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RESEARCH PAPER

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Naturalized distributions show that climatic disequilibrium is structured by niche size in pines (*Pinus* L.)

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Abstract

Aim: The assumption that the native distributions of species are in equilibrium with climate has been shown to be frequently violated, despite its centrality to many niche model applications. We currently lack a framework that predicts these violations. Here, we examine whether variation in climatic disequilibrium is structured by properties of species' native distributions and climatic niches.

Location: Global.

Methods: We built climatic niche models for 106 pine (*Pinus* L.) species, including 25 that have naturalized outside their native range. We measured the extent of climate space occupied exclusively by naturalized populations and considered what fraction of this space was available within the native continent and near the native range. We examined the consequences of disequilibrium for estimates of potential range filling and sister species niche conservatism.

Results: Most species (23 of 25) have naturalized in climate conditions outside the native niche, leading to increases in the total known suitable climate space. Increases in niche size were negatively related to native niche size. Increases were often large; one species expanded its niche by almost 10% of the global climate space. These increases were associated primarily with cooler, wetter and less seasonal climates. Increases in known niche size lowered potential range filling estimates within species' native continent and ecoregion. Naturalized data did not strengthen support for niche conservatism among sister species.

Main conclusions: Among pines, climatic disequilibrium is the norm and not the exception. The magnitude of this disequilibrium can be vast, such that the native range greatly under-represents the true climatic tolerances of some species. Fortunately, this disequilibrium can be predicted largely by the size of a species' native niche. Accounting for this disequilibrium can improve our ability to characterize ecological phenomena, including potential range filling. This is an essential step towards improving the conservation value of ecological niche models.

KEYWORDS

climate change, conservation planning, ecological niche model, niche size, phylogenetic niche conservatism, range filling, tree invasions

1 | INTRODUCTION

Species distribution models (SDMs) and the ecological niche models (ENMs) that underlie them are important tools used to predict species invasions (e.g., Broennimann et al., 2007; Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014; Peterson, 2003; Thuiller, Richardson, et al., 2005), estimate extinction risk under climate change (e.g., Thuiller, Lavorel, Lavorel, Araújo, Sykes, & Prentice, 2005) and inform conservation planning (e.g., Early & Sax, 2011; Williams et al., 2005). A primary assumption of these models, that species can survive only in areas with climatic conditions matching those where they currently occur (Busby, 1988), has been recognized since the release of the first widely used SDM package (BioClim; Nix, 1986; Booth, Nix, Busby, & Hutchinson, 2014). The current formulation of this assumption, that species distributions exist in equilibrium with their native climate (i.e., species occur in all the climates that could sustain them), has been shown to be frequently violated (Booth et al., 2015; Booth, Nix, Hutchinson, & Jovanovic, 1988; Bosci et al., 2016; Early & Sax, 2014; Gallagher, Beaumont, Hughes, & Leishman, 2010). Climatic disequilibrium can result from dispersal limitations, biotic interactions or contingencies of biogeographical history (Svenning & Skov, 2004; Wisz et al., 2013), all of which can constrain the realized niche to a nested subset of the fundamental niche. Here, we define the realized niche as the climate space occupied by the species' historical native range. We define the fundamental niche as the climate space in which a self-sustaining population can be maintained, but which may not be fully occupied owing to antagonistic biotic interactions, missing positive biotic interactions or barriers to dispersal (Sax, Early, & Bellemare, 2013).

Models that incorporate only realized conditions will generally underestimate invasion risk (Broennimann & Guisan, 2008) and overestimate the sensitivity of species to changes in climate (Araújo et al., 2013). This mismatch between realized and fundamental niche space could be ameliorated by building models that include empirical information on the fundamental niche. However, this information is generally unavailable for most species. Likewise, no predictive framework exists to estimate or model fundamental niche conditions reliably relative to realized conditions (Sax et al., 2013), although recent work pairing critical physiological limits with realized niche estimates has made progress in this regard (Soberón & Arroyo-Peña, 2017). Without such a framework, it is difficult to know how much confidence we should place in existing modelling approaches based solely on realized niche conditions.

Several lines of evidence that relate to conditions beyond the realized niche provide a partial basis for examining potential mismatches between species' realized and fundamental niches. Mechanistic models characterize the bounds of the fundamental niche by examining species' physiological limits. Such studies, on a wide variety of taxa, suggest that the fundamental niche is often much larger than the realized niche and extends into warmer and wetter climates (e.g., Araújo et al., 2013; Sunday, Bates, & Dulvy, 2012). Hindcasting approaches that compare current and past distributions can also be informative. For instance, Ivory, Early, Sax, and Russell (2016) found that fossil distributional data exposed suitable climate space that is masked from species' current ranges by human land use. Finally, considerations of the climatic conditions experienced in species' native and non-native ranges have a long history in the literature (e.g., Booth et al., 1988; Booth & McMurtrie, 1988; Grinnell, 1922). However, multiple-species comparisons in this vein have only recently emerged (e.g., Gallagher et al., 2010). This approach typically involves examining populations outside the native range that are naturalized (i.e., self-sustaining, indicating portions of the fundamental niche) or those that are adventive (i.e., growing but not self-sustaining, indicating portions of the tolerance niche; *sensu* Sax et al., 2013). Another similar and promising approach involves using data from provenance trials wherein individuals from various localities are grown outside the species' range; in particular, many tree species have been tested in this way to assess their suitability for commercial forestry (Booth, 2017; Booth et al., 2015).

Despite the nascence of this literature, two broad patterns have begun to emerge. First, there is evidence that species with small native ranges or narrow realized niches are more likely to show mismatches between their realized niche and either their fundamental or their tolerance niche. Early and Sax (2014) found strong support for this pattern among a group of 51 European plants that have naturalized in the USA. Bosci et al. (2016) found a similar pattern for plants in North America, such that species with small native ranges were most likely to have large mismatches between native climatic conditions and those in which species have become adventive. In contrast, Petitpierre et al. (2012) found that most species with large native ranges showed only minor differences between native climatic conditions and those in which the species had become established. Second, the literature examining climate conditions occupied by native and non-native populations indicates that unoccupied portions of the fundamental niche are likely to be in warmer and wetter climates than the native range, as exemplified by a study of amphibian and reptile distributions (Li, Liu, Li, Petitpierre, & Guisan, 2014). These results are consistent with mechanistic studies that examine physiological and metabolic limits (e.g., Araújo et al., 2013; Sunday et al., 2012). More work is needed, but if these patterns were widespread, a case could be made that species might fare better than previously forecast in their warming native ranges.

One of the implications of climatic disequilibrium is that areas within a species' native region or continent can be unoccupied even though they are climatically suitable. This was demonstrated in classic work by Svenning and Skov (2004), who showed that European tree species occupy only a portion of the climatically suitable area on the continent. This work and the large body of continuing work on 'range filling' has shown that most species do not fill all of the suitable area within their native region or continent (Bradley, Early, & Sorte, 2015; Dullinger et al., 2012; Nogués-Bravo et al., 2014; Svenning & Skov, 2004). However, it is important to emphasize that this work considers only the realized niche when making these comparisons (but see Bradley et al., 2015). The growing literature on native and non-native climate comparisons suggests that existing estimates of range filling underestimate the difference between realized conditions and the true climatically suitable area (Early & Sax, 2014). This means that even less of the potentially suitable area might be occupied than previously thought. However, additional work is needed to constrain better the degree to which range filling estimates based solely on native distributions might characterize range filling inaccurately.

Variation in the magnitude of climatic disequilibrium among species also has implications for the evolution of climatic niches. The idea that similarity between species should increase with relatedness has been long established, and more recent work has identified 'niche conservatism' as a general tendency for closely related species to have more similar fundamental niches or climatic tolerances than expected by chance (Holt & Gaines, 1992; Losos, 2008; Wiens et al., 2010). However, because most empirical studies on niche conservatism estimate only the realized niche (e.g., Anacker & Strauss, 2014; Peterson, Soberón, & Sánchez-Cordero, 1999), the degree to which patterns of niche conservatism extend to fundamental niche space remains unclear. For example, recent simulation studies using virtual species have demonstrated that incompletely characterized fundamental niches tend to inflate estimated rates of niche evolution (Saupe et al., 2017). Empirical investigation of the effect of climatic disequilibrium on niche conservatism requires a group of species with a finely resolved phylogeny and abundant information about the fundamental niche.

Although there are many taxonomic groups that could be used to compare native and naturalized niche conditions, the genus *Pinus* offers several advantages for such work. First, there are detailed and abundant data about where pine species are native and introduced. At least 25 species have become naturalized outside their native ranges, often in the Southern Hemisphere, where they have become invasive pests (notably in South Africa, Australia and New Zealand; Richardson & Higgins, 1998). Commercial forestry in the 19th and 20th centuries is largely responsible for these introductions, although the earliest estimates of human-mediated pine introductions range as far back as 6,000 BP (Barbéro, Loisel, Quézel, Richardson, & Romane, 1998). There is consequently a large and varied literature on the drivers of *Pinus* introduction and naturalization (Franzese & Raffaele, 2017; Nuñez & Medley, 2011; Richardson & Rejmánek, 2004), and the genus has even been proposed as a model system for studying invasion ecology (Richardson, 2006). Second, the variation in range size among pine species spans several orders of magnitude, from *Pinus squamata*, known from only a single locality, to *Pinus sylvestris*, with a native range that covers most of the Palaearctic (Farjon & Filer, 2013). Most studies thus far that compare native and naturalized niches have focused on a particular region or regions, often using an assemblage that is widely dispersed taxonomically (Early & Sax, 2014; Petitpierre et al., 2012). In contrast, pines allow study of a single genus at a global scale while still encompassing a wide range of distributional traits, niche traits and ecologies. Third, as the most economically important tree genus in the world (Richardson & Rundel, 1998), the historical native ranges of most pine species have been exceptionally well characterized (Farjon & Filer, 2013). This allows for the native climatic conditions of pines to be estimated with more confidence than for many other groups. Finally, a recently published time-calibrated phylogeny for the entire genus (Saladin et al., 2017) allows for investigation of niche relationships and conservatism.

Here, we use *Pinus* as a model system to investigate climatic disequilibrium and how it changes niche-based inference across a complete taxon. We do so by comparing the climate occupied by naturalized populations of 25 pine species with that occupied by native populations of the same species. We use naturalized (i.e., self-sustaining) populations, as opposed to those that are merely adventive, in order to focus on those conditions where it is clear that an introduced population can thrive. We ask whether climatic disequilibrium is random across species or structured by distributional or niche characteristics. We also examine the consequences of disequilibrium for regional and continental range filling estimates, and the implications for niche conservatism of sister species pairs. Finally, we explore the implications of this work for conservation of species in the face of climate change.

2 | METHODS

2.1 | Occurrence data

We acquired data on the native distribution of 109 pine species from the Conifer Database (Farjon, 2017). This carefully curated data set is built from taxonomically verified herbarium specimens, with special care taken to sample the entire distribution of each species and control for spatial sampling bias; full criteria for inclusion in the database are described by Farjon and Filer (2013). We processed these data by removing occurrences with erroneous geographical coordinates and removed three species that had either too few occurrences or too restricted a distribution to be tractable for niche modelling (*P. squamata*, *Pinus amamiana* and *Pinus maximartinezii*). To reduce the likelihood of erroneously including non-native occurrences within the native range of our focal species, we removed occurrences that fell outside a 100-km buffer around each species' native range, as defined by expert range maps. These maps were downloaded from the United States Geological Survey digitized database of North American tree species (Fryer, 2018), digitized from Critchfield and Little (1966) or supplied by Nobis, Traiser, and Roth-Nebelsick (2012). Although these range maps are derived from sources of uncertain precision, they represent decades of work by researchers at the U.S. Forest Service to finely characterize the native ranges of these species, and thus are the most complete area-based range estimates for this group. In total, our analyses include 106 species (Supporting Information Appendix S1).

Data on the naturalized occurrences of pines were collected from herbarium specimens and accounts in the literature. We began herbarium searches with the species and regions identified in the global database of invasive trees and shrubs (Rejmánek & Richardson, 2013). We searched 18 herbaria and herbarium consortia with extensive digitized pine collections and requested photographed specimens from an additional 35 herbaria (Supporting Information Appendix S2). A record was included in our database only if there was clear evidence that the specimen came from a naturalized (i.e., self-sustaining) population and if it had associated geographical coordinates (see expanded descriptions of our criteria and examples in Supporting Information Appendix S2). Finally, we performed literature searches for publications that contained references to naturalized pine populations (Supporting Information Appendix S3; Web of Science keywords: pinus *sp*; naturaliz*; invas*; exotic; alien; adventive). All records were georeferenced and localities verified in Google Earth. The complete database contains 597 naturalized occurrence records for 25 species distributed across 23 countries and five continents.

2.2 | Niche modelling

The selection of appropriate climatic variables for niche modelling or species distribution modelling is of crucial importance (Peterson et al., 2011). Recent work by Petitpierre, Broennimann, Kueffer, Daehler, and Guisan (2017) suggests that climatic variables with known ecological effects can predict plant distributions more accurately than variables selected using a model-based approach. For this reason, we selected seven climate variables indicated to be important or deterministic for pine growth and success of establishment. Owing to the long history of *Pinus* cultivation, there is a large body of literature specific to pine silviculture on which to draw (e.g., Booth et al., 1984; Poynton et al., 1977). Our final models include mean annual temperature (MAT), maximum temperature of the warmest week (MaxTemp), minimum temperature of the coldest week (MinTemp), annual precipitation (AnnPrecip), precipitation seasonality (PrecipSeas), non-summer precipitation (WinPrecip) and estimated actual evapotranspiration (AET). The first six variables are 30-year averages (1961–1990) derived from BioClim 1.2 variables downloaded from the CliMond database in June 2017 (Kriticos et al., 2012). Estimated actual evapotranspiration is supplied by the MODIS Global Evapotranspiration Project (MOD16; Mu, Zhao, & Running, 2011). All climate data were resampled to 10 arc-min resolution to match the BioClim data resolution with the lowest global error rates. We also repeated all analyses with a set of eight climate variables selected by a principal components (PCs)-based variable selection model (*sensu* Petitpierre et al., 2017), although results were not qualitatively different and are not presented here.

Choosing an ordination technique and method for characterizing niche space that suits the question is also of crucial importance. Given that we were interested in direct interspecies comparisons, all niche models needed to be built in an equivalent space (Broennimann et al., 2012). Given the global distribution of native and naturalized pines, we built all niche models in the global climate space. Following the recommendations of Broennimann et al. (2012) and Petitpierre et al. (2017), we calibrated a principal components analysis (PCA) on this global background and used the first two PC axes (containing 84.39% of the variation) as a common climate space. Given that many pines are native to the Northern Hemisphere but naturalized in the Southern Hemisphere, we also plotted the climate of each hemisphere to assess the potential for systematic differences that could influence interpretation of our niche models (Qiao, Escobar, & Peterson, 2017).

We initially built these niche models following the kernel smoothing ("KS") approach of Broennimann et al. (2012) but had concerns about potential error resulting from sampling biases and uneven sampling intensities in the native and naturalized distributions. In addition, niche models built using the KS approach are influenced by a smoothing parameter, *h*, estimated as a function of the number and mean dispersion of occurrences in climate space. Inspection of KS niche models showed niche extension into unoccupied climate space caused by systematic differences in the number and dispersion of native and naturalized occurrences. For these reasons, we used minimum convex polygons (MCPs) to characterize niche space in all the analyses presented here, for 106 native distributions and 25 combined native–naturalized distributions. Combining native and naturalized data allowed us to build a minimum estimate of the fundamental niche space outside the native realized niche (Broennimann & Guisan, 2008; Early & Sax, 2014).

2.3 | Analyses

To characterize climatic disequilibrium, we calculated the amount of climate space occupied by both native and naturalized occurrences (i.e., the extended niche, hereafter N_E), in addition to the climate space occupied by only native occurrences (i.e., the native realized niche, hereafter N_R). The difference between the extended and realized niche, ΔN, can be interpreted as the amount of suitable climate space exposed by naturalized occurrences:

$$\Delta N = N_E - N_R$$

Where N_R is a subset of N_E, which is in turn a subset of the fundamental niche, N_F:

$$N_F \supseteq N_E \supseteq N_R$$

In order to control for the anisotropy and scale dependence of climate space (Soberón & Peterson, 2011), we calculated the fraction of ΔN that is available on the native continent of each species, and the fraction of ΔN that occurs within 300 km of each species' native range (see Supporting Information Figure S4.1 for conceptual diagram). All niche spaces (N_E, N_R and ΔN) are expressed relative to the size of the global climate space (i.e., N_R of .10 indicates that the species' native realized niche encompasses 10% of the global climate space). We also calculated the vector between the geometric centroids of N_R and N_E. We emphasize that we do not consider ΔN or a large vector difference evidence of niche evolution or change per se (Petitpierre et al., 2012), but rather as evidence of fundamental niche space unoccupied by the native realized niche (Early & Sax, 2014).

Capturing all possible predictors of climatic disequilibrium in a single analysis would be difficult or impossible. Given that we were interested specifically in niche-based or distributional traits, we focused on the following variables: (a) N_R, the size of the native niche MCP in PCA climate space; (b) native range size, for which range maps were resampled to match climate data resolution, and range size was calculated as the number of occupied grid cells, $\log_{10}$-transformed for analyses; (c) native niche position, the position of the niche centroid on both PC axes; (d) native range centre latitude, the latitude of the geometric centroid of the native range; and (e) niche marginality, the climate distance from the centre of all occurrences across the genus to the centre of each species' native niche. We used a random forest regression approach to rank predictor variable importance based on the mean decrease in model accuracy across 10,000 regression trees (Genuer, Poggi, & Tuleau-malot, 2010). Random forests iteratively grow binary regression trees using bootstrapped observation samples and a random subset of predictor variables at each node (Breiman, 2001).

To assess the consequence of climatic disequilibrium on range filling estimates, we followed the procedures of Svenning and Skov (2004) and calculated range filling as the number of occupied geographical 10′ grid cells divided by the number of modelled climatically suitable grid cells. The climatically suitable area was defined as all cells that fall in climate space within the MCP niche of each species. We rasterized detailed native range maps to match the 10′ resolution of our climate data and used them to characterize the occupied area. We calculated range filling for each species using native data and combined native–naturalized data, both on the continental scale and restricted to the United Nations Food & Agriculture Organization (FAO) ecofloristic regions occupied by the species' native distribution (FAO, 2000). Given that incorporation of naturalized data can only increase the number of climatically suitable grid cells, range filling estimates made using naturalized data in addition to native data are always equal to or lower than estimates made using only native data. We calculated this difference as the proportional change in range filling when naturalized data were incorporated into the niche model.

Most methods for comparing traits across a phylogeny depend on estimation of ancestral trait values at past nodes, as in phylogenetic independent contrasts (Felsenstein, 1985). However, because a species' climatic niche is a manifestation of the interactions between traits and the environment, reconstruction of ancestral niches is difficult and beyond the scope of the present study. In addition, recent work has shown that rates of niche evolution tend to be overestimated when models depend on incompletely characterized fundamental niches (Saupe et al., 2017). For this reason, we focused phylogenetic analyses on sister species pairs (Anacker & Strauss, 2014; Peterson et al., 1999). Exploratory analyses were sensitive to differences in tree tip topology; because of this, we limited our analysis to consensus sister pairs across four phylogenies published by Saladin et al. (2017). We found 21 consensus sister species pairs in the genus, eight of which have exotic data for at least one of the species (Supporting Information Table S4.1). For those pairs, we calculated niche similarity metrics both with and without incorporation of naturalized occurrence data. There are numerous techniques for assessing niche similarity (Broennimann et al., 2012; Warren, Glor, & Turelli, 2008). Given that it remains unclear which niche similarity metric is best, we calculated the following: (a) niche centre distance, the distance in PC climate space between the geometric centroids of each niche; (b) niche overlap, the ratio of shared to total occupied climate space; and (c) niche nestedness, the proportion of the smaller species' niche that is contained within the larger niche. We compared similarity values among non-sister pairs, sister pairs with native data and sister pairs with naturalized data using Mann–Whitney *U*-tests to assess the hypothesis that the realized niche of one sister predicts the fundamental niche of the other. Given that the specific tip topology within several important *Pinus* subsections is poorly resolved (e.g., Ponderosae, Australes and Strobus sub. Strobus; Parks, Cronn, & Liston, 2012; Saladin et al., 2017), we tested for phylogenetic structure in disequilibrium among the well-supported genus subsections themselves (Parks et al., 2012; Supporting Information Figure S4.2). We used an ANOVA approach to test whether variation in ΔN was greater between subsections than within subsections. All analyses were performed in R v.3.2.4 (R Core Team, 2016).

3 | RESULTS

Among the 25 species that have naturalized outside the native range, 23 did so in climates outside the native realized niche (Figure 1; Supporting Information Appendix S1). Among those 23 species, the median ΔN was .018. The maximum increase observed, for *Pinus radiata*, was .095 (i.e., the climate space exposed by naturalized occurrences encompasses almost 10% of the global climate space; Figure 1; Supporting Information Table S4.2). The two species that showed no niche difference, *Pinus resinosa* and *Pinus thunbergii*, had only two naturalized occurrences each.

Variation in disequilibrium was non-random across our 25 species, such that ΔN was strongly related to native realized niche size, N_R (Figure 2). Generally speaking, ΔN tended to be higher and more variable among species with small native niches, and lower among those with large native niches. The proportion of ΔN that was available on species' native continent was also significantly and negatively related to N_R ($p < .01$, $R^2 = .46$; Figure 2b). This relationship was weaker (but still negative) and non-significant when the available area was pruned to within 300 km of species' native ranges ($p = .125$; Figure 2c). When compared with a null geometric expectation generated by randomizing naturalized occurrences, the observed relationship between ΔN and N_R is significantly steeper than the null model ($p = .003$; for details, see Supporting Information Figure S4.3). The randomization procedure also demonstrated that species tend to naturalize closer to the native niche than expected by chance ($p << .001$; Supporting Information Figure S4.4). The random forest model examining the potential explanatory power of range and niche characteristics did not produce significant results.

Variation in the direction of niche extension was also non-random (Figure 3). The largest shifts all occurred in a direction associated in PC climate space with lower precipitation seasonality, higher annual precipitation and cooler temperatures (Figure 3c). This climate direction was not representative of climatic differences between the Northern and Southern Hemispheres; southern climates were largely contained within the range of northern climates and displaced such that the median climate of the Southern Hemisphere was warmer and wetter than the median climate of the Northern Hemisphere (Supporting Information Figure S4.5).

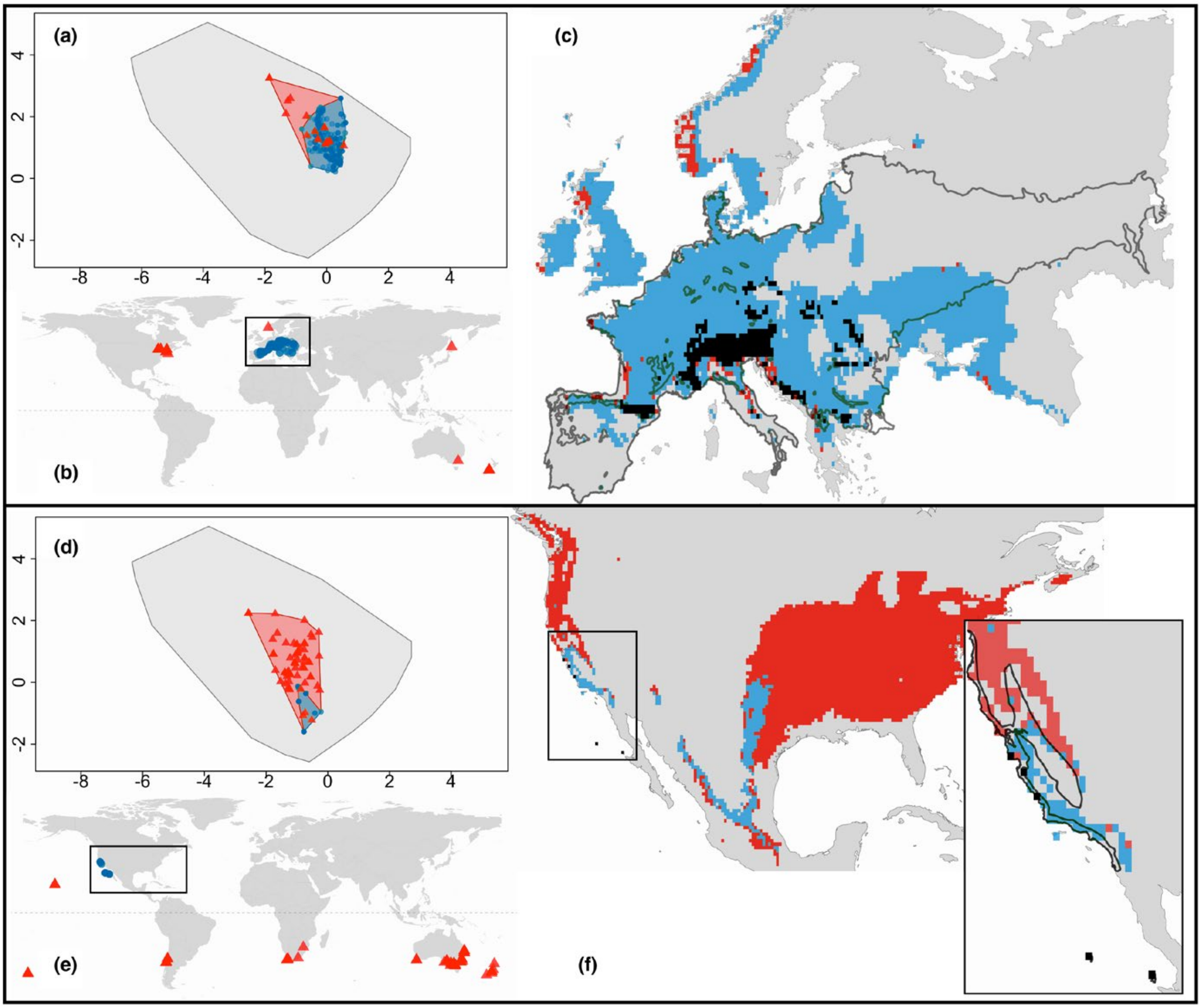

FIGURE 1 Niche models and geographical distributions for two exemplar species: *Pinus mugo* (a–c) and *Pinus radiata* (d–f). (a, d) Occurrences in climatic niche space [points and polygons correspond to native (blue) and exotic (red) occurrences, whereas the grey polygon shows the 'genus niche', the furthest extent of any species' occurrences]. Niche models are calibrated on a common principal component-transformed global climate background. (b, e) The same occurrences in the native range (blue circles) and naturalized range (red triangles). (c, f) The native distribution (black), and geographical projections of climate niche space based solely on native occurrences (blue) and based on both native and exotic occurrences (red). The dark grey line bounds the native FAO ecofloristic region (main map, panel c; inset, panel f)

The amount of range filling we found for each species was dependent on the scale of the calculation; median filling among all species in native continents and ecoregions was 16.75 and 30.62%, respectively. Adding naturalized data uniformly reduced range filling estimates, with a median percentage decrease of 13.71% on native continents and 2.89% in native ecoregions. Small-niched species showed substantial variation in their observed change in range filling (Figure 4a), such that the relationship between N_R and range filling change mirrored the relationship between N_R and ΔN. Indeed, the size of the effect that naturalized data had on range filling estimates was dependent on ΔN ($p << .001$, $R^2 = .464$). However, there was also a significant relationship between range filling change and native range size ($p << .001$, $R^2 = .55$; Figure 4b), such that the species that showed the largest range filling change had both small native niches and small geographical ranges. The relationship between N_R and range filling change also yielded a steeper relationship than expected when compared with a null geometric distribution ($p << .001$; for details, see Supporting Information Figure S4.6).

The three niche similarity metrics we used to evaluate phylogenetic niche relationships (niche centre distance, overlap and nestedness) were all significantly more similar among sister species pairs than among non-sister pairs (Figure 5; niche centre distance, $p = .006$; overlap, $p = .002$; nestedness, $p = .013$). Among the eight

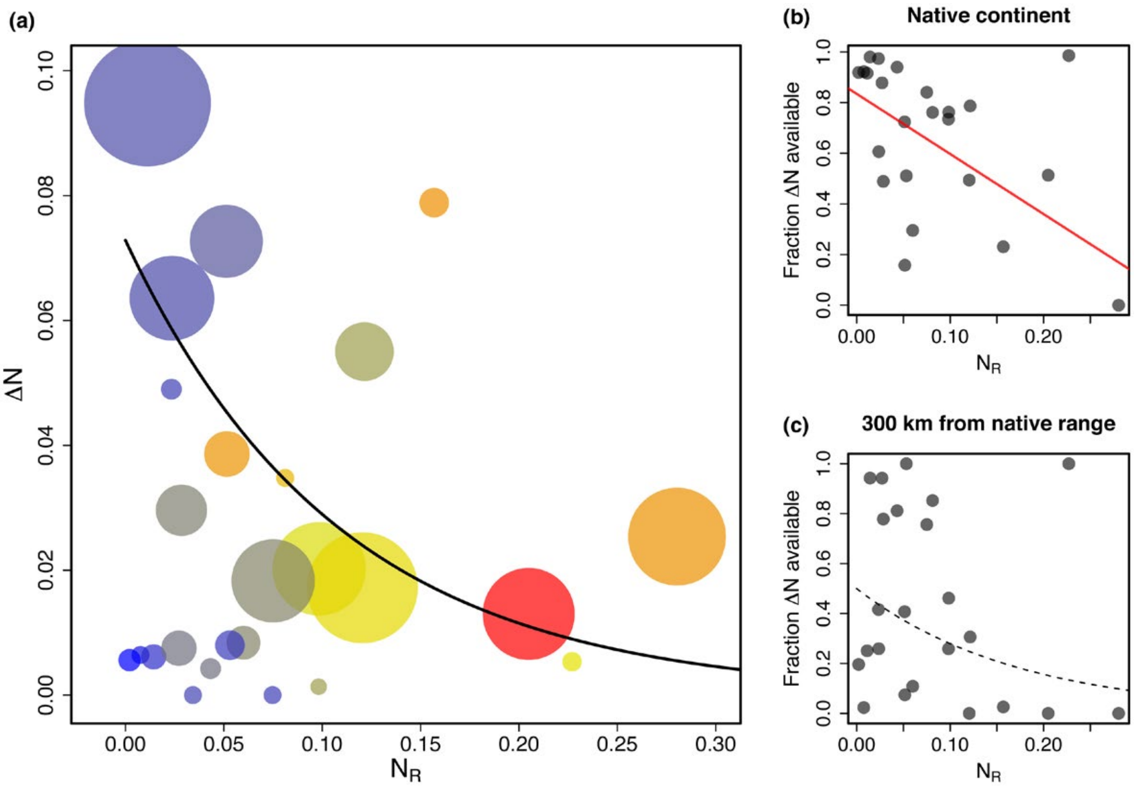

FIGURE 2 Relationships between Δ*N* (change in niche size after incorporating naturalized occurrences) and N_R (native niche size). For each species, Δ*N* is defined as the difference between the extended niche (N_E) and the native realized niche (N_R). (a) The relationship is fitted as an exponential decay function, weighted by the number of naturalized occurrences for each species ($a = .073$; $b = -9.222$; $p < .05$). Symbol size is proportional to the number of naturalized occurrences for each species, ranging from two to 77; symbol colour shows the number of native occurrences (from blue, few occurrences, to red, many occurrences). (b) Relationship between N_R and the fraction of Δ*N* that occurs on each species' native continent ($p = .0002$, $R^2 = .4613$). (c) Relationship between N_R and the fraction of Δ*N* that occurs within 300 km of each species' native range. The fitted line is an exponential decay function weighted by the number of naturalized occurrences ($a = .500$, $p = .0006$; $b = -5.814$, $p = .125$)

sister species pairs for which at least one member had naturalized occurrences, we found no significant differences in the means calculated with or without naturalized data for niche centre distance, overlap and nestedness (Figure 5). Furthermore, individual sister species pairs showed no consistent directional shift in similarity (Figure 5). None of the similarity metrics was correlated with the age of the sister pairs, for either native or native–naturalized data sets (all $p > .40$). Additionally, our ANOVA found no significant evidence that Δ*N* differed between genus subsections ($p = .55$), and genus subsections did not separate by Δ*N* or N_R (Supporting Information Figure S4.7).

4 | DISCUSSION

We found that climatic disequilibrium among pines is nearly ubiquitous and is structured in a highly non-random manner, such that species with small native realized niches are more likely to have ranges in pronounced disequilibrium with their climatic tolerances than larger-niched species. Our results are consistent with several recent studies that have found evidence of climatic disequilibrium using naturalized plant distributions (Bosci et al., 2016; Early & Sax, 2014; Gallagher et al., 2010). Our results differ from some previous studies, however, in that we found climatic disequilibrium to be nearly ubiquitous among the species we studied. Only two of our 25 naturalized species showed no evidence of disequilibrium, and these two species each had only two naturalized occurrences. Consequently, every species with three or more naturalized occurrences showed some degree of disequilibrium.

We suspect that our analysis focusing on pines provides a better test of the potential frequency and magnitude of climatic disequilibrium than most other groups or studies for several reasons. First, most other taxa are not as widely introduced outside their native range as pines (Richardson, 2006). Second, as the most economically important tree genus globally (Richardson & Rundel, 1998), the native and naturalized ranges of pines are unusually well documented. Finally, existing studies of this topic have not considered all naturalized occurrences globally, but instead focused on those within a limited and predefined region (e.g., Early & Sax, 2014; Petitpierre et al., 2012). This leads us to conclude that

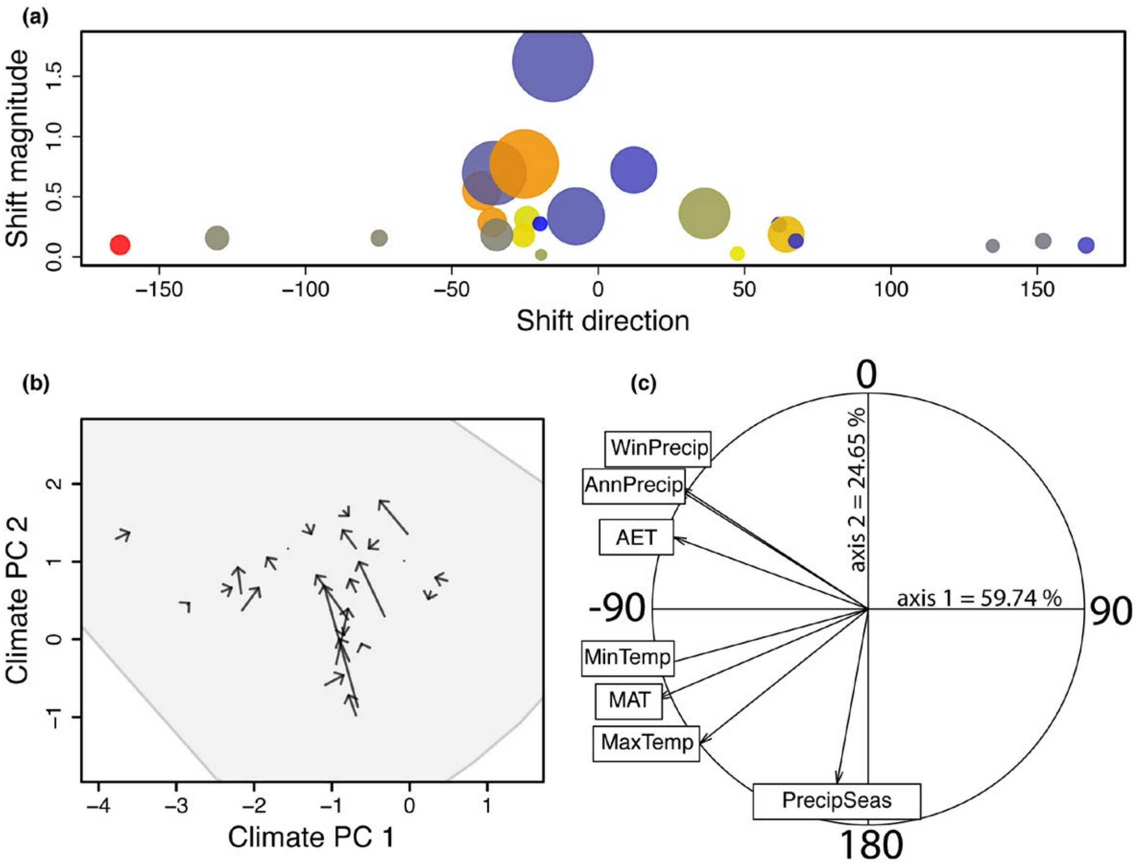

FIGURE 3 (a) Relationship between the direction and magnitude of the shift between native and native–naturalized niche centroids shows the magnitude of the shift [in units of principal component (PC) distance] related to the angular direction of the shift (c). Size of points is proportional to Δ*N*. Colour indicates number of native occurrence points and relates species to Figure 2. (b) The same shifts in climate space relative to the genus niche. (c) Loadings of climate variables on the principal components analysis background. Variables included are mean annual temperature (MAT), maximum temperature of the warmest week (MaxTemp), minimum temperature of the coldest week (MinTemp), annual precipitation (AnnPrecip), precipitation seasonality (PrecipSeas), non-summer precipitation (WinPrecip) and estimated actual evapotranspiration (AET)

climatic disequilibrium might be much more common than recognized by recent work.

Our findings also indicate that the magnitude of this disequilibrium can be estimated by native niche size. This is consistent with the results of Early and Sax (2014), who showed that native–naturalized niche expansion was negatively correlated with native niche breadth among 51 European plant species that had naturalized in the USA. Early and Sax (2014) also provided context for the findings of Petitpierre et al. (2012), who showed that large-ranged (and presumably large-niched) species showed relatively little niche expansion during intercontinental invasions. Collectively, this body of work suggests that predictions of biological invasions or species' responses to climate change that hinge on native climatic conditions might perform poorly for small-niched species even while performing well for large-niched species. For small-niched species, the level of climatic disequilibrium that we observed can be profound. In the extreme case of *P. radiata*, the size difference between N_R and Δ*N* approaches an order of magnitude, suggesting that model projections based solely on the native range are likely to be wildly misleading. Indeed, *P. radiata* is the most successful and widespread softwood forestry species in the world (Booth & McMurtrie, 1988; Richardson, 2006), while curiously also being at risk within its small native range. Although the magnitude of error is generally much lower for large-niched species, similar projections could still be misleading. Among the five species with the largest native climate niches (*Pinus contorta*, *Pinus oocarpa*, *P. sylvestris*, *Pinus ponderosa* and *Pinus patula*) we still find a mean Δ*N* equivalent to 3.55% of the global climate space.

Given that our analyses compare niches of vastly different sizes within a finite domain, we should expect to find a negative relationship between N_R and Δ*N*. We expect this relationship because random points in this domain are more likely to fall outside a small niche than a large niche. This negative relationship is indeed what we observe; however, our results depart from this null expectation in that the relationship we find between N_R and Δ*N* is significantly steeper than the random case (Supporting Information Figure S4.3). Additionally, when we consider whether species occur in close proximity to the climates encompassed by Δ*N*, we find that the small-niched species that are most likely to be in pronounced climatic disequilibrium are also those that are most likely to have unoccupied suitable climate space close to their native ranges. This provides

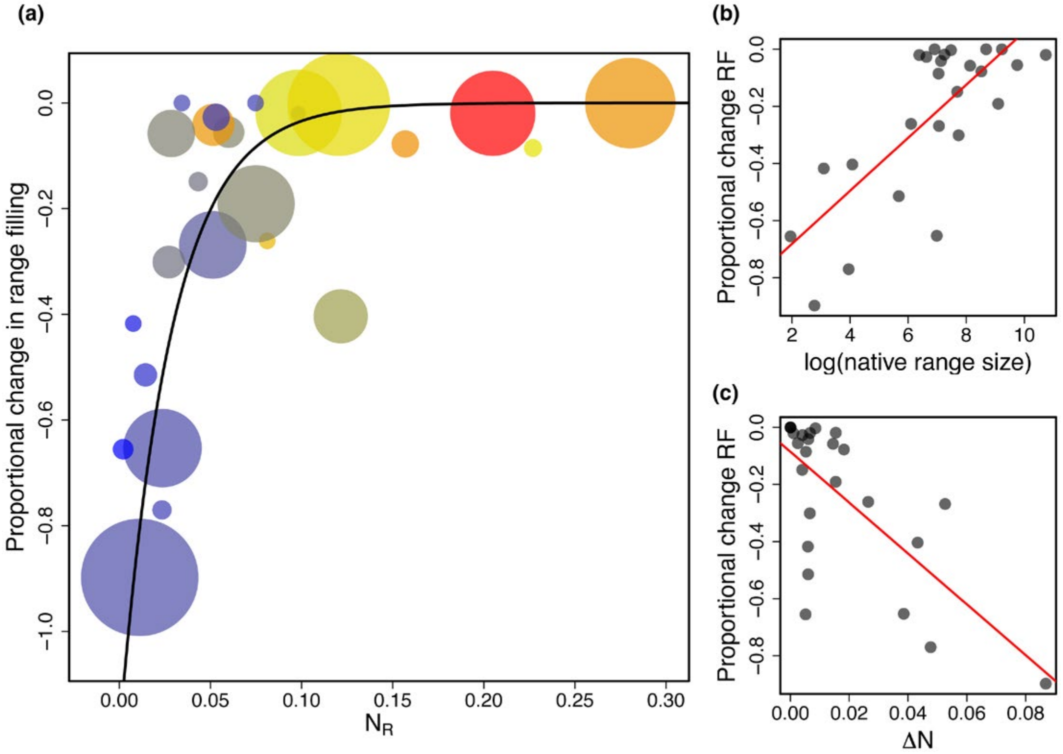

FIGURE 4 Relationship of the proportional change in range filling (RF) to N_R, native range size and ΔN. 'Proportional change in range filling' is calculated as the proportional change between range filling estimates using only native range data and those incorporating naturalized data. (a) Relationship between proportional change in range filling and N_R, fitted as a negative exponential function weighted by the number of naturalized occurrences per species ($a = -1.195$; $b = -35.559$; $p << .001$). Symbol size is proportional to the number of naturalized occurrences for each species, ranging from two to 77; symbol colour shows the number of native occurrences (from blue, few occurrences, to red, many occurrences). (b) Relationship between proportional change in range filling and native range size ($p << .001$, $R^2 = .547$). (c) Relationship between proportional change in range filling and ΔN ($p << .001$, $R^2 = .464$)

strong evidence to suggest that small-niched species are limited by non-climatic factors in their native ranges. Indeed, given the ubiquity of the disequilibrium that we observed, it raises the possibility that few, if any, species are limited entirely by climate.

Our results also provide insight into which edges of a pine species' realized niche are least likely to be determined by climate alone. We found the direction of niche extensions to be conserved across species toward cooler, wetter and less seasonal climates. Given that 19 of the 25 naturalized pine species we focused on are native in the Northern Hemisphere and naturalized in the Southern Hemisphere, it is worth considering whether general hemispheric differences in climate drove this result. This seems unlikely, however, because the global climate space we constructed does not separate by hemisphere, and the landmasses typically invaded by pine species (e.g., New Zealand, Australia) contain conditions both warmer and drier than many species' native ranges. Niche expansion into cooler and wetter conditions indicates that these portions of the fundamental niche are often unoccupied in the native range, especially for small-niched species. This is in direct contrast to studies that use mechanistic physiological models to explore species' climatic tolerances, and which generally find unoccupied niche space to be warmer and wetter than the native range (Araújo et al., 2013; Sunday et al., 2012). This is also in contrast to the findings of Booth et al. (1988), who used data from forestry trials to show that eucalypt species generally thrive outside of the native range in warmer and drier climates (although one species in their analysis, *Eucalyptus citriodora*, was successfully grown in cooler climates, and another, *Eucalyptus cladocalyx*, was successfully grown in wetter climates). Also, although forestry trials are a valuable source of information about the climates in which tree species can grow in the absence of certain biotic interactions, they generally do not provide information about the reproductive success of species (Booth, 2017). In contrast, our work explicitly examines conditions where a species can not only grow and survive, but also reproduce sufficiently well to sustain a population in the presence of both biotic interactions and other non-climatic factors. Although many pine species are long lived, and individuals may be able to survive without reproducing after significant climatic shifts, reproduction is critical to long-term population persistence (Booth, 2017; Sax et al., 2013). Indeed, examining reproductive populations is a crucial aspect of our work that allows us to characterize portions of the fundamental niche confidently. Given the limited number of studies that have investigated this issue and the disparate approaches and taxa used, it is difficult to know whether a general trend will emerge regarding patterns of

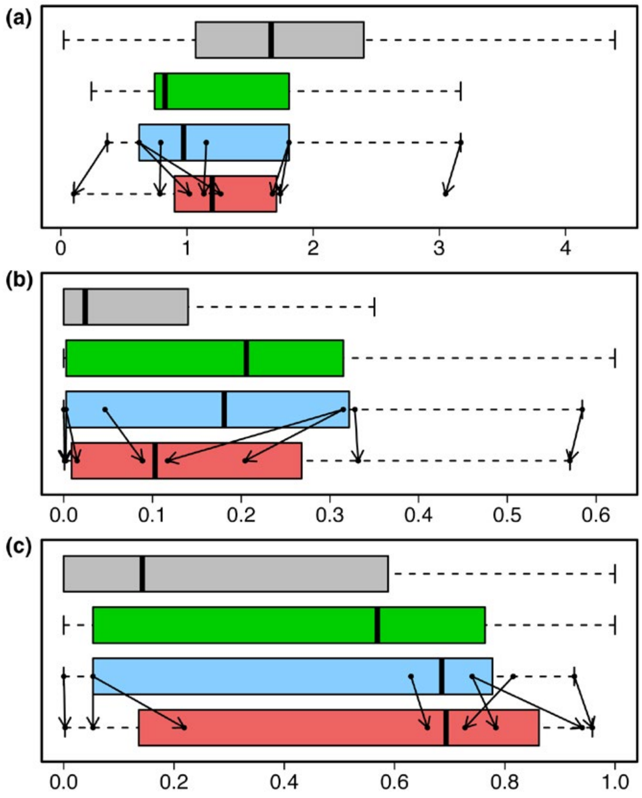

FIGURE 5 Niche similarity of sister species comparisons. In order from top to bottom, grey bars are pairwise comparisons of all non-sister species (106 species; 5,493 pairs), green bars are sister species pairs using native data only (21 pairs), blue bars are also calculated solely with native data but represent those pairs that have at least one member naturalized (eight pairs), and red bars are sister species comparisons that incorporate naturalized data (eight pairs). Arrows indicate where a sister pair comparison moved when naturalized data were incorporated. (a) Centre distance, the distance in climate space between two niche centroids. (b) Niche overlap, the ratio of shared to total occupied climate space. (c) Niche nestedness, the proportion of the smaller niche that is contained within the larger niche

unoccupied niche space. It is possible that non-climatic factors (e.g., biotic interactions or dispersal limitations) constrain species' niches in idiosyncratic ways. It is also possible that different data sources and analytical approaches will uncover different portions of the fundamental niche.

Range filling estimates have had a strong and sobering impact on the niche modelling field over the past 15 years. By showing how infrequently species fill all of the climatically suitable space within their native region or continent (Bradley et al., 2015; Svenning & Skov, 2004), these studies bring into question the applied utility of purely correlative species distribution models. Here, we show that the degree of range filling is even less extensive than previously thought for many species, particularly those with small native niches. Indeed, naturalized climate conditions show that native range data can overestimate range filling by up to 89.78% on the continental scale (e.g., *P. radiata*) and 56.11% on the ecoregional scale (e.g., *Pinus clausa*; Supporting Information Table S4.2). In contrast to these extreme examples, in some cases we found that ΔN was not associated with a substantial change in range filling estimates. This occurred when novel climate space occupied in the naturalized range did not occur on the native continent or in the native ecoregion (e.g., *Pinus taeda* is naturalized in southern Brazil, Argentina and eastern Australia but experiences conditions there that are not found on its native continent of North America; see Supporting Information Appendix S1 and Table S4.2). Such findings were more likely for large-niched species, which tended to have a smaller fraction of the climates contained in ΔN available within the native continent and ecoregion. Consequently, although N_R and ΔN are important predictors of the accuracy of range filling estimates, they are not in themselves sufficient to describe these relationships fully. The size of a species' native range provides additional information in this respect, such that small-niched species that also have small native ranges are those for which range filling estimates are least accurate.

Phylogenetic niche conservatism, the tendency for closely related species to have more similar niches than expected given their relatedness, could be leveraged to investigate the structure of fundamental niche space and climatic disequilibrium further (Losos, 2008; Wiens et al., 2010). There is some evidence to suggest that realized niche similarity underestimates fundamental niche similarity (Araújo et al., 2013; Sunday et al., 2012). Our findings, however, were not consistent with this supposition, because we found no evidence to support the conjecture that considering fundamental niche space increases the similarity of sister species. Of course, because we had only eight sister pairs with at least one naturalized species, our statistical power here is low. It is possible that another taxonomic group, if analysed in the same way, would show different results. *Pinus* is an unusually old genus, with splits among sister species that range in age from 1.4 (*Pinus hartwegii* and *Pinus pseudostrobus*) to 16.8 Myr (*Pinus halepensis* and *Pinus brutia*), among the consensus pairs we assessed (Saladin et al., 2017). It is possible that a younger genus with more recent splits would be more sensitive to the inclusion of naturalized data. Ideally, future work could investigate these relationships using different taxa with both a larger number of sister pairs and younger divergence ages.

Our approach of using naturalized occurrences to identify suitable climate space outside the native realized niche necessarily produces a minimum estimate of the fundamental niche. This is primarily a result of selective and unequal attempts at introduction; no species has been introduced with equal pressure in all possible climates. This is compounded by incomplete sampling and specimen collection across species' exotic ranges. Additionally, non-climatic factors that constrain species' realized niches in the native region (e.g., competition, soil, facilitation) may also be limiting in the introduced region, to an unknown degree. Although these are unavoidable limitations of our approach, they also mean that our methodology is especially conservative with respect to niche differences. Given that we are working with minimum estimates, we are unlikely to overestimate the frequency, magnitude or effects of climatic disequilibrium. This is in contrast to other approaches that estimate fundamental niche space from measurements of physiological limits along a single niche axis, which may overestimate the fundamental niche by failing to account for combinations of extreme conditions (Maguire, 1973). Additionally, it is possible that the coarse resolution of our climate data masks fine-scale variation and misrepresents some of the climate space occupied by populations in topoclimatically complex areas. However, this effect is unlikely to be systematic enough to produce the patterns that we observed in the magnitude, frequency and directionality of climatic disequilibrium. A final factor that could influence the interpretation of our results is the potential for rapid adaptive evolution to novel climate conditions in introduced populations, such that the native niche and the naturalized niche represent two different sets of climatic tolerances. However, because the Pinaceae are known for pronounced evolutionary conservatism and slow mutation rates (Prager et al., 1976), such concerns seem less relevant for this group. Additionally, because pines have long generation times and most intercontinental introductions have taken place within the past 200 years (Richardson & Higgins, 1998), it seems unlikely that such rapid evolution has occurred at sufficient levels to impact our results strongly. Nevertheless, we cannot completely rule out this possibility, and some fraction of the observed niche difference could be attributable to evolutionary changes (Sax et al., 2007).

Our results lead us to conclude that analyses focused solely on conditions experienced in a species' native range and region may be misleading, especially for conservation applications. This is particularly true for species with small native climatic niches and small native ranges, which we also expect to be at elevated risk from climate change and habitat loss. For these species, refining our understanding of climatic disequilibrium and its consequences for range filling estimates and niche conservatism is especially important. Our findings suggest that standard niche and species distribution modelling techniques that do not account for climatic disequilibrium are inadequate for studying small-niched species. Our findings also suggest that modelling applications that require fine-level climatic tolerances will misrepresent even large-niched species when considering native conditions alone, because these species also show some degree of climate disequilibrium. With respect to pines, our results suggest a capacity to thrive in cooler, wetter and less seasonal conditions than those known from the realized distribution alone. Unfortunately, this particular bit of fundamental niche space will not protect these species from future climatic changes, which are generally expected to produce warmer and more seasonal conditions. This implies that species currently restricted to environments where dispersal cannot occur (e.g., alpine or island endemic species) are at risk of extinction. This conclusion is consistent with Sax et al. (2013), who suggest that the relative size and placement of niche components is critical for informing current and future conservation action. Ultimately, our findings emphasize that there are large gaps in our understanding of where, when and how species occupy their fundamental niche space. To help fill this gap, we hope that future work capitalizes on the data contained in global herbarium collections and the insights afforded by species introductions and global forestry trials; doing so should lead to a better understanding of these phenomena and improve our ability to assess conservation risks accurately.

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DATA ACCESSIBILITY

The data in this paper were collected from freely available sources. Occurrence and climate data used in the analyses are available in a Data Dryad repository: https://doi.org/10.5061/dryad.1hr1n52

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BIOSKETCHES

Daniel Perret's work is motivated by the challenge of applying biogeographical insight to conservation problems. His research focuses on detangling patterns among climatic niches and geographical ranges of tree species globally.

Andrew Leslie is broadly interested in the evolution of plant reproductive morphology, using conifers as a primary study group. His work integrates phylogenetic analyses, functional morphology and data from the fossil record in order to understand the drivers of morphological diversification over million-year time-scales.

Dov Sax is a biogeographer interested broadly in conservation, with a special emphasis on understanding and preventing species extinctions. Most of his work is motivated by species invasions or climate change.

SUPPORTING INFORMATION

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

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