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Impact of climate and land use change on the distribution of orchids in Estonia

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Abstract

Habitat loss and climate change are driving global declines in terrestrial orchid populations. In Europe, predicted northward range shifts suggest that northern regions may serve as future refugia. Estonia— one of northern Europe's most orchid-rich countries—offers a valuable case study for assessing climate change impact on orchids. Using species distribution models (SDMs), we projected range changes for 31 orchid species under moderate (SSP245) and high-emission (SSP585) scenarios, integrating land use change projections through the 21st century. Currently, the western islands and coastal areas host the highest orchid diversity, forming a hotspot for calcicole tuberous species that grow preferentially in open and semi-open habitats. Under both scenarios, many of these species are expected to shift eastward. However, significant losses in orchid richness are predicted as early as 2040, severely impacting these western orchid hotspots and large parts of central and eastern Estonia, with non-calcicole rhizomatous species inhabiting forest and wet forest habitats emerging as the most vulnerable taxa. Projected changes intensify under SSP585, where 2040–2060 conditions resemble those expected under SSP245 by 2080–2100. The period up to 2040 emerges as a critical bottleneck, especially for rare and threatened species. While some recovery is projected after 2060 under high-emission scenarios, earlier population declines may lead to irreversible losses. Estonia holds promise as a northern refuge for orchids under climate change, but proactive conservation efforts are urgently needed before 2040 to avert future biodiversity loss.

Keywords Species distribution modeling · Orchids · Climate change · Land use change · Ensemble models · Estonia

Introduction

The year 2023 was the hottest on record (Witze 2024), a stark reminder that climate change scenarios are already unfolding. Climate change profoundly impacts species' physiology, distribution, survival, and the ecosystem services they provide (Chen et al. 2011; Bellard et al. 2012; Fekete et al. 2023). Predicting changes in species distributions helps researchers understand climatic patterns and their implications.

In Europe, terrestrial orchids are a protected and threatened plant family (Fay 2018; Jakubska-Busse et al. 2021; Štípková and Kindlmann 2021; Kull and Hutchings 2006; Swarts and Dixon 2009; Feldmann and Prat 2011). They are often considered flagship species (Dixon et al. 2003; Basu and Cetzal-Ix 2015; Liu et al. 2023), with 26 species currently listed as endangered (EN) or critically endangered (CR) on the IUCN Red List. Global declines in terrestrial orchids due to habitat loss and climate change are expected to worsen in the coming decades (Kindlmann et al. 2023).

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Recent studies increasingly point to climate change as a major driver of orchid population dynamics and distribution shifts (Pfeifer et al. 2006; Williams et al. 2015; van der Meer et al. 2016). Species distribution modeling has predicted northward range shifts for several orchid species under future climate scenarios, including *Orchis* spp. and *Ophrys insectifera* L. (Evans et al. 2020; Charitonidou et al. 2022). At the same time, the loss of open and semi-natural habitats due to land-use change remains a critical factor in ongoing orchid declines across Europe (Koopowitz and Hawkins 2012; Vogt-Schilb et al. 2015; Wraith and Pickering 2019; Charitonidou et al. 2022). While land-use pressures have historically played a leading role, future climate conditions are expected to become increasingly influential in determining orchid persistence and distribution. Milder warming may enable range expansions, while severe warming could cause declines or local extinctions, particularly in southern Europe. Northern Europe, including Estonia, may serve as a climatic refuge due to less harsh warming effects (van der Meer et al. 2016).

Estonia, transitioning from an oceanic to continental climate (Jaagus 1997), hosts high orchid species richness. However, of the 38 orchid species recorded in Estonia since 2000, four are classified as critically endangered (CR): *Dactylorhiza viridis* (L.) R.M. Bateman, Pridgeon & M.W. Chase, *Dactylorhiza majalis* subsp. *praetermissa* (Druce) D.M. Moore & Soó, *Dactylorhiza* × *ruthei* (M. Schulze ex Ruthe) Soó, and *Epipogium aphyllum* Sw. Two species are listed as endangered (EN): *Anacamptis morio* (L.) R.M. Bateman, Pridgeon & M.W. Chase, and *Neotinea ustulata* (L.) R.M. Bateman, Pridgeon & M.W. Chase. Additionally, ten species are classified as vulnerable (VU), and seven as near-threatened (NT) (Supplementary file df_2). Despite a low population density and protected semi-natural habitats, Estonian orchids suffered range declines of up to 62% between 1970 and 2004, averaging a 25% loss, with species typical of calcareous dry grasslands, other dry open habitats and woodlands experiencing the most significant declines, along with short-lived, shorter-statured, and rhizomatous clonal species (Kull and Hutchings 2006). According to the same authors, the species with the steepest declines during this period were *E. aphyllum* and *Corallorhiza trifida* Châtel., while some species, like *Dactylorhiza fuchsii* (Druce) Soó, showed little to no decline.

Kolanowska et al. (2017) argue that there is no universal trend in plant responses to climate change, and, as predicted by the IPCC (Intergovernmental Panel on Climate Change), global warming may have both beneficial and harmful effects depending on regional contexts. In this regard, under the current climate, the most significant threat to plant species is direct human impact, particularly the fragmentation and destruction of habitats. Habitat loss, primarily due to urbanization and the intensification of agriculture (Kull et al. 2016; Tsiftsis and Djordjević 2020), has profound consequences for many terrestrial orchid species in temperate climates (IUCN/SSC Orchid Specialist Group 1996). In Estonia, until the 20 th century, conventional practices such as clearcutting woodlands for the creation of pastures or meadows, alongside traditional agricultural activities, shaped the landscape. However, over the past few decades, extensive land-use changes have triggered vegetational successions from former pastures to shrublands and reforested areas (Palo et al. 2008). These transformations have directly impacted orchid habitats and species distributions. Specifically, the abandonment of traditional management practices for semi-natural grasslands, the drainage of wet forest habitats, and the expansion of agriculture have been major drivers in the severe decline of several orchid species in Estonia, including *Anacamptis pyramidalis* (L.) Rich., *C. trifida*, *Dactylorhiza maculata* (L.) Soó and *Neottia cordata* (L.) Rich. (Kull and Hutchings 2006).

Landscape modifications also affect habitat patches and ecological niches, likely triggering changes in soil microbial dynamics and pollinator distributions. Both of these factors are crucial for orchids, which depend on mycorrhizal symbioses for seed germination, protocorm growth, and often adult nutrition (Mccormick and Jacquemyn 2014; McCormick et al. 2018; Li et al. 2021), as well as on specialized strategies to attract specific pollinators (Jersáková et al. 2006; Schiestl and Schluter 2009). Furthermore, the interaction with climate change may also cause asynchronies between flowering and insect flight periods (Robbirt et al. 2014). Considering such ecological factors when studying current orchid distributions may lead to more accurate estimates and predictions (Kolanowska 2023).

Species Distribution Modeling (SDM) is a widely used tool for predicting species distributions under both current and future environmental conditions (Araújo et al. 2019). This is achieved by linking species distribution data to a set of environmental predictors through various modeling algorithms. In this study, we focused on Estonia as a potential northern refuge for orchids in the coming decades. We hypothesized a generalized range expansion for orchid species under mild climate change scenarios, while assuming that extreme warming scenarios would reduce suitable areas for many species.

Specifically, we aimed to: (1) model the current potential distribution of orchid species for which the Estonian Data Space for Biodiversity provided sufficient georeferenced observations from the past decade (2014–2024), using historical bioclimatic data and present-day Estonian land use/land cover (LULC) information; (2) predict future orchid distributions across Estonian territory under multiple Global Climate Models (GCMs) and two alternative CMIP6 Shared

Socioeconomic Pathways: the "middle of the road" SSP245 scenario, assuming global climate protection policies, and the "fossil-fueled development" SSP585 scenario, considered the worst-case climate scenario; (3) test the influence of orchid ecological traits (soil and habitat preference, growth form and pollination strategy) on predicted species distribution range loss or gain over time and under different future climatic scenarios.

Materials and methods

Occurrence data preparation and bias reduction for modelling

We collected georeferenced orchid occurrence records from the Estonian Data Space for Biodiversity (https://plutof.ut.ee/), excluding species with fewer than 20 records and observations prior to 2014. This resulted in 16,618 records for 31 species spanning the period 2014–2021. To reduce sampling bias and account for spatial and habitat heterogeneity, we implemented a thinning procedure based on the current land-use/land-cover (LULC) raster. The original high-resolution LULC map (0.0008°) was rescaled to match the 0.008° resolution of the WorldClim climate layers (~ 1 km²), enabling the calculation of fractional habitat cover and account for habitat heterogeneity within each coarse grid cell. We retained only one record per species and habitat category within each coarse cell. These thinned records were used in species distribution models (SDMs), while the corresponding fractional habitat covers and bioclimatic variables were incorporated into principal component analysis (PCA) workflow. We acknowledge that this approach does not fully eliminate sampling biases at spatial scales larger than 1 km. However, the Estonian Data Space for Biodiversity offers broad and even coverage across the country, reducing the risk of spatial sampling bias.

Climate and land use predictors for current and future scenarios

To assess the impact of climatic parameters on orchid distributions, we obtained 19 derived bioclimatic variables from the Worldclim2 database (Fick and Hijmans 2017) at a 30 arc-seconds resolution, covering historical (1970–2000) and future periods (2021–2040, 2041–2060, 2061-80, 2081–2100) under SSP245 and SSP585 Shared Socioeconomic Pathways (Kriegler et al. 2014; O'Neill et al. 2016; Riahi et al. 2017). To account for precipitation and temperature biases across different Global Climate Models (GCMs), we used an ensemble approach selecting three GCMs with distinct performance characteristics: MIROC6, projecting strong warming trends (Tatebe et al. 2019); MRI-ESM2-0, predicting wetter future conditions (Ossó et al. 2023); and IPSL-CM6 A-LR, offering more balanced projections (Boucher et al. 2020). We computed median habitat suitability projections across the three GCMs for each SSP and time period. Due to the unavailability of a high-resolution LULC grid for Estonia, we assembled LULC vectors from the ETD-Estonian Topographic Database (1:10,000 scale for general land use and 1:5,000 for settlement areas; Estonia Land Board, 2022) in QGIS (version 3.32.0-Lima). The resulting LULC grid was upscaled from 0.0008 to 0.008 degrees resolution to match the bioclimatic grids, enabling the calculation of habitat fractional cover per grid cell. The LULC categories included forests, shrubs, arable/agricultural land, orchards, meadows, open areas, marsh grasslands, wetlands, sandy and stony areas, peatlands, abandoned peatlands, water and urban areas.

Modelling future land-use change and habitat fragmentation index

We used the Proximity-Based Scenario Generator tool in the open-source InVEST® (Integrated Valuation of Ecosystem Services and Tradeoffs) suite developed by Stanford University (Natural Capital Project 2024) to predict future land cover changes in Estonia for the years 2040, 2060, 2080, and 2100. This tool generates land-use change maps by converting selected "focal" habitats into "replacement" habitats, based on their spatial proximity and a maximum replacement area threshold. To parameterize these thresholds, we focused on three broad land-use categories—agricultural areas, artificial surfaces (urban), and wetlands—whose expansion trends in Estonia were documented and projected by Mozaffaree Pour et al. (2022) for the period 2011–2030. These categories correspond directly to classes present in our detailed LULC dataset. To avoid introducing further bias, we applied linear regression models to the observed and projected land cover change percentages (2019–2030) to extrapolate expected changes up to 2100. The predicted percentage increases for each focal category at 2040, 2060, 2080, and 2100 were used to calculate maximum replacement areas (in hectares), which served as input thresholds in the InVEST tool. Since the Proximity-Based Scenario Generator allows one focal habitat replacement per run, we applied a three-step approach: (1) artificial surfaces were allowed to expand at the expense of all other land uses; (2) agricultural areas were allowed to replace all except wetlands and artificial surfaces; and (3) wetland expansion was modeled over all remaining land-use categories. This process reflects the future dominance of these three expanding

categories, as suggested by Mozaffaree Pour et al. (2022). The resulting LULC rasters were used as inputs in species distribution projections under future climatic and land-use scenarios.

To evaluate temporal changes in habitat fragmentation, we computed the Effective Mesh Size (MESH) index for six key land cover types relevant to orchid ecology (forest, arable land, meadow, marsh grassland, wetland, and urban) across 2040, 2060, 2080, and 2100 time points. MESH quantifies the average size of contiguous habitat patches, with lower values indicating higher fragmentation (Jaeger 2000). Analyses were performed on current and InVEST projected land-use maps. MESH was calculated using the *landscapemetrics* R package, and the total number of raster cells per land cover class was also extracted to assess temporal trends in absolute habitat extent.

Reducing predictor dimensionality and ensuring projection consistency

To assess potential risks associated with projecting beyond the training domain, we performed a Multivariate Environmental Similarity Surface (MESS) analysis using the *dismo* R package. We aimed to evaluate whether future climate conditions in Estonia would fall within the current climatic envelope of each orchid species' full European range. MESS compares each pixel of projected future climate to the historical climatic range observed across each species' known European distribution, based on IUCN data. The analysis was restricted to areas with no projected land use change and focused on four uncorrelated bioclimatic variables (BIO1, BIO7, BIO15, BIO19). For each species, MESS scores were computed for all combinations of two climate scenarios (SSP245 and SSP585) and four future time periods.

To reduce dimensionality and avoid multicollinearity among predictors, we performed a Principal Component Analysis (PCA) on standardized bioclimatic variables and land-use fractional cover data using the R package *factoextra* (Kassambara and Mundt 2020). The analysis was conducted on current conditions, including 19 bioclimatic and 14 land-use variables, after standardizing all variables to zero mean and unit variance. We retained the first four principal components (PCs), which explained the majority of the variance, and used them as environmental predictors in the species distribution modeling. To ensure consistency between current and future projections, we projected all future data into the same PCA space defined by current conditions. For each future scenario (GCM × SSP × time period), we standardized the corresponding bioclimatic and land-use input matrix using the means and standard deviations from the current PCA, and then applied the saved PCA rotation matrix to project the data into the same principal component space. This approach allows meaningful comparison and transferability between current and future PC layers. Spatial raster maps of PC1–PC4 were generated for each scenario. To better interpret the environmental space captured by the PCA, we also examined the variable loadings and spatial patterns of the first four components.

Species distribution modelling and ensemble forecasting

We built species distribution models (SDMs) for each species using four algorithms implemented in the *biomod2* R package (v.4.2–5-2): MAXNET (Maximum Entropy), GBM (Gradient Boosting Machine), ANN (Artificial Neural Networks), and MARS (Multivariate Adaptive Regression Splines). Model performance was evaluated using the True Skill Statistic (TSS) and the Area Under the Curve (AUC) metrics. Ensemble models were generated by averaging individual model outputs, weighted by TSS scores. We then projected these ensemble models onto both current and future environmental conditions under selected GCMs and SSP scenarios. All projections were binarized using the *BIOMOD_EnsembleForecasting* function, applying the threshold that maximized TSS and AUC scores (Supplementary file df_1). Each algorithm handles extrapolation into novel environmental conditions differently. MAXNET (Phillips et al. 2006) and GBM (Elith et al. 2008) extrapolate by extending their fitted response curves beyond the training data range. MARS(Friedman 1991) typically produces flat responses beyond its fitted hinge points, limiting extrapolation by maintaining constant predictions. In contrast, ANNs(Olden et al. 2004) can extrapolate but might prone to unstable outputs when predicting in novel environmental space. To buffer against these algorithm-specific differences in extrapolation behavior, we adopted an ensemble modeling strategy and summarized projections across multiple GCMs by computing the median suitability for each SSP × time period combination.

Linking ecological traits to species-level range changes

We compiled an ecological trait matrix for each orchid species, including soil preference (calcicole vs. non-calcicole), pollination strategy, growth form (tuberous vs. rhizomatous), and habitat preference. The first three traits were assigned based on expert knowledge and existing literature (Kühn et al. 2019). Habitat preferences were derived through a stepwise approach integrating both empirical and

expert-based information. First, species occurrences were mapped onto the current Estonian LULC categories to calculate the frequency of each land-use type. These detailed categories were then grouped into four broader, ecologically relevant habitat types: wetland habitats (wetlands and marsh grasslands), open habitats (meadows, open areas, agricultural land, orchards, sandy/stony areas), forests, and urban areas. Based on the distribution of occurrences across these groups, we classified species as: specialists (> 65% in a single habitat), dual-preference (> 25% in two dominant habitats), or generalists (second and third habitats between 15 and 25%) (Figs.S1, S2, S3). These initial classifications were then reviewed and validated by expert knowledge and cross-checked against habitat preference descriptions in Kühn et al. (2019) to ensure ecological consistency and robustness.

We employed Gower's distance (Gower 1971) to measure dissimilarities between species based on their categorical ecological traits, and applied Multidimensional Scaling (MDS) to the resulting Gower matrix to visualize trait-based relationships among species. To assess temporal changes in species distributions, we subtracted current-time binarized suitability maps from future median projections (averaged across three GCMs per SSP) to generate gain–loss maps for each species and future time period. These rasters indicate suitability change per grid cell, with values ranging from − 1 (loss) to + 1 (gain). Gains and losses were calculated relative to current suitability, comparing projections for the periods 2021–2040, 2041–2060, 2061–2080, and 2081–2100 against the current time baseline. For each species and scenario, we computed Net Change as the difference between the number of gained and lost cells, and Relative Net Change as the Net Change divided by the number of currently suitable cells (Relative Net Change = Net Change/Total Suitable Cells at current time). To evaluate the influence of species traits and environmental factors on predicted changes, we fitted Linear Mixed Models (LMM) with the R packages *lme4* v.1.1–35.5 and *lmerTest* v.3.1-3. We considered SSP and time period as fixed effects due to the number of levels < 5, while the species was set as a random effect. We used the following model structure: *Relative Net Change ~ Soil preference * Growth Form + Habitat * SSP * Time period + (1|Species)*. We performed post-hoc pairwise comparisons using estimated marginal means (via the *emmeans* R package) with Tukey correction. Results are reported in Table 1 and Table S1.

Table 1 Linear mixed model (LMM) fixed effects results using the formula *Relative net change ~ soil preference * Growth form + Habitat * SSP * Time_Period + (1 | Species)*. Only fixed effects with p-values < 0.05 are shown

Significant fixed effects	Estimate	Std. Error	df	t value	Pr(>|t|)
(intercept)	1.481313	0.982292	24.51	−1.508	0.14433
Open habitats : ssp585 : 2081–2100	6.38558393	1.2294932	175	5.194	5.68E-07
Open habitats	4.85105211	1.47105544	30.53	3.298	0.0025
Wetland habitats	5.36609993	1.65558883	36.04	3.241	0.0026
Rhizomatous	2.73144245	1.05112451	22.00	2.599	0.0164
Non-calcicole : Rhizomatous	−2.7134139	1.26412546	22.00	−2.146	0.0431

Results

Ecological and environmental context for model projections

To interpret the ecological meaning of species distribution model outputs and ensure the robustness of projections, we first characterized the major environmental gradients represented in the predictor dataset, assessed changes in climate and land use over time, and evaluated the extent of climatic novelty through MESS analysis. The loadings of the four principal components (PCs) used as predictors provide insight into the dominant environmental gradients shaping the species–environment space (Figs.S11, S12, S13). The first two components (PC1 and PC2) are primarily associated with climatic variables, while PC3 and PC4 reflect stronger contributions from land-use predictors. Based on variable loadings, PC1 captures gradients in annual and winter temperatures, temperature seasonality, and summer precipitation. Its spatial pattern reveals a pronounced west-to-east gradient across Estonia: western regions and coastal islands are characterized by milder annual and winter temperatures, lower seasonality, and drier summer conditions, consistent with maritime climatic influences. In contrast, eastern areas experience colder winters, greater temperature variability, and higher summer precipitation, reflecting a more continental climate. PC2 is mainly associated with precipitation seasonality and total annual precipitation. Higher precipitation seasonality is observed in eastern Estonia and parts of the western coast, where dry conditions typically occur in late winter. In contrast, central Estonia receives more evenly distributed rainfall and higher annual totals, reflecting lower seasonality. PC3 is defined by opposing loadings of forest cover versus arable land, urban areas, and meadows, highlighting a key land-use contrast across Estonia. PC4 is similarly influenced by the presence of wetland habitats in opposition to arable, urban, and meadow

land. Both components also include a summer temperature signal, which covaries with the spatial distribution of forests and wetlands. While these axes were not individually evaluated for predictive power, they provide a clear ecological interpretation of the environmental space used in the models.

Temporal projections of PC1 and PC2 across climate scenarios reveal clear spatial and directional shifts in Estonia's environmental conditions (Figs.S14–S15). For PC1, the west–east gradient remains consistent throughout the century, with a progressive eastward expansion of milder and drier summer conditions. Temperature increases and reductions in seasonality intensify across the entire territory, particularly under SSP585 by 2061–2100. Coastal islands and western regions exhibit the strongest shifts toward accelerated warming and increasing summer drought. For PC2, higher and more evenly distributed precipitation progressively expand across central Estonia, while eastern Estonia, the eastern shores of Lake Peipsi, and parts of the western coast exhibit rising precipitation seasonality, mainly due to declining winter precipitation.

We also observed diverging trends in habitat extent and fragmentation across land-cover classes over time (Fig.S4). Forests remain the dominant land cover but decline slightly in area after 2060 and show a sharp drop in the Effective Mesh Size (MESH) index, indicating increasing fragmentation in the latter half of the century. In contrast, arable land expands steadily in both area and MESH, suggesting the formation of larger, more continuous agricultural landscapes. Urban areas also increase in extent across all time periods. Natural habitats such as meadows, marsh grasslands, and wetlands retain relatively low coverage and exhibit persistently high fragmentation, with extremely low MESH values throughout the century, confirming their occurrence as small, isolated patches within the landscape.

Finally, MESS analysis—used to assess whether future climatic conditions in Estonia fall within the broader climatic envelope of each species across its European range—showed consistently positive values across scenarios (Fig.S16). Median and quartile values were well above zero, indicating that projected climates in Estonia remain within the historically observed environmental space of each species across Europe. This suggests that future conditions in Estonia do not represent novel or non-analog climates relative to the species' overall climatic tolerances (Elith et al. 2010; Guillamot et al. 2020; Owens et al. 2013).

Projected patterns of orchid species richness and suitability under future scenarios

Orchid species richness in Estonia is projected to decline markedly by 2021–2040, with the most substantial losses occurring during this initial period (Figs. 1 and 2). Large portions of western and central Estonia—currently the most diverse regions—are expected to experience significant reductions in richness. Although some areas, including the northern coast and parts of Hiiumaa island, may temporarily retain or even gain richness until 2040, these localized increases are not sustained in the following decades. From 2060 onwards under SSP585, a progressive erosion of residual richness is projected across Saaremaa island and much of the western coastline, further diminishing traditional orchid diversity hotspots.

Concurrently, a limited number of species—*Hammarbya paludosa*, *Liparis loeselii*, *Neotinea ustulata*, *Epipactis atrorubens*, and *Neottia cordata*—show marked range expansions, covering large areas of central and eastern Estonia as early as 2021–2040 (Figs.S5, S6, S7). These species largely account for the observed eastward shift and homogenization of richness patterns under both SSP scenarios. Although projections indicate a broader spatial distribution of suitable conditions over time, overall species richness remains substantially lower than under current conditions. Under the high-emission scenario (SSP585), these changes occur more rapidly, with projections for 2041–2060 resembling those expected only by 2081–2100 under SSP245.

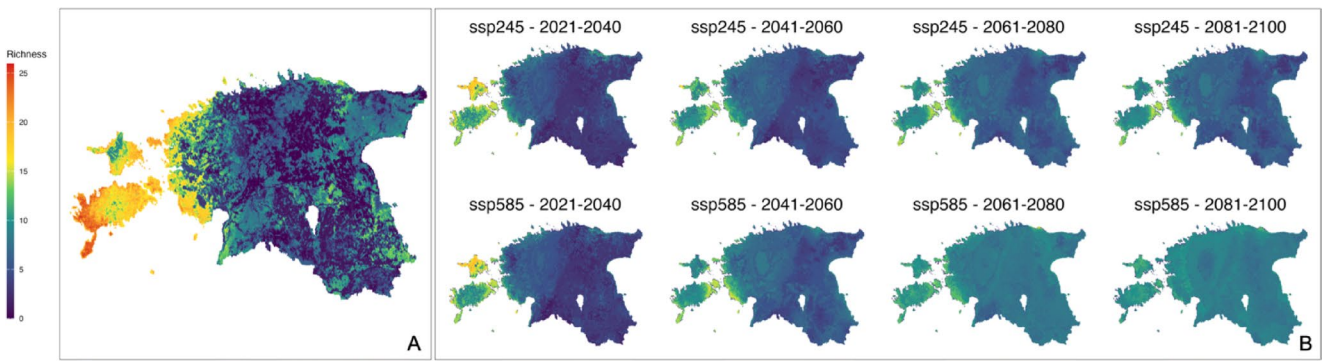

Fig. 1 Ensemble modeling of binarized orchid suitability maps, summarized by species and projected for the current period and future periods (2021–2040, 2041–2060, 2061–2080, 2080–2100) under SSP245 and SSP585. Warmer colors indicate suitability for more species (up to maximum 27 species), while cooler colors represent suitability for fewer species (down to zero)

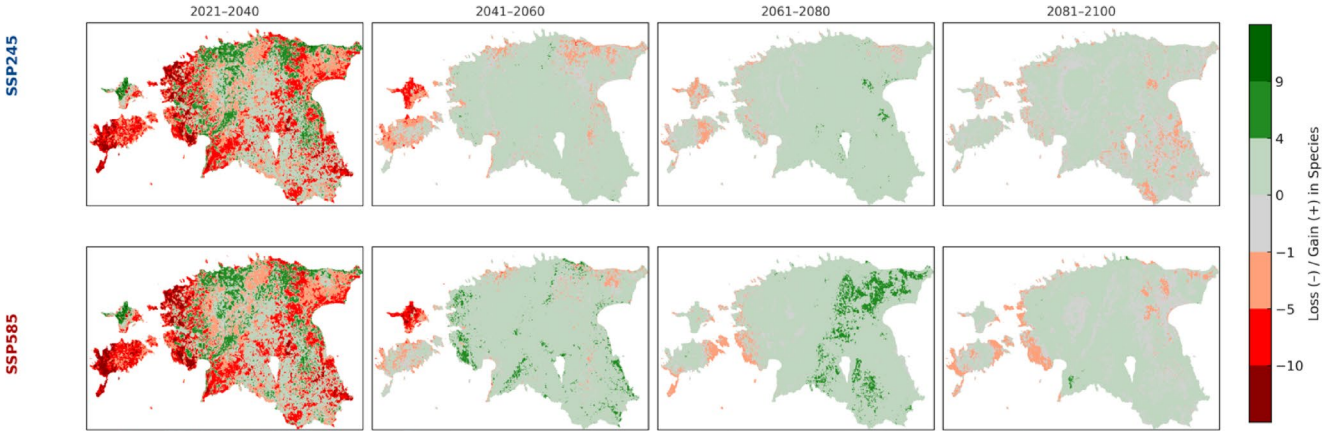

Fig. 2 Progressive loss–gain maps calculated from binarized orchid suitability maps summarized across species. Maps display changes in species richness relative to the current period, for each future time slice (2021–2040, 2041–2060, 2061–2080, 2081–2100) and emission scenario (SSP245, SSP585). Red shades indicate richness loss (fewer suitable species), while green shades indicate richness gain (more suitable species), with intensity corresponding to the number of species gained or lost per grid cell. Richness change is calculated as the difference between the future and current binary projections. SSP245 is shown in the top row, SSP585 in the bottom row

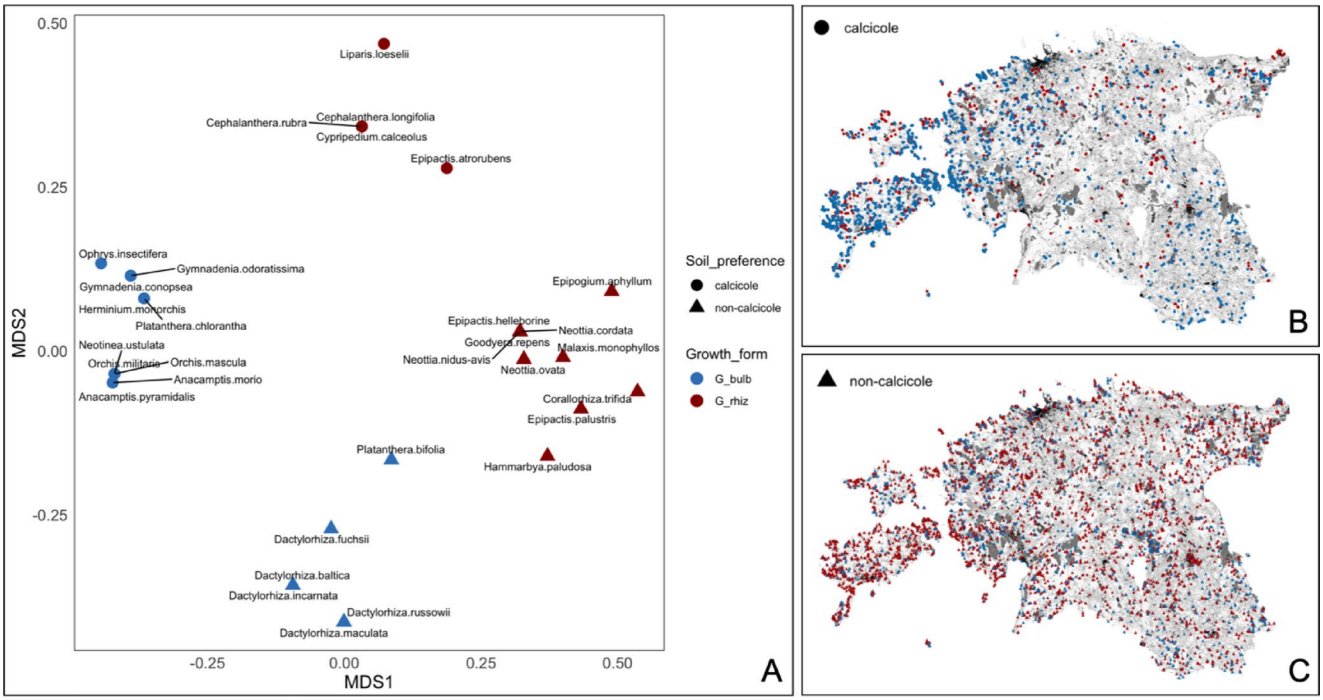

Fig. 3 A: Gower's distance-based Multidimensional Scaling (MDS) of the orchid ecological traits matrix. Circles represent calcicole species, and triangles represent non-calcicole species. Blue indicates tuberous growth form (G_bulb), and red indicates rhizomatous growth form (G_rhiz). B-C: Occurrences of calcicole and non-calcicole orchid species, respectively, plotted on the geographical space of Estonia. A grey-scale land use map is shown in the background

Trait-based variation in species' responses to global change

The MDS ordination, based on the Gower's distance matrix of ecological traits, revealed four distinct clusters that represent well-defined ecological groups of species (Fig. 3A). These clusters appear to be primarily driven by growth form and soil preference. We observed that orchid species that preferentially grow on calcareous soils (calcicole species) (Kull and Hutchings 2006; Leht et al. 2006; Landi et al. 2009; Djordjević and Tsiftsis 2019) are predominantly distributed along the Estonian west coast and the islands of Saaremaa, Hiiumaa, Muhu, and Vormsi, where calcareous substrates are abundant (Kull and Hutchings 2006; Palo et al. 2008). These species are largely associated with open or semi-open habitats and predominantly exhibit a tuberous

growth form. In contrast, non-calcicole orchid species are more geographically widespread and more frequently associated with forest and wetland habitats (Fig. 3B–C, Figs.S1, S2, S3). Ensemble modeling projections also identify the islands and west coast as a suitability hotspot for tuberous calcicole species, which make up much of the higher species richness, as well as for calcicole rhizomatous species (Fig.S10), encompassing several habitat preferences, from forest to open habitat species, the latter being more linked to the west coast and islands (Fig.S9).

The Linear Mixed Model performed using ecological traits as predictors identified several significant fixed effects influencing the relative net change in orchid suitability across species (Table 1). Open and wetland habitats were associated with higher relative net change, with the strongest effect observed for open-habitat species under the SSP585 scenario by 2081–2100. Among trait variables, rhizomatous orchids showed significantly higher relative net change compared to tuberous species. However, a significant negative interaction between rhizomatous growth form and non-calcicole soil preference revealed that this advantage does not extend uniformly across all rhizomatous orchids.

Post-hoc comparisons between trait combinations (Table S1; Fig.S8 A) clarified that calcicole rhizomatous species exhibit the highest relative net changes, significantly outperforming non-calcicole rhizomatous orchids, which showed the lowest projected values. This pattern appears driven by a small subset of species with strong predicted increases in suitability, such as *Liparis loeselii*, *Epipactis atrorubens*, and *Cephalanthera longifolia* (Fig.S8B). In contrast, many other rhizomatous orchids—especially those exclusive to forest and wetland habitats—are predicted to undergo minimal gains or decline, with some facing local extinction by mid-century. These include rare or previously declining species such as *Malaxis monophyllos*, *Epipogium aphyllum*, and *Corallorhiza trifida* (which already declined by 58% in Estonia between 1970 and 2004; Kull and Hutchings 2006). Further losses are also projected for forest-dwelling species like *Goodyera repens*, *Neottia nidus-avis*, *Epipactis helleborine*, and *Cypripedium calceolus*, as well as for open-habitat species such as *Herminium monorchis* and *Orchis mascula* in the latter half of the century.

Habitat-based trends in relative net change reveal contrasting responses among orchid groups (Fig. 4). Species associated with open habitats show the highest predicted increases in suitability over time, particularly under SSP585 by 2081–2100. This group is mainly represented by the two *Anacamptis* species, *A. morio* (EN) and *A. pyramidalis* (VU), as well as other calcicole, tuberous orchids, such as *Neotinea ustulata* (EN) and *Platanthera chlorantha*, both with preference for open or semi-opened habitats and forests. While these species benefit from expanding suitable conditions, the vulnerable dry grassland species *Gymnadenia odoratissima* (VU) is projected to undergo severe declines, with losses exceeding 96% by 2040. A strong upward trend is observed for *Hammarbya paludosa*, the only strict wetland specialist in the dataset, whose broad range expansion accounts for the significant effect of wetland habitats detected in the model. In contrast, forest-associated species and those linked to mixed forest environments tend to show slight but consistent declines across all future projections.

Discussion

Trait filters and biogeographic patterns under climate and land-use change

The ranges of many plant species are expected to shift northward in response to climate change over the coming decades. Modeling present and future potential distributions helps assess whether northern regions will provide favorable conditions for these species. Estonia lies within the northern edge of the range for many orchids and may serve as a valuable indicator of climate change impacts on plants. Alongside climate change, land use is projected to undergo significant transformations by the end of the century due to various socio-economic pressures (Veldkamp and Lambin 2001; Ton 2009; Stoate et al. 2009; Kumar et al. 2013; Haney and Cohen 2015; Borrelli et al. 2017). To address these dynamics, we predicted future geographical suitability for Estonian orchid species under combined climate and land-use change scenarios across different Shared Socioeconomic Pathways (SSPs).

The multivariate trait ordination positioning species in a functional space suggested that four clusters—broadly defined by the interaction between growth form (tuberous vs. rhizomatous) and soil preference (calcicole vs. non-calcicole)—may play a central role in shaping species' ecological strategies and potentially their geographic distributions. Current occurrence data show that calcicole tuberous species are primarily concentrated in Estonia's western islands and coastal zones (Fig. 1B–C), contributing to elevated orchid species richness in those regions. This spatial pattern is supported by species distribution models, which, despite predicting habitat suitability losses for many calcicole tuberous species, project eastward expansion for others such as *A. morio*, *A. pyramidalis* and *N. ustulata*. Similar trends are evident for some calcicole rhizomatous species, including *L. loeselii*, *E. atrorubens* and *C. longifolia*, although the latter may regress from 2060 onwards under the more extreme SSP585 scenario. Consistently, the significant interaction between soil preference and growth form in the linear mixed-effects model statistically supports

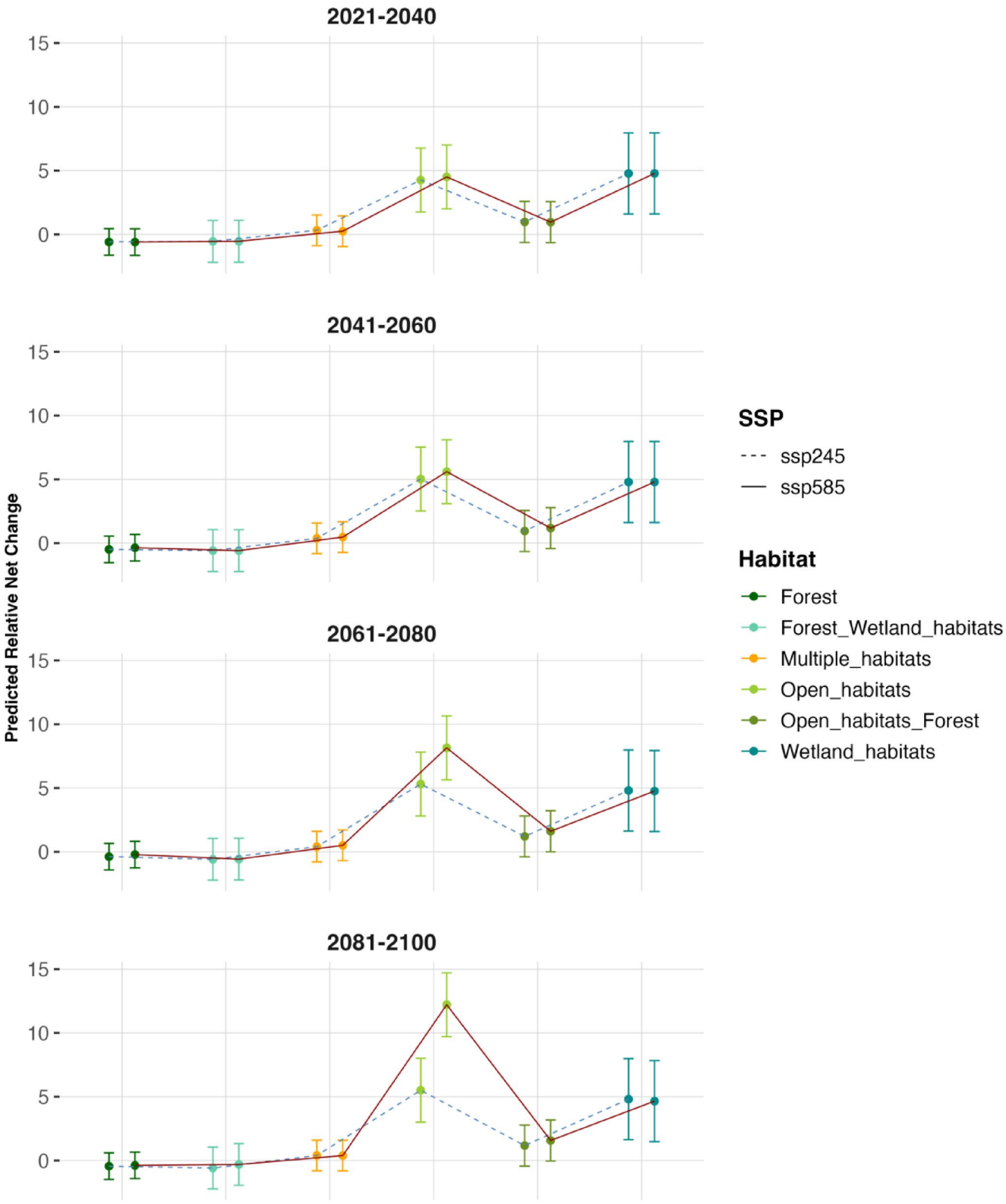

Fig. 4 Relative net range change predicted by the LMM (*Relative net change ~ Habitat + SSP * Time period + (1|Species)*). Effects are shown by habitat (A) and SSP × time period interaction (B). Error bars indicate 95% confidence intervals

the influence of these traits on projected responses to global change, particularly when considering the greater frequency of calcareous substrates in western Estonia. Although rhizomatous orchids are generally considered more resilient due to clonality, which facilitates persistence and expansion (Markus and Jürg 1997; Eriksson and Ehrlen 2001), our results suggest that under future climate and land-use change only a few of these species are likely to thrive. As shown by pairwise comparisons (Table S1), clonality alone cannot serve as a reliable proxy for conservation status; however, its interaction with soil preference may provide more meaningful insights into spatial vulnerability.

Habitat preference proved to be the most informative ecological trait in explaining future loss–gain patterns, especially in its interaction with SSPs and time periods. Species associated with forest or mixed forest habitats tend to exhibit consistent, albeit slight, reductions in suitable range. This may at least partly relate to projected forest loss and fragmentation, as highlighted by Effective Mesh Size analysis and InVEST-based land-use scenarios, and may be exacerbated by concurrent climate trends that disadvantage forest-dependent taxa. The projected increase in forest fragmentation during the latter half of the century appears closely tied to the expansion of urban and agricultural areas, which partly encroach on existing forest cores. While forest edges support rich ecotonal communities, fragmentation can increase edge unevenness, reduce core areas, and impair connectivity, factors particularly detrimental to orchid species requiring microclimatic stability or adapted to open forest margins. At the same time, the concurrent increase in MESH for arable land suggests growing spatial cohesion in agricultural landscapes, potentially displacing forest patches and reducing overall habitat heterogeneity. Urban expansion, although more limited in absolute extent, further fragments natural habitats. Additionally, the high fragmentation index for meadows, wetlands, and marsh grasslands across all time periods underscores the vulnerability of these habitats to spatial disconnection, potentially limiting their role as refugia or stepping-stone habitats for orchids under climate change. Maintaining or restoring connectivity between these patches is likely critical for long-term species persistence.

A clear example is the wide projected suitability increase of *H. paludosa*. While this may reflect a response to higher temperatures and increased precipitation evenness, the species is restricted to wet habitats. Its projected expansion may therefore be unreliable, emphasizing that even under favorable climate scenarios the conservation of specific habitat conditions is a primary goal, especially for wetlands. Similarly, *E. atrorubens* is unlikely to occupy urban or agricultural areas, limiting the plausibility of its predicted wide expansion. However, as its main habitat (forest) remains widespread in Estonia, climate warming could enhance its persistence, possibly counterbalancing the projected loss and fragmentation of forests.

The spatial trends in PC1 and PC2 across Estonia's SSP scenarios likely reflect a transition from higher snowfall regimes to increased rainfall, reduced snowcover and earlier snowmelt. Such hydrological shifts may accelerate spring runoff and reduce late-season water availability. In recent years, similar conditions—combined with reduced May–June precipitation—have already contributed to severe early summer droughts that negatively impacted orchid populations. This scenario could particularly affect species adapted to shaded and moister niches (forest and wet forest), especially during the hottest months. This may explain the predicted local extinctions and sharp declines of species such as *M. monophyllos*, *E. aphyllum*, *G. repens*, *C. trifida*, and *E. helleborine*. Conversely, species adapted to drier, open, or semi-open habitats may benefit from higher annual temperatures and eastward expansion of summer drought. *A. morio* and *A. pyramidalis*, for instance, exhibit the greatest increase in suitability—particularly under SSP585—highlighting Estonia's potential as a future refuge for these species, more common in southern Europe but currently rare in Estonia. However, these projections may underestimate habitat constraints: dry calcareous open habitats are largely confined to Estonia's islands and west coast. Previous studies (Kull and Hutchings 2006) suggest that such semi-natural habitats are vulnerable to urbanization, agricultural expansion and shrub encroachment. Maintaining connectivity and active management of open habitats is therefore essential for conserving these species.

N. ustulata further confirms this eastward expansion trend for semi-open habitat calcicole species, displaying near-complete suitability across Estonia under SSP585 from 2060 onwards. Yet, as it is currently rare and endangered in Estonia, this projection must be interpreted with caution, although it does support the notion of Estonia as a potential refuge under warming climate. Similarly, the wide predicted expansion of *L. loeselii* may relate to its multiple habitat preferences, though it is worth noting that—unlike typical open habitat orchids such as *O. militaris*, *O. mascula* and generalists like G. *conopsea*, *P. chlorantha*, *D. baltica*, *Neottia ovata* and *E. helleborine* which are relatively common in agricultural fields—*L. loeselii* current absence from agricultural and disturbed habitats weakens the plausibility of the forecasted widespread suitability. A strong signal of future climate on species distribution patterns is displayed in the range changes of *Neottia cordata*, an unfrequent non-calcicole rhizomatous species of forest and wet forest habitats, whose projected suitability gains—especially in central Estonia—closely parallel principal component PC2 climatic patterns of increased and more even precipitation in central

Estonia and secondarily the eastward temperature increase explained by PC1. Though the projection suggests a peculiar shift and expansion of suitable areas, this is unlikely to occur within a few decades, based on current population dynamics and the fact that we have no records of the species in anthropogenic or agricultural habitats. Still, the result highlights Estonia's potential as a climate refuge under appropriate conservation conditions.

When considering species richness, suitable range, and loss–gain dynamics, the period 2020–2040 may represent a near-term bottleneck under both SSPs. Many species may not benefit from later projected favorable conditions due to early range contractions or local extinctions. Even richness hotspots such as Hiiumaa may experience a decline by 2040–2060. While models suggest a slight increase in suitability across Estonia, this largely reflects a few species' potential broad suitability expansion under warmer conditions, and should not be interpreted as a reliable forecast of future distributions. Moreover, while SSP585 shows higher projected suitability after 2060, it follows a strong prior bottleneck and loss of richness by 2040. Under this worst-case scenario, suitability declines and hotspot erosion anticipated for 2080–2100 under SSP245 occur earlier, forecasting a progressive long-term erosion of western island and coastal refugia.

Overlooked ecological traits and conservation implications

Pollination strategy showed no significant effect on range predictions, though orchid distributions are undoubtedly influenced by pollinator presence (Štípková et al. 2020; Tsiftsis and Djordjević 2020; Kolanowska 2023) and by orchid–mycorrhizal associations (McCormick and Jacquemyn 2014b; McCormick et al. 2018). We recognize their ecological importance and despite the challenges in quantifying these interactions for current and future projections, we acknowledge that their future inclusion may help reduce uncertainties in model outcomes (Swarts and Dixon 2009; Vanden Broeck et al. 2014; van der Meer et al. 2016; Brzosko et al. 2017; Shefferson et al. 2020).

To address concerns about niche truncation due to regional calibration, we performed a MESS analysis, confirming that future climatic conditions in Estonia remain within each species' broader European climatic envelope. Consistently positive MESS values across scenarios suggest that projected conditions do not constitute climatic novelty at the continental scale (Elith et al. 2010; Guillaumot et al. 2020).

While this does not remove the limitations of regional modeling, it supports the idea that predicted changes occur within species' known environmental tolerances. In this regard, three additional elements support the plausibility of our projections. First, populations within the northern range of each species may show local adaptation, influencing sensitivity to climate change. Second, predicted losses align with observed declines in Estonia, likely linked to reduced snow cover and spring drought (Kull and Hutchings 2006; Jaagus 1997). Third, the absence of extrapolation suggests a conservative model: while we may underestimate persistence (i.e. fail to predict future suitability where the species could survive under broader climatic tolerances) in some areas, we are less likely to overpredict suitability (Owens et al. 2013). While long-term model projections should not be viewed as definitive forecasts, they remain valuable tools for identifying conservation priorities, guiding habitat protection and restoration, and supporting climate-adapted planning, particularly as mid-century carbon neutrality targets become increasingly unlikely (Kumar et al. 2013; O'Neill et al. 2016).

Conclusions

The highest orchid richness in Estonia is currently observed in the western islands and coastal regions of the Baltic Sea, which form a hotspot especially for calcicole species preferring open and semi-open habitats. These include tuberous species such as *A. morio*, *A. pyramidalis*, *N. ustulata*, *H. monorchis*, and *O. mascula*, and rhizomatous species such as *C. rubra* and *C. longifolia*. In general, most Estonian orchid species are currently present in these regions. Although species distribution models predict eastward range expansions for many of these species—even under the most extreme climate scenarios—these same western areas are projected to undergo severe richness losses within the next 15–20 years, with further erosion under SSP585 after 2060. The losses will not be confined to the western regions but are expected to affect large portions of the mainland, releveling medium-richness areas to lower orchid richness levels. Non-calcicole rhizomatous species typical of forests and wet forests will be the most affected by summer drought, rising average temperatures, and altered precipitation regimes, primarily due to declining snowfall. Increasing forest fragmentation and low habitat connectivity caused by urban and agricultural expansion, along with the abandonment of traditional grassland management, may further impact all orchid species, potentially threatening the rarest and most vulnerable, such as *G. odoratissima*, *M. monophyllos*, *E. aphyllum*, and *G. repens*.

The main bottleneck for Estonian orchid distributions is rapidly approaching: the most severe losses and local extinctions are projected before 2040. Many species predicted to expand may in fact be unable to meet such expectations due

to limitations such as soil type, lack of suitable or connected habitat patches, or the presence of highly anthropized landscapes. As a result, forecasted recoveries in orchid richness in the latter half of the century may be overly optimistic. By then, several species may have already undergone irreversible declines or extinctions, or may lack essential biotic interactions—such as pollinators or compatible mycorrhizal fungi—required for their persistence or expansion. Nonetheless, the positive response of some modelled species to emerging climatic trends suggests that Estonia—one of the richest northern European countries in terms of terrestrial orchid diversity—holds substantial potential as a climate refuge. For this role to be realized, however, effective conservation policies must be anticipated and implemented well before 2040.

While recognizing that ecological traits and habitat preferences can help predict current and future orchid distributions, we encourage future research and conservation strategies to integrate a broader suite of functional and ecological traits as predictors of species responses and conservation challenges.

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Author contributions D.N.V. and T.K. conceived the study, collected and selected the input data.D.N.V., S.M., C.R., M.A. and T.K. designed the methodology.D.N.V, M.A. and C.R performed the analyses in R and QGIS, with support by S.M D.N.V. wrote the first and the reviewed draft and prepared the figures.All authors contributed to the writing and to the reviewing process with suggestions and additions.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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