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Research Article

Latitudinal gradients of biodiversity and ecosystem services in protected and non-protected oak forest areas can inform climate smart conservation $\stackrel{\star}{\sim}$



GEOGRAPHY AND SUSTAINABILITY

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HIGHLIGHTS

GRAPHICAL ABSTRACT

- We substituted space-for-time to evaluate future goal fulfilment of protected areas.
- Contrary to global trends, insect and plant richness increased with latitude.
- Oak growth was not associated with latitude or area protection status.
- Protected areas did not host greater biodiversity of plants and insects.
- Alternative conservation strategies are needed to safeguard biodiversity.



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ABSTRACT

Adaptive governance of areas set aside for future protection of biodiversity, sustainable production, and recreation requires knowledge about whether and how effects of area protection are modulated by climate change and redistribution of species. To investigate this, we compare biodiversity of plants (assessed using vegetation plots) and arthropods (collected with Malaise traps, analyzed using metabarcoding) and productivity (tree growth, determined using dendrochronology) in protected and non-protected oak (Quercus spp.) forests along a latitudinal gradient (55.6 °N - 60.8 °N) in Sweden. We also compare historical, recent and projected future climate in the region. In contrast to established global latitudinal diversity gradients, species richness of plants and arthropods increased northwards, possibly reflecting recent climate-induced community redistributions, but neither was higher in protected than in non-protected areas, nor associated with contemporary ground temperature. Species composition of arthropods also did not differ between protected and non-protected areas. Arthropod biomass increased with latitude, suggesting that the magnitude of cascading effects mediated via their roles as pollinators, herbivores, and prey for other trophic levels, varies geographically and will change with a moving climate. Annual growth rate of oaks (an ecosystem service in the form of biomass increase and carbon sequestration) was independent of latitude and did not differ between protected and non-protected areas. Our findings question the efficacy of contemporary designation and management of protected oak forests, and emphasize that development and implementation of modified climate smart conservation strategies is needed to safeguard ecosystem functioning, biodiversity, and recreational values of protected forest areas against future challenges.

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1. Introduction

Climate change and the associated increased frequency of extreme weather events in combination with a growing human population pose severe threats to biodiversity, ecosystem services, socioeconomic values, and human well-being globally (Thomas et al., 2004; Scheffers et al., 2016; Pecl et al., 2017; IPCC, 2023). This emphasizes the need for more resilient and sustainable use of natural resources (Tompkins and Adger, 2004), climate smart conservation strategies that meet the new challenges (Hansen et al., 2010; Stein et al., 2014; Thomas and Gillingham, 2015; Hoffmann et al., 2019; Scheffers and Pecl, 2019; Brown et al., 2022; Pascual, 2022), and actions that mitigate future global warming (IPCC, 2023).

Regarding the consequences of climate change for biodiversity, there are three main responses. Plants and animals may undergo microevolutionary modifications and adapt to changing and novel conditions (Radchuk et al., 2019), track environmental shifts and change their geographic distribution ranges by establishing in areas where conditions are favorable (Forsman et al., 2016; Suzuki-Ohno et al., 2020; Sunde et al., 2023), or, failing that, populations and species may face local extirpations and global extinctions (Thomas et al., 2004; Scheffers et al., 2016; Pecl et al., 2017). The resulting geographic redistributions of species and alterations of community compositions can impact the functioning of ecosystems, with potentially far reaching consequences for the human societies that depend on them (Pecl et al., 2017).

The challenges for biodiversity brought about by climate change are exacerbated by the increased intensity of exploitation and modified land use, including habitat conversion, degradation, fragmentation, and loss (Maxwell et al., 2016; Horváth et al., 2019; Luedtke et al., 2023), all of which constrain the ability of species and communities to cope with the rapidly increasing number and intensity of stressors. Finding a resolution to these conflicting interests between biodiversity and societal needs is complicated further by that the spatial distribution of biological hotspots tends to coincide with human settlements, activities, and demands. Successful preservation of biodiversity cannot be delivered without simultaneously considering how humanity meets its needs (Löf et al., 2016; Scheffers and Pecl, 2019; Balmford, 2021; Bacon et al., 2023).

Conservation measures, including different forms of protected areas (henceforth PAs) with various degrees of restriction on access and utilization of natural resources, are implemented to partially resolve such conflicts (Götmark, 2013; Le Saout et al., 2013). Existing research indicates that a land-sharing approach, whereby human land use and a relaxed form of conservation efforts are combined within the same areas, is a second-best option that can complement land-sparing (Tälle et al., 2023), but studies almost invariably show that most species would fare least badly under a land-sparing approach (Phalan et al., 2011; Cannon et al., 2019; Balmford, 2021). Yet, 'softer' versions of area protection designed to allow for the coexistence of biodiversity and exploitation are dominating, in part likely due to socio-political constraints and economic considerations that often prioritize immediate human resource needs over long-term ecological benefits.

When deciding which specific areas to spare or protect it is necessary, but not sufficient, to take into consideration the conflicting needs outlined above. Due to the moving climate and changing environmental conditions, the designation of PAs is further complicated by that those areas that are particularly worthy of protection to safeguard biodiversity and ecosystem services against *future* challenges may be different from the contemporary distributions of biodiversity and PAs, and substantial mismatches between the distribution of currently PAs and future biodiversity values may pose severe challenges for conservation management (Fig. 1). Firm evaluation of the future efficacy of existing PAs would require a crystal ball. Given the impossibility of predicting the future with absolute certainty, we propose that a viable alternative approach is to use geographic location (latitude) as a proxy for climate change, and then compare biodiversity, ecosystem services, and recreational values in PAs and non-protected areas (henceforth NPAs)

along a latitudinal gradient. The underlying rationale is that both biodiversity and climate are typically correlated with latitude. Regarding biodiversity, there is evidence from different types of organisms that species richness in general increases from the poles towards the equator (Willig et al., 2003; Hillebrand, 2004; Willig and Presely, 2018; Lawrence and Fraser, 2020), likely reflecting a combination of higher productivity, longer time for evolutionary diversification, higher habitat heterogeneity, and higher temporal stability, favoring specialization (Willig et al., 2003; Jetz and Fine, 2012). Similarly, climate, both average annual temperatures, precipitation, and seasonality, show strong latitudinal patterns. With continued global warming, regional changes in mean climate and extremes will become more widespread and pronounced, increasing the severity of impacts across natural and human systems (IPCC, 2023). Combined with information on geographic variation in climatic conditions, comparative data and results on spatial patterns of biodiversity and ecosystem services generated using the study design outlined above, and employed below, have potential to reveal whether the future goal fulfillment of PAs is likely to improve or be compromised by a moving climate (Figs. 1 and 2). Such knowledge can aid the development of climate smart conservation strategies that are better adapted for future conditions (Hansen et al., 2010; Stein et al., 2014; Thomas and Gillingham, 2015; Hoffmann et al., 2019; Scheffers and Pecl, 2019; Pascual, 2022).

Here, we apply a space-for-time substitution approach (REF) using data for PAs and non-protected areas (henceforth NPAs) of deciduous forests encompassing oak in the southern part and nemoral zone of Sweden, Europe (Fig. 2). Our overarching aim is to generate insights about how climate change, biodiversity, ecosystem services (i.e., tree growth), and the efficacy of PAs are modulated by latitude, as a means to inform future climate smart conservation. A main reason for focusing on oaks is that they constitute putative forest ecosystems of the future in the boreo-nemoral climate zone that now expands northwards due to climate change (Dey, 2014; Johnson et al., 2019). Besides supporting associated biodiversity (Ranius and Jansson, 2000; Tallamy and Shropshire, 2009; Norman et al., 2010; Aerts and Honnay, 2011; Götmark, 2013; Löf et al., 2016; Johnson et al., 2019; Piovesan et al., 2022; Kozák et al., 2023; Krsnik et al., 2023) and human socio-economic interests, including tourism, recreation, and food provisioning (Norman et al., 2010; Aerts and Honnay, 2011; Löf et al., 2016), forests are key components in global policy-making to mitigate climate change, as a complement to reducing anthropogenic carbon emissions (Roebroek et al., 2023; Vieira et al., 2005; Stephenson et al., 2014; Peng et al., 2023).

Southern Sweden, where most of the human population resides, is in the temperate climate zone, characterized by relatively warm summers (average max temperatures 15 °C to 25 °C) and mild winters, compared with the northernmost part which is in the cold polar zone of the Arctic. Temperatures can drop well below freezing and snowfall is not uncommon, but the length and severity of winter differ between regions, with longer and colder winters naturally occurring in the north (WorldData, 2023). During the past 120 years, the climate in Sweden has moved northward at an alarming rate, with the temperature increase being most pronounced in the northern regions (see Fig. 2 in Sunde et al. (2023)). The changing climate has been accompanied by increments in species richness and northward shifts of species range distributions among lepidopteran insects (e.g., butterflies and macro moths) (Forsman et al., 2016; Sunde et al., 2023). However, it has not yet been evaluated whether the nature and magnitude of the moving climate, the resulting redistribution of species ranges, the alterations of community compositions, and the modifications of ecosystem services are sufficiently far reaching to question the validity of current PAs (Fig. 1).

The first aim of the present study is to investigate whether and how climate change will influence the utility of protected areas in maintaining biodiversity and ecosystem services. To this end, we first reconstruct the past, characterize the present, and project the future climatic conditions of the geographic region used for this study. This will inform



Time

Fig. 1. Conceptual illustration of how climate change and biodiversity redistribution may compromise future performance of protected areas in the northern hemisphere. Due to global warming, the latitudinal climate (temperature) gradient will move northwards. Due to expanding range margins, the negative latitudinal biodiversity trend may shift northwards, with future species richness increasing at southern and intermediate latitudes but declining in the north due to a higher rate of local extinctions than in the south (scenario a). Alternatively, due to increased local extinction both in the north and the south, future species richness may peak at intermediate latitudes (scenario b). The effects on future goal fulfillment of currently protected areas will differ depending on their spatial locations and the biodiversity redistribution.



Fig. 2. Map of study area (a) showing spatial variation in the historical (b, 1952–1972), recent (c, 1995–2014) and projected future (d, 2081–2100) climate (average annual maximum air temperature). The distribution of the 22 study sites is indicated in the middle panel (c). White diamonds represent PAs (n = 8) and gray dots NPAs (n = 14, some adjacent sites overlap on the map). Lower left panel (e) shows contemporary average maximum ground surface temperature for the different sites as a function of latitude. Blue dots indicate NPAs, red diamonds indicate PAs.

whether climatic conditions differ between PAs and NPAs, and how they vary with latitude.

The second aim is to investigate how the biodiversity of plants compares between PAs and NPAs, and how it varies according to latitude. Plants are pivotal for carbon sequestration, soil stabilization, as habitat providers, and provide food for animals, including humans. To delve further into the conservation values, we also quantify and analyze how the species richness, biomass, abundance, and species composition of arthropods compare between PAs and NPAs, and whether the differences vary according to latitude. arthropods play crucial roles as pollinators, herbivores, prey for other trophic levels in the food web, and serve as indicators of environmental health (Aerts et al., 2018; Methorst et al., 2021). We expect species richness of plants and arthropods to be higher in PAs than NPAs, based on the assumption that areas supporting high conservation values are more likely to be set aside for protection, and to decrease towards the north, in line with established latitudinal biodiversity trends (Willig et al., 2003; Mannion et al., 2014; Willig and Presely, 2018).

The third aim is to further evaluate how area protection and climate change impact some of the ecosystem services that forests provide (Krsnik et al., 2023). To this end, we collected tree-ring data from oaks using dendrochronology and analyzed how tree growth varies among areas depending on protection status and latitude. Tree growth provides important ecosystem services in the form of biomass production of socioeconomic value and carbon sequestration contributing to climate change mitigation. We expect the growth of trees to be faster in NPAs, based on the assumption that forests are managed largely to optimize productivity, and to decrease towards the north, due to the constraints imposed by the lower temperature and more pronounced seasonality.

The fourth and final aim is to use the results of the comparisons outlined above to evaluate the appropriateness of the current PAs, and discuss how our findings may inform future climate smart conservation and management. While the results presented are specific to southern Sweden, the approach has potential global application to the problem of projecting how climate change may modulate the efficacy of PAs. As our study investigates climate, tree growth (defining CO₂ uptake), and biodiversity in forests it has direct bearings on the measures required to fulfill the United Nations Sustainable Development Goals, especially goal 13 focusing on Climate action, and goal 15 focusing on Life on land (UN_DESA, 2023).

2. Materials and methods

2.1. Study area

In Sweden, PAs refer to geographically defined areas that are permanently designated, regulated, and administered to achieve specific aims and conservation goals. It is a collective term for protection under Chapter 7 of the Environmental Code (The Swedish Environmental Code (naturvardsverket.se)) and according to many of the nature conservation agreements under the Land Code (SverigesRiksdag, 2022). Formal PAs in Sweden include national parks, nature reserves, nature conservation areas, habitat protection areas, the National City Park, and Natura 2000 areas (SCB, 2023). In 2023, PAs accounted for ~ 15 % of Sweden's total land area and inland waters. In 2022, productive forest land in national parks and nature reserves with regulations for forestry covered 961,300 ha, whereas areas without regulations for forestry covered 93,800 ha (SCB, 2023). Besides supporting biodiversity values, agricultural needs, and forest productivity, PAs are important for recreation, tourism, and human well-being (Norman et al., 2010; Götmark, 2013). In 2022, one third (31 %) of the human population in Sweden lived within a 1 km zone around PAs (SCB, 2023), and 74 % of the population aged 16 years or older visited nature at least once during the period 2014-2015 (SCB, 2017). Stands of oak are among the most preferred forest habitats for recreation in Sweden, especially near urbanized areas (Norman et al., 2010).

The study was conducted in the southern region of Sweden, extending up to Gävle, the current northern range margin for naturally occurring Quercus in Sweden, covering 130,000 km² and comprising various ecological zones and a mosaic dominated by forests, farmland, and lakes. In this area, we use latitude as a proxy for a climate moving northward and compare productivity and biodiversity in PAs (n = 8) and NPAs (n = 14) deciduous forests with oak along a latitudinal gradient (55.62) °N – 60.77 °N) (Fig. 2). The 22 areas were selected to capture varying latitudes and microclimatic conditions. The eight PAs represent three forms of area protection; National parks (n = 1), Nature reserves (n = 6), and Natura 2000 areas (n = 1) (SCB, 2023) (Table 1). The mean age of PAs was 33 years, the oldest was established in 1926, and the newest in 2022. The average size of PAs was 349 ha, ranging from 5.5 ha to 1,245 ha.

2.2. Methods

2.2.1. Reconstruction of historical, characterization of recent, and projection of future climate in the study region

To quantify and compare spatiotemporal variation in climate within the study region we analyze maximum daily average temperatures (Zelinka et al., 2020) for three key periods: the historical period (1952-1972), the recent period (1995-2014), and the future projection (2081-2100). Our characterization of climate is underpinned by the comprehensive dataset from the sixth phase of the Coupled Model Intercomparison Project (CMIP6) (Tebaldi et al., 2021), which plays a pivotal role in the climate modeling community and significantly informs the Intergovernmental Panel on Climate Change's 6th Assessment Report (IPCC AR6) (Masson-Delmotte et al., 2021). CMIP6 encompasses both historical experiments and projection experiments (Ribes et al., 2021). To project the future climate, based on climate models, we integrated SSP 245, a moderate scenario aligning with current policy and technological trends by

Study sites number of	s with information on coordina dead trees, average oak tree 1	ites, type of area ieight, average o	protection (PA = ak tree height, an	 Protected Area, NPA = nd average oak birth ye 	: Non-Protected Area ar. na = not applica), year protecti əle.	on started, size of PAs, aver	age maximum g	round (surface) tem	perature, average
Site_Id	Site name	Latitude °N	Longitude °E	Area protection	Year established	Area (ha)	Surface temperature (C)	Dead trees	Tree height (m)	Tree birth year
kul	Kullaberg	56.291498	12.484459	PA, Nature reserve	1971	285	18.00	20	15.2	1887
ral	Rälla/Ekerum	56.767521	16.547704	PA, Nature reserve	2020	249	22.16	37	23.9	1905
bj	Blå Jungfrun	57.248601	16.796925	PA, National park	1926	66	21.05	27	9.6	1819
ank1	Ankarsrum1	57.673601	16.350788	PA, Nature reserve	2024	42	24.00	15	23.2	1833
fh	Filehajdar/Hejnum högård	57.694062	18.627631	PA, Natura 2000	2020	5.5	25.28	54	21.8	1871
vag	Vagnhärad	58.960674	17.602843	PA, Nature reserve	1984	448	22.00	12	19.6	1941
sth	Strömsholm	59.538610	16.273585	PA, Nature reserve	1979	1245	27.15	2	19.9	1938
tes	Testeboån	60.767224	16.978670	PA, Nature reserve	1995	449	24.27	73	21.9	1870
bjo	Björnstorp	55.618652	13.426523	NPA	na	na	21.00	1	26.6	1924
trao	Tranemåla	56.362703	14.776612	NPA	na	na	22.24	1	18.8	1926
lano	Långasjö	56.591967	15.443548	NPA	na	na	27.00	0	21.7	1857
gar	Gårdby	56.616087	16.593979	NPA	na	na	23.00	12	15.9	1926
isa	Isakull	56.682674	13.105359	NPA	na	na	19.00	8	19.7	1932
aga	Agarpsvägen	56.710100	13.112132	NPA	na	na	21.00	16	19.0	1920
str	Strömsrum	56.932726	16.391875	NPA	na	na	23.40	9	22.2	1919
tanr	Tầnnö	57.062579	14.007040	NPA	na	na	20.90	8	23.1	1927
ank2	Ankarsrum2	57.686166	16.314139	NPA	na	na	23.85	1	18.4	1920
var2	Vårgårda2	57.949305	12.832215	NPA	na	na	21.93	3	17.8	1849
varl	Vårgårda1	57.960931	12.833116	NPA	na	na	21.00	12	22.8	1893
vasv	Värmland Säby	59.067949	14.100670	NPA	na	na	19.00	14	26.6	1864
vin	Vinala	59.130601	15.385452	NPA	na	па	26.01	15	23.1	1886
vas	Väsby gård	59.164037	15.986345	NPA	na	na	20.96	4	23.4	1914

Table 1

utilizing the terra package (version 1.7-55) in R for efficient handling of large spatial raster data from climate models (Meinshausen et al., 2020; O'Neill et al., 2020; Hijmans et al., 2023). The exact_extract package (version 0.10.0) (Baston and ISciencesLLC, 2023) was used to obtain temperatures for specific areas and characterize regional climatic conditions. To visualize climate variation and change, the resulting data on historical, recent, and future maximum air temperatures were overlaid on maps of the study area (Fig. 2).

2.2.2. Analysis of ground temperature

Besides using data on maximum air temperature for analyzing largescale and long-term changes in climate, we collected higher spatial resolution data on ground surface temperature in our study area. This information was used to test for variation in climate between PAs and NPAs and according to latitude, and also to search for associations of climatic conditions with biodiversity and tree growth. Data on ground surface temperatures at our study sites were obtained from the Swedish Civil Contingencies Agency for the summer period extending from June 1 to August 31, for three years (2020-2022). These data were captured at a spatial resolution of 30 m. The temperature range was scaled in whole degrees Celsius (°C), spanning from 0 °C to +50 °C. The primary data source was Landsat 8, supplemented by Landsat 7 in areas where Landsat 8 data were unavailable. The selection of satellite scenes was contingent upon cloud coverage, with a threshold set at < 70 %. Each data point is a composite mosaic of multiple satellite scenes across different years. For information on the number of selected scenes for each year, and on the commencement and cessation dates of data collection please see the Swedish Civil Contingencies Agency (MSB, 2023). The data were analyzed using procedure GLM in SAS version 9.4. to evaluate effects of latitude, area protection status, and their interaction on maximum ground temperature.

2.2.3. Characterization of forest stands and quantification of the biodiversity of plants

2.2.3.1. Forest characterization. For each of the 22 study sites, we recorded the species and basal area and diameter of live and dead standing trees and shrubs. This was done at ten places within each study site. Those ten places surrounded and coincided with ten focal oak tree individuals that were sampled for reconstruction and quantification of growth rate using dendrochronology (see 2.2.5). To characterize the forest stands with regards to trees and bushes, we used the point relascope method with a prism 1, following the approach outlined by (Bitterlich, 1984), a method widely used for assessing forest structure and composition. We measured diameter at breast height (DBH, 1.3 m above the ground) using callipers from Haglöf. To estimate tree height, we used a clinometer, backing away 15 m from the tree. Data was collected between May 20, 2022, and September 1, 2022. Information on the number of dead trees and average tree height is provided in Table 1.

2.2.3.2. Vegetation plots. Species richness of vascular plants was quantified for each site using vegetation plots between August 10 and August 30, 2022. Data was collected for 10 individual trees at each site, using a structured grid of four vegetation plots measuring 0.5 m^2 around each of the ten trees, generating 40 plots per site. Plots were placed (using hula hoops) at a 5 m radial distance from each oak's trunk in the four cardinal directions (West, East, South, and North). Within each plot, all plant species were identified and recorded, except grasses and sedges. The data on total number of plant species per site were analyzed using procedure GLM in SAS version 9.4 to evaluate effects of latitude, area protection status, and their interaction on plant species richness.

2.2.4. Sampling the biodiversity of arthropods

To quantify variation in insect biodiversity (biomass, species richness, and size distribution) and compare community compositions across different study sites and latitudes, we deployed Malaise traps at the 22 sites, with data collection beginning on June 20, 2022, and continuing to August 9, 2022. We used Malaise traps with black (lower part) and white (top) colors, measuring 1.7 m in length and 1.2 m in width, with the highest point at 1.7 m and the lowest at 0.95 meters. The traps were emptied once, and samples were stored in ethanol in Nalgene bottles. The number of active trapping days (mean = 36, std = 4.9 days) did not vary according to latitude ($F_{1,18} = 0.25$, p = 0.62) and nor did it differ between PAs and NPAs ($F_{1,18} = 0.24$, p = 0.63). To examine size distribution and enhance the detection rate of smaller species for subsequent metabarcoding analysis, each Malaise trap sample was divided into two size fractions: arthropods smaller than 5.6 mm and those larger than 5.6 mm. This was achieved using a sieve with a 5.6 mm mesh size and a smaller mesh of 0.075 mm. To estimate productivity (arthropod biomass) in each location, we weighed the two size fractions after removing the ethanol used for preservation. To quantify the total abundance of arthropods collected at each site, we took one subsample from each of the two size fractions from each location. We then weighted both the two subsamples and the two complete size fraction samples, counted all arthropod individuals in the subsamples, multiplied the estimated number of individuals per gram in the subsamples with the weight of the complete size fraction samples, and then added the two estimated number of arthropods in the large and small size fraction per site. Thereafter, the samples were sent to the Canadian Centre for DNA Barcoding (CCDB) for metabarcoding of the mitochondrial cytochrome c oxidase (COI/COX1) marker, providing a proxy for species richness through operational taxonomic units (OTUs) and a relative abundance estimate per sample.

2.2.4.1. DNA metabarcoding for molecular species identification of arthropod bulk samples. Molecular methods, such as DNA barcoding and DNA metabarcoding, are increasingly used for species identification, particularly for species for which morphology-based taxonomy is difficult or taxa are morphologically ambiguous. These approaches can overcome the challenges associated with traditional morphological species identification and generate reliable and high taxonomic resolution in ecosystem biodiversity assessments, even based on simultaneous processing of multiple specimens or entire communities (Hebert et al., 2003; Taberlet et al., 2012; Cristescu, 2014; Creer et al., 2016; Salis et al., 2024).

Here, we used DNA metabarcoding for molecular species identification, and to estimate species richness and species composition of the bulk samples of arthropod communities collected from the different sites (see 2.2.4). To this end, DNA extraction of the bulk samples and amplification were performed according to the standard protocols used by CCDB. COI amplicon libraries were constructed using the BF3 + BR2 primer pair (Elbrecht et al., 2019), including triplicate PCR replicates as well as positive and negative controls, and sequenced on a Illumina Novaseq.

Raw reads were received as paired-end merged demultiplexed fastq files. Primers were trimmed using cutadapt v4.4 (Martin, 2011). Sequences were then processed using APSCALE v1.6.3 (Buchner et al., 2022) using default parameters. Only sequences with a length of 418 ± 10 bp and a maximum expected error of 1 passed quality filtering. Reads were dereplicated, clustered into OTUs based on 97 % similarity and chimeras were removed. OTUs were then curated to potential erroneous sequences using the LULU algorithm (Frøslev et al., 2017). Taxonomic assignment was performed using the MIDORI 2 database v GB257 (Leray et al., 2022) and the local BLAST tool implemented in APSCALE. The BLAST hits were filtered using APSCALE. Hits were filtered by evalue (retaining those with the lowest) and hits with the same taxonomy were dereplicated. Taxonomy was assigned according to the following thresholds: species \geq 98 %, genus \geq 95 %, family \geq 90 %, order \geq 85 %. Any OTUs with any remaining hits with conflicting taxonomy were then reduced to the most recent common taxonomy and checked manually. The resulting taxonomy and OTU read tables were then further processed in R v. 4.3.1 (R Core Team 2023). The tag-switching rate between

the positive controls and the other samples was calculated - there was 0.0004 %–0.002 % bleed-in from the positive controls to the samples. Thus, to account for tag-switching and cross-contamination, the read table was filtered at conservative threshold of 0.005 % (any OTUs below 0.005 % read abundance within each sample removed), and the maximum number of reads for every species in the negative controls were subtracted from the respective species' read numbers in the samples. The data set was taxonomically filtered to retain only those OTUs assigned to the phylum Arthropoda. PCR replicates and size fractions were merged to provide one sample per site. The number of OTUs in each of these samples was then used as an estimate of species richness for each site.

2.2.4.2. Statistical analyses of arthropod biodiversity. The data on arthropod diversity were analyzed using procedure GLM in SAS version 9.4 to evaluate effects of latitude, area protection status, and their interaction on each of the three response variables; species richness, total biomass, and abundance (i.e., total number of individuals) in each site. Separate GLMs were used for each response variable. Moving on from the richness and abundance of arthropods, we also analyzed community structure. To visualize how species composition of the communities varied according to area protection status and latitude, a NMDS (Non-metric MultiDimensional Scaling) analysis based on Jaccard dissimilarities (presenceabsence) was performed using the R package vegan (Oksanen et al., 2022). The effects of area protection status and latitude on community composition were evaluated using a permutational multivariate analysis of variance (PERMANOVA) based on the Jaccard dissimilarities with 999 permutations. This was performed using the adonis2 function in the package vegan. To test for homogeneity of multivariate dispersions a permutation analysis was conducted using the betadisper function. The variance of the groups (distance to the centroid of each of the protected and non-protected area groups) was not significantly different.

2.2.5. Sampling and quantification of forest productivity

We use tree-ring data obtained by dendrochronology sampling (Johnson and Abrams, 2009; Brienen et al., 2020; Anderson-Teixeira et al., 2022) to determine tree age, and to estimate how annual biomass increase of oak varies according to study site, latitude, and area protection status. To this end, we selected 10 of the dominant oak individuals, with the aim to capture the site-specific environmental variation and the size and age distribution of trees. Tree core samples were collected using an increment borer with a diameter of 5.15 mm. Cores were extracted at breast height (1.3 m above ground level) from each of 10 selected Quercus individuals within each of the 22 areas. The surface of the increment samples was prepared with industrial razor blades and in some cases, talcum powder was also used to increase the contrasts and make the boundaries between the annual rings visible. The increment samples were analyzed and data processed following standard dendrochronological procedures (Fritts, 1976; Bräker, 2002). Tree-ring widths (TRW) were measured to the nearest 0.01 mm using a digital LINTAB positioning table connected to an Olympus stereomicroscope and TSAPWin Scientific software (Rinn, 2003). Thereafter all TRW series were cross-dated for missing rings and errors using COFECHA (Holmes, 1983; Cook and Holmes, 1984). Cross-dating and statistical tests were initially made between all individual trees in an oak stand, but thereafter between all individual trees included in the study as well as between the site TRW chronologies developed from each tree stand. Each observation in the dataset represents an annual ring size measurement from individual trees located at specific sites. The data were analyzed using procedure GLM in SAS version 9.4. to evaluate effects of tree age, latitude, area protection status, and the interaction between latitude and area protection status on the average growth rate. Tree age was included as a covariate in the model to statistically account for age effects on growth rate. To visualize how tree growth varied according to latitude and area protection status, we calculated residuals from the linear regression of growth rate on tree age ($F_{1,20} = 43.04, p < 0.0001$,

 $R^2 = 0.68$) and used the residual growth rates to generate the plots. Plots were created using SigmaPlot for Windows, version 15.0.

3. Results

Overall, the results show that as a result of climate change, maximum air temperatures in the study area decrease with increasing latitude, have increased over time, and are projected to increase well above current temperatures within the next 50 years. Species richness of plants and arthropods both increased with latitude, but PAs did not host greater biodiversity of these groups than NPAs. The dendrochronological analyses showed that the average annual growth of oak trees was not associated with either latitude or area protection status, after controlling for differences in age structure. None of the biodiversity measures that we examined nor tree growth was significantly associated with contemporary average ground surface temperature. Biodiversity and tree growth was generally independent of the size and age of PAs. These findings are outlined in greater detail below.

3.1. Spatiotemporal variation in climate and independence of ground temperature with area protection status

Our characterization of the historical, recent, and future climate shows that average maximum air temperatures follow a clear latitudinal gradient and have increased considerably throughout the study area over the past 50 years (Fig. 2(a–c)). The projection of future climate also indicates that all sites included in our study will be exposed to higher temperatures towards the end of the century compared to the present situation, and within 50 years the northernmost sites will likely be warmer than the southernmost sites are today (Fig. 2(d)).

The variation among sites in contemporary maximum ground surface temperature during summer was not significantly associated with latitude, area protection status, or their interaction (GLM, full model, $F_{1,19} = 1.13$, p = 0.34, $R^2 = 0.20$; effect of latitude: $F_{1,19} = 1.69$, p = 0.21; effect of area protection: $F_{1,19} = 0.14$, p = 0.72) (Fig. 2(e)).

3.2. The diversity of plants increased with latitude but did not differ between PAs and NPAs

Species richness of plants increased with latitude ($F_{1,19} = 11.65$, p = 0.0024) but did not differ significantly between PAs (lsmeans = 26.4 ± 3.2 species) and NPAs (25.6 ± 2.1 species) areas ($F_{1,19} = 0.04$, p = 0.85) (Fig. 3). The interaction between latitude and area protection status was not significant ($F_{1,18} = 0.01$, p = 0.92).

3.3. Species richness, biomass, abundance, and community composition of arthropods in relation to latitude and PA status

Species richness of arthropods increased with increasing latitude ($F_{1,18} = 16.90$, p = 0.0007) but did not differ significantly according to area protection status ($F_{1,18} = 2.45$, p = 0.13). If anything, insect species richness tended to be lower (not higher) in PAs (Ismeans = 667 ± 64 species) than in NPAs (Ismeans = 794 ± 45 species) (Fig. 4(a)). The interaction between latitude and area protection status was not significant ($F_{1,17} = 0.33$, p = 0.57).

The biomass of arthropods increased with increasing latitude ($F_{1,18} = 8.46$, p = 0.0094) but did not differ significantly between PAs (lsmeans = 65.8 ± 10.5 g) and NPAs (lsmeans = 69.0 ± 7.4 g) areas ($F_{1,18} = 0.06$, p = 0.81) (Fig. 4(b)). The interaction between latitude and area protection status was not significant ($F_{1,17} = 2.10$, p = 0.16).

The abundance (total number of individuals) of arthropods was not associated with latitude (analyses of log-transformed data, $F_{1,18} = 0.27$, p = 0.61), but it was significantly higher in PAs (back transformed lsmeans = 13,901 ± 2,132 inds) than in NPAs (6,710 ± 1,497 inds) ($F_{1,18} = 7.03$, p = 0.0162) (Fig. 4(c)). The interaction between latitude and area protection status was not significant ($F_{1,17} = 0.16$, p = 0.69).



Fig. 3. Variation in biodiversity (species richness) of plants among study sites in relation to latitude and area protection status (blue dots indicate non-protected areas, red diamonds indicate protected areas).

Moving on to community structure of arthropods, we found a large overlap and no statistically significant difference in species composition between PAs and NPAs (permanova, $F_{1,18} = 1.11$, $R^2 = 0.05$, p = 0.19, Fig. 5). However, arthropod community composition was significantly associated with latitude ($F_{1,18} = 1.60$, $R^2 = 0.08$, p = 0.001). A visualization of these results based on Non-metric MultiDimensional Scaling (NMDS) is provided in Fig. 5.

Species richness of arthropods was not associated with species richness of plants across sites (r = 0.36, n = 21, p = 0.11, Fig. 6).

3.4. Forest productivity was independent of latitude and PA status

The average annual growth rate (mm/year) of oak trees decreased with tree age but was independent of latitude and did not differ significantly between PAs and NPAs (GLM, effect of tree age:, $F_{1,18} = 35.72$, p < 0.0001; latitude: $F_{1,18} = 0.46$, p = 0.51; area protection: $F_{1,18} = 0.37$, p = 0.55; lsmeans PAs: 1.76 ± 0.117 mm/year; lsmeans NPAs: 1.85 ± 0.087 mm/year) (Fig. 7). The interaction between latitude and area protection status was not statistically significant ($F_{1,17} = 0.09$, p = 0.77).



Fig. 5. NMDS-plot showing comparison of species composition of insect communities between protected and non-protected areas. NMDS stress = 0.13. The arrow represents the correlation between latitude and the transformed ordination space and shows that community composition depended on latitude. Blue polygon and dots indicate non-protected areas, and red polygon and diamonds indicate protected areas.

3.5. Biodiversity and tree growth was not associated with ground temperature

Of the five biodiversity and ecosystem response variables that we examined (species richness of plants, species richness, biomass and abundance of arthropods, and tree growth), none was significantly associated with the average ground temperature (Pearson correlation, all p > 0.05).

3.6. On the role of age and size of the protected areas

Of the five biodiversity and ecosystem response variables that we examined (species richness of plants, species richness, biomass and abundance of arthropods, and tree growth), none was significantly associated with the age of the PAs (Spearman correlation, all p > 0.15). Of the five response variables that we examined, only species richness of plants was significantly associated with the size of the PAs, with larger PAs having more plant species on average ($r_s = 0.88$, p = 0.004, n = 8; all other p > 0.35).



Fig. 4. Variation in insect biodiversity among study sites in relation to latitude and area protection status. The left hand frame a) displays results on species richness. The middle frame b) displays results on biomass. The right hand frame c) displays results on the number of individuals. Blue dots indicate non-protected areas, and red diamonds indicate protected areas.



Fig. 6. Species richness of arthropods was independent of species richness of plants (blue dots indicate non-protected areas, red diamonds indicate protected areas).

4. Discussion

4.1. What might explain the positive latitudinal species richness trends?

Our finding that species richness of arthropods (mainly insects) and plants increased with increasing latitude was opposite to what we predicted based on previous reports of well-established global biodiversity trends (Willig et al., 2003; Hillebrand, 2004; Willig and Presely, 2018). The positive association of species richness with latitude, observed in both arthropods and plants, along with the use of standardized sampling methods for both taxa in all areas, supports the idea that the results reflect a true underlying pattern, rather than a spurious correlation caused by, for example, variations in sampling approach or intensity. Our present findings thus add support to the conclusion and growing body of evidence that trends and redistributions of biodiversity are context specific, depending on, for example, spatial scale, organism group, and location (Forsman et al., 2016; Pecl et al., 2017; Guo et al., 2018; Hoffmann et al., 2019; Rushing et al., 2020; Suzuki-Ohno et al., 2020; Suggitt et al., 2023). Although this in itself is not surprising, it complicates the development of any generally applicable climate smart conservation strategies.

There is evidence from previous studies of both insects and plants that species range margins have moved northwards in our study area during the past century, likely attributable at least in part to climate change (Forsman et al., 2016; Auffret and Svenning, 2022; Betzholtz et al., 2023; Sunde et al., 2023). However, given that species have expanded their range margins northwards on average in response to a warmer climate, species richness should have increased throughout the latitudinal range covered by our sampling area, while maintaining a negative relationship with latitude (scenario a in Fig. 1). Our findings do not support such a scenario. This leads to the conclusion that the positive association of species richness with latitude demonstrated by our results might be representative of the alternative future scenario, with diversity peaking at an intermediate latitude (scenario b in Fig. 1). Several interacting drivers may have contributed to generating such a pattern. For example, some species may have disappeared from the southern part of our study area owing to retraction of southern range margins and an increased local extinction rate. This in turn may be the result of the combined effects of high human population density, more intense exploitation and land use, a more fragmented landscape with smaller and less connected forest areas, and more extreme abiotic stress imposed by the higher temperatures, compared with sites in the northern part of our study (Sunde et al., 2023).

Because of the trapping period used (June 20 to August 9, 2022), our samples may not have included those species that are active only during early spring or in the autumn. However, species with only early or only late phenologies likely comprise a minority of all arthropods in our study area (Jonason et al., 2014), suggesting that any underestimation of species richness should be negligible. Furthermore, the results reported for arthropods (species richness, biomass, and abundance) remain qualitatively unchanged if the number of trapping days is included as a covariate in the statistical models (not shown). We also can see no reason(s) as to how an incomplete sampling duration should create a spurious positive latitudinal species richness gradient, i.e., in a direction opposite to the general global pattern.

The finding that the species richness of plants and arthropods both increased towards the north suggests a common cause. In theory, this pattern might reflect that diversity begets diversity (Whittaker, 1975; Janz et al., 2006), with a greater variety of host plants supporting a greater variety of arthropods, and conversely with a more species rich



Fig. 7. Variation in growth rate of oak trees as a function of age, latitude and area protection status. The left hand frame (a) displays the relationship across study sites between tree growth and tree age. The right hand frame (b) displays age corrected growth (residuals from the regression of growth on age) as a function of latitude and area protection status. Blue dots indicate non-protected areas, and red diamonds indicate protected areas.

fauna of pollinators supporting a greater variety of plants. However, the diversity of these two organism groups was not significantly positively correlated across sites does not support this hypothesis.

An alternative explanation for the shared pattern in plants and arthropods is that the more northern sampling areas included in our study are situated near the so-called Limes Norrlandicus. It constitutes a biogeographical transition in central Sweden between the southern, temperate climate zone with nemoral and boreo-nemoral forests and the northern Taiga zone with boreal forests, that closely follows the northern limit of the oak, at about latitude 60 °N (Giesecke, 2005; Löf et al., 2016). The community compositions in these areas may therefore harbor an amalgamation of species that are representatives of both the nemoral and the boreal zones. Such combinations of partly distinct floras and faunas may contribute to the high diversity and positive latitudinal species richness trends shown by our results. This interpretation is also supported by the fact that the community species composition of arthropods was associated with latitude.

4.2. Why was tree growth independent of latitude?

Our results do not support the expectation that the growth rate of oak trees should decrease with increasing latitude. In principle, variation among sites likely reflect that the ontogeny of tree growth is influenced by a complex interplay of environmental constraints imposed by seasonality, light, temperature conditions, soil moisture and nutrient availability, and by community species richness and composition associated with latitude that together define phenology, the duration of the growth period, and the nature and intensity of competition (Gamache and Payette, 2004; Vieira et al., 2005; Way and Oren, 2010; Aerts and Honnay, 2011; Hulshof et al., 2015; Anderson-Teixeira et al., 2022; Mahmud et al., 2022). Much of the observed variation in growth rate among sites might therefore be due to differences in biotic and abiotic conditions that are not directly connected to latitude and that were not investigated in this study. Importantly, the lack of association with latitude was not due to a confounding effect of variation in age structure among sites, because the effect of tree age on growth rate was accounted for in the statistical model. One possible explanation for the independence of growth on latitude is that the northern populations are adapted and physiologically capable of maintaining growth at lower temperatures or can utilize the longer daylight hours during summer, but this requires further investigation. Lastly, the latitudinal range covered by our sampling sites (spanning 5 °N), despite covering the entire distribution range of oaks stands in Sweden, may have been insufficient to detect a 'true' negative relationship.

4.3. On the seemingly poor performance of area protection

4.3.1. Biodiversity. Our expectation that PAs should harbor greater biodiversity than NPAs was not supported by the results. Neither species richness of plants, nor species richness, biomass or species composition of arthropod communities differed significantly between PAs and NPAs. There are several possible explanations for this negative outcome. For example, some of the PAs may have been designated for reasons other than, or in addition to, supporting high overall diversity of these organism groups, for example targeting certain endangered species, organism groups other than those covered by our data, or to secure recreational values. The results may also reflect that the benefits of PAs are speciesspecific. For example, Santangeli et al. (2023) adopted a multi-taxon approach to compare occupancy patterns of 638 species (including birds, mammals, plants and phytoplankton) between PAs and NPAs across four decades in Finland. They report mixed impacts of area protection, with only a small proportion of species benefiting from protection. Contrary to Santangeli et al. (2023) who report that the benefits of protection are traceable to when the sites were protected, none of the measures of biodiversity that we examined was associated with the age of the PAs.

The lack of greater biodiversity in PAs may also reflect poor management, such as insufficient restrictions or solutions aiming at compromises between biodiversity values and socioeconomic needs (Götmark, 2013; Löf et al., 2016). A recent study provides an example of this from northern Gotland, where extensive and agricultural policy subsidized land use, including grazing by cattle, in PAs jeopardize the protection of biodiversity and Natura 2000 targeted species of butter-flies and orchids (Kindvall et al., 2022).

A more positive interpretation of our present findings is that the performance of PAs is not necessarily poor. Instead, some of the NPAs included in our study may be managed by private landowners with an interest in sustainable forestry and commitment to supporting biodiversity values, perhaps even if this is at the expense of forest productivity and short-term financial gain.

It might be argued that the lack of difference in biodiversity between PAs and NPAs should be interpreted with caution because the number of PAs included was relatively small. However, as demonstrated by the distribution of the data for PAs and NPAs (Figs. 3–5) the negative outcome reflected that the different aspects of biodiversity that we investigated were truly independent of area protection status, with the exception of total abundance of arthropods, and not an example of differences falling below the threshold of statistical significance due to insufficient sample size or low power. Still, additional studies based on a larger number of PAs are necessary to formally evaluate generality and reproducibility of our findings.

4.3.2. Forest productivity. Our results do not support the expectation that oak trees should grow faster in NPAs than in PAs. This might indicate that the assumption that unprotected forest areas are managed largely to maximize productivity of tree biomass is incorrect, or that such management has been unsuccessful and failed to promote tree growth (Löf et al., 2016). Alternatively, the PAs included in this study have been managed in ways that do not limit but promote forest productivity. The PAs may also have been established at sites harboring particularly viable and well functioning oak forest ecosystems with a high associated biodiversity, some of which has been lost along the way, and where the environmental conditions are beneficial and allow for fast oak growth.

The lack of a statistically significant effect on the diversity of plants and arthropods, and on tree growth, of the interaction between latitude and area protection status supports the conclusion that the performance of PAs, at least when it comes to the biodiversity values and ecosystem services considered in the present study, is independent of latitude. This spurs the questions whether the future efficacy of area protection with regards to preserving biodiversity associated with deciduous forests will be influenced by ongoing climate change, and how conservation strategies should be adapted to accommodate this.

4.4. Towards climate smart conservation

Developing climate smart conservation is complicated by the fact that there are at least two unknowns; the magnitude, rate and spatial distribution of climate change on the one hand, and the ways by which biodiversity responds to these changes on the other (Fig. 1), plus the impacts of other drivers that are modified along with climate change. The solutions also depend on the specific conservation goals and aims that the PAs are meant to fulfill, but are otherwise generally applicable and mostly well established.

When conservation targets certain endangered species in need of particular concern, this requires knowledge of their specific niche requirements combined with the identification and successful protection of areas that are likely to meet these demands in the future. If possible, PAs should be distributed in space such that the dynamics of the subpopulations is independent, as this has potential to contribute via a portfolio effect to the long-term persistence at the large scale of the 'global' population (Schindler et al., 2010; Abbott et al., 2017). In the case of the forests studied here, this means that PAs should be sufficiently separated and encompass areas for which the spatial autocorrelation of environmental variables is low. There is also a scope for modification and creation of habitats within PAs to maintain existing species and facilitate the arrival of new species (Thomas et al., 2004). Species distribution models could be used as a complement to inform such habitat engineering and to identify key locations for new PAs (Porfirio et al., 2014). In cases where *in situ* long-term persistence is unlikely and the potential for natural range expansions is limited, translocation and assisted colonization beyond the current range boundaries may be considered.

When conservation targets particularly species rich areas, the size of the PAs should be sufficient to harbor large populations and minimize negative impacts of edge effects (Belinchón et al., 2007; Ribeiro et al., 2009). Our present results suggest that species richness of plants, but not species richness of arthropods or forest productivity, increased with the size of PAs. However, additional studies of a larger number of PAs are required before a positive role of large reserve size can be questioned, and there is also recent evidence that the benefits of protection are enhanced for larger PAs (Santangeli et al., 2023). High connectivity, mediated for example via corridors, stepping stones, or high quality of the surrounding matrix that allow interpatch movements of plants and animals is likely to improve goal fulfillment (Thomas and Gillingham, 2015). In the case of the forests studied here, we did not specifically evaluate the role of connectivity for local species richness.

When conservation instead aims to maximize total species richness (gamma diversity), the spatial distribution of PAs across the landscape should cover heterogeneous and contrasting habitat types and environmental conditions that harbor different community compositions. Besides securing areas that currently harbor targeted species or constitute biodiversity hotspots, the designation of future PAs should include climate-change refugia that are relatively buffered from contemporary climate change over time and therefore may enable persistence of valued physical, ecological, and sociocultural resources (Morelli et al., 2020), as these have potential to support high biodiversity values in the future. In the case of the forests studied here, PAs should probably be prioritized in the northern part of the oak distribution.

The distribution of the localities studied here is defined by the range of oaks in Sweden, which is currently restricted to the southernmost part, covering about one third of the latitudinal span of the country. Historically, the distributional range margin of oaks in Sweden has oscillated over time, with marked range expansions and contractions depending on climatic conditions (Giesecke, 2005; Lindbladh and Foster, 2010), with projections of a future northward shift (Prentice et al., 1991). There are also reports of individual oak trees currently growing at very high latitudes (all the way up to the Arctic circle at 66.5 °N) as a result of human translocations (GBIF.org, 2023). Based on this, in combination with ongoing climate change (Fig. 2), it might be suggested that oak forests should be established beyond the current natural northern species range margin, as this has potential to provide habitats and resources that can support a high diversity of associated plants and arthropods in the future. Such assisted migration for the purpose of reforestation, afforestation and range expansions has gained much attention and been implemented as climate change adaptation strategies in production forestry for the past decades, primarily for economic reasons (Williams and Dumroese, 2013; Forster et al., 2021). By comparison, assisted migration has been used much less frequently for conservation purposes to mitigate the impacts of climate change on biodiversity, and given the potential risks associated with translocating species to new environments, more research is needed to understand the consequences of such actions for populations and communities (Thomas and Gillingham, 2015; Butt et al., 2021; Twardek et al., 2023).

5. Conclusions

In this study, we implemented a space-for-time substitution approach to evaluate the future goal fulfillment of PAs under climate change. Besides documenting past climate change, characterizing contemporary ground temperature variation and projecting the future climate, we quantified and compared biodiversity and forest productivity in protected and non-protected deciduous forests along a gradient spanning 5 degrees latitude in the nemoral and boreonemoral zones of Sweden. Contrary to some previous studies and established biodiversity gradients, we found that species richness of plants and arthropods increased with latitude and that forest productivity (oak growth rate) was independent of latitude. In opposition to our prediction, neither species richness of plants, species richness, biomass or species composition of arthropod communities, nor forest productivity differed significantly between PAs and NPAs. As such, these findings question the efficacy of contemporary designation and management of protected oak forests. However, given these unexpected results, additional research is called for before any firm recommendations towards climate smart conservation of these ecosystems can be delivered. Some of the avenues of future research that can provide important insights include investigating whether the degree of goal fulfillment of PAs depends on the type and purpose(s) of protection, and whether it is higher for threatened and conservation targeted species. To broaden inference space, future studies should also include other taxonomic groups in addition to plants and arthropods. To more directly capture the consequences of area protection, it is imperative to also use longitudinal approaches and investigate the temporal developments of biodiversity and ecosystem services. This could be achieved using historical data on species compositions to reconstruct and compare trajectories of biodiversity in PAs, and using data for neighboring NPAs as a control. Environmental niche models and species distribution models could be used to project future distributions of habitats and species, which could aid in elucidating how biodiversity patterns will change in the future and to identify potential areas of particular protection concern.

Given the ongoing redistribution of biodiversity, a major future challenge for climate smart conservation and management of PAs will be to consider the balance between actions aimed at retarding climate related declines in order to retain current species, and facilitating the expansion of species such that they can establish in new areas. This also calls for revisiting the current practice of classifying species as conservation worthy *versus* invasive based on their past distributions and recent range shifts, as well as careful consideration of whether conservation should target certain species or focus on securing functional roles, species interactions, eco-evolutionary processes, and ecosystem services.

Declaration of competing interests

The authors declare that there are no known competing financial interests or personal relationships that influenced the work reported in this paper.

Credit authorship contribution statement

Anders Forsman: Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. Johanna Sunde: Conceptualization, Methodology, Writing – review & editing. Romana Salis: Conceptualization, Methodology, Formal analysis, Writing – review & editing. Markus Franzén: Conceptualization, Data curation, Methodology, Formal analysis - climate data, Writing – review & editing.

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