SPECIAL ISSUE

Biogeographic ranges do not support niche theory in radiating Canary Island plant clades

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ABSTRACT

Aim Ecological niche concepts, in combination with biogeographic history, underlie our understanding of biogeographic ranges. Two pillars of this understanding are competitive displacement and niche conservatism. The competitive displacement hypothesis holds that very similar (e.g. closely related) co-occurring species should diverge, forced apart by competition. In contrast, according to the niche conservatism hypothesis, closely related species should have similar niches. If these are fundamental structuring forces, they should be detectable when comparing the climatic niches of endemic species in radiating clades in oceanic archipelagos, where closely related species exist in both sympatry and allopatry and the species' entire ranges are known. We took advantage of this natural experimental system to test whether the climatic niche relationships predicted by the two hypotheses are found.

Location Canary Islands.

Methods For the plant clades *Aeonium*, *Argyranthemum*, *Descurainia*, *Echium*, *Lotus* and *Sonchus*, separately, we tested relationships between phylogenetic distance and climatic niche differentiation (in temperature, precipitation and their combination), using a high-resolution dataset. We also tested for niche conservatism using Blomberg's K and Pagel's λ. We compared climatic niche differentiation between pairs of species existing in sympatry with that for pairs of species in allopatry. For each comparison, we focused on the climatic niche space available to both species.

Results The relationships between phylogenetic distance and climatic niche differentiation were mostly non-significant; some weak but significant positive relationships were found, mainly for *Aeonium* and *Sonchus*. Where differences between sympatry and allopatry were found, niche differentiation tended to be greater in allopatry.

Main conclusions The expectations from niche conservatism were frequently not met; instead our results suggest considerable climatic niche lability. All significant differences in climatic niche differentiation were opposite to the predictions from competitive displacement. These forces may be less important in structuring biogeographic ranges than is commonly thought, at least on islands.

Keywords
Adaptive radiation, climate, competition, divergence, ecological character displacement, endemic plants, ghost of competition past, niche conservatism, sister clades, speciation.

INTRODUCTION

Understanding the environmental factors that influence the local occurrence and persistence of species is one of the most fundamental tasks in ecology. Similarly, understanding what determines species' ranges is fundamental to biogeography. Prominent in both are concepts of species' niches, which relate to both environmental conditions (Grinnell, 1917) and biotic interactions (Elton, 1927). The Hutchinsonian niche concept, which views the niche as an *n*-dimensional hypervolume defined by environmentally related niche axes (Hutchinson, 1957), is the basis of current assessments of species niches (Blonder *et al.*, 2014), including species distribution modelling (Pearson & Dawson, 2003; Duputié *et al.*, 2014). Species niches are thus critical to both biogeography and ecology, and the evolution of climatic niches is an area of particular current interest (e.g. Kozak & Wiens, 2006; Algar *et al.*, 2013; Algar & Mahler, 2015).
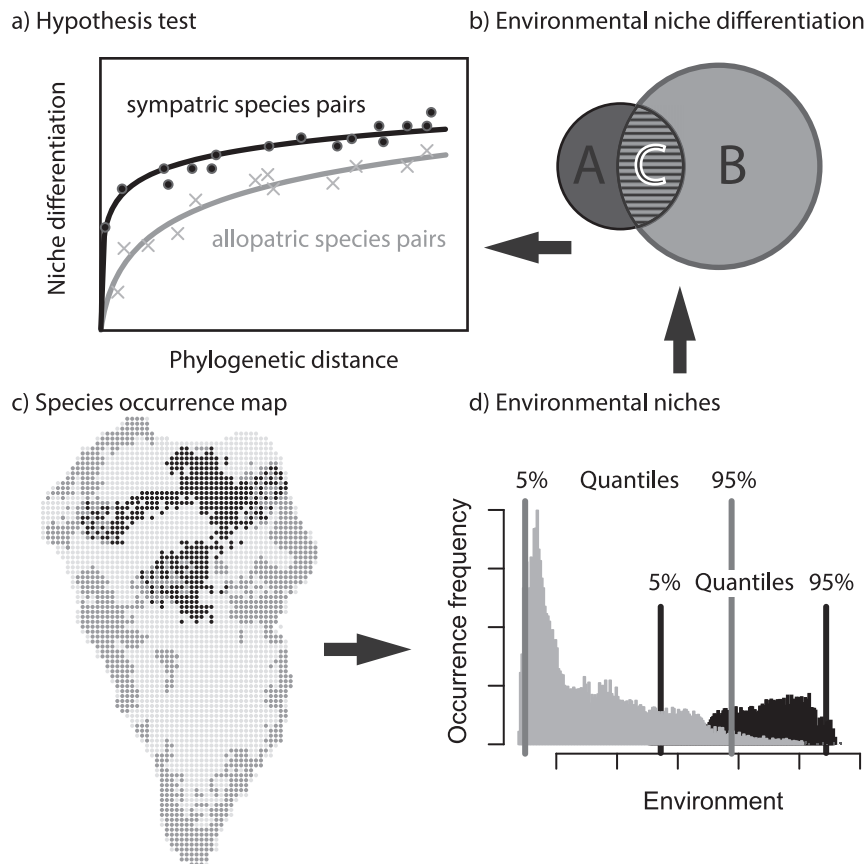
Niche theory originated in ecology, but the concepts have been applied to biogeography, based on the assumption that what happens to individuals within communities should scale up to populations and species ranges. Species distribution modelling can work well for interpolation, but is not designed to delineate the boundaries of a fundamental environmental niche (Blonder *et al.*, 2014). Such models risk calculating unbounded niches if species occurrence is modelled as increasing (unchecked) with environmental variables whose global range is not captured by the dataset being used. Further, studies with invading plant species have often not found a tight fit between native and alien niches (e.g. Broennimann *et al.*, 2007; Early & Sax, 2014), perhaps because of enemy release, suggesting that the relationship between fundamental and realized niches may be weak. Neutral theories, such as that of Hubbell (2001), demonstrate that biogeographic patterns can be modelled remarkably well without ecological differentiation between species. More generally, attempts to scale to biogeographic patterns from ecological mechanisms, determined using reductionist approaches at a very local level, have met with mixed success at best.

Niche conservatism and competitive displacement are two fundamental concepts related to niche evolution (Kozak & Wiens, 2006). The two may operate simultaneously (and independently), but differ in their hypothesized influence on the evolution of environmental niches of closely related species (Ackerly, 2009). Niche conservatism is put forward as a hypothesis to explain major biogeographic patterns such as the increase in species richness towards the tropics (latitudinal diversity gradient; Wiens & Donoghue, 2004) or the tendency of major plant clades to be restricted to one or a few biomes (Prinzing *et al.*, 2001; Donoghue, 2008). It is reasoned that closely related species should share similar environmental niche conditions (Wiens & Graham, 2005; Wiens *et al.*, 2010). Because niche lability is, to a certain degree, inevitable with time (under perfect niche conservatism there would be no evolution), niche conservatism predicts an increase in climatic niche difference (decrease in climatic niche similarity) between species with increasing phylogenetic distance.

In contrast, the idea that competition is a key structuring force in ecological communities has led to the notion of competitive displacement, the textbook argument being that ecologically similar species should rapidly diverge if they coexist in the same area (Abrams, 1983; Begon *et al.*, 2006). This could involve mechanisms of niche partitioning that allow coexistence within the same locations ('ecological character displacement'; Brown & Wilson, 1956). It could also involve geographical divergence; in an island context, the taxon cycle (Wilson, 1961; Ricklefs & Bermingham, 2002), for example, suggests that competition causes species to evolve into different environments within the same island. Given that species traits form the interface between species and their environment, and that environment (including resource distributions and climate) tends to be spatially autocorrelated, trait shifts resulting from competition between two species should be reflected in differences in their climatic niches. Thus, competitive displacement should result in a tendency for recently diverged species living on the same island to differ in their climatic niches, opposing the expectation from niche conservatism. There should be less such tendency when the species live on different islands. Similarly, within islands, niche differentiation is usually required for genetic isolation and speciation, whereas the barrier provided by the sea in archipelagos may be all that is required for speciation to happen between islands. Thus, in an oceanic archipelago setting, the theoretical expectation from these competitive divergence mechanisms is for climatic niches of recently diverged, closely related species to be more different for species of sympatric origin than for species of allopatric origin.

Oceanic archipelagos such as the Canary Islands offer an opportunity to identify links between ecological processes and emergent biogeographic patterns because they provide a natural experimental setup. This is important and required because biogeographic patterns are not amenable to manipulative experimentation. Each radiation in such archipelagos contains replicate populations (on the different islands) from replicate evolutionary episodes (speciations) that are phylogenetically controlled (the same relatively small clade) and represent the entire native range of almost all the species' populations, within approximately the same geographic setting as that in which they evolved. All of this is replicated by the different radiations. While in continental settings many species distributions may be influenced by dispersal lags from ice age refugia, and are thus in disequilibrium with their climatic niche (Normand *et al.*, 2011), the large elevational gradient and thus low climate change velocity removes this effect for islands. Utilizing these advantages offered by the Canary Islands enables us to test for signatures of key ecological and evolutionary processes by combining island biogeographic patterns and a macroecological approach across all species of radiating clades.

This approach differs fundamentally from previous studies based on the different 'natural experimental' approach of comparing pairs of species in allopatry versus sympatry to test for character displacement. Classically, the possibility of divergence driven by competition has been studied by seeking pairs of species that are more divergent in sympatry than in allopatry

a) Hypothesis test

b) Environmental niche differentiation

c) Species occurrence map

d) Environmental niches

Figure 1 Predictions of the niche conservatism (NC) and competitive displacement (CD) hypotheses for climatic niche differentiation in radiating plant clades in the Canary Islands. NC predicts a positive relationship between phylogenetic distance and climatic niche differentiation, while CD predicts that pairwise climatic niche differentiation between species should be greater for sympatric species than allopatric ones, particularly for the most closely related species. Panel (a) illustrates these predicted patterns. To produce plots like (a), we used species occurrence data from 500 m × 500 m grid cells across the Canary Islands, illustrated in panel (c) for a pair of species in La Palma, to calculate climatic niche differentiation (b) for each pair of species, using the 5% and 95% quantiles (d) (see Methods), and plotted that against their phylogenetic distance, calculated from our phylogenies. The two hypothetical species are distinguished in (b) and (d) using grey and black; in the map (c) the lightest grey dots indicate 500 m × 500 m cells in which neither species occurs, the mid-grey dots are the cells occupied by the grey species and the black dots represent both the cells occupied by the black species and those occupied by both species.

and then trying to determine whether that difference can be attributed to competition (e.g. Brown & Wilson, 1956; Schluter & McPhail, 1992). In other words, seeking cases that seem to fit the predicted pattern and then trying to infer whether the process or mechanism applies. Here, we change the perspective. We start with the mechanisms, specify the biogeographic patterns they predict and use a large set of comparisons between closely related species to test whether the predicted patterns are found more often than expected by chance. We then repeat this process for five other separate sets of comparisons (six radiations in total). To our knowledge, this is the first attempt at such an analysis, probably because it is rare to have a large set of closely related species with sufficient, systematic information on the species' climatic niches, distributions and phylogenetic relatedness, coupled with an appropriate natural experimental setup.

On island archipelagos such as the Canary Islands, the two fundamental hypotheses (niche conservatism and competitive

displacement) predict testable patterns of climatic niche differentiation among species of the same clade (where theoretically each clade results from a single colonization), in relation to the evolutionary histories and biogeographic settings of the species. For any comparison of two species, both species may exist on different islands, or on the same island(s), or there may be a mixture of co-occurrence and separate occurrence on islands across the archipelago. The mechanism of speciation (especially sympatric versus allopatric) is likely to be reflected in occurrence patterns in most within-radiation comparisons, though we cannot test for the driving mechanisms with available genetic data.

As depicted in Fig. 1, divergence hypotheses predict that two sympatric species (or sympatric populations of two species) within a clade should differ in their climatic niches more than allopatric ones. Not all niche divergence will be reflected in the climatic niche but, as argued above, a signal of it should be

detectable in the climatic niches if competitive displacement is a key structuring force. Thus we may expect greater climatic niche differentiation in sympatry than in allopatry, controlling for phylogenetic distance (Fig. 1a). If competition between the closest relatives (or most-similar species) is strongest, then this difference should be greatest for short phylogenetic distances. Sympatric–allopatric differences should modify an overall trend, predicted by the niche conservatism hypothesis, for closely related species to be more similar in their climatic niches (Fig. 1a) than more distantly related species – a trend that should be apparent for allopatric species or populations, regardless of any competitive displacement. Thus we may also expect niche difference to increase with phylogenetic distance.

Here we test these predictions using fine-resolution occurrence data for species in radiating plant lineages in the Canary Islands. Almost all these species (123 of 126) are endemic to the archipelago, and therefore our data cover their entire global range; the exceptions are species that have dispersed from the archipelago (e.g. to Madeira). The climatic niche of a species represents those climatic conditions in which a species can survive, grow and/or reproduce (depending on the definition). In most niche estimations and niche modelling techniques these climatic conditions are estimated from the occurrence records of species, an approach that is particularly suitable for non-mobile organisms (like plants).

We focus mainly on the response variable climatic niche differentiation (hereafter 'niche differentiation'). Metapopulations that develop into independent species are expected to (gradually with time) differentiate in their climatic niche. Once reproductive isolation has been effective (speciation takes place), this process of niche differentiation continues. Niche differentiation measures the degree to which the (climatic) niches of two related species have diverged during the time since splitting from a common ancestor.

METHODS

Data for species and environmental variables

We selected six clades (alliances approximating genera) in the Canary Island flora with well-resolved phylogenetic relationships: *Aeonium* (41 species), *Argyranthemum* (15 species), *Descurainia* (7 species), *Echium* (22 species), *Lotus* (14 species) and *Sonchus* (27 species). Within each clade, we statistically related phylogenetic distance to niche differentiation, as outlined in 'Analyses' below.

Phylogenies were calculated from plastid and nuclear DNA sequence alignments, based on the sequences produced by García-Maroto *et al.* (2009) for *Echium*, Lee *et al.* (2005) for *Sonchus*, Mort *et al.* (2002) for *Aeonium* and relatives, Goodson *et al.* (2006) for *Descurainia* and Ojeda *et al.* (2011) for *Lotus*. We downloaded these sequences from the GenBank database (www.ncbi.nlm.nih.gov/genbank; see Table S1.1 in Appendix S1 in the Supporting Information for details of DNA regions used). The nuclear and plastid DNA regions were first analysed separately, and in the absence of significant topological conflict

(indicated by topological differences with bootstrap values >70) the plastid and nuclear datasets were analysed in combination. We reconstructed time-calibrated phylogenies in BEAST v.1.8.0 (Drummond *et al.*, 2012) using a Bayesian relaxed clock approach with lognormal distribution. We used the GTR+G substitution model and the four Monte Carlo Markov chains were run for 50 million generations, with sampling every 1000 generations. Calibration of the clock relied on island ages and/or secondary calibration using previously published age estimates (see Table S1.1 in Appendix S1 for details). Using the program TRACER 1.5 (Rambaut & Drummond, 2010), convergence of the chains was checked by ensuring that effective sampling sizes had all exceeded 200. TREEANNOTATOR v.1.8.2, part of the BEAST package (Drummond *et al.*, 2012), was then used to remove the first 10% of the sampled trees and to compute a maximum clade credibility tree from the remaining trees, with the mean divergence ages shown at the nodes. We finally determined phylogenetic distances using the branch lengths of the resulting chronograms. Our phylogenetic distance measure thus represents the best estimate of the time since two extant species shared a common ancestor. The phylogeny for *Argyranthemum* was directly extracted from Francisco-Ortega *et al.* (1996) and is of lower quality, with the phylogenetic distance not being time-calibrated. Non-monophyletic taxa and those that we could not match to occurrence data were removed from the analysis (the number of species per clade reported in the previous paragraph excludes these removed taxa).

Species occurrence data were taken from 500 m × 500 m grid cells that span the entire Canary Islands (Atlantis 3.1) and represent a long-term governmental initiative to assemble and complete all known distribution records of species on the Canary Islands. The quality of the Atlantis data is variable, but it is particularly good for endemic-rich clades like the ones investigated here (see Appendix S6 for further information on data quality, including validation with independent data). For the species used in this study, the mean number of occupied grid cells per species was 976 (median 578) (see Table S2.1 in Appendix S2; Fig. S6.1 in Appendix S6 shows the distribution maps), which is more than sufficient for determining climatic envelopes. *Lotus* initially had 17 species, but we removed three because of their very small natural range (*Lotus eremiticus*, *Lotus maculatus*, *Lotus pyranthus*). *Lotus eremiticus*, for instance, is known to have only one natural occurrence record, which probably comprises ramets of a single genet, making the species unsuitable for niche calculations. The range in numbers of cells occupied by the remaining species was large (17–5126), with 14 of the 126 species having fewer than 100 records, including seven with fewer than 50. These species with few occurrence points are all known to have small ranges, and our experience of the islands suggests that our data represent good matches for the species' actual ranges (Fig. S6.1 in Appendix S6).

We quantified climatic niches using monthly temperature and precipitation data, which were interpolated from climate station data (provided by the Agencia Estatal de Meteorología) using spatial regression kriging (see Irl *et al.*, 2015). Given that mean grid-cell elevation is strongly collinear with mean annual tem-
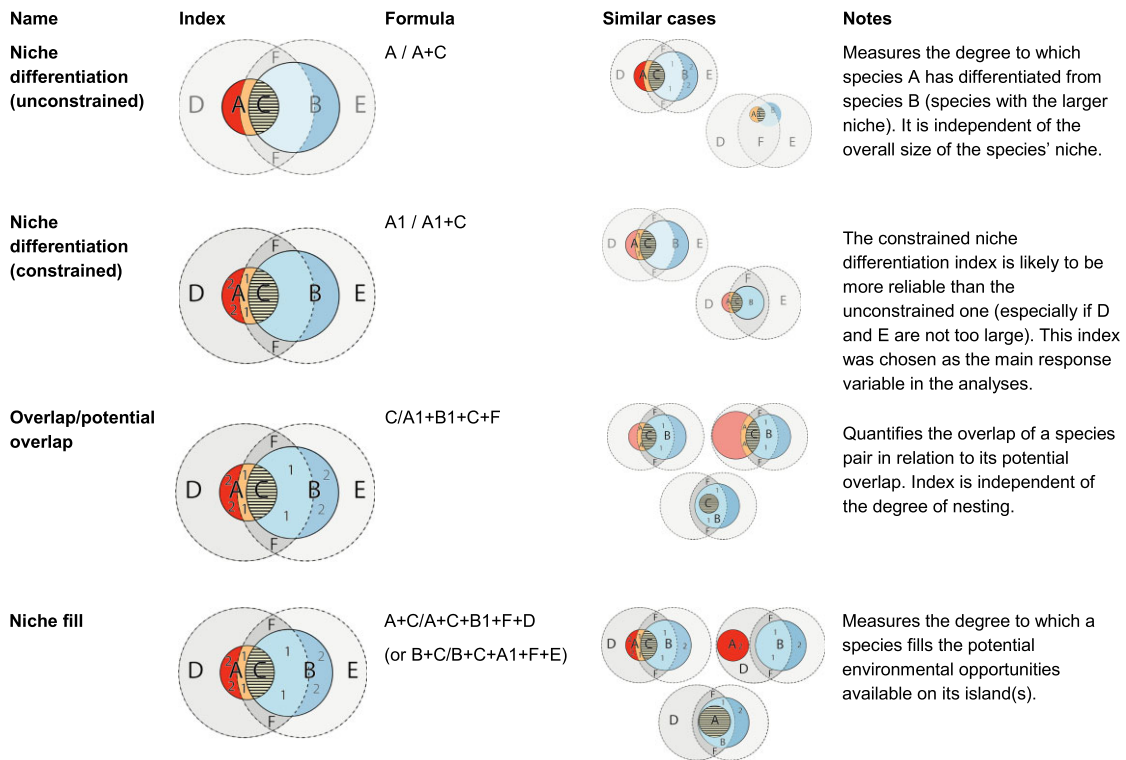
perature ($r = -0.95$), and was used in the interpolation of the temperature values from climate station data, we did not additionally include elevation in our analyses. We used six climatic variables: mean annual temperature, mean annual precipitation, mean temperature of the warmest and coldest months (August and January, respectively) and mean precipitation of the wettest and driest months (December and July, respectively). These represent both mean and extreme conditions, and perform better in accounting for species distributions than other variables (e.g. spring, summer, autumn and winter temperature and precipitation; data not shown).

Calculation of climatic niches and indices comparing climatic niches

We calculated species climatic niches using grid-cell-mean temperature and precipitation values. For each climatic variable, we measured the niche as ranging from the 5% to the 95% quantiles of all grid cells where the species was recorded as present (Fig. 1). This was to reduce bias caused by errors that would artificially inflate the estimates of niche breadth, in particular: (a) from any false presences of a species outside of its actual range and (b) from

true presences at the edges of cells with large ranges of the climatic variable. An example of (b) would be when a species restricted to relatively low elevations is recorded in a cell that has a large topographic range: its presence is at the lowest elevations but the average elevation of the cell would be well above the elevational range of the species, so the resulting value for temperature (the average for the cell) would be incorrect for the species. Other quantile thresholds (lower, 0–25%; higher, 100–75%) were also implemented and produced qualitatively similar results. In addition to these one-dimensional niche range estimations, we applied multidimensional niche range estimates using the R package HYPERVOLUME v.1.3 (Blonder *et al.*, 2014; bandwidth fixed at 0.05), using four variables: temperature of the warmest and coldest months temperature and precipitation of the wettest and driest months. Because multidimensional niche estimations are very sensitive to the choice of units and transformations (Petchey & Gaston, 2006), we rescaled untransformed environmental axes to range between 0 and 1.

Niche differentiation between two species was quantified as the percentage of the climatic niche space (niche space was measured in units of climate, e.g. °C or mm) of the smaller-niched species that does not overlap the larger one (Fig. 2). This

Name	Index	Formula	Similar cases	Notes
Niche differentiation (unconstrained)		A / A+C		Measures the degree to which species A has differentiated from species B (species with the larger niche). It is independent of the overall size of the species' niche.
Niche differentiation (constrained)		A1 / A1+C		The constrained niche differentiation index is likely to be more reliable than the unconstrained one (especially if D and E are not too large). This index was chosen as the main response variable in the analyses.
Overlap/potential overlap		C/A1+B1+C+F		Quantifies the overlap of a species pair in relation to its potential overlap. Index is independent of the degree of nesting.
Niche fill		A+C/A+C+B1+F+D (or B+C/B+C+A1+F+E)		Measures the degree to which a species fills the potential environmental opportunities available on its island(s).

Figure 2 The indices used in this study. The solid circles represent the occupied climatic niche spaces of species A and B (here shown in two dimensions, and only for cases of allopatric species pairs, for ease of visualization). The hatched area is the climatic space shared by the two species. The dashed circles represent the climatic space available on each island. Parts D, E, F in the diagrams show the climatic space of the islands not occupied by either species. Species A is always the species with the smaller occupied niche space. Each index is shown both graphically and via its formula, and some notes are given about what each index measures. The column 'Similar cases' shows different scenarios for which the index gives the same value. Some calculations are constrained to the niche space shared between islands; for these, we distinguish between the part of a species' niche that lies in the environmental space shared by the islands where both species occur (A1 or B1) and the part that lies in the unshared space (A2 or B2).

converts an approach successfully applied for geographic range overlap (Barraclough & Vogler, 2000; Anacker & Strauss, 2014) to climatic niche space. Niche differentiation was calculated for all occurrence records of the two species ('unconstrained'), and separately by restricting the analyses to the climatic space that is shared between the two sets of islands occupied by the two species ('constrained'). The results we present in this paper are for the constrained analyses; results from the unconstrained analyses are documented in Appendix S4.

In addition, we calculated 'niche fill' (measuring the degree to which each species occupies all the climatic space available on its island, or islands, within the archipelago) and 'overlap/potential overlap' of climatic niches between two species. For example, for temperature, niche fill is the range of temperatures occupied by a given species as a percentage of the range of temperatures that exist on the islands on which it occurs; 'overlap/potential overlap' is the range of temperatures shared by two species, as a percentage of the range of temperatures shared by the two sets of islands they occupy. These indices were calculated for each climatic variable separately, and for the four-dimensional niche estimation. Figure 2 illustrates these indices and gives the formulae for their calculation.

Analyses

To test for a signal of niche conservatism, we compared all species of a clade with each other (not just sister taxa) in a pairwise manner, and correlated the phylogenetic distance between them with their niche differentiation (Fig. 1a). In all cases, we related niche differentiation to phylogenetic distance using linear models with three different transformations: $y \sim x$, $y \sim \ln(x)$ and $y \sim \sqrt{x}$. These transformations were compared using diagnostic plots of model residuals; in all cases, this demonstrated little meaningful difference between the transformations and the adjusted R^2 values were very similar. In order to ensure comparability between analyses, we only report results for $y \sim x$.

To compare rates of niche differentiation between sympatric and allopatric species pairs we fitted separate regression lines for the two categories. Additionally, we directly compared niche divergence between allopatric and sympatric species pairs using permutation-based *t*-tests (R package PERM v.1.0), to reduce the problem of pseudoreplication inherent in analyses of pairwise differences.

As a second analysis of niche conservatism, we calculated niche fill for each species (see previous paragraph). In a third analysis, we tested for phylogenetic signal in each niche variable using Blomberg's K and Pagel's λ. These were calculated for all phylogenies using the function *phylosig* in the R package PHYTOOLS v.0.3–72. This analysis characterizes the niche as the mean value of the climatic variable across all occurrence points of the focal species.

To test for a signal of competitive displacement, we first classified each comparison of two species within a clade (a 'species pair'). Each species pair was classified as 'allopatric *sensu stricto*', where the species only occur on separate islands, or as 'sympatric

sensu stricto', where the two species occur on the same set of islands and share at least one grid cell on each of those islands (because within-island allopatric speciation can cause species to co-occur on an island without ever co-existing). We excluded the few cases of species pairs co-occurring on an island but not sharing any grid cells. Our definition of allopatric and sympatric species pairs is therefore based on their current occurrence patterns, and it is possible that in some cases this does not reflect their mode of speciation. For example, some sympatric pairs may result from allopatric speciation followed by secondary dispersal (Lynch, 1989; Kozak & Wiens, 2006), while an apparently allopatric pair may result from sympatric speciation followed by migration to other islands or from extinction of a sympatric sister species. We suspect such instances are few, but in the absence of sufficiently well-resolved phylogenies we do not know for sure.

In a second analysis of competitive displacement, we extended our definition of sympatry to all cases where species co-occur (sharing at least one grid cell) on any island (no matter whether they also occur alone on other islands), and that of allopatry to all cases where species occur on different islands (no matter whether they also co-occur on others). We label these 'sympatric *sensu lato*' and 'allopatric *sensu lato*', respectively.

RESULTS

Niche conservatism predicts positive relationships between phylogenetic distance and climatic niche differentiation. For our data, while none of the relationships were significantly negative, most were non-significant, and significant ones were typically weak (Figs 3 & 4 and Appendices S3 & S4). Significant positive relationships were found for allopatric populations of both *Sonchus* and *Aeonium* for most climatic variables and the four-dimensional niche, and for allopatric populations of *Argyranthemum* with respect to maximum and annual precipitation (Figs 3 & 4). For sympatric populations, significant positive relationships were found for *Sonchus* (only for sympatric *sensu stricto*) with respect to all climatic niche variables except precipitation of the driest month, and in only 2 out of the 56 tests across the other species (less than the 5% error rate). Note that the sample size tended to be larger for allopatric species pairs than sympatric. Slopes were very rarely steeper for sympatric cases than for allopatric ones.

Niche conservatism also predicts characteristic ranges of values for Blomberg's K and Pagel's λ. Values of one indicate approximate accordance to Brownian motion, and represent a minimum requirement for niche conservatism. However, some definitions require values greater than one; Losos (2008, p. 996) defined phylogenetic niche conservatism as when 'closely related species are more ecologically similar than might be expected solely as a Brownian motion evolution'. We found most values to be less than one, and none were significantly greater than one (Table 1). Most were not significantly greater than zero: of 72 tests done, only 11 were significantly greater than zero at the 5% level, and only one at the 1% level (Table 1). Values for *Argyranthemum* and *Descurainia* are consistent with Brownian
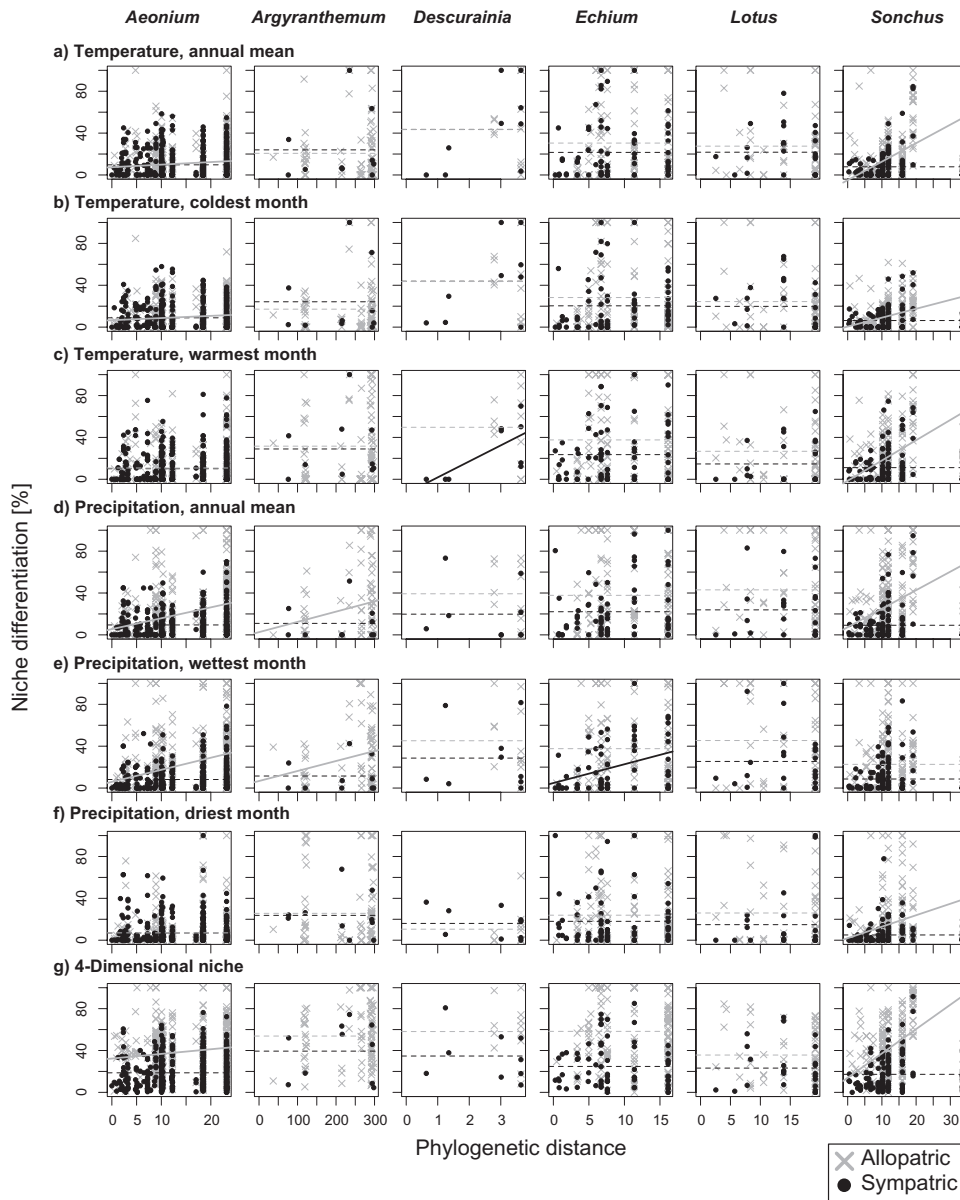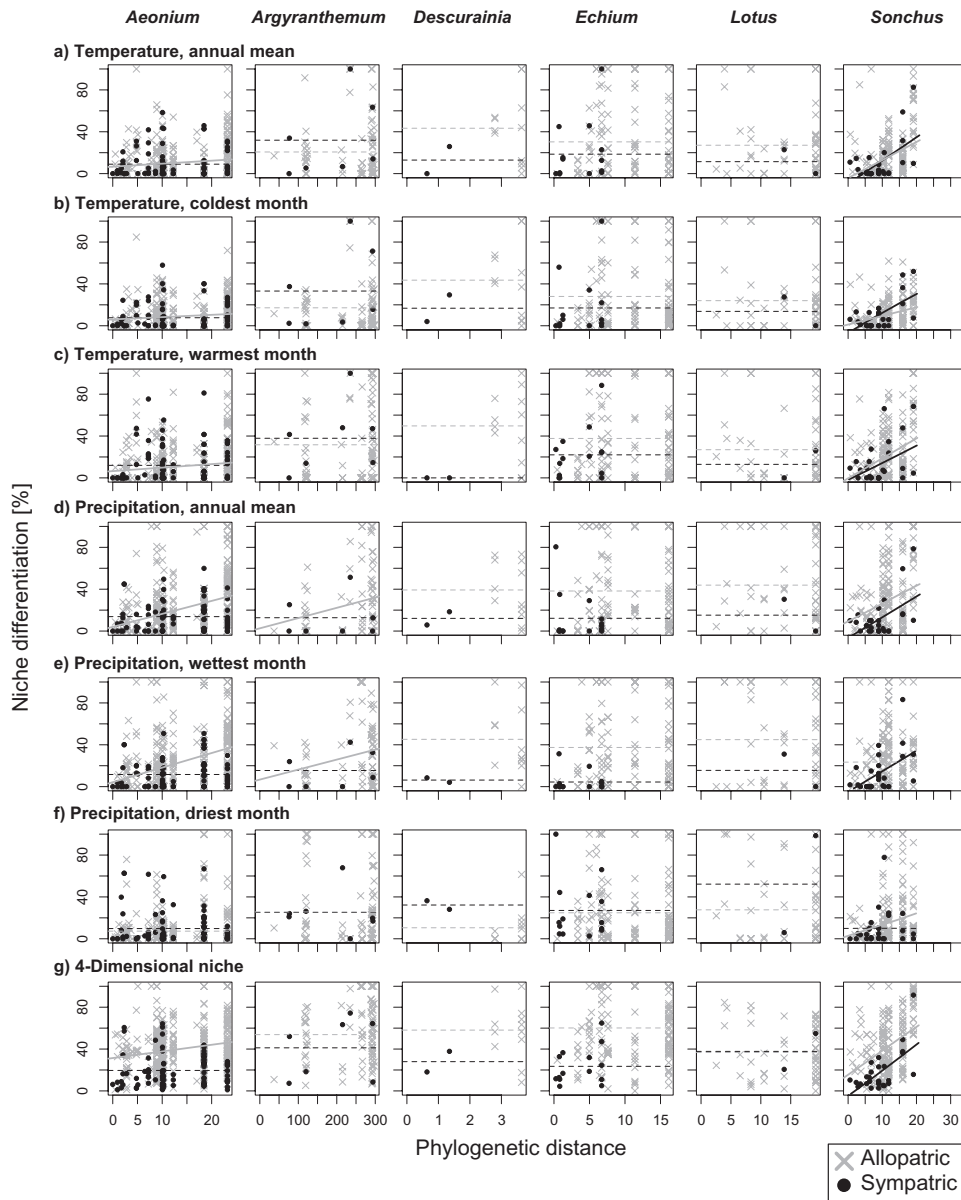
Figure 3 Niche differentiation versus phylogenetic distance for all pairwise comparisons of species within each clade, for each climatic variable. Allopatric (grey crosses, grey lines) species pairs are distinguished from sympatric (black circles, black lines) species pairs, *sensu lato* (see Methods). Solid regression lines indicate significant relationships between niche differentiation and phylogenetic distance ($P < 0.05$); dashed lines are flat and show non-significant relationships as the mean niche differentiation value.

motion-level niche conservatism for temperature, while values for the other clades across all climatic variables are more consistent with lower levels of climatic niche similarity than expected under Brownian motion evolution (Diniz-Filho *et al.*, 2012).

Another prediction of niche conservatism is that species will not fill the whole range of climates available on an island. Our measure of niche fill suggests that about 40% of the available range of temperature or precipitation is occupied by the investigated species, except for precipitation of the driest month and the four-dimensional niche, with niche fills averaging approximately 25% and 30% across the clades, respectively (Table 2).

Values of climatic niche overlap between species pairs, expressed as a percentage of the potential overlap (Table S5.1 in Appendix 5), were typically a little lower than for niche fill, but the trends in the values of the two measures were similar across climatic variables and clades.

Contrary to the prediction from the competitive displacement hypothesis, where significant differences in climatic niche differentiation between sympatry and allopatry were found in our main analyses, niche differentiation was always stronger in allopatry than in sympatry (Table 3; also compare Fig. 1a with Figs 3 & 4). These differences tended to be for precipitation in wetter periods (which correlates strongly with mean annual pre-

Figure 4 Niche differentiation versus phylogenetic distance for all pairwise comparisons of species within each clade, for each climatic variable. Allopatric (grey crosses, grey lines) species pairs are distinguished from sympatric (black circles, black lines) species pairs, *sensu stricto* (see Methods). Solid regression lines indicate significant relationships between niche differentiation and phylogenetic distance (*P* < 0.05); dashed lines are flat and show non-significant relationships as the mean niche differentiation value (note: regressions were not run for sympatric comparisons for *Descurainia* and *Lotus* because the sample size was equal to two).

cipitation) and not for temperature variables or precipitation of the driest month (Table 3), and were only manifest for the clades with the largest sample sizes (*Aeonium*, *Echium* and *Sonchus*). Using unconstrained niches produced similar but stronger results (Table S4.1, Figs S4.2 & S4.3 in Appendix S4).

DISCUSSION

Divergence of the climatic niches of closely related species was either greater in allopatry than in sympatry or not significantly different. This is in contrast to predictions based on the com-

petitive displacement hypothesis. We never found greater niche divergence in sympatry, despite conducting 42 tests (Table 3; this is also true for the equivalent 42 tests with unconstrained niches, Table S4.1 in Appendix S4). The same applied to all the near-significant differences (*P* < 0.10 or 0.20; Table 3 and Table S4.1 in Appendix S4).

There are various possible reasons for not finding the difference predicted by competitive displacement, which may help account for the fact that the majority of comparisons reported in Table 3 were not significant. The 'general dynamic model' of oceanic island biogeography (Whittaker *et al*., 2008) posits that,

Table 1 Blomberg's *K* and Pagel's *λ* for the six clades, rounded to two decimal places, for each of the six climatic variables. Values significantly greater than zero are indicated with asterisks (*0.01 < P < 0.05; **0.001 < P < 0.01); none of the values is significantly greater than one.

	Temperature			Precipitation		
	Annual	Coldest	Warmest	Annual	Wettest	Driest
Blomberg's *K*						
Aeonium	0.22	0.21	0.27*	0.23	0.18	0.20
Argyranthemum	0.99*	1.05*	0.84*	0.78	0.79	0.62
Descurainia	1.29	1.15	1.33	0.65	0.68	0.50
Echium	0.45*	0.39	0.38*	0.35	0.46**	0.14
Lotus	0.39	0.43	0.27	0.39	0.38	0.36
Sonchus	0.23	0.21	0.29*	0.41*	0.37*	0.14
Pagel's *λ*						
Aeonium	0.00	0.00	0.00	0.00	0.00	0.00
Argyranthemum	1.00	1.00*	1.00	0.59	1.00	0.15
Descurainia	1.19*	1.14	1.09	0.00	0.00	0.00
Echium	0.85	0.79	0.82*	0.69	0.73	0.00
Lotus	0.00	0.00	0.00	0.00	0.00	0.00
Sonchus	0.51	0.56	0.76	0.87	0.83	0.00

Table 2 Niche fill (see Fig. 2 for definitions and formulae) for the six climatic variables and the four-dimensional niche measure. There is one value per species, measuring niche fill across all the islands on which it occurs; the number of these datapoints (*n*) is given. Values shown are mean ± standard error of the mean (range).

Clade	Mean temperature	Mean precipitation	Four-dimensional niche
Aeonium	41.6 ± 2.3	50.8 ± 1.9	39.8 ± 3.2
n = 41	(19–74)	(23–77)	(7–86)
Argyranthemum	44.7 ± 5.1	46.9 ± 5.3	29.2 ± 5.4
n = 15	(13–74)	(26–92)	(3–65)
Descurainia	40.6 ± 5.0	41.2 ± 5.2	26.2 ± 6.1
n = 7	(22–62)	(16–55)	(12–50)
Echium	40.2 ± 4.2	45.5 ± 4.3	33.6 ± 4.8
n = 22	(14–81)	(13–80)	(2–79)
Lotus	36.8 ± 5.3	38.8 ± 5.2	26.7 ± 6.9
n = 14	(6–71)	(2–63)	(2–83)
Sonchus	39.6 ± 2.4	49.6 ± 2.9	34.9 ± 4.4
n = 27	(17–66)	(21–75)	(7–77)

	Warmest	Coldest	Wettest	Driest
Aeonium	40.7 ± 2.2	41.4 ± 2.5	47.5 ± 2.0	30.9 ± 2.6
n = 41	(18–79)	(17–76)	(25–69)	(3–63)
Argyranthemum	36.7 ± 4.1	46.3 ± 5.4	46.1 ± 4.6	25.5 ± 5.6
n = 15	(18–66)	(12–73)	(20–85)	(5–77)
Descurainia	38.1 ± 4.8	40.4 ± 5.0	43.1 ± 4.0	13.5 ± 2.6
n = 7	(26–61)	(19–59)	(30–60)	(3–23)
Echium	38.7 ± 3.9	40.5 ± 4.3	44.4 ± 3.5	26.7 ± 3.8
n = 22	(11–78)	(13–81)	(15–75)	(1–65)
Lotus	34.6 ± 5.3	36.5 ± 5.6	39.1 ± 5.1	22.0 ± 5.4
n = 14	(8–78)	(4–70)	(10–70)	(3–60)
Sonchus	41.7 ± 2.6	40.1 ± 2.7	46.8 ± 2.8	34.0 ± 3.9
n = 27	(15–70)	(16–66)	(26–72)	(3–76)

because of the geological and geomorphological dynamics of oceanic islands, environmental niche space may increase for millions of years. This would give multiple opportunities for niche differentiation and speciation without competitive displacement. Even so, classic cases of competitive displacement have been reported from oceanic archipelagos (e.g. Grant & Grant, 2006), and the flora of the Canary Islands evolved in the absence of mammalian herbivores (a characteristic of oceanic islands), which is likely to promote competition between plants, and thus competitive displacement. However, because of their isolation, oceanic islands are also characterized by low species richness, given their size and environmental setting (Whittaker & Fernández-Palacios, 2007). Further, species that colonize such islands tend to be good dispersers, but are often not good competitors (the competitive ability–dispersal capacity trade-off; Yu & Wilson, 2001).

Variable	Clade	Constrained niches
Temperature, mean annual	*Aeonium* (*n* = 41/800)	n.s.
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	n.s.
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	n.s.
Temperature, coldest month	*Aeonium* (*n* = 41/800)	n.s.
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	n.s.
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	n.s.
Temperature, warmest month	*Aeonium* (*n* = 41/800)	n.s.
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	n.s.
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	Allopatric, $P = 0.063$
Precipitation, mean annual	*Aeonium* (*n* = 41/800)	**Allopatric, *P* = 0.014**
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	**Allopatric, *P* = 0.017**
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	**Allopatric, *P* = 0.004**
Precipitation, wettest month	*Aeonium* (*n* = 41/800)	**Allopatric, *P* < 0.001**
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	**Allopatric, *P* = 0.002**
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	Allopatric, $P = 0.058$
Precipitation, driest month	*Aeonium* (*n* = 41/800)	n.s.
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	n.s.
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	n.s.
Four-dimensional niche (precipitation of wettest and driest month, temperature of warmest and coldest month)	*Aeonium* (*n* = 41/800)	**Allopatric, *P* < 0.001**
	Argyranthemum (*n* = 15/95)	n.s.
	Descurainia (*n* = 7/21)	n.s.
	Echium (*n* = 22/206)	**Allopatric, *P* < 0.001**
	Lotus (*n* = 14/73)	n.s.
	Sonchus (*n* = 27/333)	**Allopatric, *P* < 0.001**

Table 3 Whether sympatric or allopatric species pairs showed higher average niche differentiation within clades (column headed 'Constrained niches'), for the six climatic variables and the combined four-dimensional climatic niche. Where $P < 0.10$, as judged by a two-sample permutation test (function *permTs* in R-package PERM v.1.0), the type of pair (sympatric or allopatric) with the greater average niche differentiation is shown, along with the *P*-value. Those significant at the 5% level are indicated in bold; 'n.s.' indicates $P > 0.10$ (note: all n.s. were also $P > 0.20$). Note that most differences are not significant. Phylogenetic distance between pairs was not accounted for because it was largely uncorrelated with the niche differentiation indices (Figs 3 & 4). '*n*' indicates the number of sympatric/number of allopatric species pairs. Results are for constrained analyses; see Table S4.1 in Appendix 4 for results of unconstrained analyses.

While we found no evidence consistent with competitive displacement as a key process structuring biogeographic ranges, according to niche theory the divergence only needs to be in one niche dimension, which need not affect the climatic niche. However, given that trait changes underlie niche changes, and traits are the interface between species and their geographic ranges, even niche changes in non-climatic niche dimensions will tend to be reflected in changes in realized climatic niches when averaged across radiations – in the absence of strong climatic niche conservatism. And we did not find strong climatic niche conservatism; climatic niches of even the most closely related species were remarkably different, as discussed below.

In fact, there was a consistent trend in the opposite direction to that predicted by the competitive displacement hypothesis:

for significant cases, niche differentiation was always greater in allopatry than in sympatry (Table 3). The consistency of these significant (and near-significant) results is striking. Given that our analyses constrained the climatic niche space to what was available to both species in each comparison, this trend is explained neither by the relevant niche dimension being unrelated to the climatic niche nor by low levels of competition. While it is possible that the spatial regression kriging used in deriving the climate data may contribute to this finding (by making some geographically close locations artificially similar in climate), we suggest that the most parsimonious explanation starts by assuming that the climatic niches are very labile with respect to phylogeny. The numerous high niche differentiation values (Figs 3 & 4) suggest this. Climatic niches may thus

respond to the climatic opportunities on their islands (see Algar & Mahler, 2015), while the species remain range-restricted within their islands for other reasons (e.g. dispersal limitation). If so, the climatic niches of species occurring on different islands may differ more than those on the same island simply because different islands are different in many respects (e.g. age, evolutionary legacy, soils, biotic interactions).

Importantly, climatic settings may differ between islands; thus a species living in a dry, warm environment on one island might occur in warm but wetter places on another island if 'warm' is its key environmental niche condition. In such a case, populations on different islands will show greater niche differentiation in irrelevant variables (precipitation in this hypothetical example). Thus, with no phylogenetic signal we would expect allopatric cases to be most differentiated with respect to climatic variables that are less important for the species distributions. Indeed, it seems reasonable to suppose that precipitation in wetter periods (for which we find the strongest differentiation in allopatry) is less limiting than temperature or driest-month precipitation.

With respect to niche conservatism, most of the relationships between phylogenetic distance and climatic niche differentiation were not significant. Though weak at best, some relationships were significantly positive in our data, consistent with niche conservatism, and notably, none were significantly negative. In most cases the positive relationships largely reflected a lack of points in the top-left corners of the graphs (Figs 3 & 4, Appendices S3 & S4), which may indicate little more than the trivial fact that sister species have typically split recently.

Some degree of niche conservatism may be reflected in the fact that species on average filled no more than half of the climatic range available to them (Table 2). However, range restriction by dispersal limitation or other factors (e.g. human agency) could also account for such levels of niche fill. Indeed, most of the species ranges are small (Fig. S6.1 in Appendix S6). Further, values of Blomberg's K and Pagel's λ (Table 1) suggested typically less phylogenetic niche conservatism than expected from Brownian motion evolution. Although this does not definitively rule out phylogenetic niche conservatism (Wiens *et al.*, 2010), it suggests, in combination with our other findings, that niche conservatism is not a key structuring force for biogeographic ranges in these species.

Levels of climatic niche differentiation are also informative about the role of niche conservatism. These varied widely between closely related species (Figs 3 & 4, Fig. S3.1 in Appendix S3). Typically, the climatic niches of the most closely related species (phylogenetic distance near zero) were around 0–25% different. In some cases; however, the climatic niche differences of sister species were much higher, even 100% different (e.g. *Echium* for precipitation of the driest month; Fig. 3). These findings suggest that climatic niches can be very labile. The possibility of rapid changes in species niches (and thus the absence of prominent niche conservatism) is supported by the great diversity of climatic niches in the *in situ*-evolved species in this study. These demonstrate that, within a few million years, single colonizing species speciate into widely contrasting environmental settings, from harsh, high-elevation ecosystems to

dry lowland ecosystems. A prominent example is the genus *Echium*, which now fills the entire temperature and precipitation range of the Canary Islands (see also Stoecklin, 2011). Our results also mirror the rapid changes in trait variability with phylogenetic distance found by Ackerly (2009) and support scepticism towards assuming the omnipresence of niche conservatism (Losos, 2008).

The absence of a strong signal of climatic niche conservatism and the large amount of climatic niche lability therefore challenge the generality of niche conservatism as a fundamental structuring force – especially given that our results for competitive displacement are consistent with low levels of competition (strong competition would tend to separate realized niches within the same fundamental niche). These findings have potentially broad implications. For example, absent or weak influence of niche conservatism on biogeographic ranges brings into question prominent explanations for ecological phenomena like the latitudinal diversity gradient. The argument that higher tropical diversity results from the predominance of tropical-like climates during the Eocene (e.g. Wiens & Donoghue, 2004), for example, relies on climatic niche conservatism over longer time periods than those represented in our study.

Studies from continental systems (often mountains) have yielded mixed results, with some studies finding evidence consistent with niche conservatism in phylogenetically related species, and others not (Peterson *et al.*, 1999; Graham *et al.*, 2004; Kozak & Wiens, 2006). However, oceanic islands differ in several respects from continental systems, for which niche conservatism is mainly reported (e.g. Prinzing, 2001). First, oceanic islands have lower levels of biotic stress (e.g. from between-species competition, herbivory, predation and parasitism). For elevational gradients on continents, upward movement of species may typically be restricted by physiological tolerance (mainly the climatic niche), while downward range expansion is limited mainly by interspecific competition (Ghalambor *et al.*, 2006). It is possible that climatic niche conservatism mainly applies to cold (and dry) conditions. Many species face their physiological tolerance limits under drier and colder conditions (Currie *et al.*, 2004), and the diversifying clades of the Canary Islands tend to originate from non-tropical ancestors. Therefore, on oceanic islands, species may be able to evolve into a larger set of environmental conditions than in continental systems where this is hindered by the presence of more competitive species.

Our results are based on 500 m × 500 m grid cells spanning the entire archipelago, with its broad environmental ranges and phylogenetic time-scales that range back millions of years. The spatial resolution is finer than mostly used by species distribution models in macroecological analyses, but coarser than many ecological studies. Theoretically, niche differentiation at one spatial scale could be associated with niche conservatism at another, the effects cancelling each other out. For instance, populations of a species could become genetically isolated at very fine scales (e.g. by differentiating habitat preference into open and forest habitats with differing pollinators) but could retain their environmental niche on a much larger scale. However, while this would explain the absence of niche differ-

entiation in our results, it would be associated with a strong signal in niche conservatism – far from what we found.

We conclude that competitive displacement and niche conservatism may both be less important (at least for oceanic islands) in structuring biogeographic ranges than is usually considered. Given that our study is, to our knowledge, the first analysis of its type, we suggest that this is a fertile line of research, as fine-resolution datasets with more precise environmental information become available.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Supplemental material on phylogenetic data.
Appendix S2 Summary statistics per species.
Appendix S3 Niche differentiation–phylogenetic distance relationships for all species pairs.
Appendix S4 Results using unconstrained niches.
Appendix S5 Niche fill and overlap/potential overlap for four-dimensional niche space.
Appendix S6 Data quality and species distribution maps.

BIOSKETCHES

Manuel Steinbauer wants to understand biogeographic patterns and is particularly interested in scaling, dynamic communities, theoretical ecology and isolated systems like islands or mountains.

Richard Field's main interests are in biodiversity patterns, conservation biogeography (particularly with reference to tropical rain forests) and island biogeography.

Author contributions: M.S. and R.F. conceived the research, developed the methodology and wrote the manuscript. M.S. analysed the data. H.S. calculated the phylogenies. All authors contributed to the research design and commented on the results and the manuscript.

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