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## Do lichens show latitudinal patterns of diversity?



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### ABSTRACT

No previous study has directly investigated whether lichens show latitudinal patterns of diversity. We used vouchered data and MaxEnt models to compile richness estimates (species, genera, and families) across the western coastal region of the US. Nonparametric multiplicative regression then sought the geographic factors or interactions of factors that explained the most variability in lichen richness. Collection density was the strongest predictor of raw estimates of richness at all taxonomic ranks. Latitude was the overall single-best predictor of MaxEnt modeled species, generic, and familial richness in all models. MaxEnt modeling was necessary to minimize collection bias, which otherwise obscured any other patterns of diversity. While geography explained a sizable portion of variance in lichen richness, it does not trend linearly with latitude. Instead, lichen diversity may be influenced by a compilation of regional and local factors including climate, disturbance, and competition.

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### Introduction

Perhaps the most fundamental and ubiquitous large-scale biogeographic pattern is latitudinal gradients of decreasing diversity with increasing latitude (Pianka, 1966; Hillebrand, 2004; Jablonski et al., 2006). First recognized in the early 19th century by Von Humboldt (Hawkins, 2001), this pervasive pattern of biodiversity has been documented in fauna dating back to the Paleozoic (Cecca et al., 2005; Leighton, 2005). Furthermore, latitudinal diversity gradients have been demonstrated in nearly every taxonomic group and in every imaginable environment (Roy et al., 1998; Willig et al., 2003; Hillebrand, 2004; Qian et al., 2009). Latitudinal diversity trends in fungi, however, tend to be less clear; endophytes follow traditional gradients (Arnold and Lutzoni, 2007), soil fungal diversity does not vary with latitude (Dennis et al., 2012), while ectomycorrhizas show reverse trends with the greatest diversity at high latitudes (Tedersoo and Nara, 2009).

Few studies, however, have investigated latitudinal gradients of lichen diversity. Lichens, the symbiosis of fungi, green algae and/or cyanobacteria, serve a critical role in ecosystems by contributing to diversity and vegetative biomass (Holt et al., 2007; Ellis, 2012), serving as a source of fixed nitrogen in nutrient poor ecosystems (Hobara et al., 2006), contributing to the water-cycle (Ellis, 2012), and providing forage and shelter to other organisms (Brodo et al., 2001). However, coarse-scale studies on patterns of lichen diversity are notably lacking. The few exceptions are studies where such gradients were elucidated upon analysis and were not the research objective (Goward and Spribille, 2005; Elvebakk and Bjerke, 2006; Green et al., 2011; Smykla et al., 2011). In the southern hemisphere, patterns of lichen species richness appear unrelated to latitude (Cannone, 2004; Smykla et al., 2011; Casanovas et al., 2013), or more strongly correlated to land area than latitude (Aptroot, 2009). At the other end of the globe, studies of northern lichens found latitude did not

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explain variation in coastal epiphytes, yet inland corticolous lichens demonstrated a reverse gradient of decreasing species richness with decreasing latitude (Vucetich et al., 2000; Goward and Spribille, 2005).

Some reports indicate that the greatest documented lichen diversity occurs at high northern latitudes (Elvebakk and Bjerke, 2006; Spribille et al., 2010). However, this prediction may simply reflect the size of the principal lichen life form coupled with their abundance on the landscape. Specifically, arctic ecosystems often lack trees, and large mat-forming fruticose or foliose lichens predominate. Alternatively, tropical systems house a multitude of inconspicuous micro-lichens, which tend to be overlooked and understudied (Aptroot, 2001; Lücking and Matzer, 2001). While work in the past decade and a half has helped elucidate the tremendous diversity of lichens that exists in the tropics (e.g., Aptroot, 2001; Lücking and Matzer, 2001; Lücking et al., 2009; van den Boom et al., 2011; Plata and Lücking, 2013), work is still needed to compare complete diversity estimates globally or over large geographic scales.

Even on the continental or country-scale, studies comparing lichen diversity across several latitudes has not been done. The US represents a relatively well-studied country, which provides a reasonable canvas by which to begin such comparisons. Moreover, floristic inventories within the US suggest that no one region (i.e., northern versus southern US) is lichenologically more rich (Lücking et al., 2011); therefore, we had no preconceived notion that lichens should follow classic increasing patterns of diversity with decreasing latitude as has been documented for many other taxonomic groups.

Our goal was to compile estimates of lichen species richness across ca. 436,000 km<sup>2</sup> of the western temperate US, and correlate these patterns with latitude. Specifically, we questioned: (1) do raw estimates of lichen richness based on vouchered collections show latitudinal gradients?; (2) do maximum entropy modeled estimates of lichen richness show latitudinal gradients?; and (3) how do estimates of species, generic, and familial lichen richness differ in their association with latitude?

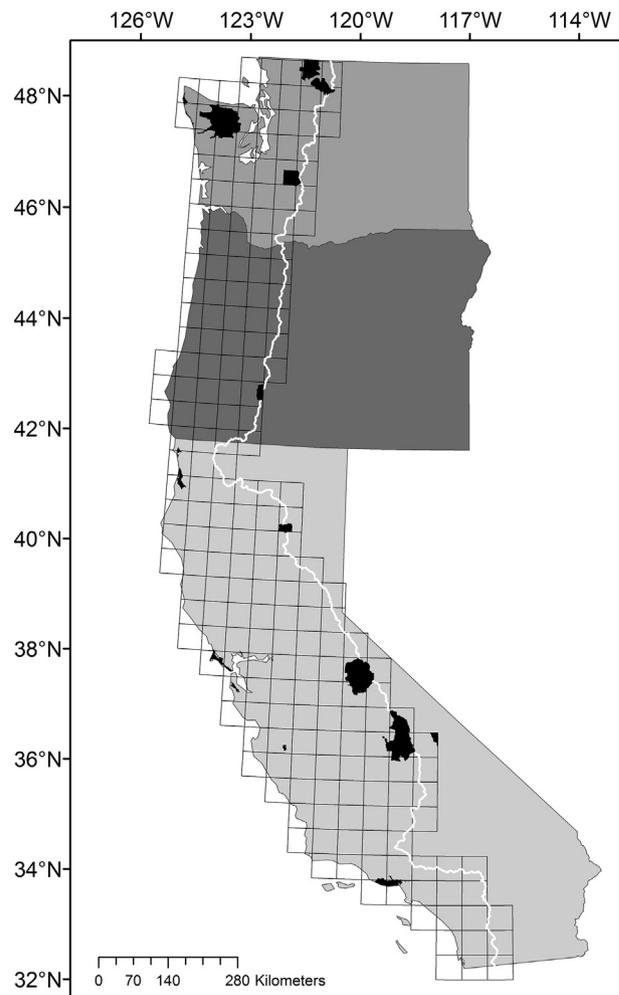
## Materials and methods

### Study area

The study area included western California, Oregon, and Washington; it was roughly delineated by US national borders to the north and south and the coastline and Pacific Crest trail to the west and east (32.331–48.978°N, 116.077–124.323°W). Due to its large size, the study area was quite heterogeneous. The hottest and driest portion is near Fresno, CA (mean maximum Jul. temperature: 36.9 °C, mean annual precipitation: 29.9 mm), while the coolest and driest portion lies atop Mount Rainier (closest weather-station at Longmire, WA; mean minimum Dec. temperature: –3.0 °C, mean annual precipitation: 199.6 mm; NCDC, 1992–2011). This area was selected because it represents a well-studied region of the US, supported by vast collections of lichen data across a large geographic area. In addition, the ridge of the Cascade and

Sierra Nevada Mountains was chosen as the inland boundary, as a natural break between more coastal-influenced systems and those driven by orographic patterns to the east.

To better compare regional diversity estimates, a grid was created using GIS, covering the entire study area (Fig 1). The grain size of this grid was approximately 50 × 50 km, which has been demonstrated as the largest cell size that will offer adequate resolution for landscape-level diversity estimates comparable to other methods (Graham and Hijmans, 2006). The grid followed latitudinal and longitudinal lines to facilitate data extraction. Each of the 218 grid cells was not exactly a 2 500 km<sup>2</sup> square, owing to the convergence of longitudinal lines northward, as well as variation in the terrain and bodies of water and coastline reducing land area in some grid cells. In the full analysis, grid cells were included regardless of final size (63–2 563 km<sup>2</sup>; mean = 2 001 km<sup>2</sup>). Reduced analyses were



**Fig 1 – Map of the study area including western Washington, Oregon and California. Fine black lines indicate the grid delineating the 218 cells used to calculate diversity in roughly equal-area blocks across the area. The thick white line represents the Pacific Crest Trail which served as the eastern-most boundary, which roughly follows the crest of the Cascade and Sierra Nevada Mountains. Solid black polygons represent the 13 national parks used to determine the thresholds (Table 1).**

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