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Niche syndromes reveal climate-driven extinction threat to island endemic conifers

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Anthropogenic climate change is predicted to cause many extinctions worldwide[1]. Although species endemic to islands or archipelagos have high conservation value and are vulnerable to human impacts[2,3], there has been no global analysis of climate-driven extinction risk focused on island endemics. Here, we use conifers as a model system to assess extinction risk among island endemics under climate projections for 2070. We employ the emerging technique of combining native and non-native occurrence data to model climatic conditions under which each species can sustain a population[4–7] and also incorporate horticultural data to model the broader range of conditions that allow short-term survival. Our projections indicate that some species will retain suitable climatic conditions, some will experience conditions completely precluding survival and others will experience intermediate-risk conditions that lead to population decline and eventual extinction. Based on different climate change models, we report island size thresholds of 400 to 20,000 km², below which extinction risks increase. These patterns are driven by correlations among island area and the breadth of species' realized, fundamental and tolerance niches. Notably, realized and fundamental niche breadth are positively correlated. Our results highlight management interventions needed to protect species from climate-driven extinction across islands of different sizes.

The severity of climate-driven extinction risk is uncertain for island endemics. They have limited ranges and dispersal opportunities, which could confer high risk, particularly on small islands[8]. Indeed, some island endemics appear seriously threatened (see, for example, Ferreira et al.[9]) and if future conditions fall beyond those currently present on a given island, the extinction threat could intensify[10]. However, early species distribution modelling research demonstrated the importance of investigating species' ability to thrive in conditions beyond those reflected by their native distributions (reviewed by Booth[11]). Later studies confirm that habitability of conditions outside those experienced in the native range, termed niche disequilibrium, is widespread[6,11–14], indicating that species may be more resilient to climate change than their native ranges suggest. Intriguingly, a global analysis of herpetofauna showed that island endemics exhibit especially strong disequilibrium[15], which may have helped them persist through Pleistocene climate swings. Additionally, recent work suggests species inhabiting narrow climatic conditions in their native ranges exhibit the greatest niche disequilibrium[7,16], which could lessen risk for small-island endemics, since small-ranged species have narrow niches[17]. However, it is unclear whether island endemics exhibit sufficient niche disequilibrium to withstand predicted warming.

Given the evidence for climatic niche disequilibrium, Sax et al.[4] suggest that assessments of climate-driven extinction risk should consider 'niche syndromes', that is, the size and positioning of three nested components of a species' niche, which they define as the present conditions in the native range (realized niche), the broader range of conditions under which a species could sustain a population (fundamental niche) and the even broader range of conditions under which some individuals survive but reproductive rates are insufficient to sustain populations (tolerance niche). Fundamental and tolerance niches are important for island endemics, because when the climate of a species' native island shifts beyond the realized niche the new conditions could still overlap the fundamental niche, allowing persistence, or the tolerance niche, triggering gradual attrition as death rates overtake recruitment rates[4]. Unfortunately, fundamental and tolerance niches are difficult to quantify because species' realized niches underrepresent them by unknown amounts[5,16,18]. No study has quantified all three niche components, although some have examined realized and fundamental[15,18] or realized and tolerance[5], or lumped fundamental and tolerance niches[6]. Together, these studies highlight promising techniques that could be combined to quantify species' full niche syndromes, including fundamental and tolerance niches[4]. For naturalized species, researchers can estimate the fundamental niche by circumscribing the range of climatic conditions under which each species has self-sustaining populations, both native and non-native. For plants grown horticulturally, researchers can estimate the tolerance niche by circumscribing the set of conditions under which mature individuals survive unassisted, but reproduction is insufficient to sustain a population. If all three niche components are estimated, these estimates could be compared with future climate projections to improve assessments of climate-driven extinction risk.

Conifers are an ideal system for evaluating climate-driven extinction risk among island endemics due to their diversity (157 island endemics globally[19]), horticultural popularity, propensity for naturalization and strong representation in occurrence databases. Conifers are widely planted and many are naturalized[20], affording valuable opportunities to quantify their fundamental and tolerance niches. Furthermore, their native and non-native distributions are well documented[19,20], facilitating thorough sampling.

Here, we evaluate climate-driven extinction risk among island endemic conifers by modelling their realized, fundamental and tolerance niches from native, naturalized and horticultural occurrences, and determining whether predicted climate conditions in 2070 coincide with species' estimated niches. We also analyse relationships among niche breadth, island size and available climate space to disentangle the drivers of extinction and advance niche theory.

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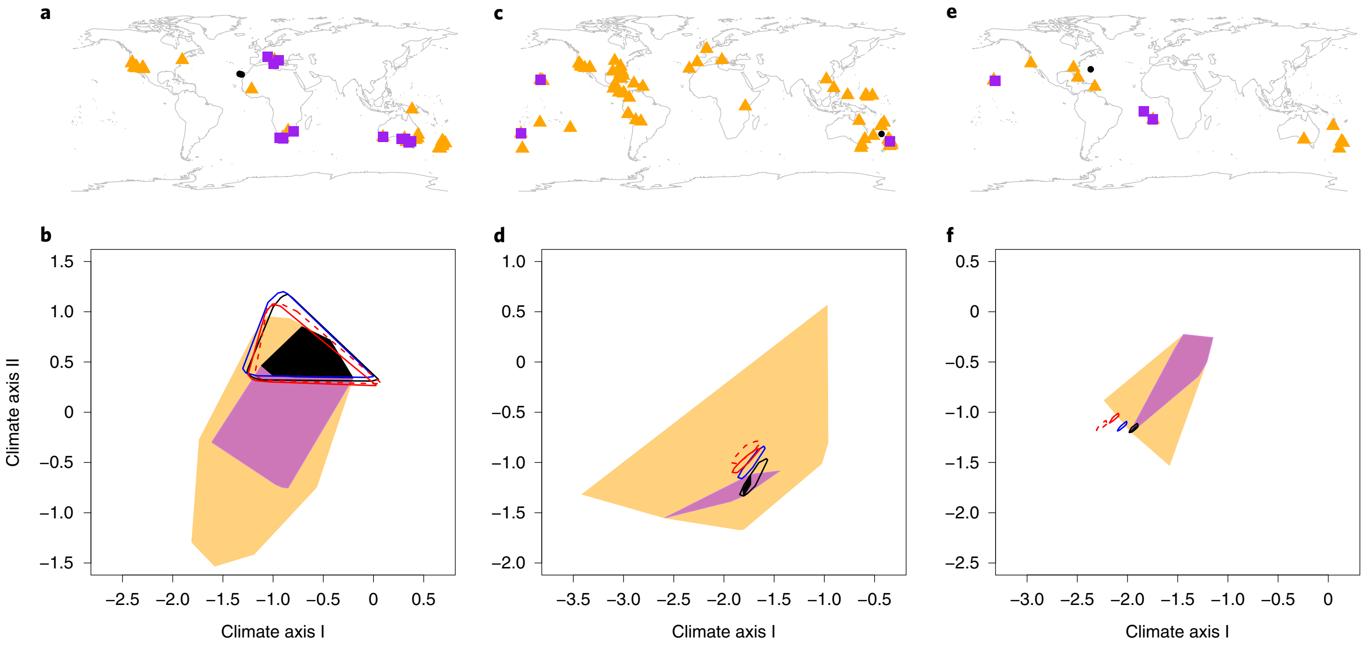


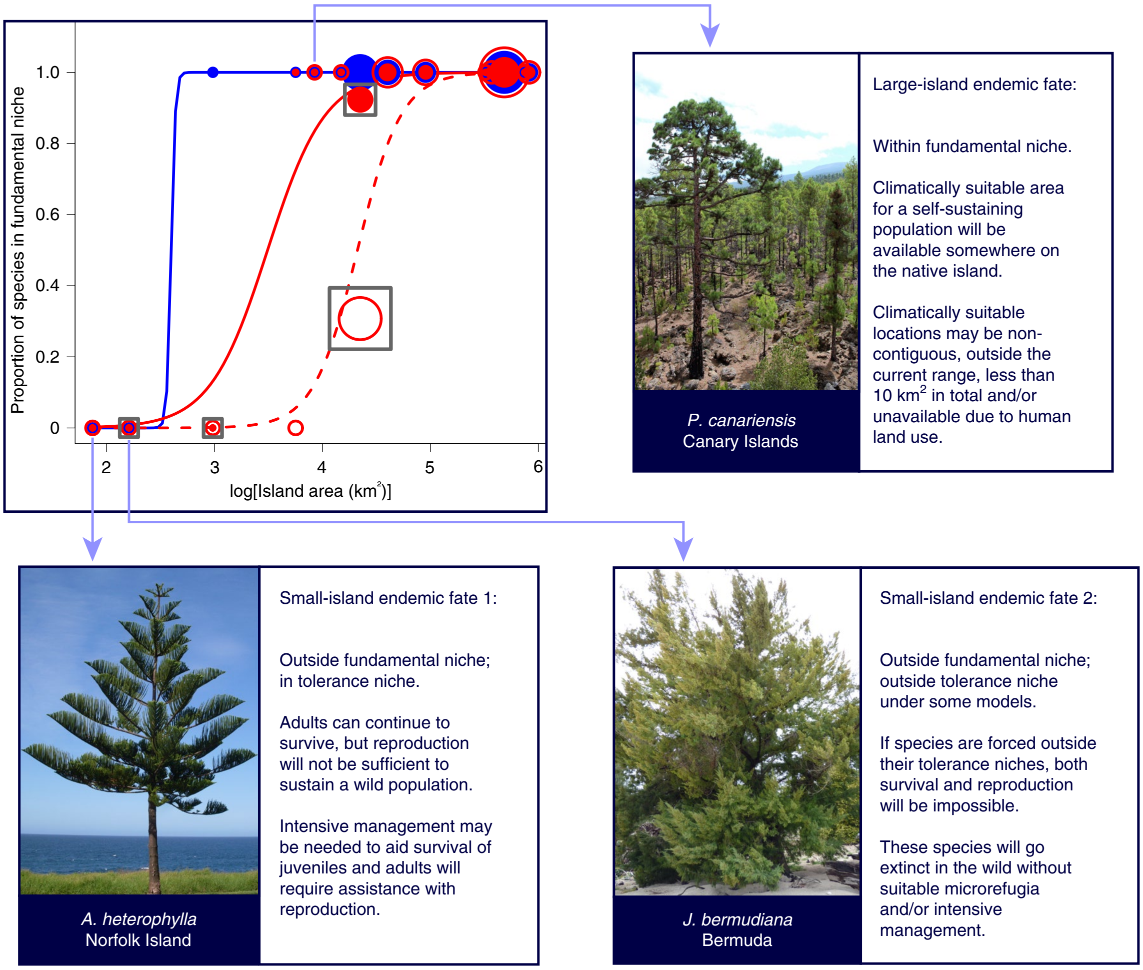
Fig. 1 | Occurrence data and niche models for three exemplar species. a–**f**, The species plotted are *P. canariensis*—Canary Islands (**a**,**b**), *A. heterophylla*—Norfolk Island (**c**,**d**) and *J. bermudiana*—Bermuda (**e**,**f**). Occurrences (and corresponding niche space) are classified as native (black, corresponding to the realized niche), naturalized (purple, corresponding to the fundamental niche) or non-naturalized but climatically tolerated (orange, corresponding to the tolerance niche). Climate space available on islands is shown with polygon outlines for current conditions (black), as well as for 2070 under RCP2.6 (blue), RCP8.5 (red) and the most severe individual model results for RCP8.5 (dashed red). Note that under all scenarios, *P. canariensis* retains fundamental niche space on its native island, whereas *A. heterophylla* and *J. bermudiana* are excluded from their fundamental niches, with *A. heterophylla* retaining tolerance niche space under all scenarios and *J. bermudiana* losing all overlap with its tolerance niche under the most severe scenario.

Native and non-native occurrence data were gathered from online herbaria and primary literature. Data were obtained for 55 species endemic to 14 islands and archipelagos worldwide (see Methods). Of these species, eight have naturalized populations. We built niche models using CHELSA climate data[21]. Focusing on variables of known importance to our study taxa (*sensu* Petitpierre et al.[22]), we considered mean temperature of warmest quarter, mean temperature of coldest quarter, mean annual precipitation and precipitation seasonality. Using a principal component analysis calibrated to global climate, we constructed a two-dimensional climate space capturing 84.5% of global variation (Supplementary Fig. 1). For each species, we estimated realized and tolerance niches by plotting relevant occurrence data (see Methods) in this climate space and circumscribing minimum convex polygons (MCPs). We estimated fundamental niches in the same way for the eight naturalized species. Each island's present and predicted climate spaces were also defined using MCPs. Climate forecasts for 2070 were downloaded from CHELSA using four CMIP5 models (see Methods). We considered three future scenarios, listed here in increasing severity of climate change: the ensemble mean of all four models under Representative Concentration Pathway (RCP)2.6, the RCP8.5 ensemble mean and, for each species, the individual model that generates the least overlap between the species' fundamental niche (when available; otherwise we used the realized niche) and the projected climate of the native island under RCP8.5 (see Methods).

Niche syndromes and future predictions for our study species fall into three categories. Some species have large realized, fundamental and tolerance niches and are predicted to stay within their fundamental niches (for example *Pinus canariensis*; Fig. 1a,b). Others have smaller realized and fundamental niches but large tolerance niches and are predicted to be outside their fundamental niches but within their tolerance niches (for example *Araucaria heterophylla*; Fig. 1c,d). A third set of species has small realized and fundamental niches but also smaller tolerance niches, and they are predicted to be outside even their tolerance niches under some scenarios (for example *Juniperus bermudiana*; Fig. 1e,f). Supplementary Fig. 2 shows plots of all other study species. All except *Lagarostrobos franklinii* exhibit niche disequilibrium (Supplementary Fig. 2).

The proportion of species falling into each category above depends on the future climate scenario, with more species outside their fundamental and tolerance niches under more severe scenarios. By 2070, 3.6–23.6% of the conifer species we studied are predicted to be outside their fundamental niches (Supplementary Table 1). The severity of the climate change scenario also informs the likelihood of falling outside the tolerance niche, with none of our conifer species in this category under the least severe scenario, only one under the intermediate scenario and 20% under the most severe scenario (Supplementary Table 1). With one exception (see Supplementary methods), the predicted climates of the 47 species that lack fundamental niche estimates all fall within the realized niche or outside the tolerance niche (Supplementary Fig. 2), making fundamental niche estimates unnecessary for predicting these species' fates (see Methods).

Island area predicts whether a species will remain in its fundamental niche. When logistic regression was used to model the proportion of species on a given island expected to remain in their fundamental niches (Fig. 2; for all regressions, $n = 55$, McFadden's pseudo-R^2 ranges from 0.53 to 1.00 and AIC evidence ratio ['ER'; see Methods] > 1,900/1), we found that the point at which half an island's species are predicted to be outside their fundamental niches—that is, any given species on an island is equally likely to be outside or inside its fundamental niche—corresponds with an island size threshold that varies with severity of climate change: 400 km^2 (RCP2.6), 3,000 km^2 (RCP8.5 ensemble mean) and 20,000 km^2 (RCP8.5 individual model).



Large-island endemic fate:

Within fundamental niche.

Climatically suitable area for a self-sustaining population will be available somewhere on the native island.

Climatically suitable locations may be non-contiguous, outside the current range, less than 10 km^2 in total and/or unavailable due to human land use.

Small-island endemic fate 1:

Outside fundamental niche; in tolerance niche.

Adults can continue to survive, but reproduction will not be sufficient to sustain a wild population.

Intensive management may be needed to aid survival of juveniles and adults will require assistance with reproduction.

Small-island endemic fate 2:

Outside fundamental niche; outside tolerance niche under some models.

If species are forced outside their tolerance niches, both survival and reproduction will be impossible.

These species will go extinct in the wild without suitable microrefugia and/or intensive management.

Fig. 2 | Island size and climate change severity determine the proportion of species remaining within their fundamental niches, as well as management needed to avoid climate-driven extinction. Islands are shown as circles (scaled by number of species studied from each island) positioned with logistic regressions under each of three climate change scenarios for 2070: RCP2.6 (solid blue circles and curve), RCP8.5 (solid red circles and curve) and the most severe individual model results for RCP8.5 (red circular outlines and dashed red curve). For each island, the blue circles are scaled to be smallest, the solid red to be intermediate and the red outlines largest, so that when all three future scenarios yield the same prediction for a given island, all three points can be visible. A grey box around a circle indicates that at least one species from the given island is projected to be outside its tolerance niche. The species accounts describe three possible future fates. Credit: Photos are from https://www.flickr.com (José Mesa Acosta (*P. canariensis*), John Tann (*A. heterophylla*) and Forest and Kim Starr (*J. bermudiana*)). All photos are licensed under Creative Commons (https://creativecommons.org/licenses/by/2.0/) and have been cropped but are otherwise unaltered from their original forms.

The strong correlation we found between island area and the predicted fates of island endemics is driven by positive relationships among the breadths of the three niche components, island area and available climate space (Fig. 3). These findings reinforce prior work reporting a positive relationship between niche breadth and range size[17,23], a factor related to island size. We also corroborate previous studies[7,16] showing that species with small realized niches exhibit the greatest niche disequilibrium between realized and fundamental niches (Supplementary Fig. 3; $n=8$, $R^2=0.86$, AICc ER > 180/1). However, our results add a new caveat: species with smaller realized niches still have smaller fundamental niches in spite of their high niche disequilibrium (Fig. 3a; $n=8$; $R^2=0.89$ and 0.74 for realized and fundamental; AICc ER > 400/1 for both; slopes significantly different at $P<0.001$). Since species with small realized and fundamental niches are found on small islands (Fig. 3a,b; for realized niches in Fig. 3b, $n=55$; $R^2=0.44$ and AIC ER > 2,500,000/1), which offer a limited range of climatic conditions (Fig. 3c; $n=14$; $R^2=0.86$; AICc ER > 100,000/1), small-island endemics are especially likely to be forced out of their fundamental niches when climate shifts (Fig. 2). This finding echoes earlier reports suggesting that narrow-niched species are most threatened by climate change[24]. In contrast, our tolerance niche estimates are not strongly correlated with island size, although we found a non-significant positive trend (Fig. 3a,b; AICc and AIC do not favour slope models). Because all observed tolerance niches are relatively large, few species are outside their tolerance niches under most 2070 scenarios (Supplementary Table 1).

Although our characterizations of fundamental and tolerance niches represent minimum estimates, they retain important predictive value. Fundamental niche breadth is uncorrelated with the number of naturalized occurrences used to generate the estimates, indicating that if we had more data, our estimates would not be larger (Supplementary Fig. 4a). This finding suggests that even if some occurrences we classified in the tolerance niche eventually (with more time since introduction) prove to be within the fundamental niche, our fundamental niche estimates would not change appreciably. Additionally, the positive correlation we found between realized and fundamental niche breadth is robust to randomized resampling of naturalized occurrence data (Fig. 3d; $n=8$, slope for real data is

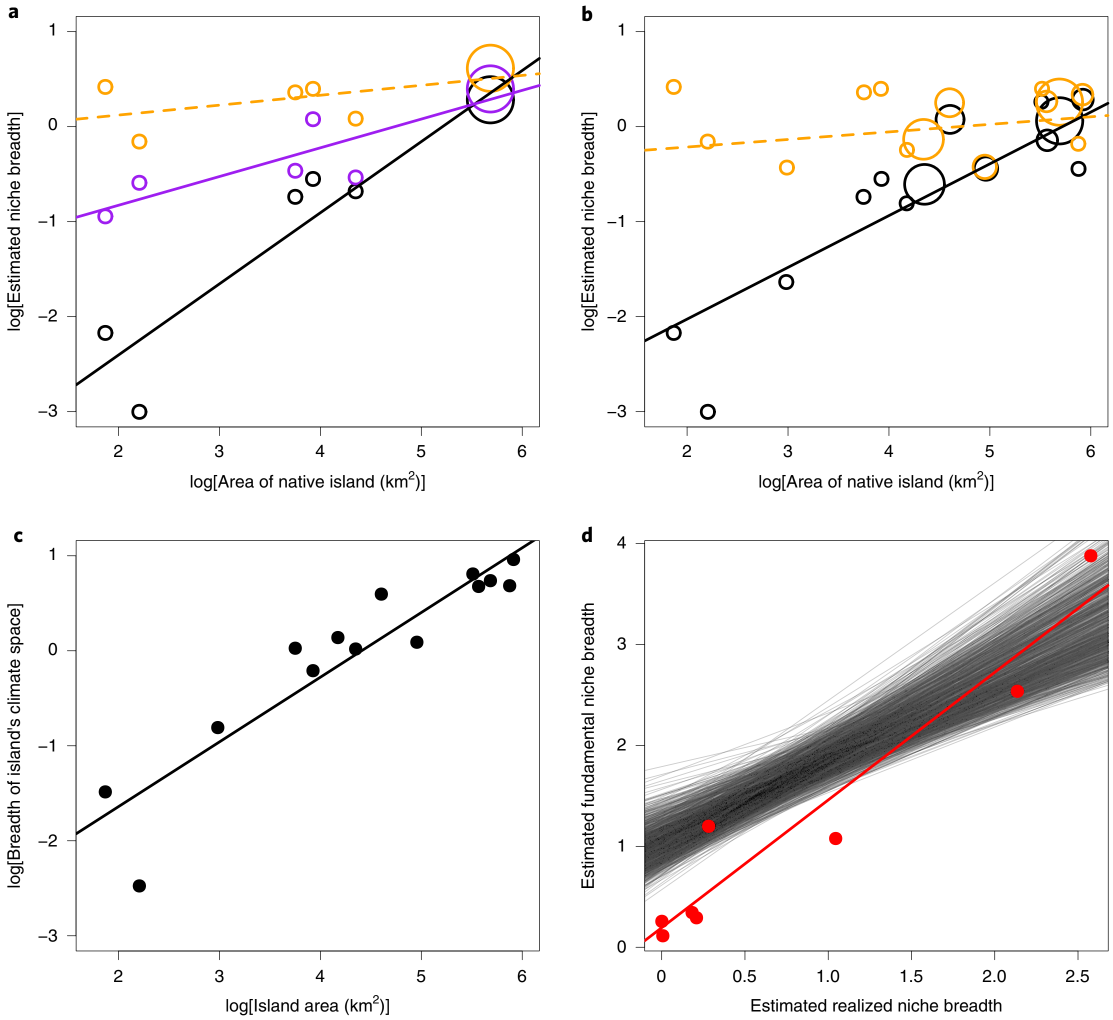


Fig. 3 | Correlations among island area, species' realized and fundamental niche breadth and total available climate space. a–c, Continuous lines represent linear regression models favoured over intercept-only alternatives by AIC or AICc evidence ratios and dotted lines represent non-favoured regression models. **a**,**b**, Regressions fit island size against the breadth of individual species' realized (black), fundamental (purple) and tolerance (orange) niches. Circles show the mean among species on an island, with circle size scaled by number of species. **a**, Relationships among eight species that have fundamental niche estimates. **b**, Relationships among all 55 study species. The *x* and *y* coordinates of circles have been jittered to improve visibility. **c**, Breadth of climatic conditions currently occurring island-wide for all islands studied. **d**, The linear regression slope for estimated fundamental niche breadth versus estimated realized niche breadth is steeper than expected by chance. Red points represent the real data, and the red trend line represents a linear model fitted to the real data. The grey lines represent linear models for 1,000 simulated datasets (points not shown), in which each species' realized niche model was built from the real data, and each fundamental niche model was built by adding seven randomly assigned locations.

greater than 99.6% of slopes for random scenarios, $R^2 = 0.92$, AIC ER > 1,700/1; see Methods), indicating that the patterns we found for the fundamental niche are unlikely to be artefacts of sampling bias. In contrast, estimated tolerance niche breadth is positively correlated with the number of non-native occurrences used for each species, indicating that if we had more data, our tolerance niche estimates would probably be larger (Supplementary Fig. 4b; $n = 55$, $R^2 = 0.23$, AIC ER > 500/1). Consequently, we have high confidence that species predicted to remain in their tolerance niches will do so, but less confidence in cases where species are predicted to fall outside their tolerance niches.

Our results highlight the urgent threat of climate-driven extinction for endemic species on small islands, as well as opportunities for impactful conservation management. Due to the relationships we have found among island characteristics and niche breadth (some previously unreported; see above), climate change is predicted to force small-island endemics outside their fundamental niches by 2070. Once these species are outside their fundamental niches, death rates will exceed reproductive rates, imposing a climate-driven extinction debt[25] paid by population attrition. Although attrition could take centuries for long-lived taxa like conifers, extinction is likely without intervention. If other vascular plants behave similarly, a substantial portion of global plant diversity will disappear, particularly from small islands. For example, under the RCP8.5 ensemble mean scenario, a small island like Mauritius (1,865 km^2), with 287 endemic vascular plant species[26], would be expected to lose 199 by attrition. While some species might evolve quickly enough to keep pace with climate change[27], those with longer life cycles, like conifers, seem unlikely to do so[28]. Moreover, species predicted to remain in their fundamental niches may still struggle, as climate change could exacerbate negative biotic interactions—for example, North American forests are suffering from climate-driven range expansion of the southern pine beetle[29]. Non-climatic threats like habitat modification could also make more areas unsuitable. On the other hand, islands may contain micro-refugia, which retain favourable climatic conditions amidst larger regional shifts[30]. Given these possibilities, targetted conservation will be essential for averting climate-driven extinction. Areas predicted to fall within species' realized niches could take top conservation priority, so that existing populations can be protected and expanded. Areas predicted to fall within the fundamental niche could take next priority, with managers seeking and protecting micro-refugia. For species predicted to fall within only their tolerance niches, conservation measures could aid recruitment of offspring. Some species may persist only in a semi-wild state; nonetheless, helping island endemics endure climate change could pay dividends for global biodiversity.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0530-9.

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Author contributions

K.C.R. and D.F.S. designed the study and wrote the manuscript. K.C.R. collected the data and performed the analyses. D.L.P. helped design the data collection approach, contributed to some analyses, assisted in interpretation and contributed to writing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Species occurrence data. Among the 157 species of conifers that are endemic to islands globally, we selected all species (55 in total) for which we could obtain verified occurrence data in both the native and non-native ranges. Verified data sources included herbaria, the primary literature and communications with botanical experts (see below).

Native occurrence records were gathered primarily from the Conifer Database[19,31]. This database has been curated to reflect as robustly as possible the full native distributions of conifer species. The Conifer Database yielded 2,152 native occurrences for our 55 study species, or approximately 39 occurrences per species (Supplementary Table 2).

An additional 88 native records for 9 underrepresented native species (approximately 10 per species), along with all 418 non-native records across all 55 species (approximately 8 per species; Supplementary Table 2), came from a primary literature search, as well as searches of the following online herbaria and consortia: the Southeast Regional Network of Expertise and Collections[32], the Consortium of Northeast Herbaria[33], the Consortium of Pacific Northwest Herbaria[34], the New York Botanical Garden[35], the Smithsonian National Museum of Natural History[36], Tropicos[37], the Harvard University Herbarium[38], the Consortium of California Herbaria[39], the University of Michigan Herbarium[40], the Australasian Virtual Herbarium[41], the Allan Herbarium[42], the Auckland Museum[43], the National Forestry Herbarium[44], the Botanical Database of Southern Africa[45], Kew[46], the Royal Botanic Garden Edinburgh[47], the French Muséum National d'Histoire Naturelle[48] and the Swedish Naturhistoriska Riksmuseet[49]. Full citations for primary literature sources are included in the References[50–76]. These sources are identified in Supplementary Note 1. Although the Global Biodiversity Information Facility (GBIF) is a valuable repository for species occurrence data, a large proportion of these data are not suitable for our purposes and thus would have had to be filtered out during our data collection process (see below), which is highly labour-intensive. Consequently, we opted to focus on the more specific sources listed above. Additionally, some of our sources do not contribute to GBIF, and thus by querying them directly we were able to find additional data that would not have otherwise been available.

Occurrences were only counted as naturalized, and thus used in fundamental niche models, if there was clear evidence of a self-sustaining population—that is, a wild population in which sufficient reproduction occurs to sustain the population without human aid. For example, one record of *Pinus canariensis* was used in the fundamental niche model because the specimen remarks include 'Abundantly naturalized (hundreds of plants) in road reserve and adjoining plantation on farm from which naturalized', demonstrating that the species is reproducing regularly beyond its planted origin. Occurrences lacking clear evidence of naturalization were not used to estimate the fundamental niche, but were instead incorporated into tolerance niche models whenever we could confirm that at least one adult individual was surviving without irrigation or other human assistance. These confirmations of occurrences indicating the tolerance niche were made in two ways. First, for some specimens, there was evidence of some unassisted reproduction, but recruitment was insufficient to demonstrate with certainty that a fully wild population could be sustained. For example, one record of *A. heterophylla* was used in the tolerance niche model but not the fundamental niche model because the specimen remarks include 'Seedlings and saplings common along an old road leading to a disused water tower above sugar refinery. A stand of adult trees occurs nearby', indicating that unassisted reproduction is occurring, but has not exceeded one generation beyond the parent generation, which was likely to have been planted. Second, in other cases, cultivated specimens were counted whenever we could determine, through personal communication with collectors and/or horticulturalists, that irrigation or any other human assistance had ceased after the sapling stage. Personal communication was used for 248 specimens, including at least one of each species. In general, horticultural data must be interpreted with caution, since horticulturalists sometimes select microsites to optimize growing conditions, thereby potentially limiting the effectiveness of coarse-scale interpolated climate estimates for capturing the conditions actually experienced by individual trees[11].

Niche modelling. We characterized the niche space occupied by each species using MCPs. This approach is often used in characterising niche space[13,77] and is particularly useful when species' occurrence density might be driven by variation in collection effort, as opposed to variation in environmental suitability. In contrast, kernel-smoother estimates are particularly useful when density of occurrences reflects a species' true tolerances[78], but we did not use this approach here because results can be strongly swayed when collection effort is variable[79]—as is undoubtedly the case across the many regions of the world where island endemic conifers are native or naturalized.

We were able to determine the predicted climate niche status of all 55 species studied under all three 2070 scenarios—with one exception (see Supplementary methods)—because, although we lack fundamental niche estimates for most species, predictions for these species tend to be either within the realized niche or outside the tolerance niche (Supplementary Fig. 2). Due to the nested configuration of the three niche components, any species inside its realized niche is also inside the other two by default. Similarly, any species outside its tolerance niche is outside the other two by default. These two predicted fates (inside the realized niche and outside the tolerance niche) are common because, for many species, the climate of the native island is predicted to move in a direction in climate space that is mismatched with the orientations of species' fundamental and tolerance niches. In other words, as hypothesized by Booth[11], many species do not show niche expansion beyond the realized niche in all directions in climate space, and the climate of the native island is often predicted to move toward (or beyond) these areas of the realized niche that lack expansion—that is, areas where the realized, fundamental and tolerance niche edges all coincide (Supplementary Fig. 2).

There were idiosyncratic modelling issues for two species, *Pinus luchuensis* and *Afrocarpus mannii*. We discuss these issues, and how they were addressed, in the Supplementary methods.

Climate data and forecasts. Baseline climate data from CHELSA[21] are model outputs for the period 1979–2013 downscaled to 30-arcsec resolution.

Projections for our four climate variables (mean temperature of warmest quarter, mean temperature of coldest quarter, mean annual precipitation and precipitation seasonality) in 2070 were downloaded from CHELSA. We used CMIP5 models that received the maximum global performance rating from McSweeney et al.[80]: CCSM4, GFDL-CM3, GFDL-ESM2G and GFDL-ESM2M.

In identifying the 'most severe' model for 2070 under RCP8.5 for each species, we ranked models by the predicted degree of overlap they generated between the fundamental niche and the climate of the native island. The less overlap was predicted by a given model between the fundamental niche and the island's climate, the higher the model was ranked in severity. Whenever two models predicted the same degree of overlap with the fundamental niche, we broke the tie by calculating the degree of overlap with the tolerance niche.

Statistical analyses. All analyses were performed in R v.3.4.3 (ref. [81]) using 11 packages in total (details below).

To import and process climate data in raster format from CHELSA[21], we used several functions in the raster package[82], including raster (to read in raster files), rasterToPoints (to convert rasters into data frames for further processing and statistical analysis), area (to calculate the land area of islands, as well as climatically suitable regions within islands), brick (to group raster layers into multi-layer objects), overlay (to generate ensemble mean climate predictions from the four models), stack (to group climate data layers for principal component analysis) and writeRaster (to write raster files for the ensemble mean predictions we generated). We used QGIS[83] to clip rasters of individual islands from global layers and to link georeferenced species occurrences to climate data (in raster form) through point sampling.

Our principal component analysis was calibrated to the current global climate background, as represented by CHELSA's data for our four climate variables (mean temperature of warmest quarter, mean temperature of coldest quarter, mean annual precipitation and precipitation seasonality), using the rasterPCA function in the RStoolbox package[84]. To circumscribe MCPs for species' niche models, as well as individual islands' climate spaces, we used the mcp function in the adehabitatHR package[85]. We used the gIntersection function in the rgeos package[86] to find the intersections between species' niche models and the climate spaces of their native islands.

All correlations we report among variables were assessed using linear regression (for continuous response variables) or logistic regression (for binary response variables), with common-log transformations of predictor and/or response variables where appropriate to meet regression assumptions. All variables that were log-transformed are labelled as such in the relevant figures.

For each linear or logistic regression model, we computed an AIC or AICc ER using the akaike.weights function in the qpcR package[87] in order to compare against an alternative intercept-only model. AICc was used instead of AIC when the ratio of n (the number of observations) to k (the number of predictors) was less than 40/1. Thus, since our models have one predictor each, we used AICc for all models with $n<40$. We computed these values using the AICc function in the AICcmodavg package[88].

The pR2 function in the pscl package[89] was used to compute McFadden's pseudo-R^2 values for logistic regression models. We used seemingly unrelated regression (SUR) analysis, conducted with the systemfit function in the systemfit package[90] and the glht function in the multcomp package[91], to determine whether the regression slopes for fundamental and realized niche breadth were significantly different from each other when these variables were plotted against island area (see Fig. 3a,b).

In Supplementary Fig. 4b, the point in the bottom left corner could be regarded as an outlier. As such, we repeated the regression analysis with and without it. The differences in results were negligible. Thus, we report results for the full dataset, including the point in question.

In order to eliminate the possibility that species on larger islands have larger fundamental niche estimates because they are simply planted more widely, we plotted total exotic occurrences (including cultivated occurrences) against island area for all species with fundamental niche estimates, confirming that these variables are uncorrelated (Supplementary Fig. 5).

We used the symbol.size function in the simba package to adjust the symbol sizes in our figures[92]. To create the global maps in Fig. 1, we used the map function in the maps package[93].

Randomized resampling of occurrence data. In order to confirm that the positive correlation we found between realized and fundamental niche breadth is not an artefact of sampling bias among naturalized occurrences, we resampled 1,000 times from the overall pool of naturalized occurrences across all species, assigning each species a random set of seven occurrences (the mean number observed in the real dataset), and reanalysing the relationship between realized and fundamental niche breadth for each randomly generated dataset using simple linear regression. For example, when we randomly reassigned naturalized occurrences to *Juniperus bermudiana*, its simulated naturalized range included seven locations randomly selected from the pool of locations where any species in our dataset, not just *J. bermudiana*, had been recorded as naturalized. We compared the slopes of the regression models for the random scenarios (grey lines, Fig. 3d) to the regression slope for the real data (red points and line, Fig. 3d) to confirm that the observed relationship for the real data is unlikely to have arisen by chance.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Some herbaria and consortia we queried for species occurrence data do not allow dissemination of their data beyond the user, so we are unable to publish the portion of our dataset derived from these online sources. However, these data are publicly available for download, so we provide information on where to access data from each herbarium and consortium in the references. For full details on herbarium consortia, including lists of individual participating herbaria whose data we used, see Supplementary Note 2. We also provide in the Supplementary Data a version of our species occurrence dataset that contains only the data derived from personal communication and our primary literature search. CHELSA climate data are publicly available at http://www.chelsa-climate.org and at the Dryad Digital Repository at https://doi.org/10.5061/dryad.kd1d4.

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