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Climatic niche limits and community-level vulnerability of obligate symbioses

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Abstract

Aim: Communities with many species at their climatic niche limits may be vulnerable to species losses, suggesting that niche-based measures can inform vulnerability assessments. We aimed to quantify spatial variation in community-level vulnerability indices based on niche limits, not just central tendencies, to predict where climate changes will produce rapid, pronounced shifts in ecological communities.

Location: North America.

Taxon: Epiphytic lichenized fungi.

Methods: We integrated broad-extent herbarium data (46,343 North American sites, for estimation of realized niches) with systematic, whole-community macrolichen surveys from the U.S. Forest Inventory and Analysis inventory (6,474 U.S. sites, for standardized vulnerability estimation). We introduce three niche-based vulnerability indices describing (a) percentage of vulnerable species occurring at their upper climatic limits, (b) community-mean percentile, and (c) deviation of local conditions from community-mean upper limits. We also performed sensitivity analyses and evaluated vulnerability in future climate change scenarios.

Results: Sensitivity of indices to uncertainty in climate variables was minor. Present-day vulnerability was greatest in north-central California, in the Southwest along the western Colorado Plateau, and on the Southeastern coastal plain—locations where climatically-induced compositional changes will become most evident. Under future warming scenarios (+0.5 to + 3.6°C increases), the percentage of U.S. epiphytic macrolichen communities exceeding critical values grew from about 2%–20%.

Main conclusions: In all scenarios the most vulnerable communities were concentrated in low-elevation and southerly locations, suggesting that many ostensibly “warm-adapted” communities may be close to exceeding their climatic limits. Findings indicate that warming and moisture changes will modify community compositions through the local loss of intolerant species pushed beyond their niche limits. Assessing vulnerability of bioindicators such as lichens will help prioritize locations where the greatest climate-induced changes in species distributions and diversity will occur.

KEYWORDS

climate exposure, climate sensitivity, epiphytes, forest inventory, lichens, niche limits, range limits, species distributions, vulnerability



1 | INTRODUCTION

Emerging global changes are sparking the need to discriminate how and where basic ecosystem properties, such as species diversity, will change. This need underpins climate adaptation strategies in fields as diverse as agriculture, forestry and commercial fisheries. Climatic changes selectively alter the composition of ecological communities by favouring some species and eliminating others (Vellend, 2016). Therefore, characterizing climatic limits to species' distributions will help identify which taxa are most at risk of local extinctions, and will identify locations where communities are most vulnerable to compositional changes. Climate change vulnerability assessments commonly incorporate exposure, sensitivity and adaptability to determine extinction risks at the species level (Ellis, 2013; Foden et al., 2013; Pacifici et al., 2015); however, we also need to understand global change responses at the community-level. For example, in the absence of migration or adaptation, warming climates may force the local extinction of cold-tolerant species while warm-tolerant species thrive, a process termed the "thermophilization" of floras (Gottfried et al., 2012). Even warm-tolerant communities might be vulnerable to drastic changes if species currently living very near their upper operational limits lack the capacity to acclimate or adapt (Deutsch et al., 2008; Overgaard, Kearney, & Hoffman, 2014). Quantifying how communities will respond to changes in climate regimes is now vital for identifying where biological responses will be greatest, given that warming air temperatures and concurrent moisture changes are expected in virtually all U.S. locations over the next century (Melillo, Richmond, & Yohe, 2014).

Temperature and moisture conditions impose critical physiological constraints on epiphytic organisms directly exposed to atmospheric fluctuations. Epiphytic lichens, for example, are fungus–photobiont symbioses with a lifestyle defined by nutritional and metabolic dependency on atmospheric conditions, making them excellent bioindicators of climatic variation. Epiphytic lichens are particularly consequential because of their disproportionate impact on forest functions, such as the cycling of carbon, nitrogen, phosphorous and water (Berryman & McCune, 2006), and because they may regulate canopy environments that improve water use by vascular plants (Stanton et al., 2014). Therefore, changes in lichen communities can have profound consequences for other forest processes. Atmospheric warming and drying alter lichen reproductive allocation (Martinez et al., 2012) and cause rapid growth declines and mortality (Smith, Nelson, Jovan, Hanson, & McCune, 2018; Song, Liu, & Nadkarni, 2012). Temperature and moisture shifts can therefore lead to differential species gains and losses (Ellis, Yahr, & Coppins, 2009). At regional scales, the greatest changes in lichen community composition are expected where colder/drier areas transition to warmer/wetter conditions (Root, McCune, & Jovan, 2014), or where climatic warming expands host tree distributions faster than epiphytes can track (Greenwood, Chen, Chen, & Jump, 2016). Approaching continental scales, variation in lichen community diversity is highly correlated with mean annual air temperature, continentality, precipitation and moisture deficits (Coyle & Hurlbert, 2016; Smith, Jovan,

& McCune, 2017), suggesting that national monitoring of lichens will be effective for detecting the biological effects of global changes on forests. Given lichens' multiscale relationships with climate, we employed niche-based vulnerability analyses to determine how and where lichen community diversity is expected to change under contemporary climates and future scenarios.

Climate change vulnerability assessments are predicated on sufficient knowledge of species' realized climate niches. Early 20th-century Russian and European vegetation workers developed semi-quantitative "ecological indicator values" to rank plant species' optimum positions along environmental gradients (Ellenberg, 1974; Ramensky, Tsatsenkin, Čížikov, & Antipov, 1956), an approach later extended to lichens and other fungi (Barkman, 1958; Wirth, 2010). More recently, workers have combined remotely sensed or gridded climate products with species occurrences to yield fully quantitative measures based on the centre (mean) of a climate niche for single species, or else the community-weighted average of species' niche centres (Elmendorf et al., 2015). Evaluating changes in central tendencies of realized niches can reveal whether shifts in organisms' distributions might keep pace with observed rates of warming (Devictor, Julliard, Couvet, & Jiguet, 2008; Feeley, Hurtado, Saatchi, Silman, & Clark, 2013; Savage & Vellend, 2015). Yet niche centrality measures, which focus on mean values, may ignore information in other portions of realized niches, such as the upper and lower bounds that describe species' climatic constraints. It is these constraints, and the climate changes that violate them, that determine how local extinctions will occur.

We sought a simple approach to estimate niche-based climate change vulnerability for any set of ecological communities. By way of example, we examine communities of climate-sensitive epiphytic forest macrolichens across the United States. Organisms may respond to global changes by persisting or else dying under altered conditions, dispersing to suitable conditions, and/or adapting to altered conditions. Since long-term rates of dispersal and adaptation are logistically prohibitive to obtain for all the taxa that could occur in a region (especially for lichenized fungi), we sought an approach that avoided arbitrarily parameterizing dispersal and adaptation. Although molecular evidence reveals that long-distance (often trans-oceanic) dispersal occurs among lichens on evolutionary time-scales (Leavitt et al., 2018), we do not know the frequency or distance of dispersal in sufficient resolution to predict it on ecological time-scales for a sufficiently large number of species. Over short time periods, relaxing the need to specify local adaptation is also sufficient because of the gaping mismatch between rates of evolutionary change and the unprecedented velocity of recent climate changes (Jezkova & Wiens, 2016; Parmesan, 2006; Saupe et al., 2014).

Our primary objective was to define and implement three niche-based community vulnerability indices that estimate the location and magnitude of community compositional changes. Secondary objectives were: (a) to evaluate the effects of geographical extent on potential niche underestimation ("truncation") prior to vulnerability analyses; (b) to test the expectation that vulnerability is greater at lower elevations and latitudes; (c) to evaluate sensitivity of indices

to uncertainty in climate variables; and (d) to apply the vulnerability indices to expected future climates across the United States. We further discussed how this approach can be extended to comparatively evaluate the relative vulnerability of different organism groups to global changes.

2 | MATERIALS AND METHODS

2.1 | Data for U.S. lichens and climate

Complete data and algorithms are available in a free, open-source software repository (<https://github.com/phytomosaic/vuln/>), with “fuzzed” plot coordinates provided to protect landowner privacy. All analyses were performed in R version 3.5.1 (R Development Core Team, 2018). Inferences apply to epiphytic macrolichen communities on forested lands in the United States sampled as part of the U.S. Forest Service's Forest Inventory and Analysis (FIA) lichen program. The National FIA Lichen Database gives abundances of all epiphytic macrolichen species recorded over the period 1989–2012 at 8,344 plots across the United States. Prior to analysis, we first excluded 1,870 externally contributed plots that did not adhere to the systematically random FIA sampling design, yielding a final FIA lichen dataset with 75,740 unique occurrences of 443 species at 6,474 sites (plots). The FIA lichen sampling design is systematically random and geographically representative: one site is randomly located in each 39,072-ha hexagonal grid cell of a hexagonal grid covering the U.S., and a plot (the sample unit) is then measured at each forested site (defined as $\geq 10\%$ potential tree cover on undeveloped land ≥ 0.41 ha area and ≥ 36.6 m wide). This design is representative of many different kinds of geography, land ownerships and disturbance histories across U.S. forests. Field sampling consisted of a 2-hr, time-constrained, exhaustive inventory of a circular, 0.379-ha fixed-area plot in which technicians collected and assigned quasi-logarithmic abundance values (0–4) for all epiphytic macrolichen species growing on trees above 0.5 m. Abundance values were: 0 = not present; 1 = 1–3 individuals observed; 2 = 4–10 individuals observed; 3 = more than 10 individuals observed but on <50% of available branches and stems; and 4 = individuals observed on >50% of available substrates. Because its goal is complete inventory of all species present (within measurement time constraints), the FIA method provides “informative absences” that facilitate predictive species modeling.

All climate data originated from the ClimateNA database (Wang, Hamman, Spittlehouse, & Carroll, 2016). For all FIA lichen plot locations, we extracted (or calculated) 17 lichen-relevant climate values as 30-year annual normals covering the period 1980–2010 (Appendix S1). These included two focal variables used for vulnerability analyses. Mean Warmest Month Temperature (MWMT hereafter) is the 30-year mean air temperature of each year's warmest month, and approximates the hottest potentially-lethal temperatures to which lichens are exposed. Climatic moisture deficit (CMD) is a proxy of drought stress that reflects differences between available moisture and temperature-driven evaporative demand, and therefore captures the interaction between precipitation and temperature. We

focused on these two variables because lichen mortality depends both on absolute heat tolerance when lichen thalli are dry, and on net photosynthetic carbon balance when thalli are hydrated (Kershaw, 1983; MacFarlane & Kershaw, 1978; Zotz, Schultz, & Rottenberger, 2003).

2.2 | Species' climatic niche measures

For each of the 443 U.S. macrolichen species, we calculated realized climatic niche space as an empirical cumulative distribution function (ECDF) with respect to climate. We can describe the probability of encountering a given species at any point along a continuous environmental gradient as an empirical probability density function shown as a ‘solid’ curve; the ECDF is simply the cumulative area under this curve (Figure 1). For a vector X describing a continuous random environmental variable, the ECDF gives the proportion of observations less than or equal to any value x :

$$F_X(x) = P(X \leq x).$$

The inverse CDF, or quantile function, describes the x value for a given percentile τ in the interval (0,1):

$$Q(\tau) = F_X^{-1}(\tau).$$

This data-driven, nonparametric approach makes no assumptions about any statistical distribution, and allows species niche responses to be nonlinear, polymodal or asymmetrical in a way that realistically portrays the rich and individualistic climate responses of many species (Whittaker, 1967). From each species' ECDF, we determined sample quantiles of interest for each species' $Q(0.50)$ as the climatic median (centre), $Q(0.75) - Q(0.25)$ as the interquartile range (spread), and $Q(0.05)$ and $Q(0.95)$ as the 5th and 95th percentiles (lower and upper limits). Interquartile range (75th percentile minus 25th percentile) is a measure of niche breadth indicating where a species falls on a specialist–generalist spectrum; it is analogous to a SD statistic but is more robust to outliers, non-normal distributions and skewed distributions (Zwillinger, 2012).

2.3 | Niche coverage: Truncated versus extended climate niches

Fundamental niches may appear “truncated” (i.e., underestimated) if the full range of climate conditions do not exist, are incompletely sampled, or if a species' geographic centre of mass is outside the study area (Feeley & Silman, 2010; Peterson et al., 2011). Because the FIA dataset is restricted to the United States, it may underestimate (“truncate”) thermal niches for southern-centred species, and overestimate thermal niches for northern-centred species. Therefore, we “extended” the coverage of species climate niches by introducing 361,865 lichen herbarium records for the entirety of North America (U.S., Mexico and Canada), sourced from the Consortium of North American Lichen Herbaria database (<http://lichenportal.org/portal/>). Further extension to the global scale

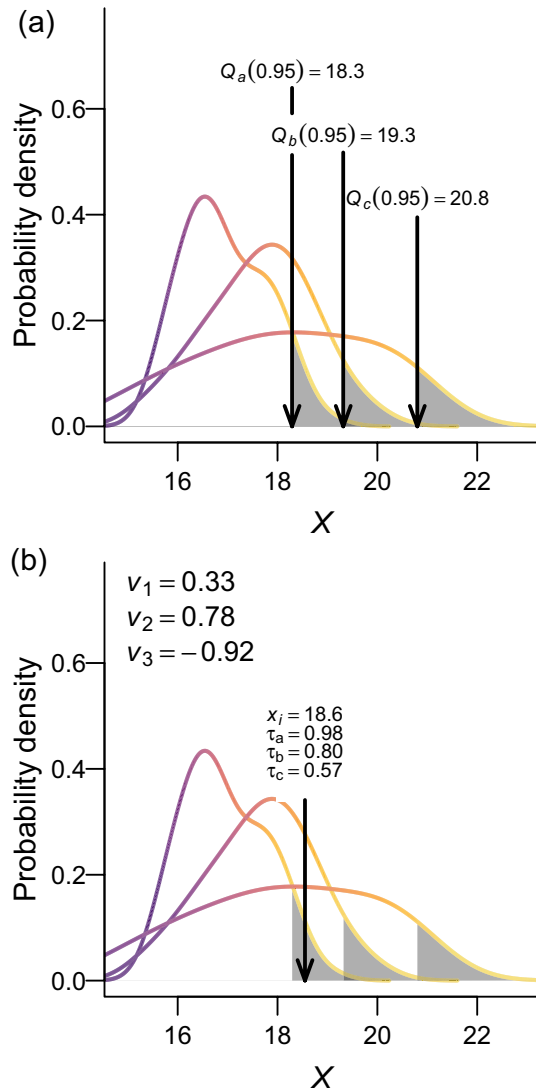


FIGURE 1 Conceptual example of species' niches and community vulnerability. Along climate gradient X , each of three hypothetical species a , b , c has a probability distribution function (solid curves) describing the proportion of sites in which the species occurs across the gradient, interpreted here as the realized niche. Cumulative area under each curve is the empirical cumulative distribution function. Each species has a unique climatic upper limit defined by its 95th percentile value, $Q(0.95)$ (a). A species is "vulnerable" to incremental climate changes wherever populations exceed $Q(0.95)$ (grey areas in the tails; a). At any given X value, say $x_i = 18.6$ in (b), community vulnerability can be estimated with three indices: v_1 is the proportion of vulnerable species occurring at their upper climatic limits, v_2 is the community-mean percentile (τ), and v_3 is the deviation of local conditions from community-mean upper limits. These vulnerability indices integrate the climate exposure of each site (from observed or expected values) with the collective sensitivities of constituent species (from individually estimated niches) [Colour figure can be viewed at wileyonlinelibrary.com]

would be desirable if high-quality data at sufficient extent and density were available. Of the more than 70 genera in the largest macrolichen clade (Parmeliaceae, Lecanoromycetes, Ascomycota), approximately 28% are cosmopolitan, 37% occur in North America,

and 7% occur only in North America (Elix, 1993). We assumed that continental (rather than global) sampling would adequately sample most climatic niches because intercontinental lichen species tend to occur within latitudinal bands exhibiting similar climates (Feuerer & Hawksworth, 2007), and occupy a defined set of climatic habitats regardless of geography (Fačková, Senko, Svitok, & Guttová, 2017). We meticulously pre-processed the herbarium data by removing any records that lacked georeferenced localities, were exact duplicates, were outside species' known ranges, or were incorrectly georeferenced (52.4% of records were removed). We then harmonized species names to be consistent with taxonomic concepts in the FIA dataset. The final cleaned and filtered herbarium dataset (excluding the FIA plots) had 172,127 unique occurrences of 443 macrolichen species at 46,343 North American sites (plots) spanning 14° to 85° North latitude.

Herbarium observations are not systematically sampled, therefore some species and locations are under- or over-represented given collector biases, and any absences are ambiguous (uninformative). For example, an absence could mean that no lichens existed at a site thoroughly searched (true negative), or that many lichens truly existed but the site was never visited (false negative). To reconcile the issue of unequal sampling efforts, we rasterized (binned) all point occurrences into coarse-grained grid cells (approximately 50×50 km) projected over North America. Coarse spatial grain sizes reduce sampling biases associated with herbarium data (Engemann et al., 2015), while retaining information otherwise lost by thinning, filtering or subsetting observations. From climate data (Wang et al., 2016) at each point occurrence, we calculated the mean climate value per grid cell per species. We then recalculated species niche measures as above in parallel with the FIA dataset, giving two sets of niche measures calibrated either with the "truncated" FIA data or "extended" herbarium data. We repeated this procedure at varying spatial grain-sizes, finding that 50×50 km was an acceptable compromise between balancing unequal sampling efforts and the risk of losing climate information by over-smoothing (both of which increase with size of grid cells). It was not necessary to estimate the complete species composition per grid-cell because ECDF niche estimation was for each species individually, and ECDFs do not explicitly depend on co-occurrence information. To evaluate extended versus truncated niche coverage, we estimated niche overlap as the Sørensen similarity of the truncated and extended probability distribution functions. To evaluate the effects of niche coverage on multi-species vulnerability estimates, we compared site-wise vulnerability using range-standardized MAD (mean absolute deviation expressed as a proportion of each range of "extended" values).

2.4 | Vulnerability indices

2.4.1 | v_1 : Vulnerable species percentage

The first vulnerability index (v_1) is defined here as the percentage of all co-occurring species that locally exceeded their upper climatic limits. We focused on the upper limits because this edge of the niche is

expected to be most vulnerable to forecasted climate changes; other niche measures are given in Appendix S2. Upper limits are defined by local climate values (MWMT or CMD) exceeding the 95th percentile of each species' ECDF. On a 0%–100% scale, v_1 can be interpreted as the potential community-level effect of incrementally raising warm-season temperatures or moisture deficits, where higher values indicate greater vulnerability and 100% indicates that all species are vulnerable. The numerator describes the number of vulnerable species approaching their upper climatic limits at a site, and the denominator describes the total number of species present.

$$v_{1i} = \left(\frac{\sum_{j=1}^n a_{ij} l_{ij} [x_i \geq Q_j(0.95)]}{\sum_{j=1}^n a_{ij}} \right) \times 100$$

where a_{ij} is the presence (0 or 1) of species j in site i , l_{ij} is an indicator function taking the value 1 when the bracketed quantity is true and 0 when false, $Q_j(0.95)$ is the 95th percentile climate value from the set of all climate values in which species j occurs (upper climate tolerance of species j), x_i is the climate value of site i , and n is the total number of species observed over all sites.

2.4.2 | v_2 : Community-mean percentile

Rather than an index based on discrete cut-offs, an index based on averaging percentiles of all species at a given temperature would provide insight about the *degree* of vulnerability, applicable even to relatively less-vulnerable communities. By this logic, we defined a second vulnerability index (v_2) as the community-mean of all species' percentiles at a given local climate value, where higher values indicate greater average vulnerability.

$$v_{2i} = \left(\frac{\sum_{j=1}^n a_{ij} F_j(x_i)}{\sum_{j=1}^n a_{ij}} \right) \times 100$$

where a_{ij} is the presence (0 or 1) of species j in site i , $F_j(x_i)$ is the percentile of species j given site climate value x_i , x_i is the climate value of site i , and n is the total number of species we observed over all sites.

2.4.3 | v_3 : Safety margin

Finally, a third vulnerability index (v_3) was the climatic “safety margin”, defined as the deviation of local climate values from community-mean upper tolerances (95th percentile values). Positive v_3 indicates that local conditions exceed average community upper tolerances (i.e., “vulnerable” communities), while negative values indicate that local conditions are less than average tolerances (communities with a margin of safety). The magnitude of v_3 indicates how far the average community upper tolerances depart from local conditions.

$$v_{3i} = x_i - \left(\frac{\sum_{j=1}^n a_{ij} Q_j(0.95)}{\sum_{j=1}^n a_{ij}} \right)$$

where a_{ij} is the presence (0 or 1) of species j in site i , $Q_j(0.95)$ is the 95th percentile climate value from the set of all climate values in which

species j occurs (upper climate tolerance of species j), x_i is the climate value of site i , and n is the total number of species we observed over all sites. Previous workers used a nearly identical “thermal bias” measure, except they reversed the order of terms making it negatively related to vulnerability (Stuart-Smith, Edgar, Barrett, Kininmonth, & Bates, 2015). Blonder et al. (2017) refer to a similar measure as “community climate lag” when integrating change over time.

2.5 | Elevational and latitudinal variation of vulnerability

Of interest was whether “cold-adapted” communities at higher elevations and northerly latitudes would be more or less vulnerable relative to “warm-adapted” communities at lower elevations and more southerly locations. After estimating vulnerability across the United States study area, we used nonparametric quantile regressions to estimate 95th percentile vulnerability, conditional on the interaction of elevation and latitude. Resulting regression surfaces represented the greatest expected vulnerability as a continuous nonlinear function of elevation $\times$ latitude combinations.

2.6 | Sensitivity of vulnerability

Measurement and model error can propagate to uncertainty in climate variables and estimated vulnerability. We evaluated uncertainty using sensitivity analyses in which we added noise to the original climate data inputs, then measured corresponding effects on vulnerability outputs. Added noise was uniformly-distributed with bounds $\pm 5\%$ or $\pm 10\%$ the range of the original climate values. Sensitivity (s) was the range-standardized mean absolute deviation of original versus noise-added vulnerability values, expressed as a proportion of the range of original values.

$$s = \left(\frac{\sum_{i=1}^n |v_{\text{noise}_i} - v_{\text{orig}_i}|}{n | \max v_{\text{orig}_i} - \min v_{\text{orig}_i} |} \right) \times 100$$

where v_{noise} and v_{orig} are vulnerability values for site i , respectively, resulting from noise-added and original data, and n is the total number of sites. Sensitivity (s) is interpreted as the proportion of change in the v response caused by a corresponding change in the climate variable. Values of $s = 0\%$ would mean that climate uncertainty has no effect on the response, while $s = 100\%$ would mean that a change in climate variables results in an average vulnerability change of equal magnitude. For each of the three vulnerability indices, we calculated the average sensitivity of 100 noise-added datasets.

2.7 | Future climate change scenarios

We evaluated changes in thermal vulnerability under four future climate change scenarios. For consistency, we refer to each of the four alternative warming scenarios by their mean warming increment (+0.5, +1.0, +2.5, +3.6°C). First, we incrementally added +0.5, and +1.0°C to contemporary MWMT to mimic small amounts of uniform warming



across sites. Second, since real warming is not likely to be spatially uniform, we also used data derived from coupled climate models that were not added incrementally to each site, but rather which incorporated spatial variation in warming. For this, we queried MWMt values for the 30-year period spanning 2041–2070 from two realistic ensemble model projections based on low-(CMIP5-RCP4.5) and high-(CMIP5-RCP8.5) greenhouse gas emissions scenarios (IPCC [Intergovernmental Panel on Climate Change], 2014). We chose the CMIP5 model because of its comprehensive spatial coverage at high resolution, demonstrated hindcast skill, and its inclusion of a full range of potential future climates while accounting for historical variability (Snober et al., 2013). Ensemble model projections were obtained from ClimateNA (Wang et al., 2016). Finally, for each warming scenario we then estimated the percentage of “very vulnerable” communities where vulnerability exceeded subjective critical values ($v_1 \geq 50\%$, $v_2 \geq 95\%$, $v_3 \geq 0^\circ\text{C}$).

3 | RESULTS

3.1 | Species' climatic niche measures

Epiphytic macrolichen species of the United States exhibited a broad array of realized climate niches for 17 different variables, which we collected into one database (Appendix S2). Beyond the present application to vulnerability, realized niche values should prove useful for studies of climatic niche evolution, trait analyses and climate-based distributional mapping. We focus hereafter on climatic niches defined by MWMt and CMD.

3.2 | Niche coverage: Truncated versus extended climate niches

Niche overlap between extended versus truncated niches exceeded 75% for greater than half of the species in the United States macrolichen flora (Appendix S3). Niche estimation most affected warm-tolerant lichen genera (*Heterodermia*, *Sticta*, *Teloschistes*) whose geographical distributions extended south of the FIA study area. By contrast, extremely common temperate species exhibited little difference in coverage between truncated versus extended niches (Appendix S3), where “extremely common” species refer to those occurring in $\geq 20\%$ of all plots: *Flavoparmelia caperata*, *Punctelia rudecta* and *Phaeophyscia rubropulchra* in the eastern U.S.; *Melanohalea subolivacea*, *Hypogymnia imshaugii* and *Letharia vulpina* in the western U.S.; and *Parmelia sulcata*, *Physcia adscendens* and *Hypogymnia physodes* throughout. The niche estimation steps assume that the realized niche, as observed in a finite area, will adequately describe species' climate sensitivities; before proceeding with such an analysis, workers should ensure that the finite area is representative of the true range of climates under which the species may persist.

Vulnerability from extended versus truncated niche estimation disagreed by 3.2%–3.4% (range-standardized MAD for v_1), 6.2%–8.7% (v_2) and 3.7%–7.2% (v_3) (Figure 2), suggesting that broadening niche estimation from the United States to the North American continent had minor but substantive effects on estimated vulnerability.

Robustness to niche coverage differed among the vulnerability indices (v_2 had slightly greater disagreement than v_1 or v_3). Truncated niches gave higher vulnerability relative to extended niches (Figure 2). Based on niche breadths (interquartile ranges), a mixture of specialist and generalist species tolerated upper extremes of the climatic gradients (Appendix S4). Lichens of the eastern U.S. tended to have higher upper thermal tolerances relative to western species. After accounting for possible niche truncation by extended niche estimation, very few macrolichen species tolerated conditions in excess of 28°C MWMt or 1,250 mm/year CMD (Appendix S4).

3.3 | Vulnerability indices

Based on the FIA lichen survey sites with extended niche estimation, all three v indices agreed qualitatively: vulnerability by any index was consistently greatest in northern and central California, in the Southwest along the Sonoran–Colorado Plateau interface, and to a lesser degree on the Southeastern coastal plain (Figure 3). High vulnerability in these regions indicates where community compositions are most expected to change as a result of specific climate changes. Vulnerability based on temperature alone (MWMt) was broadly distributed throughout the United States, while vulnerability based on temperature-dependent moisture limitation (CMD) was more pronounced in the U.S. West (Figure 3).

3.4 | Elevational and latitudinal variation of vulnerability

All three vulnerability indices reached maxima at low elevations and low latitudes (Figure 4), regardless of whether the extended or truncated niche estimation was employed. The first vulnerability index (v_1 : vulnerable species percentage) exhibited the steepest geographical gradient of vulnerability at low-elevation and southerly locations, whereas v_2 and v_3 varied more gradually. Lichen communities below 2,000 m elevation and south of 40° latitude had the greatest vulnerability in all cases.

3.5 | Sensitivity of vulnerability

Sensitivity (s) is the proportion of change in the v response caused by a corresponding change in the climate variable (where $s = 0\%$ means no effect of climate uncertainty, and $s = 100\%$ means equal-magnitude change in v resulting from uncertainty in climate variables). Vulnerability index v_2 was more than twice as sensitive to climate uncertainty as the other indices. After adding $\pm 5\%$ noise to the three original climate variables to mimic uncertainty, the sensitivities of v_1 , v_2 and v_3 were respectively 1.4%–1.9%, 6.1%–8.1% and 2.3%–2.5%. After adding $\pm 10\%$ noise, sensitivity was 3.2%–4.5%, 11.8%–14.2% and 4.5%–5.0%, respectively.

3.6 | Future climate change scenarios

Thermal vulnerability increased under future climate warming scenarios (+0.5, +1.0, +2.5, +3.6°C), with the greatest changes in lichen

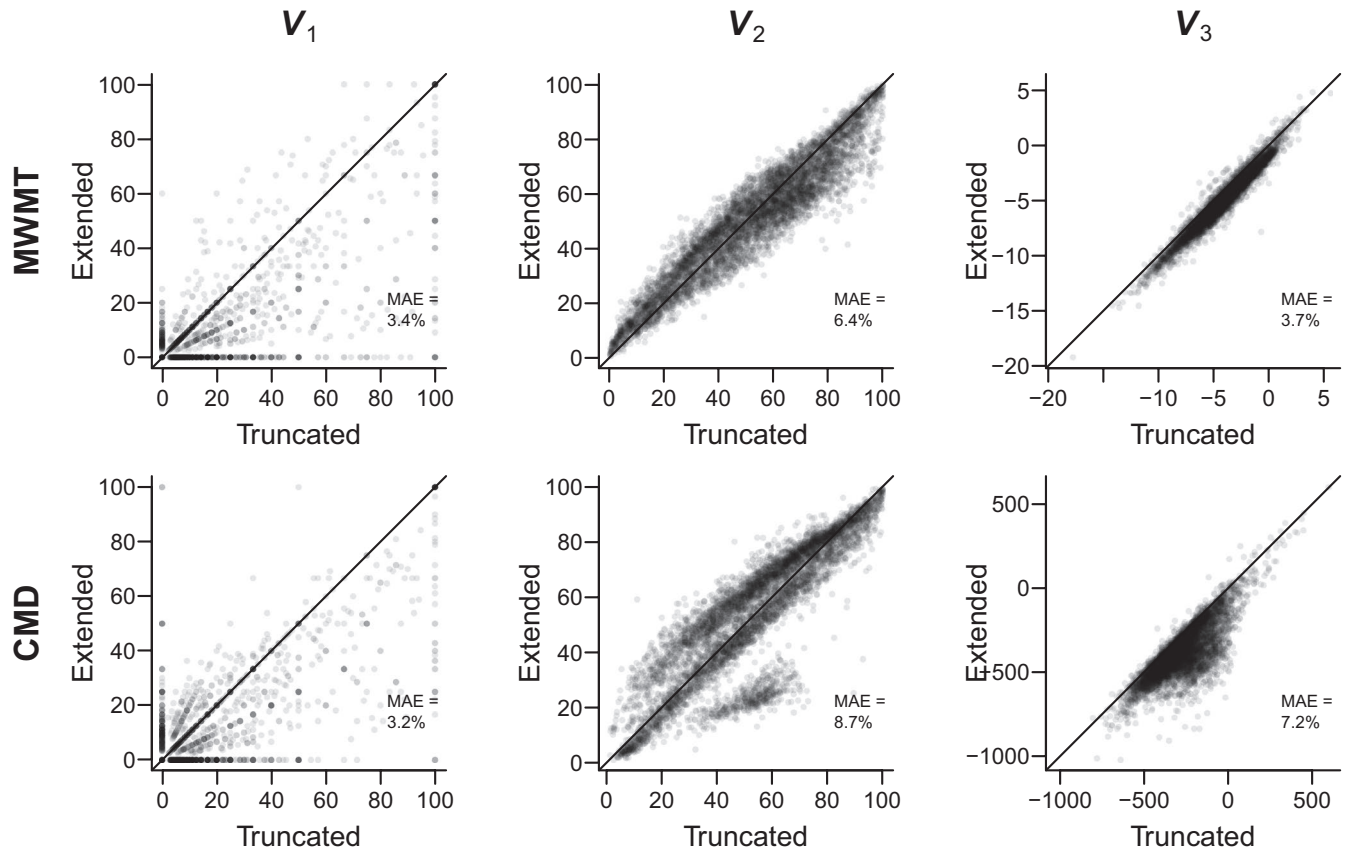


FIGURE 2 Niche coverage effects on climate vulnerability of US lichen communities. Truncated niches (horizontal axes) from the United States and extended niches (vertical axes) from all of North America were used to estimate vulnerability values at 6,474 Forest Inventory and Analysis lichen community sites. Three indices (columns) and two focal climate variables (rows) showed minor disagreement of vulnerability between truncated versus extended niches, largely because extended niches more completely characterized the realized niche

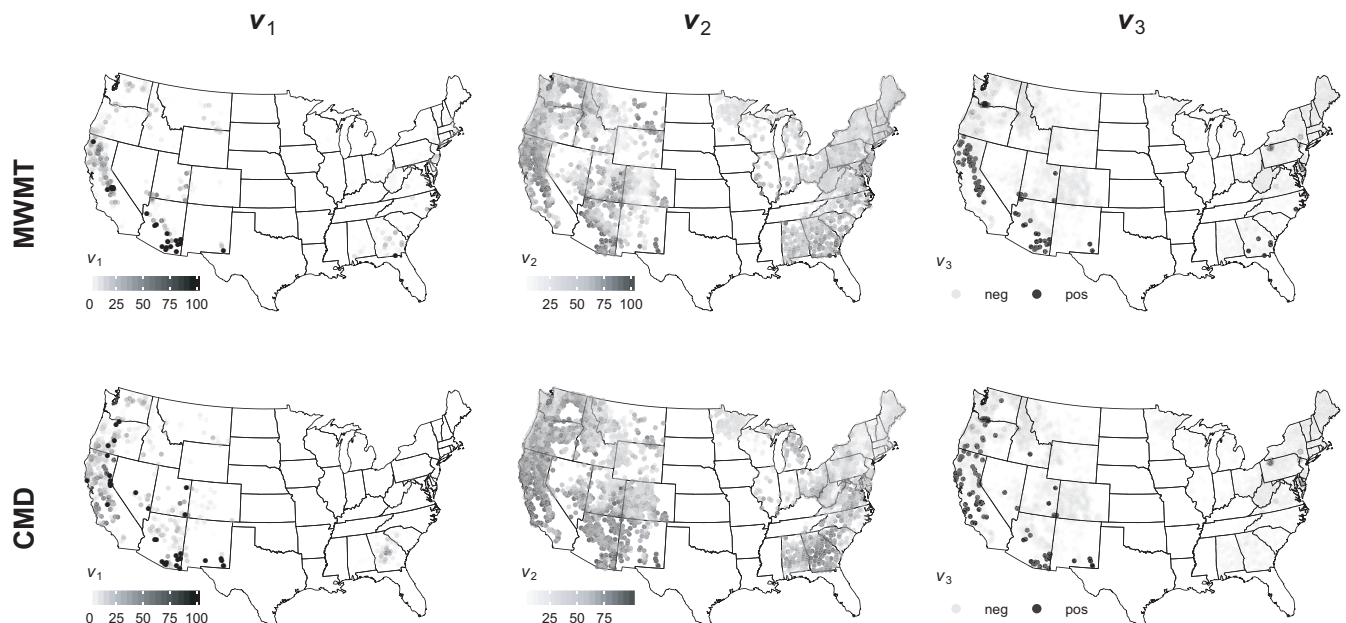


FIGURE 3 Mapped climatic vulnerability of U.S. lichen communities. Vulnerability by any of the three indices (columns) and two climate variables (rows) was consistently greatest in northern and central California, in the Southwest along the western Colorado Plateau, and to a lesser degree on the Southeastern coastal plain. Alaska not shown for brevity. Each point is one epiphytic macrolichen plot from the Forest Inventory and Analysis program, where completely blank areas were not sampled. Albers equal-area projection

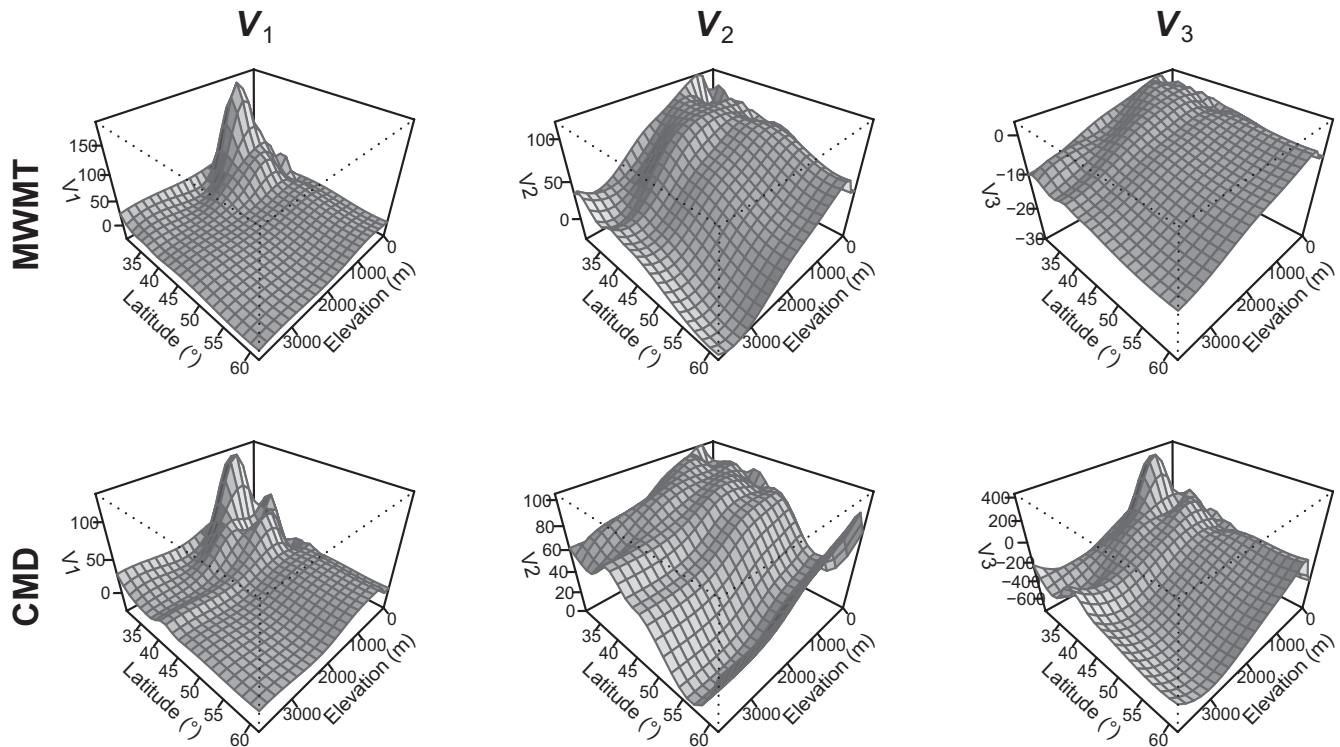


FIGURE 4 Climatic vulnerability of U.S. lichen communities across elevation and latitude. Based on three indices (columns) and two distinct climate variables (rows), maximal vulnerability of epiphytic macrolichen communities occurred at low-elevation sites and southerly latitudes of the United States. Surfaces are conditional 95th percentiles from nonparametric quantile regressions

communities expected for the U.S. Southeast, Southwest, California and the Intermountain West (Figure 5). The percentage of “very vulnerable” sites exceeding critical values also increased with warming. For example, the percentage of U.S. communities with more than half of all species vulnerable ($v_1 \geq 50\%$) increased from 1.9% to 32.4%. The percentage of communities at excessive community-mean thermal percentiles ($v_2 \geq 95\%$) increased from 1.3% to 20.4%. The percentage of communities exceeding thermal safety margins ($v_3 \geq 0^\circ\text{C}$) increased from 1.8% to 28.7% (Figure 6). Collectively, the three vulnerability indices indicated that at least one-fifth of all U.S. epiphytic macrolichen communities would meet the criteria for severe loss of species within the 30-year period 2041–2070 given high-emissions scenarios.

4 | DISCUSSION

Overall, our findings suggest that lichen communities with the greatest vulnerability of warming- and drought-related species losses are those at low-elevation and southerly locations in the United States. This finding contradicts a commonly accepted view that climatic vulnerability should be greatest among high-elevation and high-latitude communities possessing species not adapted to warm conditions. High-elevation lichens have long been a conservation focus because of high endemism and rarity (Allen & Lendemer, 2016), and because of assumptions that communities dominated by

cold-tolerant species should be more sensitive than warm-tolerant communities to increasing temperatures (Aptroot & van Herk, 2007; Hauck, 2009; van Herk, Aptroot, & van Dobben, 2002). By contrast, we found that warm-tolerant lichen communities are nevertheless quite commonly very near to exceeding their upper climatic limits. This echoes similar findings among warm-adapted arthropods, amphibians, reptiles, molluscs and fish in the tropics, which are simultaneously tolerant of currently warm conditions but also at-risk of further incremental warming (Overgaard et al., 2014; Sunday, Bates, & Dulvy, 2011; Tewksbury, Huey, & Deutsch, 2008). Vulnerability of warm-tolerant species near their upper climatic limits may be aggravated by a limited capacity for acclimation given the often narrow range of climatic variation towards lower latitudes (Deutsch et al., 2008).

The climate change vulnerability of warm-tolerant vegetation communities requires critical re-thinking. For example, tropical lowland macrolichens are at risk from global changes because they often occur in physiologically marginal locations that would become too hot to support species if exposed to even minor amounts of warming (Zotz & Bader, 2009). Controlled experiments (Zotz et al., 2003) confirm that the negative impacts of minor warming are not merely an artefact of underestimating fundamental niches in the absence of hotter current conditions (Feeley & Silman, 2010), but instead reflect real physiological limits and a lack of plasticity. Others have invoked greater vulnerability of tropical and subtropical vegetation because of dominance by thermal specialists (Perez,

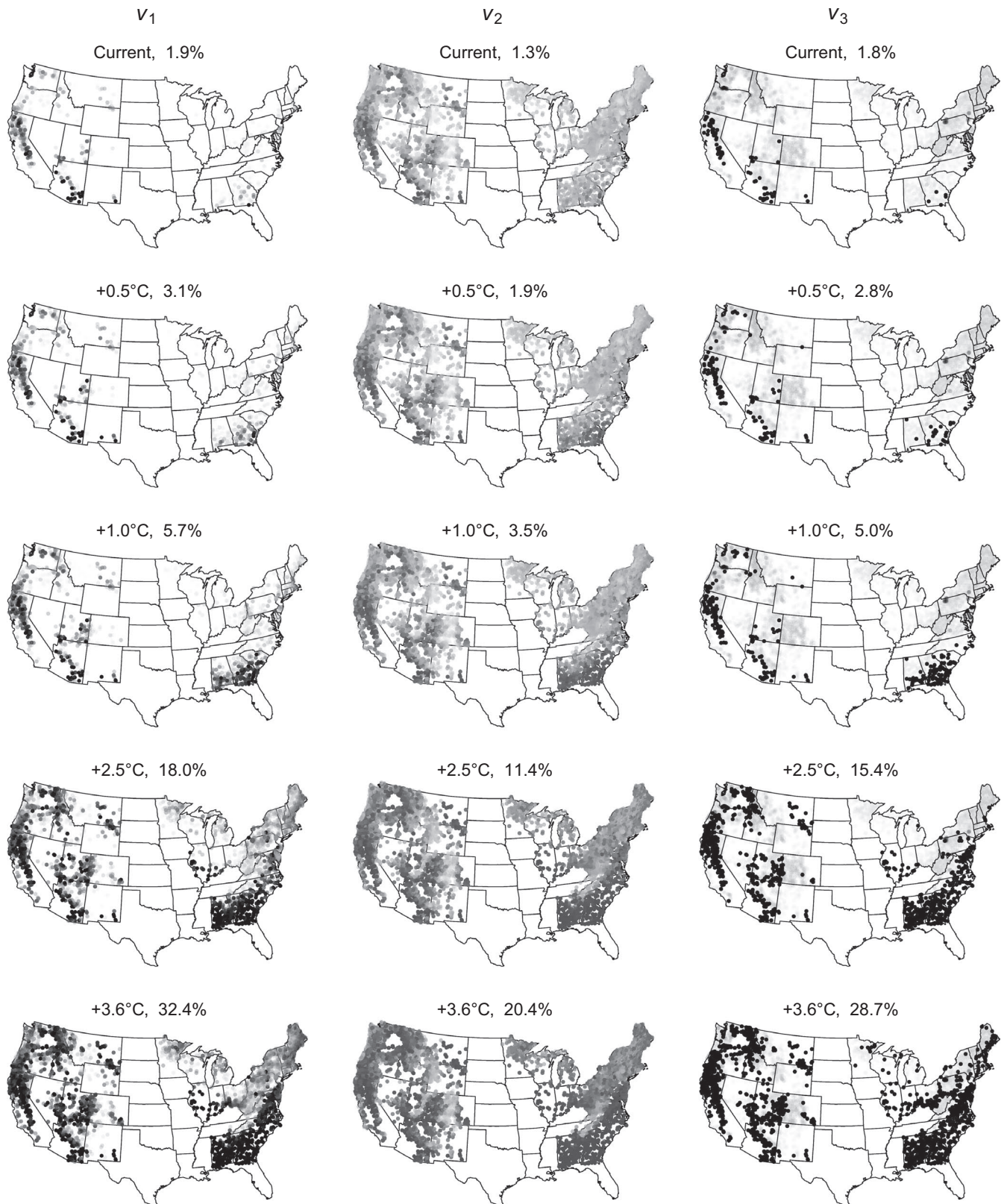


FIGURE 5 Warming effects on thermal vulnerability of U.S. lichen communities. Four warming scenarios (+0.5, +1.0, +2.5, +3.6°C) were compared to the contemporary baseline. Percentages are the number of 6,474 sites identified as “very vulnerable” communities exceeding critical values (more than half of all species vulnerable = $v_1 \geq 50\%$; community-mean thermal percentile extremely high = $v_2 \geq 95\%$; exceeded thermal safety margin = $v_3 \geq 0^\circ\text{C}$). Alaska not shown for brevity. Each point is one epiphytic macrolichen plot from the Forest Inventory and Analysis program, where completely blank areas were not sampled. Albers equal-area projection

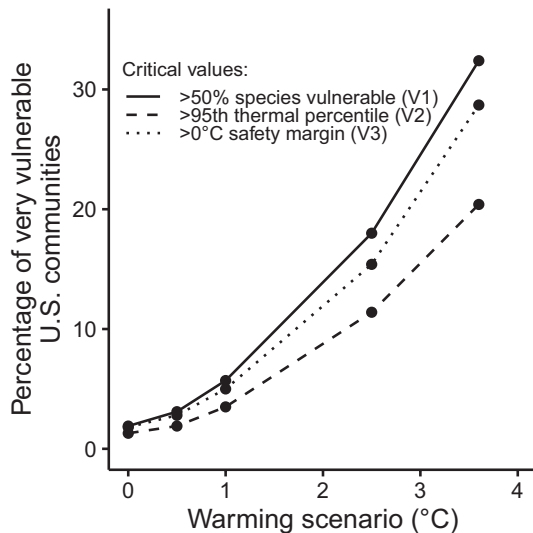


FIGURE 6 Percentage of very vulnerable U.S. lichen communities exceeding critical values. Percentages are the number of 6,474 sites identified as very vulnerable communities exceeding critical values, corresponding to Figure 5. Critical values were defined as: more than half of all species vulnerable = $v_1 \geq 50\%$; community-mean thermal percentile extremely high = $v_2 \geq 95\%$; exceeded thermal safety margin = $v_3 \geq 0^\circ\text{C}$. Warming scenario data originated from ClimateNA (Wang et al., 2016) based on IPCC (2014) emissions scenarios

Stroud, & Feeley, 2016), though we found inconclusive support in this study because both generalists and specialists occurred at warmer temperatures. Aside from direct physiological impacts, atmospheric warming may also have indirect effects on lowland lichen communities due to rising sea levels (Lendemer & Allen, 2014) or shifts in moisture regimes (Follmann, 1995). Similar to cold-tolerant and temperate species, the only recourse for warm-tolerant lichen species would be upward or northward range expansion, as seems to be recently underway in western Europe where long-term records exist (Aptroot & van Herk, 2007; van den Broeck, 2010; van Herk et al., 2002; Söchting, 2004; Wolfskeel & van Herk, 2000). Maintaining populations via range expansion assumes that species' dispersal rates can track suitable climates. Yet, for at least some species, dispersal and establishment rates necessary to maintain populations may lag behind rates of climate change (Greenwood et al., 2016).

Warming scenarios when combined with our vulnerability indices revealed that the local consequences of climate changes will not be solely restricted to warm areas. High-elevation montane areas and high-latitude areas also became increasingly vulnerable with progressive warming, despite that our analyses did not include rock- or ground-dwelling species which may be least adapted to warm conditions (Hauck, 2009). Suitable montane and alpine habitats may become increasingly limited in places like the Appalachian Mountains of the U.S. Southeast (Allen & Lendemer, 2016). To the extent that dispersal allows, climate migration in the mountainous U.S. West could involve both poleward and upward shifts, but poleward shifts may be the only feasible route in the U.S. East where

mountains are much lower and less extensive. The loss of epiphytic macrolichens from boreal and montane forests would likely have repercussions on forest functions such as water retention, cycling of carbon, nitrogen and phosphorous, and the provision of wildlife habitat (Berryman & McCune, 2006, and sources therein). Therefore, the potential for lichen species decline implies direct consequences for other forest processes.

Under future emission scenarios leading to warming (+0.5, +1.0, +2.5, +3.6°C), the greatest increases in thermal vulnerability were concentrated in lichen communities of the U.S. Southeast, Southwest, California and the Intermountain West. Intriguingly, those high-vulnerability areas appeared to coincide with predicted climate-change "hotspots" (Williams, Jackson, & Kutzbach, 2007), which suggests that vulnerability metrics integrating both climatic exposure and species' sensitivities are consistent with independent metrics based solely on climate. Under plausible high-emissions scenarios (+3.6°C), we found that a large fraction (nearly one-fifth) of all U.S. lichen communities could lose half their current lichen species by the late-21st century, based on exceedances of upper thermal tolerances. A similar proportion of lichen communities exceeded thermal safety margins, meaning that local warm-season temperatures are expected to exceed the average upper thermal tolerances of these communities by the end of the century. Taken together, these findings suggest that multiple strategies for stabilizing greenhouse gas concentrations (e.g., emissions reductions, afforestation, shifts to renewable energy; Pacala & Socolow, 2004) could, in part, help address the warming-related decline of forest diversity over broad areas of the United States.

Resource managers and policy makers need a rapid way to score sites according to climate change extinction risks. Ideally, such a method would avoid the burden of specifying in detail each species' demography or assumed climate response traits (Pacifi et al., 2015). Our approach was to model species responses individually (as nonparametric cumulative distribution functions of niches) and simultaneously (as collective vulnerability indices for each site). This approach differs from most other ecological response approaches by modelling species occurrence probabilities via cumulative distribution functions, rather than regression functions. Cumulative distribution functions realistically portray 'solid' response curves where many zero or low-abundance values can occur even at a species' optimum on one niche axis, due to constraints on other, possibly unobserved niche axes (McCune & Grace, 2002; Whittaker, 1967). In the process of estimating species niches this way, we found subtle but important effects of extending niche coverage to avoid truncation. Correcting for niche truncation lowered the perceived degree of vulnerability in this study and others (Feeley & Silman, 2010), leading to more realistic vulnerability estimates. Bias is always a risk when estimating the climatic niche of any single species. For example, observations restricted to a temperate region may underestimate the thermal niche of a tropic-centred species, but also overestimate that of a boreal-centred species. However, niche biases among multi-species mixtures may on average tend to cancel when calculating vulnerability at the community-level. An ongoing

challenge remains to account for novel climate combinations not yet observed in realized ranges. Given that existing species' distributions represent the accumulated legacy of historical climates, novel climates unlike any in the recent historical record may complicate forecasts. Parameterizing forecasts would ultimately benefit from ecophysiological experiments across a combinatorial range of climates, which may or may not be logistically practical for hundreds of taxa simultaneously.

Vulnerability indices show the degree to which climatic changes will impinge on species tolerances to affect community compositions. Evaluating temperature and moisture impacts is important because these are the two most critical factors that limit the warm edges of species geographic distributions (Cahill et al., 2014). Developing a multivariate generalization that admits interactions among multiple climate drivers is warranted and will be forthcoming. While the univariate version described here requires assuming only that change at extreme values of one variable will be biologically limiting, the multivariate version requires non-trivial assumptions about the direction and magnitude of a climate-change vector across multiple axes (assumptions both biological and analytical). Sensitivity analysis found that our vulnerability indices were largely robust to moderate uncertainty in climate data, which would otherwise lead to spurious conclusions about community climate-change responses (Rodríguez-Sánchez, De Frenne, & Hampe, 2012). Like other niche-based methods, our approach assumes that species' realized niches are indicative of potentially habitable climate space (Peterson et al., 2011), and that dispersal and adaptation are not overwhelming influences on species' local persistence. Our vulnerability metrics consider species losses but not gains, and therefore they give conservative estimates of compositional change (i.e., they account only for local extinctions of existing species, and do not account for immigrations that would further change community compositions relative to baseline). We view this conservative property as desirable, both philosophically (to avoid overestimating potential changes) and operationally (to avoid dependence on parameterizing dispersal kernels, distances to known populations, rates of propagule production and release, etc.). Nonetheless, improved knowledge of dispersal and adaptation processes could strengthen our vulnerability approach, given the mutual importance of both dispersal and strong environmental filtering during establishment for explaining lichen biogeographic distributions (Leavitt & Lumbsch, 2016; Tripp, Lendemer, Barberán, Dunn, & Fierer, 2016; Werth et al., 2006). We explored the possible effects of climatic changes in removing species from local communities, but future modifications might also incorporate other ecological processes that may remove species, such as competitive selection and ecological drift, or processes that can introduce species, like immigration and speciation (Vellend, 2016). Gaining adequate knowledge of such hard-to-measure processes would permit more precise forecasting of future forest conditions.

The consensus view is that epiphytic lichen communities are excellent bioindicators of both air quality and climate in forests

(McMurray, Roberts, & Geiser, 2015). Yet the question remains whether lichens will be more sensitive to climate change than other kinds of vegetation, such as vascular plants. Rapid population turnover in lichens (Larsson & Gauslaa, 2011) suggests that climate-related responses could manifest in lichen communities before longer-lived vegetation such as trees. Our approach could be used for comparatively ranking climate change vulnerability among different groups of organisms with contrasting life histories (e.g., trees vs. understory vs. epiphytic vegetation) that may respond at different rates. We posit that forest trees, understory plants, and epiphytic lichens (in that order) would be increasingly vulnerable because of different population growth-rates and life histories.

In conclusion, niche-based climate change vulnerability indices are useful for scoring whole communities (sites), specific habitats and geographic regions according to the joint vulnerability of all species present. Vulnerability in this sense is based on both the climate exposure of each site and the sensitivity of constituent species. Environmental constraints limit species membership in ecological communities, and are central to predicting diversity changes. Among epiphytic forest macrolichen communities of the United States, climatic constraints in current and future scenarios appear to most strongly limit species membership in low-elevation and southern locations, although high-elevation and northern locations are not exempt. Vulnerability analyses are one avenue toward anticipating how the strength of climate selection may change over time.

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DATA AVAILABILITY STATEMENT

All data (species occurrences, community inventories and climate data) and computer code (R format) are available in a self-contained, open-access, public repository at: <https://github.com/phytomosaic/vuln>.

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BIOSKETCHES

Robert J. Smith is a poet and postdoctoral ecologist who asks how changes to disturbance and climatic regimes alter the distribution, persistence and co-occurrence of species; this work is a contribution to his doctoral dissertation. **Sarah Jovan**, an ecologist with the US Forest Service, focuses on developing metrics for indicating air quality and climate based on lichen and bryophyte communities and chemistry. **Bruce McCune** is professor in the Department of Botany and Plant Pathology at Oregon State University; he works on biodiversity and ecology of lichens and bryophytes as well as tools for analysis of multivariate ecological data and niche modelling.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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