>Gonepteryx rhamni</i>	<i>DynReg</i>	IPSL	High	381.6	379.9	415	428
<i>Hesperia comma</i>	<i>DynReg</i>	GFDL	Low	61	60.4	84.4	89.4
<i>Hesperia comma</i>	<i>DynReg</i>	GFDL	High	193.4	189.5	225.2	233.4
<i>Hesperia comma</i>	<i>DynReg</i>	IPSL	Low	97.3	96.4	123.4	130.2
<i>Hesperia comma</i>	<i>DynReg</i>	IPSL	High	342.1	340.9	369.2	376.8
<i>Hipparchia semele</i>	<i>DynReg</i>	GFDL	Low	87.7	83.1	120	133.6

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Hipparchia semele</i>	DynReg	GFDL	High	196.8	192.6	226.8	239.1
<i>Hipparchia semele</i>	DynReg	IPSL	Low	94	90.3	134.3	146.5
<i>Hipparchia semele</i>	DynReg	IPSL	High	329.1	325.9	367.7	380.6
<i>Maniola jurtina</i>	DynReg	GFDL	Low	77.8	76.1	96.3	101.6
<i>Maniola jurtina</i>	DynReg	GFDL	High	161.5	156.7	191.1	201.2
<i>Maniola jurtina</i>	DynReg	IPSL	Low	90.7	89.8	115.5	127.8
<i>Maniola jurtina</i>	DynReg	IPSL	High	288	287	314.7	325.5
<i>Aglais io</i>	DynReg	GFDL	Low	85.4	83.9	100.8	112.5
<i>Aglais io</i>	DynReg	GFDL	High	201.8	199.1	223.4	231.9
<i>Aglais io</i>	DynReg	IPSL	Low	88.6	88.9	106.5	113.5
<i>Aglais io</i>	DynReg	IPSL	High	349.3	348.1	374.2	383.1
<i>Anthocharis cardamines</i>	DynReg	GFDL	Low	87.4	86.1	104.4	110.2
<i>Anthocharis cardamines</i>	DynReg	GFDL	High	155.2	153.8	177.1	185.4
<i>Anthocharis cardamines</i>	DynReg	IPSL	Low	85.1	84.6	105.7	110.9
<i>Anthocharis cardamines</i>	DynReg	IPSL	High	251.5	250.9	270.2	276.3
<i>Lycaena phlaeas</i>	DynReg	GFDL	Low	95	93.8	114.8	122.5
<i>Lycaena phlaeas</i>	DynReg	GFDL	High	175.3	172.9	194.9	206.5
<i>Lycaena phlaeas</i>	DynReg	IPSL	Low	84.8	84.4	100.1	103.5
<i>Lycaena phlaeas</i>	DynReg	IPSL	High	290.8	290.3	308.3	314.1
<i>Lycaena virgaureae</i>	DynReg	GFDL	Low	100.3	98	124.5	134.6
<i>Lycaena virgaureae</i>	DynReg	GFDL	High	182.2	178.2	212	220.1
<i>Lycaena virgaureae</i>	DynReg	IPSL	Low	86.4	82.5	112.9	124.7
<i>Lycaena virgaureae</i>	DynReg	IPSL	High	297.4	295.9	326.1	333.8
<i>Pararge aegeria</i>	DynReg	GFDL	Low	83.3	81.5	104.6	110
<i>Pararge aegeria</i>	DynReg	GFDL	High	154.1	152.1	169.9	180
<i>Pararge aegeria</i>	DynReg	IPSL	Low	78.1	76.9	90.8	95.3
<i>Pararge aegeria</i>	DynReg	IPSL	High	261	260.4	276.9	282.2
<i>Phengaris alcon</i>	DynReg	GFDL	Low	114.2	113.9	141	147.7
<i>Phengaris alcon</i>	DynReg	GFDL	High	180.7	180.2	207.1	211.6
<i>Phengaris alcon</i>	DynReg	IPSL	Low	122.8	117.2	158.3	163.1
<i>Phengaris alcon</i>	DynReg	IPSL	High	265	258.5	301	314.8
<i>Plebejus idas</i>	DynReg	GFDL	Low	108.7	105.8	128.6	139.7
<i>Plebejus idas</i>	DynReg	GFDL	High	261.6	256.6	313.3	334.3
<i>Plebejus idas</i>	DynReg	IPSL	Low	123.6	117.1	158.1	182.8
<i>Plebejus idas</i>	DynReg	IPSL	High	487.3	485.7	533.9	548.8

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Polygonia c-album</i>	DynReg	GFDL	Low	115	110.9	149.8	159.9
<i>Polygonia c-album</i>	DynReg	GFDL	High	214.1	212.1	233.8	243
<i>Polygonia c-album</i>	DynReg	IPSL	Low	101	98.6	122.6	127.5
<i>Polygonia c-album</i>	DynReg	IPSL	High	362.8	362.5	387	396.1
<i>Polyommatus amandus</i>	DynReg	GFDL	Low	46.2	45.8	63.1	70.6
<i>Polyommatus amandus</i>	DynReg	GFDL	High	196.5	197.7	220.3	227.5
<i>Polyommatus amandus</i>	DynReg	IPSL	Low	83	83.6	101.8	107.5
<i>Polyommatus amandus</i>	DynReg	IPSL	High	371	371	403.6	412.8
<i>Speyeria aglaja</i>	DynReg	GFDL	Low	52.4	52.5	71.7	77.3
<i>Speyeria aglaja</i>	DynReg	GFDL	High	239.8	241.7	273.3	280.5
<i>Speyeria aglaja</i>	DynReg	IPSL	Low	96	96.1	121.4	128.4
<i>Speyeria aglaja</i>	DynReg	IPSL	High	458.6	458.8	500.7	512.1
<i>Pieris napi</i>	DynReg	GFDL	Low	86.5	87.1	103.8	107.2
<i>Pieris napi</i>	DynReg	GFDL	High	140.6	138	160.7	167.2
<i>Pieris napi</i>	DynReg	IPSL	Low	83.5	82.5	98.5	102.4
<i>Pieris napi</i>	DynReg	IPSL	High	230.6	230	248.4	253.2
<i>Favonius quercus</i>	DynReg	GFDL	Low	110.9	111.1	127.1	131.2
<i>Favonius quercus</i>	DynReg	GFDL	High	200.6	194.7	238.3	258.2
<i>Favonius quercus</i>	DynReg	IPSL	Low	109	106.5	145.2	157.2
<i>Favonius quercus</i>	DynReg	IPSL	High	310.8	304.9	356.9	370
<i>Aphantopus hyperantus</i>	StatNest	GFDL	Low	158.3	159.6	181	184.3
<i>Aphantopus hyperantus</i>	StatNest	GFDL	High	170	171.9	191	198.2
<i>Aphantopus hyperantus</i>	StatNest	IPSL	Low	136.2	136.8	154.3	159.6
<i>Aphantopus hyperantus</i>	StatNest	IPSL	High	181.9	176.4	208.8	216.6
<i>Aporia crataegi</i>	StatNest	GFDL	Low	126.7	127.9	153.1	161.8
<i>Aporia crataegi</i>	StatNest	GFDL	High	138.4	136	186.1	194.5
<i>Aporia crataegi</i>	StatNest	IPSL	Low	136.1	135.3	174.1	179.3
<i>Aporia crataegi</i>	StatNest	IPSL	High	153.4	153.1	184.8	188.8
<i>Argynnis paphia</i>	StatNest	GFDL	Low	145.9	147.6	163.9	169.3
<i>Argynnis paphia</i>	StatNest	GFDL	High	162.6	165.7	179.5	183.5
<i>Argynnis paphia</i>	StatNest	IPSL	Low	130.8	131.1	147.4	151.3
<i>Argynnis paphia</i>	StatNest	IPSL	High	175.9	173.3	195.9	199.8
<i>Boloria euphrosyne</i>	StatNest	GFDL	Low	91.3	92	107.7	111
<i>Boloria euphrosyne</i>	StatNest	GFDL	High	84.1	83.9	109.4	114.1
<i>Boloria euphrosyne</i>	StatNest	IPSL	Low	86.8	88.8	109.1	114.3

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Boloria euphrosyne</i>	StatNest	IPSL	High	89.2	87.4	110.8	115.9
<i>Brenthis ino</i>	StatNest	GFDL	Low	203.9	204	238.7	250.3
<i>Brenthis ino</i>	StatNest	GFDL	High	225.3	223.7	264.2	278
<i>Brenthis ino</i>	StatNest	IPSL	Low	177.6	171.7	214	227
<i>Brenthis ino</i>	StatNest	IPSL	High	234.8	236.6	273.3	286.5
<i>Celastrina argiolus</i>	StatNest	GFDL	Low	137.2	138.2	158.2	166.1
<i>Celastrina argiolus</i>	StatNest	GFDL	High	154.8	152	184.5	193.7
<i>Celastrina argiolus</i>	StatNest	IPSL	Low	132.3	129.1	159.8	168.8
<i>Celastrina argiolus</i>	StatNest	IPSL	High	163.9	160.3	190.6	197.1
<i>Coenonympha tullia</i>	StatNest	GFDL	Low	232.4	235.4	270.5	281.5
<i>Coenonympha tullia</i>	StatNest	GFDL	High	234.7	232.6	299.3	328.4
<i>Coenonympha tullia</i>	StatNest	IPSL	Low	234.6	231.1	290.6	311.2
<i>Coenonympha tullia</i>	StatNest	IPSL	High	240.9	235.3	299.8	319.5
<i>Cupido minimus</i>	StatNest	GFDL	Low	143.2	144.6	162.5	165.4
<i>Cupido minimus</i>	StatNest	GFDL	High	152.5	155.9	169.3	172.7
<i>Cupido minimus</i>	StatNest	IPSL	Low	126.2	125.8	144.3	148.8
<i>Cupido minimus</i>	StatNest	IPSL	High	160.5	157.4	176.7	181.4
<i>Cyaniris semiargus</i>	StatNest	GFDL	Low	151.7	152	171.7	179.9
<i>Cyaniris semiargus</i>	StatNest	GFDL	High	168.1	165.8	192.2	199.8
<i>Cyaniris semiargus</i>	StatNest	IPSL	Low	145.8	142.7	173.3	179.1
<i>Cyaniris semiargus</i>	StatNest	IPSL	High	164.1	160.7	185.8	194.6
<i>Euphydryas aurinia</i>	StatNest	GFDL	Low	151.9	153.3	174.1	182.4
<i>Euphydryas aurinia</i>	StatNest	GFDL	High	174	175.7	193.1	204
<i>Euphydryas aurinia</i>	StatNest	IPSL	Low	130.5	132.4	146.9	149.7
<i>Euphydryas aurinia</i>	StatNest	IPSL	High	173.9	173.6	195.2	199.2
<i>Fabriciana adippe</i>	StatNest	GFDL	Low	165.9	165.7	191.4	199.5
<i>Fabriciana adippe</i>	StatNest	GFDL	High	192.2	190.7	217.8	228.4
<i>Fabriciana adippe</i>	StatNest	IPSL	Low	141.3	139.7	161.4	168.1
<i>Fabriciana adippe</i>	StatNest	IPSL	High	203.8	208.1	228.6	233.2
<i>Fabriciana niobe</i>	StatNest	GFDL	Low	147.4	148.2	166.2	170.8
<i>Fabriciana niobe</i>	StatNest	GFDL	High	159.4	158.2	192.1	201.8
<i>Fabriciana niobe</i>	StatNest	IPSL	Low	155.6	155.5	178.9	187.3
<i>Fabriciana niobe</i>	StatNest	IPSL	High	164.7	163.4	191.3	199.1
<i>Gonepteryx rhamni</i>	StatNest	GFDL	Low	129	130.4	146.8	152.3
<i>Gonepteryx rhamni</i>	StatNest	GFDL	High	141.4	141.3	172.1	183.5

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Gonepteryx rhamni</i>	StatNest	IPSL	Low	133.3	130.8	158.6	167.9
<i>Gonepteryx rhamni</i>	StatNest	IPSL	High	150.8	148.8	179.3	189.7
<i>Hesperia comma</i>	StatNest	GFDL	Low	26.5	26.4	35.4	37.6
<i>Hesperia comma</i>	StatNest	GFDL	High	29.1	25.8	49.4	50.9
<i>Hesperia comma</i>	StatNest	IPSL	Low	24.2	21.6	39.8	41.6
<i>Hesperia comma</i>	StatNest	IPSL	High	38.9	38.4	56.9	61.8
<i>Hipparchia semele</i>	StatNest	GFDL	Low	122.3	122	143.7	152.4
<i>Hipparchia semele</i>	StatNest	GFDL	High	142.3	139.6	170.7	182.2
<i>Hipparchia semele</i>	StatNest	IPSL	Low	117.9	114.3	145.3	153.4
<i>Hipparchia semele</i>	StatNest	IPSL	High	155	150.1	182.2	187.1
<i>Maniola jurtina</i>	StatNest	GFDL	Low	117.8	117.6	137	141.8
<i>Maniola jurtina</i>	StatNest	GFDL	High	126.8	124.9	158.1	166.5
<i>Maniola jurtina</i>	StatNest	IPSL	Low	123.7	121.3	149.6	156
<i>Maniola jurtina</i>	StatNest	IPSL	High	137.3	135.1	161.2	169.1
<i>Aglais io</i>	StatNest	GFDL	Low	147.4	148	168	171.6
<i>Aglais io</i>	StatNest	GFDL	High	158.3	161.6	175.8	179.6
<i>Aglais io</i>	StatNest	IPSL	Low	128.4	128.9	145	149
<i>Aglais io</i>	StatNest	IPSL	High	165.6	162.6	182	187.3
<i>Anthocharis cardamines</i>	StatNest	GFDL	Low	135.3	135.9	154.9	162.5
<i>Anthocharis cardamines</i>	StatNest	GFDL	High	152.3	150.7	176	183.6
<i>Anthocharis cardamines</i>	StatNest	IPSL	Low	129.5	127.1	154.8	163.1
<i>Anthocharis cardamines</i>	StatNest	IPSL	High	153.2	150	175.6	186.2
<i>Lycaena phlaeas</i>	StatNest	GFDL	Low	133.9	135.1	149.5	155.9
<i>Lycaena phlaeas</i>	StatNest	GFDL	High	147.6	149.7	164.4	168
<i>Lycaena phlaeas</i>	StatNest	IPSL	Low	117.9	117	135	139.8
<i>Lycaena phlaeas</i>	StatNest	IPSL	High	158.5	158.5	170.9	175.3
<i>Lycaena virgaureae</i>	StatNest	GFDL	Low	164.6	163.5	201	211.1
<i>Lycaena virgaureae</i>	StatNest	GFDL	High	187.1	184.1	225.6	239.5
<i>Lycaena virgaureae</i>	StatNest	IPSL	Low	145.9	138.3	183.1	193.5
<i>Lycaena virgaureae</i>	StatNest	IPSL	High	185.8	186	216	227.1
<i>Pararge aegeria</i>	StatNest	GFDL	Low	181.4	181.3	212.4	222.7
<i>Pararge aegeria</i>	StatNest	GFDL	High	212.9	207.9	257.2	264.6
<i>Pararge aegeria</i>	StatNest	IPSL	Low	138.7	137.6	163.7	169
<i>Pararge aegeria</i>	StatNest	IPSL	High	207.2	203.5	250.5	257.7
<i>Phengaris alcon</i>	StatNest	GFDL	Low	158.5	158.8	179.1	186.7

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Phengaris alcon</i>	StatNest	GFDL	High	171.8	169.2	202.9	214.8
<i>Phengaris alcon</i>	StatNest	IPSL	Low	157.9	154.8	187.6	195.5
<i>Phengaris alcon</i>	StatNest	IPSL	High	177.6	170.4	209.6	217.6
<i>Plebejus idas</i>	StatNest	GFDL	Low	160.6	162.4	182.4	189.4
<i>Plebejus idas</i>	StatNest	GFDL	High	167.5	165.3	209	227
<i>Plebejus idas</i>	StatNest	IPSL	Low	165.7	165.9	197.3	209.2
<i>Plebejus idas</i>	StatNest	IPSL	High	170	165.6	208.1	218.8
<i>Polygonia c-album</i>	StatNest	GFDL	Low	141.8	142.4	160.9	164.5
<i>Polygonia c-album</i>	StatNest	GFDL	High	151.7	154.8	167.3	170.5
<i>Polygonia c-album</i>	StatNest	IPSL	Low	120.2	121.2	135.1	140.2
<i>Polygonia c-album</i>	StatNest	IPSL	High	154.6	151.7	172.1	175.5
<i>Polyommatus amandus</i>	StatNest	GFDL	Low	33.4	32.7	44.2	46.7
<i>Polyommatus amandus</i>	StatNest	GFDL	High	39.6	37.6	62.8	64.6
<i>Polyommatus amandus</i>	StatNest	IPSL	Low	34.2	31.8	49.7	52.1
<i>Polyommatus amandus</i>	StatNest	IPSL	High	50.8	50.8	69.6	74.2
<i>Speyeria aglaja</i>	StatNest	GFDL	Low	18.6	18.7	23.7	25.1
<i>Speyeria aglaja</i>	StatNest	GFDL	High	19.8	15.4	39.9	43.8
<i>Speyeria aglaja</i>	StatNest	IPSL	Low	18.7	17.5	28.1	29.5
<i>Speyeria aglaja</i>	StatNest	IPSL	High	21.3	19.3	37.6	41.9
<i>Pieris napi</i>	StatNest	GFDL	Low	142.6	143.7	163.8	171.3
<i>Pieris napi</i>	StatNest	GFDL	High	159.9	156.5	190.7	207.8
<i>Pieris napi</i>	StatNest	IPSL	Low	139	135.6	171.2	182.6
<i>Pieris napi</i>	StatNest	IPSL	High	170.2	163.4	208.6	219.8
<i>Favonius quercus</i>	StatNest	GFDL	Low	156.4	156.1	181	188.2
<i>Favonius quercus</i>	StatNest	GFDL	High	184.4	182.6	212.4	218.6
<i>Favonius quercus</i>	StatNest	IPSL	Low	135.1	130.8	161.1	167.7
<i>Favonius quercus</i>	StatNest	IPSL	High	202.2	203.4	230.8	239.1
<i>Aphantopus hyperantus</i>	DynNest	GFDL	Low	25.3	23.3	36.6	41.2
<i>Aphantopus hyperantus</i>	DynNest	GFDL	High	36.6	33.1	56.4	62.5
<i>Aphantopus hyperantus</i>	DynNest	IPSL	Low	22.2	21	34.9	38.1
<i>Aphantopus hyperantus</i>	DynNest	IPSL	High	44.9	43	59.6	63.7
<i>Aporia crataegi</i>	DynNest	GFDL	Low	27	26	37.7	41.1
<i>Aporia crataegi</i>	DynNest	GFDL	High	26.5	23.5	46.1	49.4
<i>Aporia crataegi</i>	DynNest	IPSL	Low	27.1	25.8	41.9	44.5
<i>Aporia crataegi</i>	DynNest	IPSL	High	44.4	42	59.8	73.2

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Argynnis paphia</i>	DynNest	GFDL	Low	25.2	23.9	35.8	38.6
<i>Argynnis paphia</i>	DynNest	GFDL	High	38.3	35.6	57.1	59.9
<i>Argynnis paphia</i>	DynNest	IPSL	Low	24.1	24.4	34.8	37.3
<i>Argynnis paphia</i>	DynNest	IPSL	High	48.7	44.9	76.4	87.7
<i>Boloria euphrosyne</i>	DynNest	GFDL	Low	12.8	11.9	20.1	23.2
<i>Boloria euphrosyne</i>	DynNest	GFDL	High	13	11.7	20.5	26.9
<i>Boloria euphrosyne</i>	DynNest	IPSL	Low	13.5	11.8	22.1	27.2
<i>Boloria euphrosyne</i>	DynNest	IPSL	High	12.1	10.5	21.6	26.7
<i>Brenthis ino</i>	DynNest	GFDL	Low	29.5	27.2	43.8	51
<i>Brenthis ino</i>	DynNest	GFDL	High	41.4	39.4	61	68
<i>Brenthis ino</i>	DynNest	IPSL	Low	27.9	26.3	43.1	48.3
<i>Brenthis ino</i>	DynNest	IPSL	High	58.2	55.6	82.9	90.8
<i>Celastrina argiolus</i>	DynNest	GFDL	Low	29.7	26.9	45.8	51.2
<i>Celastrina argiolus</i>	DynNest	GFDL	High	42.1	38.6	60	68.5
<i>Celastrina argiolus</i>	DynNest	IPSL	Low	30.2	27.5	50.1	53.4
<i>Celastrina argiolus</i>	DynNest	IPSL	High	52.3	48.4	77.2	83.9
<i>Coenonympha tullia</i>	DynNest	GFDL	Low	31.2	29.4	45.2	48.6
<i>Coenonympha tullia</i>	DynNest	GFDL	High	46.9	42.5	70.2	75.6
<i>Coenonympha tullia</i>	DynNest	IPSL	Low	36.4	33.8	52.1	56.3
<i>Coenonympha tullia</i>	DynNest	IPSL	High	79.2	79	98.8	106.9
<i>Cupido minimus</i>	DynNest	GFDL	Low	26	24.8	38.2	41.6
<i>Cupido minimus</i>	DynNest	GFDL	High	38.5	36.9	55.7	61
<i>Cupido minimus</i>	DynNest	IPSL	Low	25.1	25	35.2	37.4
<i>Cupido minimus</i>	DynNest	IPSL	High	59.1	56.1	83.2	86.7
<i>Cyaniris semiargus</i>	DynNest	GFDL	Low	31.2	28.1	46.6	50.4
<i>Cyaniris semiargus</i>	DynNest	GFDL	High	43.5	40.5	64.2	70.4
<i>Cyaniris semiargus</i>	DynNest	IPSL	Low	34.5	31.3	51.2	56.8
<i>Cyaniris semiargus</i>	DynNest	IPSL	High	58.7	55	80.6	87.1
<i>Euphydryas aurinia</i>	DynNest	GFDL	Low	17.8	17.8	24.2	25.4
<i>Euphydryas aurinia</i>	DynNest	GFDL	High	18.7	17.8	26	30.2
<i>Euphydryas aurinia</i>	DynNest	IPSL	Low	22	22.3	29.4	30.4
<i>Euphydryas aurinia</i>	DynNest	IPSL	High	31.2	31.4	37	38.1
<i>Fabriciana adippe</i>	DynNest	GFDL	Low	30.1	28	46.1	52.5
<i>Fabriciana adippe</i>	DynNest	GFDL	High	43.7	43	63	66.8
<i>Fabriciana adippe</i>	DynNest	IPSL	Low	31.1	29.7	42.3	46.4

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Fabriciana adippe</i>	DynNest	IPSL	High	50	49.2	61.8	65.9
<i>Fabriciana niobe</i>	DynNest	GFDL	Low	29.2	29.9	38.6	41.7
<i>Fabriciana niobe</i>	DynNest	GFDL	High	39.9	37.3	54.7	61.6
<i>Fabriciana niobe</i>	DynNest	IPSL	Low	32.9	30.9	46.2	51.6
<i>Fabriciana niobe</i>	DynNest	IPSL	High	39.5	38.4	51	55.2
<i>Gonepteryx rhamni</i>	DynNest	GFDL	Low	25.4	23.3	37.8	40.8
<i>Gonepteryx rhamni</i>	DynNest	GFDL	High	38.6	34.9	61.9	67
<i>Gonepteryx rhamni</i>	DynNest	IPSL	Low	29.1	26.9	43.7	46.9
<i>Gonepteryx rhamni</i>	DynNest	IPSL	High	50.3	48.8	67.2	79.8
<i>Hesperia comma</i>	DynNest	GFDL	Low	10	9.5	15.3	17.5
<i>Hesperia comma</i>	DynNest	GFDL	High	16.2	14.7	26.3	32.6
<i>Hesperia comma</i>	DynNest	IPSL	Low	13.2	12.6	19.2	24.6
<i>Hesperia comma</i>	DynNest	IPSL	High	25.4	24.2	38	47
<i>Hipparchia semele</i>	DynNest	GFDL	Low	29.1	27.3	41.6	47.7
<i>Hipparchia semele</i>	DynNest	GFDL	High	37	32.5	63	71.7
<i>Hipparchia semele</i>	DynNest	IPSL	Low	30.9	29.3	46.2	49.9
<i>Hipparchia semele</i>	DynNest	IPSL	High	51.4	51.4	65.5	69.5
<i>Maniola jurtina</i>	DynNest	GFDL	Low	24.6	22.6	38.3	42
<i>Maniola jurtina</i>	DynNest	GFDL	High	35.5	32.9	52.7	69.4
<i>Maniola jurtina</i>	DynNest	IPSL	Low	29.3	26.4	46	49.3
<i>Maniola jurtina</i>	DynNest	IPSL	High	39.3	37.1	56.2	63
<i>Aglais io</i>	DynNest	GFDL	Low	25	23.2	37.5	41.1
<i>Aglais io</i>	DynNest	GFDL	High	34.5	34.1	52.8	58.8
<i>Aglais io</i>	DynNest	IPSL	Low	23.7	23.3	34.5	37.7
<i>Aglais io</i>	DynNest	IPSL	High	46.2	46.1	58	61.7
<i>Anthocharis cardamines</i>	DynNest	GFDL	Low	26.2	24.2	39.9	43.8
<i>Anthocharis cardamines</i>	DynNest	GFDL	High	38.9	37.7	54.9	64.4
<i>Anthocharis cardamines</i>	DynNest	IPSL	Low	28.4	26.5	42.5	45.3
<i>Anthocharis cardamines</i>	DynNest	IPSL	High	47.1	43	72.3	77.2
<i>Lycaena phlaeas</i>	DynNest	GFDL	Low	25	22.8	37.8	44.3
<i>Lycaena phlaeas</i>	DynNest	GFDL	High	36.2	32.5	56.8	64.3
<i>Lycaena phlaeas</i>	DynNest	IPSL	Low	23.4	21.8	35.8	39.8
<i>Lycaena phlaeas</i>	DynNest	IPSL	High	52.8	52.3	63.1	65.3
<i>Lycaena virgaureae</i>	DynNest	GFDL	Low	24.1	22.8	34.3	38.2
<i>Lycaena virgaureae</i>	DynNest	GFDL	High	33.8	32.8	51.6	55.4

Species	Framework	GCM	SSP	Mean	Median	P90	P95
<i>Lycaena virgaureae</i>	DynNest	IPSL	Low	24.4	23.6	33.3	36.8
<i>Lycaena virgaureae</i>	DynNest	IPSL	High	52.5	49.3	78.3	85.1
<i>Pararge aegeria</i>	DynNest	GFDL	Low	23.8	23.2	31.8	35.3
<i>Pararge aegeria</i>	DynNest	GFDL	High	35.4	32.5	52.2	59
<i>Pararge aegeria</i>	DynNest	IPSL	Low	23.1	21.8	33.8	37.4
<i>Pararge aegeria</i>	DynNest	IPSL	High	51.1	50.8	61.7	64.7
<i>Phengaris alcon</i>	DynNest	GFDL	Low	50.8	46.8	75.3	78.9
<i>Phengaris alcon</i>	DynNest	GFDL	High	63.3	55	99.9	106.1
<i>Phengaris alcon</i>	DynNest	IPSL	Low	58.1	54.3	80.1	84
<i>Phengaris alcon</i>	DynNest	IPSL	High	79.2	71.7	113.6	117.9
<i>Plebejus idas</i>	DynNest	GFDL	Low	35.6	32.7	52.3	58.7
<i>Plebejus idas</i>	DynNest	GFDL	High	47.8	44.3	72.5	88
<i>Plebejus idas</i>	DynNest	IPSL	Low	39.8	36.8	59.6	69.9
<i>Plebejus idas</i>	DynNest	IPSL	High	57.7	51.8	86.4	96.3
<i>Polygonia c-album</i>	DynNest	GFDL	Low	22.9	21.2	34.7	38.7
<i>Polygonia c-album</i>	DynNest	GFDL	High	32.2	27.7	55.3	59.5
<i>Polygonia c-album</i>	DynNest	IPSL	Low	21.4	19.3	33.6	37.1
<i>Polygonia c-album</i>	DynNest	IPSL	High	46.5	47.5	63	67.9
<i>Polyommatus amandus</i>	DynNest	GFDL	Low	12.5	12	19	23.1
<i>Polyommatus amandus</i>	DynNest	GFDL	High	23.2	22.6	36.5	43.5
<i>Polyommatus amandus</i>	DynNest	IPSL	Low	17.8	17.3	26.9	29.8
<i>Polyommatus amandus</i>	DynNest	IPSL	High	32	29.6	45.4	53
<i>Speyeria aglaja</i>	DynNest	GFDL	Low	8.6	7.9	13.9	16.1
<i>Speyeria aglaja</i>	DynNest	GFDL	High	13	11.6	23.2	26.1
<i>Speyeria aglaja</i>	DynNest	IPSL	Low	9.8	8.9	16.4	18.5
<i>Speyeria aglaja</i>	DynNest	IPSL	High	18.1	16.8	28.9	34.1
<i>Pieris napi</i>	DynNest	GFDL	Low	28	26.4	40.1	43.5
<i>Pieris napi</i>	DynNest	GFDL	High	41.6	39.2	61.7	70.3
<i>Pieris napi</i>	DynNest	IPSL	Low	29.6	27.7	41.3	45.8
<i>Pieris napi</i>	DynNest	IPSL	High	55.4	53.2	72.6	76.5
<i>Favonius quercus</i>	DynNest	GFDL	Low	30.7	28.3	48.6	51.8
<i>Favonius quercus</i>	DynNest	GFDL	High	49.4	45.8	72.3	76.1
<i>Favonius quercus</i>	DynNest	IPSL	Low	29.6	27.7	44.1	47.4
<i>Favonius quercus</i>	DynNest	IPSL	High	72.6	68.8	94.7	102.1

S6. Agreement among future projections

Spearman correlations quantify the similarity of pixel-wise suitability rankings between framework pairs within each GCM-SSP combination. Values were averaged across species. Lower correlation indicates greater sensitivity to framework choice, not lower forecast accuracy.

Table S6. Mean pixel-wise Spearman correlation (ρ) between pairs of continuous future suitability projections, averaged across 28 species for each GCM-SSP combination in 2071–2100.

GCM	SSP	Framework 1	Framework 2	Mean ρ
GFDL-ESM4	SSP1-2.6	<i>StatReg</i>	<i>StatNest</i>	0.719
GFDL-ESM4	SSP1-2.6	<i>StatReg</i>	<i>DynReg</i>	0.728
GFDL-ESM4	SSP1-2.6	<i>StatReg</i>	<i>DynNest</i>	0.736
GFDL-ESM4	SSP1-2.6	<i>StatNest</i>	<i>DynReg</i>	0.945
GFDL-ESM4	SSP1-2.6	<i>StatNest</i>	<i>DynNest</i>	0.970
GFDL-ESM4	SSP1-2.6	<i>DynReg</i>	<i>DynNest</i>	0.969
IPSL-CM6A-LR	SSP1-2.6	<i>StatReg</i>	<i>StatNest</i>	0.691
IPSL-CM6A-LR	SSP1-2.6	<i>StatReg</i>	<i>DynReg</i>	0.707
IPSL-CM6A-LR	SSP1-2.6	<i>StatReg</i>	<i>DynNest</i>	0.706
IPSL-CM6A-LR	SSP1-2.6	<i>StatNest</i>	<i>DynReg</i>	0.941
IPSL-CM6A-LR	SSP1-2.6	<i>StatNest</i>	<i>DynNest</i>	0.965
IPSL-CM6A-LR	SSP1-2.6	<i>DynReg</i>	<i>DynNest</i>	0.963
GFDL-ESM4	SSP5-8.5	<i>StatReg</i>	<i>StatNest</i>	0.721
GFDL-ESM4	SSP5-8.5	<i>StatReg</i>	<i>DynReg</i>	0.736
GFDL-ESM4	SSP5-8.5	<i>StatReg</i>	<i>DynNest</i>	0.735
GFDL-ESM4	SSP5-8.5	<i>StatNest</i>	<i>DynReg</i>	0.938
GFDL-ESM4	SSP5-8.5	<i>StatNest</i>	<i>DynNest</i>	0.965
GFDL-ESM4	SSP5-8.5	<i>DynReg</i>	<i>DynNest</i>	0.961
IPSL-CM6A-LR	SSP5-8.5	<i>StatReg</i>	<i>StatNest</i>	0.733
IPSL-CM6A-LR	SSP5-8.5	<i>StatReg</i>	<i>DynReg</i>	0.745
IPSL-CM6A-LR	SSP5-8.5	<i>StatReg</i>	<i>DynNest</i>	0.744
IPSL-CM6A-LR	SSP5-8.5	<i>StatNest</i>	<i>DynReg</i>	0.941
IPSL-CM6A-LR	SSP5-8.5	<i>StatNest</i>	<i>DynNest</i>	0.965
IPSL-CM6A-LR	SSP5-8.5	<i>DynReg</i>	<i>DynNest</i>	0.963

S7. ODMAP protocol

The workflow is documented following the Overview, Data, Model, Assessment and Prediction structure of Zurell et al. (2020). The forward temporal holdout is distinguished from full-period calibration and spatial cross-validation.

ODMAP element	Contents
Authorship	Authors: Camila Rocabado, Derek Corcoran, Trine Bilde, Samuel J. L. Gascoigne, Signe Normand, Marjo Saastamoinen, Santiago J. E. Velazco, Damaris Zurell, Roslyn Henry and Greta Bocedi. Contact: camilarocabado7@gmail.com Title: Beyond static species distribution models: temporally dynamic, spatially nested species distribution models reduce extrapolation for future projections
Model objective	Objectives: to compare four species distribution modelling frameworks in a factorial design crossing temporal (long-term averages <i>versus</i> year-matched predictors) and spatial (regional <i>versus</i> spatially nested calibration) dimensions; to quantify predictive performance, climatic niche truncation, environmental novelty under future climates and sensitivity of spatial projections to framework choice. Target outputs: continuous habitat-suitability predictions for Denmark, cross-validation metrics, climatic niche-unfilling estimates, environmental-novelty diagnostics (Shape metric) and pairwise spatial correlations among future projections.
Taxon	Twenty-eight resident Danish butterfly species (Lepidoptera). Migratory species whose Danish distributions were excluded from the candidate set.
Location	European calibration domain for the range-wide component of nested models and Denmark as the regional modelling and projection domain.
Scale of analysis	Spatial extent: Europe, -31.28 to 68.93 degrees E and 18.97 to 81.85 degrees N; Denmark, 7.88 to 15.60 degrees E and 54.35 to 57.81 degrees N. Spatial grain: approximately 1 km (30 arcseconds) for European climate models and 100 m for regional Danish models. Temporal extent: occurrence and historical environmental data, 1990-2018; future climate, 2071-2100. Forward temporal validation: regional calibration, 1990–2009; evaluation, 2010–2018. Temporal grain: annual for temporally matched models; 1990-2018 averages for static models. Extent boundary: geographic European modelling extent and the administrative boundary of Denmark.

ODMAP element	Contents
Conceptual model / hypotheses	Regional training datasets can truncate the climatic conditions represented across a species' wider range (Adde et al. 2023), while long-term environmental averages can omit interannual conditions associated with observations (Milanesi et al. 2020). Spatial nesting and temporal matching were therefore expected to broaden complementary dimensions of the training domain. Their combination was expected to reduce environmental novelty most strongly when projecting to future climates.
Assumptions	The fitted correlative relationships are informative for spatial and temporal transfer and remain applicable under future conditions. GBIF filtering and thinning reduce, but do not eliminate, heterogeneous sampling effort across space and time. Generated pseudoabsences represent available environmental conditions rather than confirmed absences. Climate and land use capture important distributional constraints, but dispersal, biotic interactions, demography, adaptation and evolutionary change are not modelled. Lower extrapolation indicates stronger environmental support, not demonstrated future accuracy.
Biodiversity data overview	Response type: species presences from GBIF and generated pseudoabsences. European and Danish occurrence datasets were prepared separately to match the spatial grain of the respective model components. Pseudoabsence replicates were balanced to the number of presences.
Biodiversity data	Taxon names: <i>Aglaia io</i>; <i>Anthocharis cardamines</i>; <i>Aphantopus hyperantus</i>; <i>Aporia crataegi</i>; <i>Argynnis paphia</i>; <i>Boloria euphrosyne</i>; <i>Brenthis ino</i>; <i>Celastrina argiolus</i>; <i>Coenonympha tullia</i>; <i>Cupido minimus</i>; <i>Cyaniris semiargus</i>; <i>Euphydryas aurinia</i>; <i>Fabriciana adippe</i>; <i>Fabriciana niobe</i>; <i>Favonius quercus</i>; <i>Gonepteryx rhamni</i>; <i>Hesperia comma</i>; <i>Hipparchia semele</i>; <i>Lycaena phlaeas</i>; <i>Lycaena virgaureae</i>; <i>Maniola jurtina</i>; <i>Pararge aegeria</i>; <i>Phengaris alcon</i>; <i>Pieris napi</i>; <i>Plebejus idas</i>; <i>Polygonia c-album</i>; <i>Polyommatus amandus</i>; and <i>Speyeria aglaja</i>. Ecological level: species. Data source: GBIF occurrence records for Europe and Denmark, restricted to 1990-2018. Candidate Danish resident species followed Eskildsen et al. (2015).
Biodiversity-data processing	Records without usable coordinates, duplicates, coordinate centroids, institutional coordinates and records flagged by <i>CoordinateCleaner</i> were removed (Zizka et al. 2019). Coordinate uncertainty had to be below the modelling grain (approximately 1 km in Europe and 100 m in Denmark). At most one presence was retained per grid cell and year within two-year periods; static datasets were additionally thinned to one record per cell across 1990-2018. Species required at least 30 regional records and temporal coverage spanning the study period. Potential biases: GBIF records have heterogeneous sampling effort through space and time; filtering and thinning reduce but cannot remove this bias.

ODMAP element	Contents
Data partitioning	Spatial validation used five spatial blocks. Species-specific block size was based on the estimated spatial autocorrelation range using <i>cv_spatial_autocor()</i> , and blocks were assigned to folds with <i>cv_spatial()</i> in <i>blockCV</i> (Valavi et al. 2019). Forward temporal evaluation fitted regional models using 1990–2009 records and scored all frameworks against a common pooled 2010–2018 presence–pseudoabsence dataset. Dynamic annual predictions were averaged before scoring; static climate was averaged separately for the training and evaluation periods. Pseudoabsences were generated by species and year in ten replicates, with equal numbers of presences and pseudoabsences, within a convex hull expanded by 20% of its area.
Type of predictors	European components: bioclimatic predictors. Regional components: downscaled bioclimatic predictors, proportional grassland, wetland, cropland and forest cover, plus European climatic suitability as an additional covariate in nested frameworks.
Predictor variables	Climate: monthly minimum temperature, maximum temperature and precipitation from CHELSA v2 (Karger et al. 2017) were used to derive 19 annual bioclimatic variables; variables 8, 9, 18 and 19 were excluded because combined temperature-precipitation variables can contain spatial discontinuities (Booth 2022). Annual layers were generated for 1990–2018; static layers were their period means. Future CHELSA v2 climate represented 2071–2100 for GFDL-ESM4 and IPSL-CM6A-LR under SSP1-2.6 and SSP5-8.5. Land use: proportional grassland, cropland and forest cover derived from 25 m Danish categorical maps for ten time steps between 1990 and 2018 (Levin et al. 2014, Levin and Gylsten 2022). Spatial preprocessing: European climate retained its approximately 1 km grain; regional climate was bilinearly downscaled and land use aggregated to 100 m.
Predictor alignment and transformation	All spatial layers were aligned to the relevant European or Danish modelling grid. Dynamic models extracted climate and land-use conditions for the year assigned to each presence and pseudoabsence. Static models used 1990–2018 averages. Nested models transferred predictions from the European climatic model to the regional grid as an additional suitability predictor. Proportional land-cover variables were calculated from categorical rasters during aggregation.
Variable pre-selection / multicollinearity	Predictors were screened separately for every species and spatial extent using variance inflation factors. Variables were removed iteratively with <i>vifstep()</i> in <i>usdm</i> (Naimi et al. 2014), so the retained European and Danish predictor sets could differ among species and model components.
SDM algorithms	Random Forest classification models, implemented in the R package <i>sdm</i> (Breiman 2001; Naimi and Araújo 2016). Full-period calibration used 1,000 trees.

ODMAP element	Contents
Model workflow	Four frameworks were fitted for each species and pseudoabsence replicate. <i>StatReg</i> used Danish occurrences with climate and land use averaged across 1990-2018. <i>DynReg</i> used Danish occurrences, pseudoabsences, climate and land use matched by year. <i>StatNest</i> first fitted a Europe-wide climatic model using averaged climate, then used its climatic-suitability prediction as an additional covariate in a static Danish model. <i>DynNest</i> fitted a Europe-wide model with annually matched climate, generated annual climatic-suitability layers and used these with annually matched regional climate and land use in the Danish model. Frameworks were evaluated using niche coverage to calculate unfilling (Di Cola et al. 2017), spatial cross-validation and a common forward temporal validation (Roberts et al. 2017, Valavi et al. 2019), future environmental novelty (Velazco et al. 2024) and agreement among continuous future projections.
Model settings	Full-period models used 1,000 trees, bootstrap sampling and default classification settings (mtry equal to the square root of the number of predictors; terminal node size 1). Models were fitted by species, framework and pseudoabsence replicate.
Model estimates	Primary estimates were continuous habitat-suitability values.
Software, code and data	Software: R 4.4.0. Principal packages included <i>sdm</i> , <i>terra</i> , <i>dismo</i> , <i>CoordinateCleaner</i> , <i>usdm</i> , <i>blockCV</i> , <i>ecospat</i> , <i>flexsdm</i> , <i>lme4</i> , <i>lmerTest</i> and <i>emmeans</i> . Occurrence data: GBIF downloads https://doi.org/10.15468/dl.kqavhr (Europe) and https://doi.org/10.15468/dl.79t5mt (Denmark).
Non-independence correction / analyses	Spatial and temporal structure were addressed using spatial block cross-validation and a common forward temporal holdout validation scheme. Comparative performance analyses used linear mixed-effects models with temporal strategy, spatial strategy and their interaction as fixed effects and species as a random intercept. Type-III F-tests and estimated marginal means were used; pairwise p-values were adjusted using the Benjamini-Hochberg procedure.
Performance statistics	Performance was evaluated using AUC, TSS, SSI and CBI, separately for spatial cross-validation and the forward temporal holdout. Forward-holdout metrics were computed using <i>flexsdm::sdm_eval()</i> , with <i>max_sens_spec</i> thresholds for threshold-dependent scores. Metric values were averaged over pseudoabsence replicates for each species and framework before mixed-effects analysis. Type-III tests, estimated marginal means and the six pairwise framework contrasts are reported in Section S4. Pairwise p-values were Benjamini-Hochberg-adjusted within metric and evaluation design. Residual-versus-fitted and normal Q-Q plots were inspected. Models with AUC ≥ 0.7 and TSS ≥ 0.4 were retained for future projection.

ODMAP element	Contents
Prediction output	Prediction unit: continuous habitat suitability on a 0-1 scale for Denmark. Future projections covered 2071-2100 for two GCMs and two SSPs. Environmental novelty was quantified with Mahalanobis-distance Shape using <i>extra_eval()</i> in <i>flexsdm</i>, with summaries in Section S5. Spatial agreement was quantified using pixel-wise Spearman correlations between each pair of frameworks within species and GCM–SSP combination, then averaged across species (Section S6). Neither lower Shape nor higher agreement establishes future predictive accuracy.

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