Proactive Tundra Conservation Strategy for a Rapidly Changing Arctic

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Abstract

Warming-induced forest expansion, permafrost thaw, and human activities are major drivers affecting the biodiversity and ecosystem functions of the Arctic tundra. While the pace of climate warming is fastest in the Arctic, some important stressors, like forest expansion, seem relatively slow. The slow response might provide the opportunity to safeguard Arctic biodiversity and ecosystem function via a strategic and conservation action, taking future dynamics into account. This strategy requires a comprehensive synthesis of how these pressures may threaten the tundra's unique biodiversity, its ecosystem functions and services, including its global climate-regulating role, and the sustainability of Indigenous land use. Developing an effective conservation strategy also requires knowledge of past and projected changes across the tundra and a well-coordinated communication process between scientists, Indigenous people and local communities, and further stakeholders. Here, we outline the essential knowledge base and implementation pathways needed to prioritize areas for protection in such a rapidly changing environment, avoid conflicts of interest, and ensure that tundra biodiversity and associated ecosystem functions and services endure the future warming period.

Introduction

The Arctic tundra ecosystems provide key functions and services, including carbon sequestration, protecting permafrost, providing wildlife habitat, and supporting the land traditions and livelihoods of Indigenous communities [1–3]. However, it is a highly fragile environment [4–6] and is experiencing the world's fastest rate of warming [7]. As a result, tundra biodiversity, ecosystem functions, and Indigenous cultural heritage face serious threats [8].

Large parts of the Arctic tundra are relatively undisturbed by direct human impact, but the potential for today's tundra biodiversity to endure and adapt to rapid warming remains uncertain. There is little doubt that driven by warmer temperatures and changes in precipitation regimes, the Arctic tundra may undergo significant transformations over the next decades and centuries [5,9]. However, some ecosystems might respond rapidly [10,11], while other processes are likely to respond more slowly [12]. Thus, protecting Arctic tundra to safeguard its biodiversity and ecosystem functions and services requires scientifically driven strategic planning based on how the Arctic ecosystem is predicted to respond to climate change and direct human impact over the next decades and centuries.

Currently, only about 16% of the Arctic tundra areas are covered by some form of legal protection (Figure 1), which is well below the 30% target set in the Convention on Biological Diversity's Strategy to 2030 [13]. Furthermore, the current protected area estate does not adequately represent today's tundra ecoregions (Figure 1, supplementary material S1). Moreover, cultural inheritance and practices and future dynamics of tundra-related threats and functions have so far received little attention in conservation strategies [14]. With global commitments to the 30% protection target, a timely opportunity exists to design a comprehensive conservation strategy for the Arctic tundra. Such an approach should aim at the conservation of tundra biodiversity and ecosystem functions under different forms of land use, identification and consideration of their trajectories under climate change, to ultimately identify and prioritize potential refugia.

Here, we illustrate and discuss how warming-induced forest expansion, changes in ecosystem features such as their species assemblages, and economic developments will result in the squeezing of today's Arctic tundra areas, associated with a potential loss of biodiversity, ecosystem functions and services. Developing a framework to prioritize areas for conservation based on projected future dynamics is a critical step for the long-term identification of resilient tundra areas. Here, we aim to highlight key knowledge gaps that must be addressed to develop effective strategies for identifying priority areas for protection. Finally, we propose a systematic prioritization process for selecting these areas, considering future dynamics and potential management practices, emphasizing the importance of minimizing potential land-use conflicts. This involves communication pathways among scientists, Indigenous peoples and local communities, stakeholders and policymakers to collaboratively discuss conservation opportunities, planning tools, and procedures for tundra conservation.

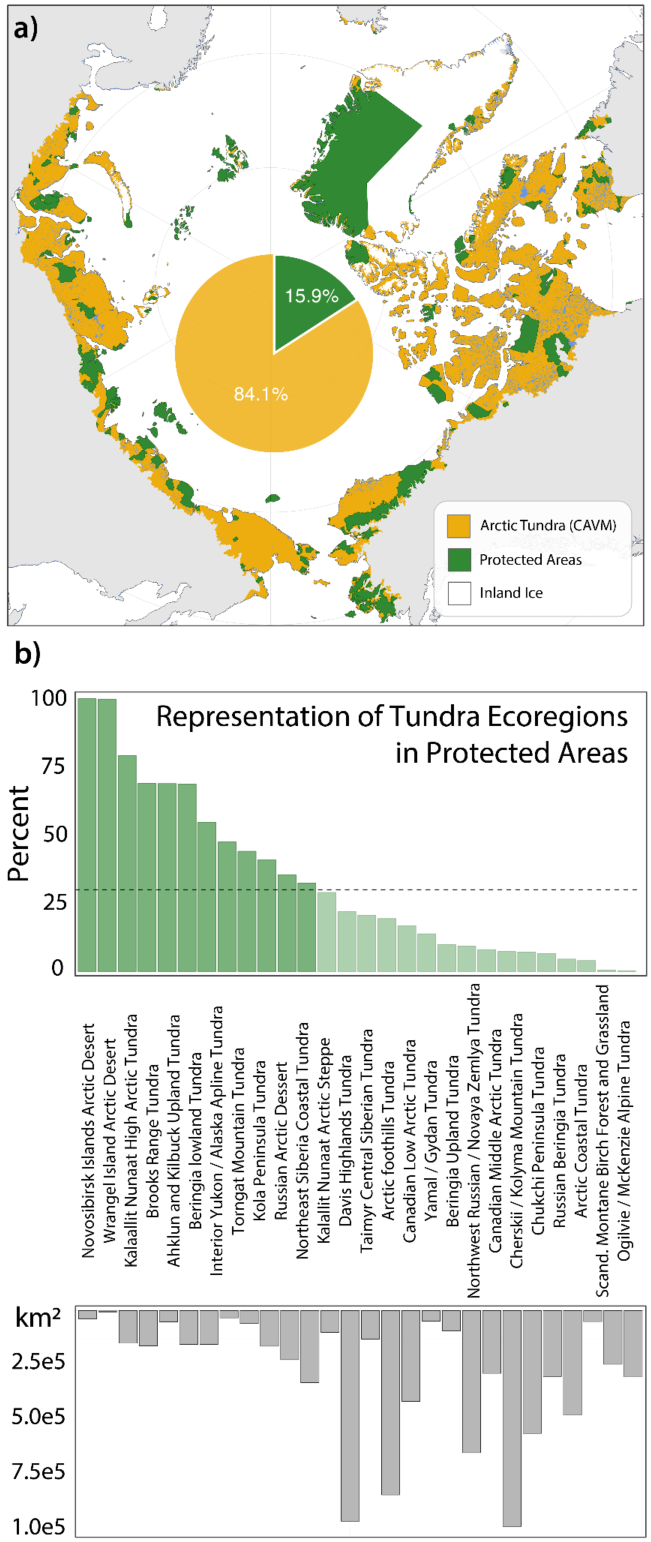

Figure 1: (a) Arctic tundra(orange) as defined by the Circum Arctic Vegetation Mapping project [15], with protected areas (green; UNEP-WCMC and IUCN [16]) and the relative area of tundra protection (pie chart). (b) Tundra ecoregions based on classification by Dinnerstein et al. [17], and their relative representation within protected areas, and the extent of the ecoregion in km^2. Map created with the natural earth dataset.

Major threats for Arctic tundra biodiversity, ecosystem functions and services

The Arctic is warming faster than the global average [7], and warming is expected to accelerate in the near future [18]. Given that the tundra biome, and notably the transition zone from the boreal forests to the treeless tundra, is strongly temperature-constrained, we expect that the tundra will be squeezed by forest expansion towards the north [12,19]. In addition, long-term field studies document recent increases in plant cover, plant growth, and overall biomass, partly associated with large-scale shrubification [20–22]. Rates of treeline advances from field studies range between 3 to 40 meters per year [23] with some exceptions of up to 100 meter per year [24]. Modeling studies led to similar rates, and investigations for northeastern Siberia have shown that forest invasion is much slower than the northward and upward progression of the forest temperature niche [12]. Theoretically, if the treeline matched the speed of warming, much of the Arctic tundra would have already experienced a drastic biome shift towards boreal forests, and open tundra areas with their specific biodiversity would get lost within the next century [12]. Since this is not the case, observations and modeling studies support the idea of a disequilibrium with climate [25], and a time lag in the expansion of forests that might even be on a millennial time scale representing postglacial forest dynamics [26].

A simplified circum-arctic grid-based model parameterized with realistic migration rates (Kruse et al. 2022) for different climate change scenarios (RCPs) [27] highlights the possible tundra loss in the subarctic (Figure 2, supplementary material S2). Depending on the scenario, the Arctic tundra area in Eurasia will significantly decline until 2300, with larger areas remaining in the very east of Siberia, the Taymyr Peninsula and on Novaya Zemlya. However, most of the treeless tundra might remain in Canada due to large land areas at higher latitudes. The remaining treeless tundra regions can provide an initial filter to identify resilient tundra areas that will at least not be affected by forest expansion from the south. This simplified model ignores important factors such as regional-specific climatic conditions, fires (Payette *et al.* 2007), light and nutrient limitation or spatial heterogeneity (Reichle *et al.* 2018), that need to be implemented in future circum-Arctic modeling approaches.

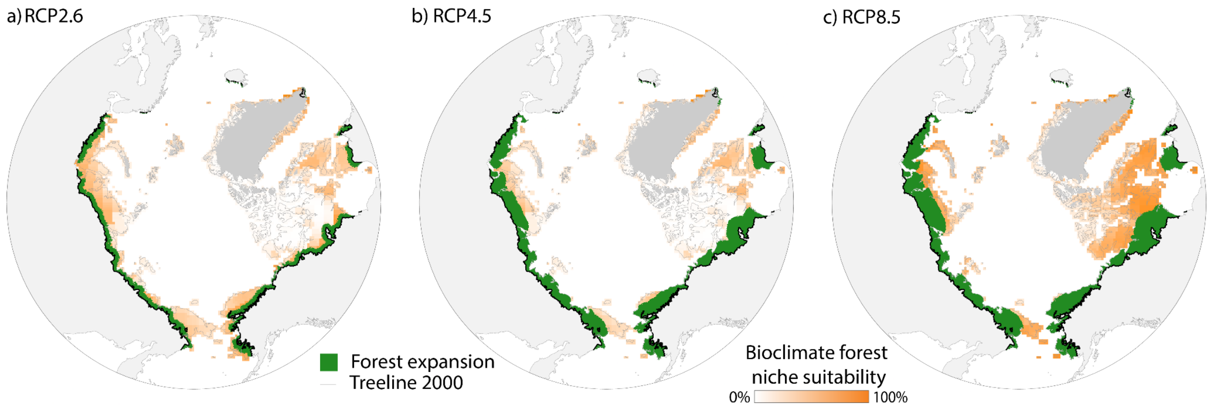

Figure 2: Predicted forest expansion into the Arctic tundra in 2300, under different climate change scenarios (RCP2.6, 4.5, 8.5). Starting point represented by the treeline defined in 2000 [15]. Predictions are based on tree migration rates from individual based model output [12]. Niche suitability for 2300 is extrapolated from the current bioclimatic niche of the treeline. Maps are created with the natural earth dataset.

Permafrost, the permanently frozen ground, is a major foundation of Arctic tundra ecosystems. Even under conservative climate change scenarios (stabilization at 2°C of warming, as aimed for with the Paris Agreement), approximately 40% of the near-surface permafrost ist still projected to thaw [30]. Observed and projected changes in Tundra biodiversity and ecosystem functions are partially related to permafrost thaw [2]. While gradual thaw can increase decomposition of organic soils, releasing nutrients and changes below ground community change and vegetation composition [31], abrupt thaw can even lead to local soil surface collapse, leading to mortality and drastic vegetation change [32–34].

In contrast to traditional land-use practices such as hunting, gathering, and reindeer herding, the expansion of industrialized mining activities and associated infrastructure has a more profound impact on tundra landscapes [35–38]. Due to climate change, natural resources such as oil, gas, and minerals, have become more accessible, leading to increased exploration and extraction activities [36]. The development of new industries poses significant risks to the environment, including habitat destruction and pollution [39]. Even more, the infrastructure to support these industries, including roads, railways, and pipelines facilitates easier access to previously remote areas amplifying land use changes [40].

Missing data and future scenarios to identify candidate areas for Arctic tundra protection

Arctic tundra regions that are less affected by rapid change or are somewhat resilient to change, are considered prime candidates for protection. To identify such areas, a thorough assessment of the dynamics and consequences of tundra stressors is mandatory but also highly challenging.

We lack specific understanding of how forest expansion, shrub encroachment, and permafrost thaw impact the diversity and distribution of tundra species across the Arctic. Recent paleoecological studies using sedimentary ancient DNA [41] and pollen (supplementary material S3) suggest that the expansion of woody taxa has led to a widespread community change and reduced vascular plant diversity after the last glacial maximum. With the range expansion of southern species towards the north and due to the relatively low competitive abilities of cold-adapted species in the north [42–44], tundra specialists may vanish regionally or may even become globally extinct.

Current understanding of Arctic biodiversity changes and ecosystem functions remains incomplete, particularly regarding regional variations and underlying mechanisms. In addition, it remains largely unclear which areas of the Arctic could serve as refugia for endemic species during climate shifts, particularly for endemics. Empirical data collection and remote sensing applications can provide necessary data on plant traits, tundra biodiversity, and the speed of ongoing changes (e.g., forest expansion and biodiversity change within the transition from the boreal forest to the open tundra, supplementary material S4). Such data provide the basis for mechanistic and statistical models that will help to understand how forest expansion, shrub encroachment as well as migration of southern plant species, alters functional diversity and productivity of tundra communities (impacts of treeline shifts on mosses and lichens, supplementary material S5). Besides forecasting future biodiversity across the Arctic, these models can also help to predict the status and changes in key ecosystem functions, including permafrost stability [45] and fire regimes [46,47], and investigate the effects of land use practises that, in case of traditional reindeer grazing, may help conserve specific areas [48].

Forest expansion, shrub encroachment, and abiotic changes in snow and ice and permafrost conditions resulting from climate warming will increasingly impact indigenous people and their traditional land use by reducing the accessibility for domesticated reindeer grazing [49], decreasing access to traditional hunting, trapping, and berry harvesting areas, changing the landscape that the plants and animals that Indigenous peoples use to survive depend upon, increase the risk of using the land, disrupt the transmission of Indigenous knowledges [50] and increasing the likelihood of exotic and re-emerging disease transmission [51,52]. Indigenous knowledge of plant responses to Arctic climate change has highlighted the effects of ongoing warming [53], and Indigenous knowledge and voices can play an active role in scientific data collection and interpretation [54]. Mapping the needs, culturally important areas and future projection of important herding, hunting, and harvesting sites will be crucial to incorporate in tundra conservation and management strategies. Similarly, pan-Arctic mapping of industrial sites and infrastructure, combined with a prediction of risks, for example, induced by permafrost thaw [39], will enable the identification of regions with conflict potential regarding the establishment and management of existing and future protected areas.

Dynamic and systematic conservation planning in the rapidly changing Arctic

The establishment and management of protected areas are central to the conservation of biodiversity and ecosystem functions [14,55,56]. Protected areas have a long history in the Arctic, beginning with the creation of Afognak Island State Park in Alaska in 1892. However, by 1980, only 5.6% of the terrestrial Arctic was under some form of protection, which has slowly increased to 21.2% today [57]. Yet, protection is unevenly distributed across tundra ecoregions (Figure 1) and in some cases also insufficient to safeguard tundra biodiversity and ecosystem functions [14,42]. Specifically, the Canadian Middle Arctic Tundra, Canadian High Arctic Tundra, and Canadian Low Arctic Tundra, along with 13 other ecoregions, are insufficiently protected, with protected area coverage falling short of the 30% target. To meet a 30% coverage target, 0.43 million square kilometers (the approximate size of Sweden or Yemen) of new protected areas are needed.

Dynamic and systematic conservation planning offers an efficient framework for prioritizing protected areas by synthesizing environmental, cultural, and economic factors with climate projections, land-use models, and Indigenous knowledge [58,59]. This approach is especially appropriate under global climate change, where shifting species ranges, evolving ecosystem functions, and altering ecosystem services demand adaptive, forward-looking strategies. By enabling protected areas and conservation initiatives to adapt dynamically, conflicts among stakeholders—such as developers, Indigenous communities, and conservationists—can be mitigated. Concurrently, this adaptability strengthens the long-term resilience, ecological representativeness, and effectiveness of biodiversity preservation efforts.

Figure 3 illustrates a spatially explicit decision support framework that operationalizes systematic conservation planning. This framework incorporates an optimization model that integrates ecological, societal, and economic values while accounting for relevant constraints [59,60], allowing a co-design strategy and effective tracking of progress towards conservation targets [56,61].

The modeling system combines biodiversity conservation with ecosystem functions and human benefits derived from land use. Using multiple data layers, it defines the possibility space for conservation actions while assessing their relationship to societal welfare. Ecological inputs include current distributions of ecosystems and biodiversity features alongside outputs from process-based models simulating tundra systems' ecological interactions under scenarios such as forest expansion, shrub encroachment, and land-use changes. Socioeconomic data—such as population densities, infrastructure development, agricultural activities, mining operations, and industrial activities—are also incorporated to ensure a comprehensive understanding of human impacts. Indigenous communities' perspectives are integrated through stakeholder dialogues to ensure their needs are addressed within the planning framework.

The identification of candidate areas for protection follows a structured process designed to ensure dynamic adaptability over the planning horizon. After the quantitative assessment of **conservation opportunities**, an overall **conservation target** is defined to guide prioritization efforts across vulnerable ecological features and resilient tundra regions that maintain biodiversity and ecosystem functions. This approach ensures **balanced representation** across ecoregions while addressing **human benefits and costs**. Land-based goods and services—such as hunting and agriculture—are evaluated alongside direct costs and opportunity costs associated with conservation actions. Future benefits are adjusted to their present value using equity factors to account for regional disparities in socioeconomic conditions.

To reflect real-world limitations, land-use constraints are explicitly incorporated into the model through zoning laws, preservation policies, and urban development needs. This ensures alignment with political, social, and environmental objectives while preventing overexploitation of natural resources. Certain land-use activities that provide indirect ecological benefits are also considered in decision-making processes to optimize biodiversity outcomes without compromising human needs. The model tracks commodity balances to allocate goods and services effectively across demand regions while maintaining ecological integrity.

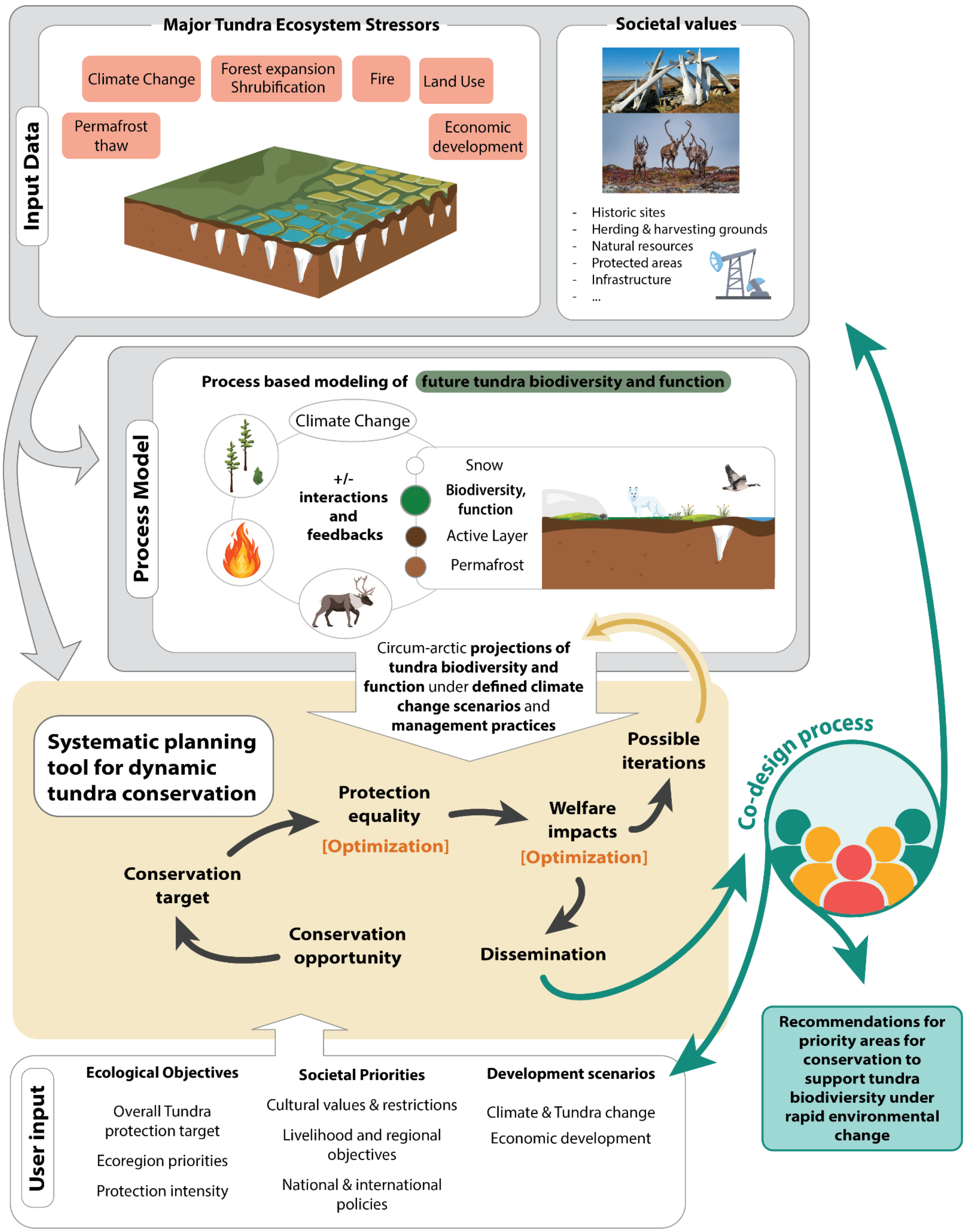

Figure 3: This framework supports the planning of protected area networks by integrating climate and ecological projections with anthropogenic demands. Inputs (top grey box) include spatial data on environmental, societal, and economic factors. These inputs are used to derive ecological stressors, which feed into a process model (second box) that simulates the evolution of tundra-

related biodiversity and ecosystem functions. The systematic conservation planning model (middle beige box) defines the opportunity space for conservation by combining primary data inputs, outputs from the process model, user-defined targets, rightsholder priorities, and development scenario options (bottom box). Using a multi-objective optimization approach, the planning model allocates protected areas by setting protection targets, ensuring a balanced ecological distribution, and maximizing welfare through trade-offs between benefits and costs. The final output identifies priority conservation areas. The entire process is co-designed with stakeholders, Indigenous peoples, and policymakers, who contribute data, define goals, refine outputs, and recommend collaborative protection strategies.

Given the potential for rapid environmental change in the Arctic, with climate warming that may exceed 8˚C over the next decades [7], we consider a dynamic optimization of protected areas necessary. This can either be realised by optimizing across time simultaneously or by iterating the optimization process with the process based modeling output, accounting for changes in land use, management practices and policies.

Co-design process

Community and stakeholder engagement is recognized as an essential component of nature conservation projects [62]. A co-design - the process of producing usable outputs through collaboration between knowledge users and creators [63] - throughout the process, helps to align conservation efforts with community values and enhance the effectiveness and acceptance of conservation measures. In the Arctic, we consider an active involvement of the local Indigenous communities, their regional councils, and representatives crucial for successful Arctic tundra conservation [64]. Besides scientific datasets that include mapped base layers and the development of models to predict future dynamics, the optimization process should be guided by the knowledge and interests of the respective communities [65]. Indigenous guidance and governance allows for the specific needs of communities to be met, including economic stability, sustainable development and food security, while playing a crucial role in conserving and restoring ecosystems. Hunting, trapping, and berry picking, as well as economic developments that include tourism, infrastructure are key factors to maintain and improve the livelihoods of the local people. While some human activities and economic developments might harm Arctic tundra biodiversity and ecosystem function, others (e.g., grazing) can promote their resilience and are effective tools for conservation. With the choice of model input, the discussion of targets, and the cooperative synthesis of the model-based prioritization, the different scenarios and conservation potential strategies can be understood, refined and can ultimately lead to an agreeable solution for the implementation of new protected areas.

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Supplementary Material

Proactive Tundra Conservation Strategy for a Rapidly Changing Arctic

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S1: Tundra ecoregion representation in current protected areas

To understand how well-protected areas cover the arctic tundra's biodiversity, and identify any gaps, we quantified the overlap of protected areas (UNEP-WCMC and IUCN, 2024) with the ecoregions on land (Dinerstein et al. 2017). The assessment included 28 ecoregions within the tundra biome, defined by the Arctic tundra region's boundaries (Circum Arctic Vegetation Map; Raynolds et al. 2019). The R package 'wdpar' (Hanson, 2022) was used to retrieve and clean PA data, and the R package 'ConsTarget' (Jantke et al., 2018) was used to calculate the metric mean target achievement (MTA).This metric evaluates how well conservation targets are met across all terrestrial ecoregions in the Arctic tundra. The metric outputs a value ranging from 0% to 100%, where 0% means that none of the ecoregions are protected at all, and 100% means each ecoregion meets its specific representation target (Jantke et al., 2019). To align with the 30x30 target goals, we assessed the MTA metric based on a 30% protected area coverage goal for each terrestrial ecoregion. We found that more than half of the ecoregions (16 out of 28) in the Arctic tundra are below the 30% target and thus, insufficiently represented by existing protected areas (Figure S1.1). The Ogilvie-MacKenzie alpine tundra in Canada and the Scandinavian montane birch forest and grasslands in Norway are the least protected, with protected area coverage of less than 1%. The coverage of 12 ecoregions exceeded the 30% target. These ecoregions are mainly located in Alaska, Greenland, the northeast Siberian coast, and the archipelagos in the Arctic Ocean. Both the Novosibirsk Islands Arctic desert and the Wrangel Island Arctic desert have achieved complete protection. The MTA for the entire Arctic tundra region is 64% when the conservation target is set at 30%, suggesting that an additional 0.69 million km2 (13.25% of the whole region) is needed to achieve the 30% representation across all ecoregions. The MTA is greater than the percentage of ecoregions that meet the target (42.9%), indicating the presence of ecoregions with very high target achievement. For instance, in the Davis Highlands Tundra, PA coverage has reached 29.2% (Fig. S1.1), accomplishing 97.3% of the conservation target. Therefore, an expansion of only 767 km2 (0.8% of its area) in this ecoregion can fulfill 100% of the conservation target. Conversely, due to insufficient protected area coverage and their large sizes, the Canadian Middle Arctic Tundra, Canadian High Arctic Tundra, and Canadian Low Arctic Tundra require the most significant increase in protected areas, totaling 0.43 million square kilometers. This accounts for more than three-fifths of the total additional protected areas needed for the entire Arctic tundra.

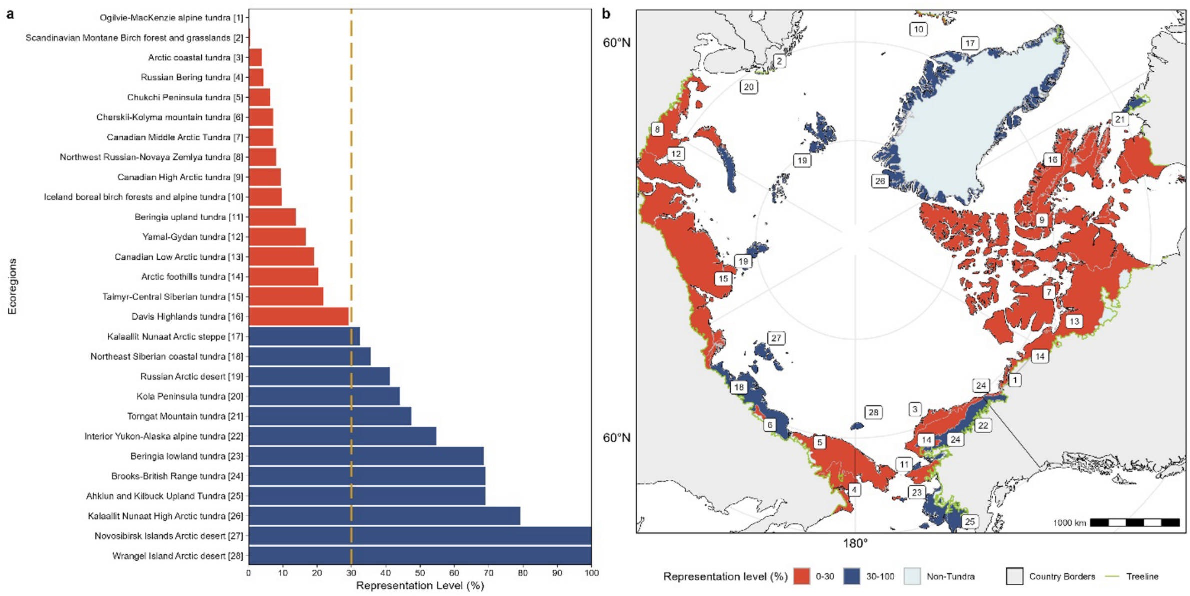

Figure S1.1: Representation of ecoregions by protected areas in the Arctic tundra. (a) Representation of ecoregions in relation to the 30x30 target. Red color indicates under-representation, and blue color indicates well-representation. (b) Spatial distribution of ecoregion representation in the Arctic tundra. The labels correspond to the ecoregion numbers in plot (a).

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S2: Treeline and Bioclimatic niche projection

We simulated possible treeline advances using a grid-based approach. First, the a raster with equal area projection (Sphere_ARC_INFO_Lambert_Azimuthal_Equal_Area) and a resolution of 2 km was created for the northern hemisphere. The treeline for 2010 was defined as the southern border of the Circum Arctic Vegetation Mapping dataset, providing tundra vegetation types on a 1 km resolution. Next, the migration rates of boreal forest was extracted from Kruse et al. 2022 (Table S2.1) for different RCP climate change scenarios.

S2.1 Table of different treeline migration rates inferred from individual based modeling (Kruse et al. 2022).

Scenario	Median Mig. Rate
RCP 2.6	1.4 km / decade
RCP 4.5	6.3 km / decade
RCP 8.5	9.6 km / decade

In time steps of 10 years, the distance of each tundra cell to the closest tree covered cell was calculated. Based on a gaussian probability (parameters in Table S2.1) and according to the climate change scenario, a cell becomes forest if a random number between 0 and 1 is smaller than the distance related gaussian probability (median treeline rate and 2.5 SD).

Code is available on Github:
https://github.com/PolarTerrestrialEnvironmentalSystems/treelineMigration

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S3: Forest Cover and Tundra Biodiversity

Paleoecological data derived from sedimentary fossil pollen records indicate a negative relationship between forest cover and plant species richness in landscapes north of 60°N. An increase in forest cover within tundra regions, driven by anthropogenic climate change, could therefore result in significant biodiversity loss.

Sedimentary fossil pollen records provide a time series of past vegetation through the stratified accumulation of pollen grains in sediments over time. Sediment cores are typically collected from lakes or peatlands and generally reflect regional vegetation signals. For Figure S4, we utilize a global synthesis of pollen records (LegacyPollen 2.0, Li et al., 2024), including records north of 60°N and with samples younger than 14 ka BP (before present) — totaling 331 records.

Pollen-type richness is a reliable proxy for plant species richness (Abraham et al., 2022; Birks et al., 2016). However, it represents only pollen-producing plants, excluding cryptogams. These communities are particularly diverse in tundra landscapes, meaning the negative relationship in Figure S4 may even be underestimated (Alatalo et al., 2020; Cornelissen et al., 2001). The dataset used here has been harmonized to ensure consistent taxonomic resolution. Most taxa are represented at the family level, with tree taxa identified at the genus level. Richness depends on the total number of pollen grains counted — more grains yield more detected taxa. To account for this, we applied rarefaction to equalize grain counts across all samples (Hsieh et al., 2016).

Forest cover data is derived from vegetation reconstructions based on the same pollen dataset (Herzschuh et al., 2025; Schild et al., in press). This reconstruction accounts for taxon- and basin-specific biases, adjusting the pollen composition for greater accuracy. Forest cover is calculated by summing the coverages of all arboreal taxa (Schild et al., in press). Both richness and forest cover data were rasterized to 1°x1° cells in 500-year time slices (Schild, 2024). Figure S2.1 presents 1,892 richness and forest cover values from 101 distinct cells.

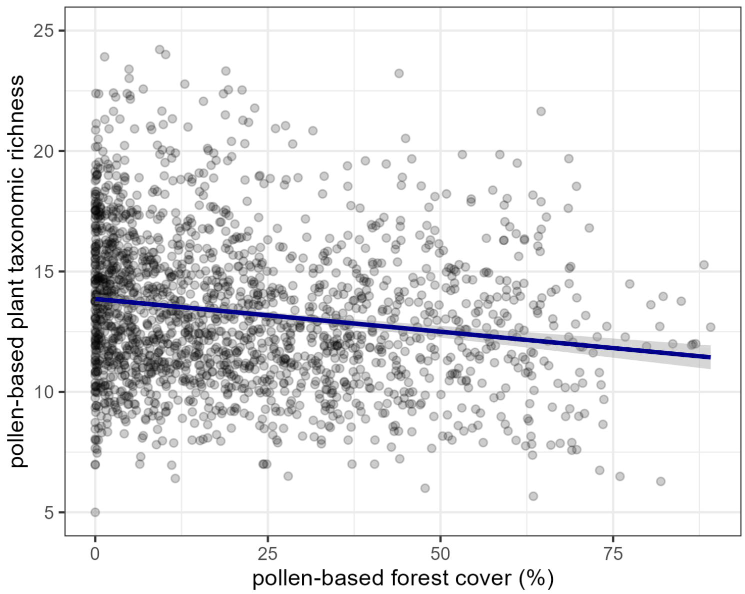

Fig. S2.1: Plant taxonomic richness as a function of forest cover using gridded paleoecological samples (n = 1892) based on sedimentary fossil pollen records.

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S4: Defining the high-latitude treeline

The high-latitude biome boundary at the forest and tundra interface is represented by the forest-tundra ecotone , also defining the southern limit of the Arctic Bioclimate Zone (Reynolds et al. 2019, Walker et al., 2005). Spatially explicit and measurable properties characterize the status of forest-tundra ecotone features, such as biomass, vegetation height, stand age or cover fractions. Most empirical observations from these vegetation changes within the forest-tundra ecotone rely on field-related monitoring, dendrological methods and field-photo based and airborne photo surveys (e.g. Rees et al. 2002, 2020, Garbarino et al. 2023, Timoney and Mamet, 2020). Garbarino et al. (2023) counted that 10% of treeline ecology studies worldwide applied remote sensing tools, with the majority of them relying on local high-spatial resolution airborne remote sensing surveys, and very few of the studies were successful in satellite remote sensing applications. Only few studies could locally map high-latitude treelines, depending on the landscape and the forest type, as shown in the review scientific papers of Bartsch et al. (2016), Chetri et al. (2019) and Rees et al. (2002). Callaghan et al. (2002) summarize that there exist different definitions for high-latitude treelines, forest lines and the forest-tundra ecotone, already recommending the upcoming consistently defined ‘Arctic treeline’ from the major community effort of the CAFF Circum Arctic Vegetation Map (CAVM) project (CAVM team 2003). The CAVM products are based on a joint manual mapping initiative by regional experts (for Canada, Greenland, Iceland, Norway including Svalbard, European Russia, West Siberia, East Siberia, Chukotka and Alaska) who defined tundra vegetation boundaries on the base of an Advanced Very High Resolution Radiometer (AVHRR) false colour infrared mid-summer composite (1:4 M scale) (more details in Walker et al. 2002, Walker et al. 2005). The delineation of the CAVM treeline product was in addition guided by the compilation of regional treeline and botanical maps (Walker et al. 2002, 2005). Reynolds et al. (2019) retain the original CAFF CAVM treeline in their updated CAVM gridded version, as there is up to date no other consistently derived, internationally accepted Arctic treeline dataset. The CAFF CAVM treeline (Walker et al., 2005, Reynolds et al., 2019) is also the basis of our study.

A gradient-based product derived from boreal tree cover or forest productivity could be additionally also defined as a southern boundary of the treeless tundra, as also proposed in Rees et al. (2002), Reynolds et al. (2019), Montesano et al. (2016, 2020). There are available remote sensing datasets that hold the potential to reflect the forest productivity changes in the Northern forest edge over time on large spatial extent such as the Global Forest Change dataset (GFC, Hansen et al. 2013) and the Tree Canopy Cover and Stand Age Boreal Forest Biome dataset from the Arctic-Boreal Vulnerability Experiment (ABoVE, Feng et al. 2022) Both tree cover datasets estimate the proportion of tree canopy defined with >5 m in height with a spatial resolution of 30 m x 30 m. The GFC raster data (Hansen et al., 2013) provide pixel-wise Tree-Cover (status 2000) and annual forest change data from 2000 to the present on a global scale. GFC is primarily based on Landsat imagery and uses a combination of multi-temporal metrics and spectral data to detect changes in forest cover. GFC Forest gain represents the establishment of tree canopy from a non-forest state. The ABoVE raster data (Feng et al. 2022) provide tree canopy cover estimates for the circum-arctic boreal zone from 1984 to 2020 at annual temporal resolution. Like the GCF dataset, it is derived from Landsat imagery while tree canopy cover was further locally calibrated for boreal forests.

Independent accuracy assessments of land cover products for high latitude regions have been extremely scarce (Montesano et al. 2016, Bartsch et al. 2016, 2024). Channan et al. (2015), Hansen et al. (2003), Sexton et al. (2013) reveal in their accuracy assessments that Landsat and MODIS tree cover products show confusion between dense herbaceous and sparse tree cover and systematic underestimation of tree cover in the forest-tundra ecotone. We used a high spatial resolution quasi-true Red Green Blue imagery map (World Imagery, ESRI) to perform an evaluation of the GFC (Hansen et al. 2013) and the ABoVE (Feng et al., 2022) tree cover products. Based on visual assessment at example areas in Alaska, Canada, Eastern Siberia, we found large differences in tree cover estimations for the exact same areas between the GFC and AboVE data. Major challenges became apparent as shrubs were mapped as trees and therefore increased the percentages of pixel-wise tree cover estimates, whereas open needleleaf woodland areas were not mapped as tree cover. This is likely caused by the fact that sparsely growing needleleaf trees are much darker in the Near Infrared than areas with green dense shrub coverage t This might cause difficulties in the classification process of the used algorithms. Further, we found that tree cover was mapped in both products in places where neither trees or shrubs grow based on visual interpretation of the high resolution imagery (see Fig. S2, especially part b). While both datasets offer important insights in broad scale forest change dynamics, they also have clear limitations when used as a basis for the delineation of high-spatial resolution forest features such as forest islands within the forest-tundra ecotone in the circum-arctic region.

. The currently available remote sensing products derived from passive optical remote sensing lack structural information, such as forest structure or vegetation height, that could be valuable for characterizing dynamics of the forest-tundra ecotone. This could be achieved by using RADAR sensors (Radio detection and ranging), such as the TanDEM-X/TerraSAR-X or Sentinel-1 constellations or a combination of radar sensors or radar and optical sensors and detailed digital elevation models (for example see Fassnacht et al. 2021; Bartsch et al. 2020; Bartsch et al. 2024). Also the Ice, Cloud, and Elevation Satellite-2 (ICESat-2) lidar-point derived terrain and canopy height products for boreal forests (Neuenschwander et al. 2020) provide forest structure that was used to derive the current gradient of the Northern forest edge (Montesano et al. 2024). Exploring their potential for spatially detailed vegetation height mapping could help to characterize forest-tundra transition zones and their changes over time on large spatial extents.

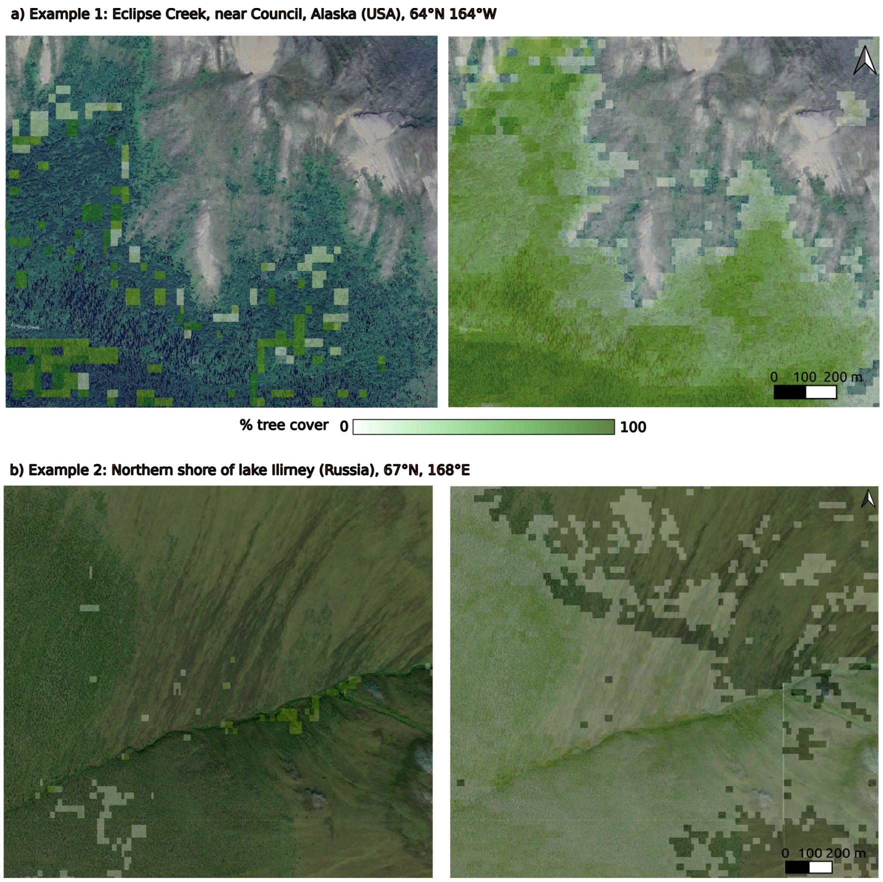

Figure S4.1: Two example regions for a visual assessment of the GFC (Hansen et al. 2013, **left column**) and ABoVE (Feng et al. 2022, **right column**) tree cover datasets. In example 1, the GFC data does not cover trees, while shrubs are being classified as trees. The ABoVE data shows a more consistent classification of tree cover, while shrubs are being considered trees in this dataset. This must be considered with caution when used for forest-tundra ecotone classification or localisation of the high-latitudinal treeline. In example 2, the GFC data fails to provide reliable tree cover estimates along a slope on the Northern shore of lake Illirney, Chukotka Autonomous Okrug, Russia. While shrubs along the river are (mis)classified as trees, the forest along the slope is only marginally considered. The ABoVE data shows more promising tree cover estimates at this example region. Between both datasets, the percentage of treecover differs substantially.

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S5: Modeling arctic tundra vegetation change, climate interactions and feedbacks

Acknowledging these limitations, we conducted preliminary simulations using the current version of the LiBry -DGVM (Dynamic Global Vegetation Model for non-vascular vegetation; Porada et al., 2013) to gain initial insights into the potential impacts of forest invasion on tundra vegetation. Specifically, we utilized the treeline expansion projections generated by the treeline migration model discussed in the previous section (Kruse et al., 2022). We conducted two separate modeling scenarios under the RCP8.5 climate scenario: one using treeline projections for 2020 and another for 2300. Importantly, to isolate the impact of tree invasion on the Arctic tundra, we used recent past climate data (1958–2001) for both simulations rather than projected future climate data. By incorporating these treeline expansion projections as prescribed tree cover into our mechanistic model, we assessed the impacts on tundra vegetation under consistent climate conditions.

Our simulations ran over 200 years and included 300 physiological strategies of mosses and lichens to represent their functional diversity and range of traits. By comparing the outputs of the 2020 and 2300 scenarios, we found that increased tree cover leads to reductions in ground vegetation biomass (from 0.65 to 0.51 Gt), net primary productivity (from 0.26 to 0.19 Gt/year), and the number of functional strategies. These results are illustrated in Fig. S4, which compares the spatial distributions of these variables between the two scenarios. Our findings suggest that tree invasion may significantly diminish the functional diversity and productivity of ground-level communities, potentially affecting key ecosystem functions (Tape, Sturm, & Racine, 2006; Myers-Smith et al., 2011).

Building upon this need for improved simulations, we acknowledge that while our mechanistic model for moss and lichen communities has been valuable (Porada et al., 2013, 2017, 2018, 2019), it currently lacks several critical components. One significant limitation is the absence of interactions with other plant types native to Arctic tundra ecosystems, such as shrubs and grasses (Chapin III et al., 1995; Dormann & Woodin, 2002). This lack of representation of functional diversity hinders our ability to effectively link changes in species composition to biogeochemical functions, including soil temperature regulation and carbon cycling (Chapin III et al., 2000; De Deyn, Cornelissen, & Bardgett, 2008). Additionally, the model does not account for dispersal mechanisms or immigration processes that are vital for predicting species range shifts under climate change (Harsch et al., 2009; Walck et al., 2011).

To address these gaps, we plan to enhance the model by incorporating interactions among different plant types, including shrubs, grasses, mosses, and lichens. This integration will enable us to simulate more realistic community dynamics and competitive relationships. Furthermore, we aim to couple soil thermal dynamics—specifically active layer depth and permafrost—with vegetation processes to better understand feedback mechanisms in tundra ecosystems (Koven et al., 2011; Schuur et al., 2015).

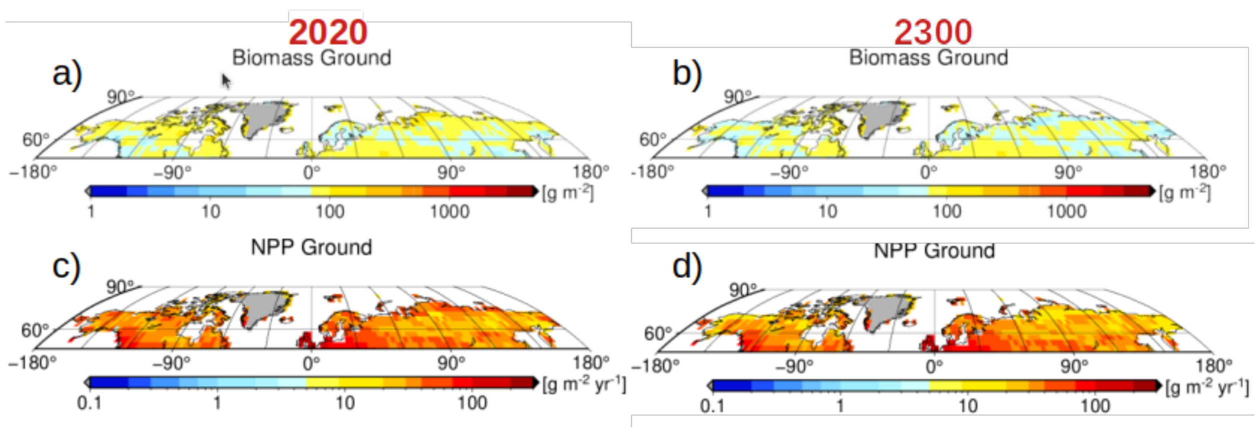

Fig. S5.1: Spatial distributions of (a) ground vegetation biomass, and (c) ground net primary productivity (NPP), in the Arctic tundra under the 2020 treeline scenario; and (b), and (d) the same variables under the 2300 treeline scenario.

S6: Description of Systematic Conservation Planning Tool

Systematic conservation planning (SCP) is a structured, scientific approach to identifying and prioritizing areas for conservation to ensure the long-term protection of biodiversity. In the face of global biodiversity loss and climate change, SCP has become increasingly important for effective environmental management. This approach involves a comprehensive process that balances ecological, economic, and social factors to make informed decisions about conservation actions (Margules and Pressey 2000, Pressey and Bottrill 2009).

<u>Background</u>

Various approaches and tools have been developed to identify priority areas for conservation such as Marxan, Zonation, ConsNet, and C-Plan (Ciarleglio et al. 2009, Pressey et al. 2009, Watts et al. 2009, Lehtomäki and Moilanen 2013). Below, we describe a constrained optimization technique in a generic way that can be adapted to specific regions and biodiversity surrogates. This technique has been applied in several previous conservation planning studies in Europe (Jantke and Schneider 2010, Jantke 2011, Jantke et al. 2011, Jantke and Schneider 2011, Müller et al. 2018, 2020).

Key Principles

The model incorporates the following principles:

1. Conservation goals typically involve expanding existing protected areas, with already protected areas remaining safeguarded.
2. Land use restrictions agreed upon by stakeholders and rightsholders take precedence over ecological or economic considerations.
3. The optimization process follows three lexicographic steps:
    a. Specification of the overall conservation target (e.g., 30% protected area coverage of biodiversity features according to the Kunming-Montreal Global Biodiversity Framework).
    b. Iterative exploration of contributions from individual biodiversity features to meet the overall target in an ecologically balanced way.
    c. Allocation of additional conservation areas based on economic objectives, maximizing net benefits while considering opportunity costs from competing land use demands.

<u>Model Structure</u>

The model optimizes conservation decisions in order to maximize a combination of ecological features and anthropogenic utility, subject to a series of constraints reflecting real-world limitations and requirements. The model is resolved over space and time to account for geographical variations in land and biodiversity characteristics and future developments of environmental conditions and land use demands. The model considers a range of land-based ecosystem services (e.g., biodiversity conservation, carbon sequestration) alongside anthropogenic goods and services (e.g., agricultural production, urban development, recreational uses).

Mathematical Notation

In the model's mathematical structure:

1. Lowercase letters represent parameters (fixed values or coefficients).
2. Uppercase letters denote variables (quantities that can change or are solved for).
3. Subscripts denote sets (indices of parameters, variables, and equations).

List of Tables

Table S1 Equation Structure and Scope[1]

Equation	Mathematical Structure	Dimensions
Equ 1	$Z = w_1 \cdot E + w_2 \cdot U$	singular
Equ 2	$U = \sum_{t,p,y} \left(\frac{1}{(1+d_t)^t} \cdot f_{p,y} \cdot \left(\begin{array}{l} \int v_{t,p,y}\left(S_{t,p,y}\right) d(\cdot) \\ -\sum_{u}\left(c_{t,r,u} \cdot L_{t,r,u}\right) \\ -\sum_{\tilde{r},y}\left(c_{t,r,u} \cdot T_{t,r,\tilde{r},y}\right) \end{array} \right) \right)$	singular
Equ 3	$0 \le E \le B_{t,e}$	$\forall t, e \in e_1$
Equ 4	$E \ge B^*_{t,e}$	$\forall t, e \in e_2$
Equ 5	$0 \le B_{t,e} = \sum_{r,u}\left(a_{t,r,u,e} \cdot L_{t,r,u}\right)$	$\forall t, e$
Equ 6	$0 \le B_{t,r,u} \le,=,\ge l_{t,r,u_o}$	$\forall t, r, u$

[1] The scope or dimensions of equations refer to the indexes used in the equations, indicating how many times an equation is repeated across different elements of one or more indexes. For example, an equation indexed over time (t) and ecoregion (e) is applied to all possible combinations of elements from both t and e.

Equ 7	$\sum_{u}\left(a_{t,r,u,i}\cdot L_{t,r,u}\right)\le m_{t,r,i}$	$\forall t,r,i$
Equ 8	$0\le S_{t,p,y}+\begin{pmatrix}\sum_{\tilde{p}} T_{t,p,\tilde{p},y}\\ -\sum_{\tilde{p}} T_{t,\tilde{p},p,y}\end{pmatrix}-\sum_{r\in p,u}\left(a_{t,r,u,y}\cdot L_{t,r,u}\right)\le k_{t,p,y}$	$\forall t,p,y$

Table S2 Equation Description

Equation	Description
Equ 1	Objective Function Equation This equation computes the objective function value to be maximized. The objective function weights (w_1, w_2) determine the relative importance of ecological objectives (associated with variable 'E') and anthropogenic utility (associated with variable 'U') in the maximization process. While a joint maximization (with both weights non-zero) is technically possible, the standard procedure follows a lexicographic approach. This means the optimization is performed in two sequential steps: First, ecological features are targeted by setting 'w_1' to a non-zero value while 'w_2' remains zero. Once the ecological target optimization is complete, 'w_2' is set to one while 'w_1' is set to zero to maximize anthropogenic utility.
Equ 2	Anthropogenic Net Benefit Accounting Equation This equation determines the net benefits of land use across space and time. The term within the outer parentheses consists of two key components: 1. Anthropogenic utility from goods and services The first component calculates utility by integrating the inverse demand function from zero to the optimized point of consumption. This integration captures the total utility associated with the consumption of land-based goods and services. 2. Costs of land use and trade The second component accounts for the costs associated with land use and land-based commodity trade between demand regions. The overall summation across space and time incorporates a rate of time preference, often referred to as a discounting factor, which adjusts future benefits to their present

	value. Additionally, an equity rate is included to allow for normative corrections of monetary disparities across regions.
Equ 3	<u>Ecological Target Equations</u> This equation computes an ecological objective value (E). The value of 'E' is constrained by the lowest performance (e.g. protected area) across all considered biodiversity features (e.g. ecoregions or species) and time periods, represented by the variable 'B'. Here, 'B' is indexed over both biodiversity feature (e1) and time. When the model maximizes E, it effectively raises the lowest-performing biodiversity feature to its highest possible level. This approach ensures that conservation actions are prioritized for the most critical or underperforming biodiversity feature.
Equ 4	<u>Biodiversity Feature Minimum Protection Restrictions</u> This equation sets minimum values for biodiversity features not currently optimized in the ecological target equation (Equ 3). These biodiversity features have already been addressed in earlier iterations of the model, where their maximum contributions were determined. By enforcing these minimum values, the equation ensures that the conservation gains made for these biodiversity feature in previous optimization rounds are maintained while allowing the model to focus on improving other biodiversity feature in the current iteration. This approach helps to balance the conservation efforts across all ecoregions over multiple rounds of optimization.
Equ 5	<u>B</u>iodiversity Feature<u> Accounting Equations</u> This equation calculates how different land uses contribute to the protection of biodiversity features. The variable 'L' represents land uses, while 'B' denotes the protected area of biodiversity features. The contribution coefficient 'a' is a key factor in this equation, indexed over time, land unit, and land use type. This coefficient serves two essential functions: 1. It indicates whether a specific land use region (r) is part of a particular biodiversity feature occurrence area (e). 2. It determines whether a given land use (u) provides adequate protection to be considered as contributing to the biodiversity feature's protected status.
Equ 6	<u>Land Use Constraint Equations</u> These equations set boundaries on regional land use, allowing it to be equal to, less than, or greater than the initial land use allocation or other land use agreements. These constraints are designed to reflect the following:

	1. Communal views and preferences regarding land development and conservation actions 2. Political instruments and targets, such as zoning regulations or growth management policies The equations ensure that land use changes align with local priorities and regulatory frameworks, balancing development needs with community desires and environmental considerations. This approach allows for flexibility in land use planning while maintaining control over changes' extent and direction. By incorporating these constraints, the model can better represent real-world limitations on land use changes, including factors such as: ● Preservation of agricultural land for food security ● Maintaining the protection of ecologically sensitive areas ● Accommodation of housing and infrastructure development needs
Equ 7	<u>Resource Constraint Equations</u> These equations account for and limit the physical utilization of land and other resources across different land use categories. They ensure that the total resources used do not exceed the available endowments. For instance, it guarantees that the combined area of protected and unprotected land does not surpass the total available land area in each region.
Equ 8	<u>Commodity Balance Equations</u> These equations describe the physical balance between the provision of local land use and the consumption of goods and services across all demand regions. ● The variable S represents the consumption of goods and services for a given period (t), demand region (p), and good or service (y). ● Local production is calculated as the product of land-use area and land-use yield. All locally produced goods or services are allocated to demand regions. ● Trade between regions is represented by the variable T. The consumption in a demand region cannot exceed the sum of local production in that region plus imports from other regions minus exports to other regions. Additionally, the parameter k accounts for exogenous supply-demand impacts, which may arise if the model does not endogenously include all regions connected through trade.

Table S3 Explanation of Mathematical Symbols

Sets

Symbol	Description	Notes
t	time index	Number of explicit periods. Individual time elements usually depict rather large periods, e.g., 30-year periods.
r	landuse region index	The set of land use regions, often defined by environmental or ecological boundaries.
p	demand region index	The set of demand regions, which can range from small community areas to larger market regions.
u	landuse index	Elements include agricultural, cultural, mining, industrial, and conservation land uses.
e	biodiversity feature index	Elements include biodiversity surrogates such as ecoregions, species, taxonomic groups, or other biodiversity indicators
i	resource index	Land and other resources for land use. Elements include land cover types such as tundra vegetation, bare ground, wetlands and peatlands, shrubland, sparse forest transition, or settlements. Further elements may consist of labor, mineral, and infrastructure resources.
y	good & service index	Land-based commodities and services that contribute to livelihoods and well-being.

Parameters

Symbol	Description	Notes
a	technical coefficient	Land use coefficients which describe input requirements and commodity or service productivities for land use options.
c	cost coefficient	Direct costs of land use and trading activities. Land use costs are measured in monetary units per area unit; trading costs are measured in monetary units per unit of product.
d	rate of time preference	A unitless weighting term that accounts for the time value of money and individual preferences. It reflects the principle that benefits or resources received in the future are typically valued less than the same amount received today. This parameter is crucial for comparing values across different time periods and is often used in calculating discount factors for long-term decision-making.

f	equity weight	The equity weight is a unitless parameter often calculated by dividing the average global per-capita income by the per-capita income of a specific demand region. This calculation results in weights above one for poor demand regions and below one for richer demand regions. Equity weights are particularly important for non-market goods such as human health. Their purpose is to adjust utility calculations to account for income disparities between regions, ensuring a more balanced representation of value across different economic contexts.
k	exogenous good supply	This parameter represents the net supply of goods from trading partners that are excluded from the model. Positive values indicate net imports (goods entering the demand region), while negative values represent net exports (goods leaving the demand region). It is typically measured in physical units, such as tons or units of a specific good. This parameter is essential for capturing the influence of external trade flows on the system being analyzed, ensuring that excluded regions' contributions are appropriately accounted for in the model.
m	resource endowments	This parameter represents the physical quantities of natural resources available within a given production area. It includes land resources, such as different types of land (e.g., arable land, forests, grasslands), as well as other resources like water, minerals, or energy sources. Resource endowments are typically measured in physical units appropriate to each resource type, such as hectares for land or cubic meters for water resources.
w	objective weight	A weighting parameter which controls whether ecological or economic objectives are maximized.

Functions

Symbol	Description	Notes
v	demand function	A marginal utility function with associated parameters that can represent: ● Normal (downward sloping) demand: Reflects decreasing marginal utility as quantity increases.

		● Perfectly elastic demand: Horizontal demand curves with constant prices ● Perfectly inelastic demand: Vertical demand curve without price sensitivity; quantity demanded remains constant No demand: Represents external goods and services (also known as externalities); no direct market demand but may have indirect effects on utility or costs.

Variables

Symbol	Description	Notes
Z	overall objective variable	Variable to be maximized. It depicts the weighted sum of monetary and ecological outcomes.
U	anthropogenic objective variable	This variable accounts for the net anthropogenic benefits derived from economic activities. It is calculated by subtracting the costs of production and trade from the benefits of consuming goods and services. The key components include the value gained from the consumption of goods and provision of services (benefits) and the expenses associated with production and trade activities (costs). Typically measured in monetary units, this variable provides a quantifiable measure of human-derived economic value.
E	ecological objective variable	This variable accounts for ecological benefits, typically measured in physical values. It quantifies conservation outcomes of a given action or policy. For example, if the ecological value being measured is the spatial extent of protected areas, then the variable would be expressed in area units (e.g., hectares or square kilometers). Other possible measures could include biodiversity indices, carbon sequestration rates, or water quality indicators, depending on the specific ecological focus of the model.
B	protected biodiversity feature variable	This variable quantifies the total protected area across all depicted biodiversity surrogates over multiple time periods. It is expressed in area units (e.g., hectares, square kilometers) and covers all biodiversity features included in the model. The variables track changes over

		different time periods and serve as indicators of conservation efforts. It provides a spatial and temporal representation of protected areas.
L	land-use variable	This variable represents the allocation of land for different uses across various regions and time periods. Typically expressed in area units (e.g., hectares, square kilometers), it covers different types of land use, such as agriculture, forestry, urban development, or conservation. The variable tracks changes in land allocation over time.
S	good & service variable	This variable quantifies the consumption of goods and services in all demand regions. Typically expressed in physical quantities, it encompasses land-based products and services. The variable tracks changes in consumption over time.
T	commodity trade variable	This variable represents the flow of commodities between different regions or countries. Typically expressed in physical quantities, it covers various types of commodities, such as agricultural products, minerals, or energy resources. The variable accounts for both imports and exports over different time periods.

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