



## Drivers of high-latitude plant diversity hotspots and their congruence



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### ABSTRACT

Determining the drivers, patterns and hotspots of biodiversity can be of critical importance in supporting regional conservation planning. However, as biodiversity hotspots can be described with several different metrics, it is important to investigate their congruence as well as the spatial overlap of hotspots with protected areas. Here, by using extensive data on climate, topography, soil characteristics and vascular plants combined with boosted regression tree models, we determine the patterns and key drivers of plant diversity hotspots along broad environmental gradients in northernmost Europe spanning from taiga landscapes to treeless tundra. We assess plant diversity with four metrics – species richness, range-rarity richness, threatened species richness, and local contribution to beta diversity – and examine their congruence with each other as well as with contemporary conservation areas.

We found that climate plays an important role in governing species diversity, though topo-edaphic are highlighted alongside climatic predictors in determining the diversity patterns of many threatened, near-threatened, and range-restricted species. Importantly, the different diversity metrics have contrasting drivers and, overall, their hotspots have low congruence. Furthermore, existing protected areas appear to offer limited coverage for hotspots of vascular plant diversity.

Modelling the various facets of diversity and their drivers, such as the topo-edaphic setting, may provide useful information to help conserve diversity in a changing climate. Projected patterns of different aspects of diversity and their congruency can provide insights into the processes underlying biodiversity and be employed to assess the representativeness of protected area networks.

### 1. Introduction

The successful conservation of biodiversity depends on our ability to understand and predict the properties and distribution of diversity and, in particular, the hotspots thereof. This calls for continuous efforts to determine the key drivers of biodiversity (Gould, 2000; Smith et al., 2001; Zellweger et al., 2015). Identifying biodiverse regions, i.e. diversity hotspots, can also be useful in recognizing priority areas for conservation (Prendergast et al., 1993; Myers et al., 2000). Hotspots can be identified via assessments of diversity patterns across landscapes. They are commonly quantified through different diversity metrics, such as measures of the total, rare, narrow-ranged, or threatened species richness occurring at a given site (Prendergast et al., 1993; Williams et al., 1996; Reid, 1998; Armsworth et al., 2004; Ceballos and Ehrlich, 2006). Total species richness, combined with rarity or endemism data, has traditionally had a central role in conservation assessments (Myers et al., 2000; Stein et al., 2000), but the degree to which diversity features overlap remains contradictory (Bonn et al.,

2002; Orme et al., 2005). A less investigated but potentially valuable diversity metric is the measure of a site's local contribution to  $\beta$ -diversity (LCBD: Legendre and Cáceres, 2013; Legendre, 2014), which has yet to be applied in terrestrial plant diversity hotspot analyses. LCBD highlights ecologically unique sites contributing more than the mean to  $\beta$ -diversity. An important application in mapping different diversity hotspots is the comparison of their distributions with existing Protected Areas (PAs) to determine potential conservation shortfalls (Scott et al., 1993; Flather et al., 1997; Virkkala et al., 2013; Huang et al., 2016).

Total species richness (TSR), a direct proxy for  $\alpha$ -diversity (i.e. local diversity at a given site), is widely used to depict the biodiversity and conservation value of an area (Whittaker, 1972; Steck et al., 2007; Magurran and Dornelas, 2010). However, TSR may be insufficient in representing local aggregations of rare species (Reid, 1998). This is a potentially critical deficiency as spatially restricted species and species of elevated conservation concern contribute greatly to biological uniqueness and are often classified as having a greater extinction risk than common species (Csuti et al., 1997; Lamoreux et al., 2006; Peters et al.,

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2015). Thus, hotspots of such species are considered to have a higher conservation value than areas where species richness is similar but composed of mainly common species (Lennon et al., 2004; Malcolm et al., 2006; Mouillot et al., 2013). The richness of spatially restricted species can be represented by range-rarity richness (RRR), also known as rarity-weighted richness and rarity score. RRR is a frequently used biodiversity metric to quantify and locate areas richest in species with the most restricted ranges (Williams et al., 1996; Myers et al., 2000; Levin et al., 2007). The richness of species of high conservation concern, including both the threatened and near threatened species (THR) of a given site can be exemplified by the amount of Red Listed species present (Gjerde et al., 2004). TSR, RRR and THR are commonly used in diversity studies (Bonn et al., 2002; Orme et al., 2005), but often utilized separately. A more recent metric, LCBD indicates a site's relative contribution to overall  $\beta$ -diversity (the variation in species composition across sites: Anderson et al., 2011). A high LCBD may indicate distinctive conditions or combinations of species with high conservation value, or degraded species-poor sites in need of ecological restoration (Legendre and Cáceres, 2013; Legendre, 2014).

Identifying the drivers of biodiversity and assessing differences between diversity indicators can help focus field surveys and conservation efforts, or aid in detecting threats to biodiversity (Brooks et al., 2006; Cañadas et al., 2014). Previous studies have shown that various environmental factors influence species richness patterns (Wohlgemuth, 1998; Lobo et al., 2001; Loidi et al., 2015) and that observed biodiversity hotspots generally showcase low congruence (e.g. Feng et al., 2011; Daru et al., 2015). Thus there is growing interest in finding a more comprehensive way to identify diversity hotspots, but knowledge is still lacking regarding what drives different diversity metrics, their hotspots and congruence, and how these manifest across extensive environmental gradients at high latitudes (Orme et al., 2005; Magurran, 2013).

Here we address these information gaps by seeking further understanding on which factors govern vascular plant diversity patterns and the congruence of different diversity hotspots in high-latitude continental Europe. This study combines a statistical modelling approach with extensive data of regional environmental attributes and a unique dataset of vascular plant species based on field observations. We examine the drivers and patterns of four diversity metrics: overall species richness (Prendergast et al., 1993), range-rarity richness (Myers et al., 2000), richness of species of elevated conservation concern (Gjerde et al., 2004), and local contribution to  $\beta$ -diversity (Legendre and Cáceres, 2013). By determining the effects of climatic, topographic and edaphic parameters along a broad gradient spanning from forested taiga to treeless tundra, we identify what drives discernable patterns and differences between the metrics. Furthermore, we quantify the congruence of diversity hotspots to examine their value for conservation efforts. Lastly, as hotspots falling outside areas currently protected can help define conservation gaps in a geographically explicit way (Flather et al., 1997), we overlay our results with current PAs to evaluate their efficiency in preserving vascular plant diversity within the studied high-latitude region.

## 2. Materials and methods

### 2.1. Study area

The study area, located in northernmost Europe between 67°N and 69°N, is influenced by the Arctic Ocean, the proximal Scandes Mountains (Fig. 1), the Polar Front, and the warm North Atlantic current (Aalto et al., 2014). The region hosts a variety of climatic, topographic and edaphic gradients and has an elevational gradient of 72 to 1365 m.a.s.l.. Average July temperatures range from 6.1 °C to 15.2 °C and mean annual precipitation from 449 mm to 600 mm (1981–2010 means: Pirinen et al., 2012). The study area encompasses a boundary area between northern boreal and arctic-alpine habitats, and the

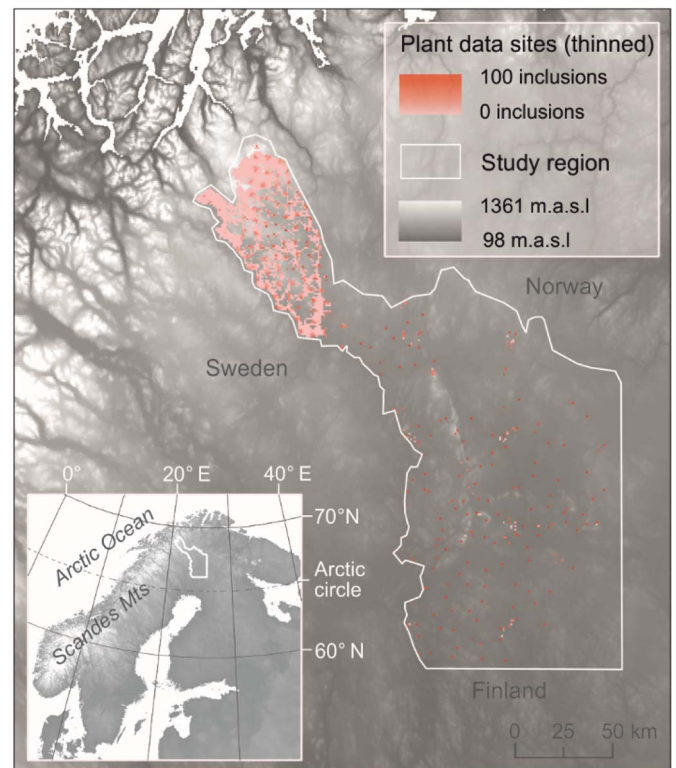


Fig. 1. The location and elevation of the study area in northernmost Europe. The grid cells with available vascular plant data ( $n = 2073$ , spatial resolution 1 km  $\times$  1 km) for which data thinning was applied are also shown. In total, 812 data points were included in the models.

vegetation varies accordingly from spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) forests in the south to mountain birch (*Betula pubescens* subsp. *czerepanovii*) and alpine tundra above the tree-line in the north (Sormunen et al., 2011; le Roux et al., 2012). See Niskanen et al. (2017a, 2017b) for further details on the study area.

### 2.2. Vascular plant species data

Occurrence records for 593 vascular plant species in 1 km  $\times$  1 km cells ( $n = 2073$ ) served as the basis for this study (Fig. 1). Species data was collected for each cell by professional botanists and supplemented by exploration of species records from scientific literature and herbaria with the floristic material being maintained in the Kastikka-database, property of the Botanical Museum (University of Helsinki, Finnish Museum of Natural History). Ranging from taiga to treeless tundra, all the main biotopes found in the study region are represented by the species data. The northern parts of the study region were subjected to a higher sampling intensity. To account for the possible effects of this sampling bias, we utilized spThin, an R package for spatially thinning species occurrence records for use in SDMs (Aiello-Lammens et al., 2015). The data were thinned 100 times with points randomly removed from within a given radius (here, 5 km). The resulting thinned data samples retained 214 sites each.

Based on the species data, we calculated four easily replicated diversity metrics (TSR, RRR, THR, and LCBD: Table 1) to capture different aspects of biodiversity. Metric equations and corresponding details are listed in Table 1 and the summary statistics are presented in Table 2. The TSR metric was calculated as the total number of vascular plant species occurring in a given grid cell (Prendergast et al., 1993; Gaston, 2000). The RRR metric, following terminology suggested by Guerin and Lowe (2015), was built up by first calculating the range-rarity richness of a single species as the inverse of range size (Williams, 2000), here substituted with the estimated range cover of each species within

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