



The University of
Nottingham

UNITED KINGDOM · CHINA · MALAYSIA

Steinbauer, Manuel J. and Field, Richard and Fernández-Palacios, José-Maria and Irl, Severin D.H. and Rüdiger, Otto and Schaefer, Hanno and Beierkuhnlein, Carl (2016) Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Global Ecology and Biogeography*, 25 (7). pp. 792-804. ISSN 1466-8238

Access from the University of Nottingham repository:

http://eprints.nottingham.ac.uk/34329/1/GEB-2014-0306_R4%20Steinbauer%20et%20al.pdf

Copyright and reuse:

The Nottingham ePrints service makes this work by researchers of the University of Nottingham available open access under the following conditions.

This article is made available under the University of Nottingham End User licence and may be reused according to the conditions of the licence. For more details see: http://eprints.nottingham.ac.uk/end_user_agreement.pdf

A note on versions:

The version presented here may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the repository url above for details on accessing the published version and note that access may require a subscription.

For more information, please contact eprints@nottingham.ac.uk



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

Journal:	<i>Global Ecology and Biogeography</i>
Manuscript ID	GEB-2014-0306.R4
Manuscript Type:	Special Issue Article
Date Submitted by the Author:	21-Nov-2015
Complete List of Authors:	Steinbauer, Manuel; University of Bayreuth, Department of Biogeography Field, Richard; University of Nottingham, School of Geography; Fernandez-Palacios, Jose-Maria; Universidad de La Laguna, Instituto Universitario de Enfermedades Tropicales y Salud Pública. de Canarias (IUETSPC) Irl, Severin; University of Bayreuth, Disturbance Ecology Otto, Rüdiger; Universidad de La Laguna, Instituto Universitario de Enfermedades Tropicales y Salud Pública. de Canarias (IUETSPC) Schäfer, Hanno ; Technische Universität München, Biodiversitaet der Pflanzen Beierkuhnlein, Carl; University of Bayreuth, Department of Biogeography
Keywords:	competition, niche conservatism, ecological character displacement, climate, endemic plants, sister clades, adaptive radiation, speciation, divergence, ghost of competition past

1
2
3 1 **Biogeographic ranges do not support niche theory in radiating**
4 2 **Canary Island plant clades**

5
6 3 Manuel J. Steinbauer^{1,2*}, Richard Field^{3*}, José-Maria Fernández-Palacios⁴, Severin D.H. Irl¹,
7 4 Rüdiger Otto⁴, Hanno Schaefer⁵, Carl Beierkuhnlein¹

8
9 5 ¹ *Department of Biogeography, Bayreuth Center of Ecology and Environmental Research*
10 6 *BayCEER, University of Bayreuth, D-95447 Bayreuth, Germany*

11 7 ² *Section Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, DK-*
12 8 *8000 Aarhus, Denmark*

13 9 ³ *School of Geography, University of Nottingham, University Park, Nottingham, UK*

14 10 ⁴ *Island Ecology and Biogeography Research, Group, Instituto Universitario de*
15 11 *Enfermedades Tropicales y Salud Pública de Canarias, Universidad de La Laguna,*
16 12 *La Laguna, 38206, Tenerife, Spain,*

17 13 ⁵ *Department of Ecology and Ecosystem Management, Technische Universitaet Muenchen,*
18 14 *D-85354 Freising, Germany*

19 15
20 16 ** Both authors equally contributed to the manuscript*

21 17
22 18 **Running title:** Niche theory in radiating Canary Island plant clades

23 19 **Corresponding author:** Manuel Steinbauer (Manuel.Steinbauer@bios.au.dk)

24 20 **Words count Abstract:** 300

25 21 **Word count main text:** 5402

26 22 **References:** 53
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

23 Abstract

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

34 **Location:** Canary Islands.

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

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

46 **Main conclusions:** The expectations from niche conservatism were frequently not met;
47 instead our results suggest considerable climatic niche lability. All significant differences in
48 climatic niche differentiation were opposite to the predictions from competitive displacement.

1
2
3 49 These forces may be less important in structuring biogeographic ranges than is commonly
4
5 50 thought, at least on islands.

6
7 51

8
9
10 52 **Keywords:** competition, niche conservatism, ecological character displacement, adaptive
11
12 53 radiation, climate, endemic plants, sister clades, speciation, divergence, ghost of competition
13
14 54 past.

15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Peer Review

55 Introduction

56 Understanding the environmental factors that influence the local occurrence and persistence
57 of species is one of the most fundamental tasks in ecology. Similarly, understanding what
58 determines species' ranges is fundamental to biogeography. Prominent in both are concepts
59 of species' niches, which relate to both environmental conditions (Grinnell, 1917) and biotic
60 interactions (Elton 1927). The Hutchinsonian niche concept, which views the niche as n-
61 dimensional hypervolume defined by environmentally related niche axes (Hutchinson, 1957)
62 is the fundament of current assessments of species' niches (Blonder et al., 2014), including
63 species distribution modelling (Pearson & Dawson, 2003; Duputié et al., 2014). The niches of
64 species are thus critical to both biogeography and ecology, and the evolution of climatic
65 niches is an area of particular current interest (e.g. Kozak & Wiens, 2006; Algar et al., 2013;
66 Algar & Mahler, 2015).

67 Niche theory originated in ecology, but the concepts have been applied to
68 biogeography, based on the assumption that what happens to individuals within communities
69 should scale up to populations and species' ranges. Species distribution modelling can work
70 well for interpolation, but is not designed to delineate the boundaries of a fundamental
71 environmental niche (Blonder et al., 2014). Such models risk calculating unbounded niches if
72 species' occurrence is modelled as increasing (unchecked) with environmental variables
73 whose global range is not captured by the dataset being used. Further, studies with invading
74 plant species have often not found a tight fit between native and alien niches (e.g.
75 Broennimann et al., 2007; Early & Sax, 2014), perhaps because of enemy release,
76 suggesting that the relationship between fundamental and realized niches may be weak.
77 Neutral theories, such as Hubbell's (2001), demonstrate that biogeographic patterns can be
78 modelled remarkably well without ecological differentiation between species. More generally,
79 attempts to scale to biogeographic patterns from ecological mechanisms, determined using
80 reductionist approaches at very local level, have met with mixed success at best.

1
2
3 81 Niche conservatism and competitive displacement are two fundamental concepts
4
5 82 related to niche evolution (Kozak & Wiens, 2006). The two may operate simultaneously (and
6
7 83 independently), but differ in their hypothesized influence on the evolution of environmental
8
9 84 niches of closely related species (Ackerly 2009). Niche conservatism is put forward as a
10
11 85 hypothesis to explain major biogeographic patterns such as the increase in species richness
12
13 86 towards the tropics (latitudinal diversity gradient; Wiens & Donoghue, 2004) or the tendency
14
15 87 of major plant clades to be restricted to one or few biomes (Prinzing et al., 2001; Donoghue,
16
17 88 2008). It is reasoned that closely related species should share similar environmental niche
18
19 89 conditions (Wiens & Graham, 2005; Wiens et al., 2010). Because niche lability is inevitable to
20
21 90 a certain degree with time (under perfect niche conservatism there would be no evolution),
22
23 91 niche conservatism predicts an increase in climatic niche difference (decrease in climatic
24
25 92 niche similarity) between species with increasing phylogenetic distance.

26
27
28 93 In contrast, the idea that competition is a key structuring force in ecological
29
30 94 communities has led to the notion of competitive displacement, the textbook argument being
31
32 95 that ecologically similar species should rapidly diverge if they coexist in the same area
33
34 96 (Abrams 1983, Begon et al., 2006). This could involve mechanisms of niche partitioning that
35
36 97 allow coexistence within the same locations ('ecological character displacement'; Brown &
37
38 98 Wilson, 1956). It could also involve geographical divergence; in an island context, the taxon
39
40 99 cycle (Wilson 1961; Ricklefs & Bermingham, 2002), for example, suggests that competition
41
42 100 causes species to evolve into different environments within the same island. Given that
43
44 101 species' traits form the interface between species and their environment, and that
45
46 102 environment (including resource distributions and climate) tends to be spatially
47
48 103 autocorrelated, trait shifts resulting from competition between two species should be
49
50 104 reflected in differences in their climatic niches. Thus, competitive displacement should result
51
52 105 in a tendency for recently diverged species living on the same island to differ in their climatic
53
54 106 niches, opposing the expectation from niche conservatism. There should be less such
55
56 107 tendency when the species live on different islands. Similarly, within islands, niche

1
2
3 108 differentiation is usually required for genetic isolation and speciation, whereas the barrier
4
5 109 provided in archipelagos by the sea may be all that is required for speciation to happen
6
7 110 between islands. Thus, in an oceanic archipelago setting, the theoretical expectation from
8
9 111 these competitive divergence mechanisms is for climatic niches of recently diverged, closely
10
11 112 related species to be more different for species of sympatric origin than for species of
12
13 113 allopatric origin.

14
15 114 Oceanic archipelagos such as the Canary Islands offer an opportunity to identify links
16
17 115 between ecological processes and emergent biogeographic patterns because they provide a
18
19 116 natural experimental setup. This is important and required because biogeographic patterns
20
21 117 are not amenable to manipulative experimentation. Each radiation in such archipelagos
22
23 118 contains replicate populations (on the different islands), from replicate evolutionary episodes
24
25 119 (speciations) that are phylogenetically controlled (same relatively small clade) and represent
26
27 120 the entire native range of almost all the species' populations, within approximately the same
28
29 121 geographic setting as that in which they evolved. All of this is replicated by the different
30
31 122 radiations. While in continental settings many species' distributions may be influenced by
32
33 123 dispersal lags from ice age refugia, and thus in disequilibrium with their climatic niche
34
35 124 (Normand et al., 2011), the large elevational gradient and thus low climate change velocity
36
37 125 removes this effect for islands. Utilizing these advantages offered by the Canary Islands
38
39 126 enables us to test for signatures of key ecological and evolutionary processes, by combining
40
41 127 island biogeographic patterns and a macroecological approach across all species of radiating
42
43 128 clades.

44
45
46 129 This approach differs fundamentally from previous studies that were based on the
47
48 130 different 'natural experimental' approach of comparing pairs of species in allopatry versus
49
50 131 sympatry to test for character displacement. Classically, the possibility of divergence driven
51
52 132 by competition has been studied by seeking pairs of species that are more divergent in
53
54 133 sympatry than in allopatry and then trying to determine whether that difference can be
55
56 134 attributed to competition (e.g. Brown & Wilson, 1956; Schluter & McPhail, 1992). In other

1
2
3 135 words: seeking cases that seem to fit the predicted pattern and then trying to infer whether
4
5 136 the process or mechanism applies. Here, we change the perspective. We start with the
6
7 137 mechanisms, specifying biogeographic patterns they predict, and use a large set of
8
9 138 comparisons between closely related species to test whether the predicted patterns are
10
11 139 found more often than expected by chance. We then repeat this process for five other,
12
13 140 separate sets of comparisons (six radiations in total). To our knowledge, this is the first
14
15 141 attempt at such an analysis, probably because it is rare to have a large set of closely related
16
17 142 species with sufficient, systematic information on the species' climatic niches, distributions
18
19 143 and phylogenetic relatedness, coupled with an appropriate natural experimental setup.

20
21
22 144 On island archipelagos such as the Canary Islands, the two fundamental hypotheses
23
24 145 (niche conservatism and competitive displacement) predict testable patterns of climatic niche
25
26 146 differentiation among species of the same clade (where theoretically each clade results from
27
28 147 a single colonization), in relation to the evolutionary histories and biogeographic settings of
29
30 148 the species. For any comparison of two species, both species may exist on different islands,
31
32 149 or on the same island(s), or there may be a mixture of co-occurrence and separate
33
34 150 occurrence on islands across the archipelago. The mechanism of speciation (especially
35
36 151 sympatric vs. allopatric) is likely to be reflected in occurrence patterns in most within-
37
38 152 radiation comparisons, though we cannot test for the driving mechanisms with available
39
40 153 genetic data.

41
42 154 As depicted in Figure 1, divergence hypotheses predict that two sympatric species (or
43
44 155 sympatric populations of two species) within a clade should differ in their climatic niches
45
46 156 more than allopatric ones. Not all niche divergence will be reflected in the climatic niche, but
47
48 157 as argued above, a signal of it should be detectable in the climatic niches if competitive
49
50 158 displacement is a key structuring force. Thus we may expect greater climatic niche
51
52 159 differentiation in sympatry than in allopatry, controlling for phylogenetic distance (Figure 1a).
53
54 160 If competition between the closest relatives (or most-similar species) is strongest, then this
55
56 161 difference should be greatest for short phylogenetic distances. Sympatric–allopatric

1
2
3 162 differences should modify an overall trend, predicted by the niche conservatism hypothesis,
4
5 163 for closely related species to be more similar in their climatic niches (Figure 1a) than more
6
7 164 distantly related species – a trend that should be apparent for allopatric species or
8
9 165 populations, regardless of any competitive displacement. Thus we may also expect niche
10
11 166 difference to increase with phylogenetic distance.

12
13
14 167 Here we test these predictions using fine-resolution occurrence data for species in
15
16 168 radiating plant lineages in the Canary Islands. Almost all these species (123 of 126) are
17
18 169 endemic to the archipelago, and therefore our data cover their entire global range; the
19
20 170 exceptions are species that have dispersed from the archipelago (e.g. to Madeira). The
21
22 171 climatic niche of a species represents those climatic conditions in which a species can
23
24 172 survive, grow and/or reproduce (depending on the definition). In most niche estimations, and
25
26 173 niche modelling techniques, these climatic conditions are estimated from the occurrence
27
28 174 records of species, an approach particularly suitable for non-mobile organisms (like plants).

29
30 175 We focus mainly on the response variable climatic niche differentiation (hereafter
31
32 176 'niche differentiation'). Metapopulations that develop into independent species are expected
33
34 177 to (gradually with time) differentiate in their climatic niche. Once reproductive isolation has
35
36 178 been effective (speciation takes place), this process of niche differentiation continues. Niche
37
38 179 differentiation measures the degree to which the (climatic) niches of two related species have
39
40 180 diverged during the time since splitting from a common ancestor.

41
42
43 181

44 45 182 **Methods**

46 47 48 183 **Data for species and environmental variables**

49
50
51 184 We selected six clades (alliances approximating genera) in the Canary Island's flora with
52
53 185 well-resolved phylogenetic relationships: *Aeonium* (41 species), *Argyranthemum* (15
54
55 186 species), *Descurainia* (7 species), *Echium* (22 species), *Lotus* (14 species) and *Sonchus* (27

1
2
3 187 species). Within each clade, we statistically related phylogenetic distance to niche
4
5 188 differentiation, as outlined in the 'Analyses' section below.
6

7
8 189 Phylogenies were calculated from plastid and nuclear DNA sequence alignments,
9
10 190 based on the sequences produced by García-Maroto et al. (2009) for *Echium*, Lee et al.
11
12 191 (2005) for *Sonchus*, Mort et al. (2002) for *Aeonium* and relatives, Goodson et al. (2006) for
13
14 192 *Descurainia*, and Ojeda et al. (2011) for *Lotus*. We downloaded these sequences from the
15
16 193 GenBank database (www.ncbi.nlm.nih.gov/genbank; see Table S1.1 for details of DNA
17
18 194 regions used). The nuclear and plastid DNA regions were first analysed separately, and in
19
20 195 the absence of significant topological conflict (indicated by topological differences with
21
22 196 bootstrap values > 70) the plastid and nuclear datasets were analysed in combination. We
23
24 197 reconstructed time-calibrated phylogenies in Beast v. 1.8.0 (Drummond et al., 2012) using a
25
26 198 Bayesian relaxed clock approach with lognormal distribution. We used the GTR+G
27
28 199 substitution model and the four Monte Carlo Markov chains were run for 50 million
29
30 200 generations, with sampling every 1000 generations. Calibration of the clock relied on island
31
32 201 ages and/or secondary calibration using previously published age estimates (see Table S1.1
33
34 202 for details). Convergence of the chains was checked by ensuring that effective sampling
35
36 203 sizes had all exceeded 200 using the program TRACER 1.5 (Rambaut & Drummond, 2010).
37
38 204 TreeAnnotator v. 1.8.2, part of the BEAST package (Drummond et al., 2012), was then used
39
40 205 to remove the first 10 % of the sampled trees and to compute a maximum clade credibility
41
42 206 tree from the remaining trees, with the mean divergence ages shown at the nodes. We finally
43
44 207 determined phylogenetic distances using the branch lengths of the resulting chronograms.
45
46 208 Our phylogenetic distance measure thus represents the best estimate of the time since two
47
48 209 extant species shared a common ancestor. The phylogeny for *Argyranthemum* was directly
49
50 210 extracted from Francisco-Ortega et al. (1996) and is of lower quality, with phylogenetic
51
52 211 distance not time-calibrated. Non-monophyletic taxa and those that we could not match to
53
54 212 occurrence data were removed from the analysis (the numbers of species per clade reported
55
56 213 in the previous paragraph exclude these removed taxa).
57
58
59
60

1
2
3 214 Species' occurrence data were taken from 500m x 500m grid cells that span the
4
5 215 entire Canary Islands (Atlantis 3.1) and represent a long-term governmental initiative to
6
7 216 assemble and complete all known distribution records of species on the Canary Islands.
8
9 217 Quality of the Atlantis data is variable but is particularly good for endemic-rich clades like the
10
11 218 ones investigated here (see supporting information S6 for further information on data quality,
12
13 219 including validation with independent data). For the species used in this study, the mean
14
15 220 number of occupied grid cells per species was 976 (median 578; see Table S2.1; Figure
16
17 221 S6.1 shows the distribution maps), which is more than sufficient for determining climatic
18
19 222 envelopes. *Lotus* initially had 17 species, but we removed three because of their very small
20
21 223 natural range (*L. eremiticus*, *L. maculatus*, *L. pyranthus*). *Lotus eremiticus*, for instance, is
22
23 224 known to have only one natural occurrence record, which probably comprises ramets of a
24
25 225 single genet, making the species unsuitable for niche calculations. The range in numbers of
26
27 226 cells occupied by the remaining species was large (17–5126), with 14 of the 126 species
28
29 227 having fewer than 100 records, including seven with fewer than 50. These species with few
30
31 228 occurrence points are all known to have small ranges, and our experience of the islands
32
33 229 suggests that our data represent good matches for the species' actual ranges (Figure S6.1)

34
35
36 230 We quantified climatic niches using monthly temperature and precipitation data, which
37
38 231 were interpolated from climate station data (provided by Agencia Estatal de Meteorología)
39
40 232 using spatial regression kriging (see Irl et al., 2015). Given that mean grid-cell elevation is
41
42 233 strongly co-linear with mean annual temperature ($r = -0.95$), and was used in the
43
44 234 interpolation of the temperature values from climate station data, we did not additionally
45
46 235 include elevation in our analyses. We used six climatic variables: mean annual temperature,
47
48 236 mean annual precipitation, mean temperature of the warmest and coldest months (August
49
50 237 and January, respectively) and mean precipitation of the wettest and driest months
51
52 238 (December and July, respectively). These represent both mean and extreme conditions, and
53
54 239 perform better in accounting for species' distributions than other variables (e.g. spring,
55
56 240 summer, autumn and winter temperature and precipitation; data not shown).

241

242 Calculation of climatic niches and indices comparing climatic niches

243 We calculated species' climatic niches using grid-cell-mean temperature and precipitation
244 values. For each climatic variable, we measured the niche as ranging from the 5% to the
245 95% quantiles of all grid cells where the species was recorded as present (Figure 1). This
246 was to reduce bias caused by errors that would artificially inflate the estimates of niche
247 breadth, in particular: (a) from any false presences of a species outside of its actual range;
248 and (b) from true presences at the edges of cells with large ranges of the climatic variable.
249 An example of (b) would be when a species restricted to relatively low elevations is recorded
250 in a cell that has a large topographic range: its presence is at the lowest elevations but the
251 average elevation of the cell would be well above the elevational range of the species, so the
252 resulting value for temperature (the average for the cell) would be incorrect for the species.
253 Other quantile thresholds (lower: 0–25%; higher: 100–75%) were also implemented and
254 produced qualitatively similar results. Additionally to these one-dimensional niche range
255 estimations, we applied multidimensional niche range estimates using the R package
256 *hypervolume* version 1.3 (Blonder et al., 2014; bandwidth fixed at 0.05), using four variables:
257 warmest-month and coldest-month temperature, wettest-month and driest-month
258 precipitation. Because multidimensional niche estimations are very sensitive to the choice of
259 units and transformations (Petchey & Gaston, 2006), we rescaled untransformed
260 environmental axes to range between 0 and 1.

261 Niche differentiation between two species was quantified as the percentage of the
262 climatic niche space (niche space was measured in units of climate, e.g. °C or mm) of the
263 smaller-niched species that does not overlap the larger one (Figure 2). This converts an
264 approach successfully applied for geographic range overlap (Barraclough & Vogler 2000;
265 Anacker & Strauss, 2014) to climatic niche space. Niche differentiation was calculated for all
266 occurrence records of the two species ('unconstrained'), and separately by restricting the
267 analyses to the climatic space that is shared between the two sets of islands occupied by the

1
2
3 268 two species ('constrained'). The results we present in the paper are for the constrained
4
5 269 analyses; results from the unconstrained analyses are documented in the Supplementary
6
7 270 material.

8
9 271 In addition, we calculated 'niche fill' (measuring the degree to which each species
10
11 272 occupies all the climatic space available on its island, or islands, within the archipelago) and
12
13 273 'overlap/potential overlap' of climatic niches between two species. For example, for
14
15 274 temperature, niche fill is the range of temperatures occupied by a given species as a
16
17 275 percentage of the range of temperatures that exist on the islands on which it occurs;
18
19 276 'overlap/potential overlap' is the range of temperatures shared by two species, as a
20
21 277 percentage of the range of temperatures shared by the two sets of islands they occupy.
22
23 278 These indices were calculated for each climatic variable separately, and for the four-
24
25 279 dimensional niche estimation. Figure 2 illustrates these indices and gives the formulae for
26
27 280 their calculation.

28
29
30 281

31 32 282 **Analyses**

33
34
35 283 To test for a signal of niche conservatism, we compared all species of a clade with each
36
37 284 other (not just sister taxa), in a pairwise manner, and correlated the phylogenetic distance
38
39 285 between them with their niche differentiation (Figure 1a). In all cases, we related niche
40
41 286 differentiation to phylogenetic distance using linear models with three different
42
43 287 transformations: $y \sim x$, $y \sim \ln(x)$ and $y \sim \sqrt{x}$. These transformations were compared using
44
45 288 diagnostic plots of model residuals; in all cases, this demonstrated little meaningful difference
46
47 289 between the transformations and the adjusted R^2 values were very similar. In order to ensure
48
49 290 comparability between analyses, we only report results for $y \sim x$.

50
51
52 291 To compare rates of niche differentiation between sympatric and allopatric species
53
54 292 pairs, we fitted separate regression lines for the two categories. Additionally, we directly
55
56 293 compared niche divergence between allopatric and sympatric species pairs using

1
2
3 294 permutation-based t-tests (R package *perm* version 1.0), to reduce the problem of
4
5 295 pseudoreplication inherent to analyses of pairwise differences.
6

7 296 As a second analysis of niche conservatism, we calculated niche fill for each species
8
9 297 (see previous paragraph). In a third analysis, we tested for phylogenetic signal in each niche
10
11 298 variable using Blomberg's K and Pagel's λ . These were calculated for all phylogenies using
12
13 299 the function *phylosig* in the R package *phytools* version 0.3-72. This analysis characterizes
14
15 300 the niche as the mean value of the climatic variable across all occurrence points of the focal
16
17 301 species.
18

19
20 302 To test for a signal of competitive displacement, we first classified each comparison of
21
22 303 two species within a clade (a 'species pair'). Each species pair was classified as 'allopatric
23
24 304 *sensu stricto*', where the species only occur on separate islands, or as 'sympatric *sensu*
25
26 305 *stricto*', where the two species occur on the same set of islands and share at least one grid
27
28 306 cell on each of those islands (because within-island allopatric speciation can cause species
29
30 307 to co-occur on an island without ever co-existing). We excluded the few cases of species
31
32 308 pairs co-occurring on an island but not sharing any grid cells. Our definition of allopatric and
33
34 309 sympatric species pairs is therefore based on their current occurrence patterns, and it is
35
36 310 possible that in some cases this does not reflect their mode of speciation. For example,
37
38 311 some sympatric pairs may result from allopatric speciation followed by secondary dispersal
39
40 312 (Lynch, 1989; Kozak & Wiens, 2006), while an apparently allopatric pair may result from
41
42 313 sympatric speciation followed by migration to other islands or from extinction of a sympatric
43
44 314 sister-species. We suspect such instances are few, but in the absence of sufficiently well-
45
46 315 resolved phylogenies, we do not know for sure.
47

48
49 316 In a second analysis of competitive displacement, we extended our definition of
50
51 317 sympatry to all cases where species co-occur (sharing at least one grid cell) on any islands
52
53 318 (no matter whether they also occur alone on other islands), and that of allopatry to all cases
54
55 319 where species occur on different islands (no matter whether they also co-occur on others).
56
57 320 We label these 'sympatric *sensu lato*' and 'allopatric *sensu lato*', respectively.
58

1
2
3 3214
5 322 **Results**

6
7
8 323 Niche conservatism predicts positive relationships between phylogenetic distance and
9 324 climatic niche differentiation. For our data, while none of the relationships were significantly
10 325 negative, most were non-significant, and significant ones were typically weak (Figures 3–4
11 326 and Supplements S3–S4). Significant positive relationships were found for allopatric
12 327 populations of both *Sonchus* and *Aeonium* for most climatic variables and the four-
13 328 dimensional niche, and for allopatric populations of *Argyranthemum* with respect to maximum
14 329 and annual precipitation (Figures 3–4). For sympatric populations, significant positive
15 330 relationships were found for *Sonchus* (only for sympatric *sensu stricto*) with respect to all
16 331 climatic niche variables except driest-month precipitation, and in only two out of the 56 tests
17 332 across the other species (less than the 5% error rate). Note that the sample size tended to
18 333 be larger for allopatric species pairs than sympatric. Slopes were very rarely steeper for
19 334 sympatric cases than for allopatric ones.

20
21
22
23
24
25
26
27
28
29
30
31
32
33 335 Niche conservatism also predicts characteristic ranges of values for Blomberg's K
34 336 and Pagel's λ . Values of 1 indicate approximate accordance to Brownian motion, and
35 337 represent a minimum requirement for niche conservatism. However, some definitions require
36 338 values greater than 1; Losos (2008: 996) defined phylogenetic niche conservatism as when
37 339 'closely related species are more ecologically similar than might be expected solely as a
38 340 Brownian motion evolution'. We found most values to be less than 1, and none were
39 341 significantly greater than 1 (Table 1). Most were not significantly greater than 0: of 72 tests
40 342 done, only 11 were significantly greater than 0 at the 5% level, and only one at the 1% level
41 343 (Table 1). Values for *Argyranthemum* and *Descurainia* are consistent with Brownian motion-
42 344 level niche conservatism for temperature, while values for the other clades across all climatic
43 345 variables are more consistent with lower levels of climatic niche similarity than expected
44 346 under Brownian motion evolution (Diniz-Filho *et al.*, 2012).

1
2
3 347 Another prediction of niche conservatism is that species will not fill the whole range of
4
5 348 climates available on an island. Our measure of niche fill suggests that about 40% of the
6
7 349 available range of temperature or precipitation is occupied by the investigated species,
8
9 350 except for driest-month precipitation and the four-dimensional niche, with niche fills
10
11 351 averaging approximately 25% and 30% across the clades, respectively (Table 2). Values of
12
13 352 climatic niche overlap between species pairs, expressed as a percentage of the potential
14
15 353 overlap (Table S5.1), were typically a little lower than for niche fill, but the trends in the
16
17 354 values of the two measures were similar across climatic variables and clades.

18
19
20 355 Contrary to the prediction from the competitive displacement hypothesis, where
21
22 356 significant differences in climatic niche differentiation between sympatry and allopatry were
23
24 357 found in our main analyses, niche differentiation was always stronger in allopatry than in
25
26 358 sympatry (Table 3; also compare Fig. 1a with Figs 3–4). These differences tended to be for
27
28 359 precipitation in wetter periods (which correlates strongly with mean annual precipitation), and
29
30 360 not for temperature variables or driest-month precipitation (Table 3), and were only manifest
31
32 361 for the clades with the largest sample sizes (*Aeonium*, *Echium* and *Sonchus*). Using
33
34 362 unconstrained niches produced similar but stronger results (Table S4.1; Figs S4.2–S4.3).

35
36
37 363

38 39 364 **Discussion**

40
41
42 365 Divergence of the climatic niches of closely related species was either greater in allopatry
43
44 366 than in sympatry or not significantly different. This is in contrast to predictions based on the
45
46 367 competitive displacement hypothesis. We never found greater niche divergence in sympatry,
47
48 368 despite conducting 42 tests (Table 3; this is also true for the equivalent 42 tests with
49
50 369 unconstrained niches, Table S4.1). The same applied to all the near-significant differences
51
52 370 ($P < 0.10$ or 0.20 ; Tables 3 and S4.1).

53
54
55 371 There are various possible reasons for not finding the difference predicted by
56
57 372 competitive displacement, which may help account for the fact that the majority of

1
2
3 373 comparisons reported in Table 3 were not significant. The 'General Dynamic Model' of
4
5 374 oceanic island biogeography (Whittaker *et al.*, 2008) posits that, because of the geological
6
7 375 and geomorphological dynamics of oceanic islands, environmental niche space may
8
9 376 increase for millions of years. This would give multiple opportunities for niche differentiation
10
11 377 and speciation without competitive displacement. Even so, classic cases of competitive
12
13 378 displacement have been reported from oceanic archipelagos (e.g. Grant & Grant, 2006), and
14
15 379 the flora of the Canary Islands evolved in the absence of mammalian herbivores
16
17 380 (characteristic for oceanic islands), which is likely to promote competition between plants,
18
19 381 and thus competitive displacement. However, because of their isolation, oceanic islands are
20
21 382 also characterized by low species richness, given their size and environmental setting
22
23 383 (Whittaker & Fernández-Palacios, 2007). Further, species that colonize such islands tend to
24
25 384 be good dispersers, but are often not good competitors (competitive ability–dispersal
26
27 385 capacity trade-off; Yu and Wilson, 2001).

28
29
30 386 While we found no evidence consistent with competitive displacement as a key
31
32 387 process structuring biogeographic ranges, according to niche theory the divergence only
33
34 388 needs to be in one niche dimension, which need not affect the climatic niche. However, given
35
36 389 that trait changes underlie niche changes, and traits are the interface between species and
37
38 390 their geographic ranges, even niche changes in non-climatic niche dimensions will tend to be
39
40 391 reflected in changes in realized climatic niches when averaged across radiations – in the
41
42 392 absence of strong climatic niche conservatism. And we did not find strong climatic niche
43
44 393 conservatism; climatic niches of even the most closely related species were remarkably
45
46 394 different, as discussed below.

47
48
49 395 In fact, there was a consistent trend in the opposite direction of that predicted by the
50
51 396 competitive displacement hypothesis: for significant cases, niche differentiation was always
52
53 397 greater in allopatry than in sympatry (Table 3). The consistency of these significant (and
54
55 398 near-significant) results is striking. Given that our analyses constrained the climatic niche
56
57 399 space to what was available to both species in each comparison, this trend is explained

1
2
3 400 neither by the relevant niche dimension being unrelated to the climatic niche, nor by low
4
5 401 levels of competition. While it is possible that the spatial regression kriging used in deriving
6
7 402 the climate data may contribute to this finding (by making some geographically close
8
9 403 locations artificially similar in climate), we suggest that the most parsimonious explanation
10
11 404 starts by assuming that the climatic niches are very labile with respect to phylogeny. The
12
13 405 numerous high niche differentiation values (Figs 3–4) suggest this. Climatic niches may thus
14
15 406 respond to the climatic opportunities on their islands (see Algar & Mahler, 2015), while the
16
17 407 species remain range-restricted within their islands for other reasons (e.g. dispersal
18
19 408 limitation). If so, the climatic niches of species occurring on different islands may differ more
20
21 409 than those on the same island simply because different islands are different in many
22
23 410 respects (e.g. age, evolutionary legacy, soils, biotic interactions).

24
25
26 411 Importantly, climatic settings may differ between islands; thus a species living in dry,
27
28 412 warm environments on one island might occur in warm but wetter places on another island if
29
30 413 ‘warm’ is its key environmental niche condition. In such a case, populations on different
31
32 414 islands will show greater niche differentiation in irrelevant variables (precipitation in this
33
34 415 hypothetical example). Thus, with no phylogenetic signal we would expect allopatric cases to
35
36 416 be most differentiated with respect to climatic variables that are less important for the
37
38 417 species’ distributions. Indeed, it seems reasonable to suppose that precipitation in wetter
39
40 418 periods (for which we find the strongest differentiation in allopatry) is less limiting than
41
42 419 temperature or driest-month precipitation.

43
44
45 420 With respect to niche conservatism, most of the relationships between phylogenetic
46
47 421 distance and climatic niche differentiation were not significant. Though weak at best, some
48
49 422 relationships were significantly positive in our data, consistent with niche conservatism, and
50
51 423 notably, none were significantly negative. In most cases the positive relationships largely
52
53 424 reflected a lack of points in the top-left corners of the graphs (Figures 3–4 and Supplements
54
55 425 S3–4), which may indicate little more than the trivial fact that sister species have typically
56
57 426 split recently.

1
2
3 427 Some degree of niche conservatism may be reflected in the fact that species on
4
5 428 average filled no more than half of the climatic range available to them (Table 2). However,
6
7 429 range restriction by dispersal limitation or other factors (e.g. human agency) could also
8
9 430 account for such levels of niche fill. Indeed, most of the species' ranges are small (Fig. S6.1).
10
11 431 Further, values of Blomberg's K and Pagel's λ (Table 1) suggested typically less
12
13 432 phylogenetic niche conservatism than expected from Brownian motion evolution. Although
14
15 433 this does not definitively rule out phylogenetic niche conservatism (Wiens *et al.*, 2010), it
16
17 434 suggests, in combination with our other findings, that niche conservatism is not a key
18
19 435 structuring force for biogeographic ranges in these species.

20
21 436 Levels of climatic niche differentiation are also informative about the role of niche
22
23 437 conservatism. These varied widely between closely related species (Figures 3–4 and S3.1).
24
25 438 Typically, the climatic niches of the most closely related species (phylogenetic distance near
26
27 439 0) were around 0–25% different. In some cases, however, the climatic niche differences of
28
29 440 sister species were much higher, even 100% different (e.g. *Echium* for driest-month
30
31 441 precipitation; Figure 3). These findings suggest that climatic niches can be very labile. The
32
33 442 possibility of rapid changes in species' niches (and thus the absence of prominent niche
34
35 443 conservatism) is supported by the great diversity of climatic niches in the *in situ*-evolved
36
37 444 species in this study. These demonstrate that, within a few million years, single colonizing
38
39 445 species speciate into widely contrasting environmental settings, from harsh, high-elevation
40
41 446 ecosystems to dry lowland ecosystems. A prominent example is the genus *Echium*, which
42
43 447 now fills the entire temperature and precipitation range of the Canary Islands (see also
44
45 448 Stoecklin, 2011). Our results also mirror the rapid changes in trait variability with
46
47 449 phylogenetic distance found by Ackerly (2009) and support scepticism towards assuming
48
49 450 omnipresence of niche conservatism (Losos, 2008).

50
51
52 451 The absence of a strong signal of climatic niche conservatism and the large amount
53
54 452 of climatic niche lability therefore challenge the generality of niche conservatism as a
55
56 453 fundamental structuring force – especially given that our results for competitive displacement
57
58
59
60

1
2
3 454 are consistent with low levels of competition (strong competition would tend to separate
4
5 455 realised niches within the same fundamental niche). These findings have potentially broad
6
7 456 implications. For example, absent or weak influence of niche conservatism on biogeographic
8
9 457 ranges questions prominent explanations for ecological phenomena like the latitudinal
10
11 458 diversity gradient. The argument that higher tropical diversity results from the predominance
12
13 459 of tropical-like climates during the Eocene (e.g. Wiens & Donoghue, 2004), for example,
14
15 460 relies on climatic niche conservatism over longer time-periods than those represented in our
16
17 461 study.

18
19
20 462 Studies from continental systems (often mountains) have yielded mixed results, with
21
22 463 some studies finding evidence consistent with niche conservatism in phylogenetically related
23
24 464 species, and others not (Peterson et al., 1999; Graham et al., 2004; Kozak & Wiens 2006).
25
26 465 However, oceanic islands differ in several respects from continental systems, for which niche
27
28 466 conservatism is mainly reported (e.g. Prinzing et al., 2001). First, oceanic islands have lower
29
30 467 levels of biotic stress (e.g. from between-species competition, herbivory, predation and
31
32 468 parasitism). For elevational gradients on continents, upward movement of species may
33
34 469 typically be restricted by physiological tolerance (mainly the climatic niche), while downward
35
36 470 range expansion is limited mainly by interspecific competition (Ghalambor et al., 2006). It is
37
38 471 possible that climatic niche conservatism mainly applies to cold (and dry) conditions. Many
39
40 472 species face their physiological tolerance limits under drier and colder conditions (Currie et
41
42 473 al. 2004) and the diversifying clades of the Canary Islands tend to originate from non-tropical
43
44 474 ancestors. Therefore, on oceanic islands, species may be able to evolve into a larger set of
45
46 475 environmental conditions than in continental systems where this is hindered by the presence
47
48 476 of more competitive species.

49
50
51 477 Our results are based on 500x500m grid cells spanning the entire archipelago, with
52
53 478 its broad environmental ranges and phylogenetic timescales that range back to millions of
54
55 479 years. The spatial resolution is finer than mostly used by species distribution models in
56
57 480 macroecological analyses, but coarser than many ecological studies. Theoretically, niche

1
2
3 481 differentiation at one spatial scale could be associated with niche conservatism at another,
4
5 482 the effects cancelling each other out. For instance, populations of a species could become
6
7 483 genetically isolated at very fine scales (e.g. by differentiating habitat preference into open
8
9 484 and forest habitats with differing pollinators) but could retain their environmental niche on a
10
11 485 much larger scale. However, while this would explain the absence of niche differentiation in
12
13 486 our results, it would be associated with a strong signal in niche conservatism – far from what
14
15 487 we found.

16
17
18 488 We conclude that competitive displacement and niche conservatism may both be less
19
20 489 important (at least for oceanic islands) in structuring biogeographic ranges than is usually
21
22 490 considered. Given that our study is, to our knowledge, the first analysis of its type, we
23
24 491 suggest that this is a fertile line of research, as fine-resolution datasets with more precise
25
26 492 environmental information become available.

27
28 493

29 30 31 494 **Acknowledgements**

32
33
34 495 The Agencia Estatal de Meteorología provided climate station data within the frame of the
35
36 496 Danish Carlsbergfondet Project Number CF14-0148, which supported M.J. Steinbauer.

37
38 497

39 40 41 498 **References**

42
43
44 499 Abrams, P. (1983) The theory of limiting similarity. *Annual Review of Ecology, Evolution, and*
45
46 500 *Systematics*, **14**, 359–376.

47
48 501 Ackerly, D. (2009) Conservatism and diversification of plant functional traits: evolutionary
49
50 502 rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences*
51
52 503 *USA*, **106**, 19699–19706.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 504 Algar, A.C. & Mahler, D.L. (2015) Area, climate heterogeneity, and the response of climate
505 niches to ecological opportunity in island radiations of *Anolis* lizards. *Global Ecology
506 and Biogeography*, Early View: DOI: 10.1111/geb.12327.
- 507 Algar, A.C., Mahler, D.L., Glor, R.E. & Losos, J.B. (2013) Niche incumbency, dispersal
508 limitation and climate shape geographical distributions in a species-rich island
509 adaptive radiation. *Global Ecology and Biogeography*, **22**, 391–402.
- 510 Anacker, B. & Strauss S. (2014) The geography and ecology of plant speciation: Range
511 overlap and niche divergence in sister species. *Proceedings of the Royal Society-B*,
512 **281**, 20132980.
- 513 Atlantis 3.1. Gobierno de Canarias. Banco de Datos de Biodiversidad de Canarias
514 (<http://www.biodiversidadcanarias.es/atlantis>) accessed November 2013
- 515 Barraclough, T.G. & Vogler, A.P. (2000) Detecting the Geographical Pattern of Speciation
516 from Species-Level Phylogenies. *The American Naturalist*, **155**, 419–434.
- 517 Begon, M., Townsend, C.R. & Harper, J.L. (2006) *Ecology: from individuals to ecosystems*,
518 4th edn. Blackwell Publishing, Oxford.
- 519 Blonder, B., Lamanna C., Violle C. & Enquist, B.J. (2014) The n-dimensional hypervolume.
520 *Global Ecology and Biogeography*, **23**, 595–609.
- 521 Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A.
522 (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**,
523 701–709.
- 524 Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **5**, 49–64.
- 525 Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A.,
526 Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turne, J.R.G. (2004)
527 Predictions and tests of climate-based hypotheses of broad-scale variation in
528 taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

- 1
2
3 529 Diniz-Filho, J.A.F., Santos, T., Rangel, T.F. & Bini, L.M. (2012) A comparison of metrics for
4
5 530 estimating phylogenetic signal under alternative evolutionary models. *Genetics and*
6
7 531 *Molecular Biology*, **35**, 673–679.
- 8
9 532 Donoghue, M.J. (2008). A phylogenetic perspective on the distribution of plant diversity.
10
11 533 *Proceedings of the National Academy of Sciences USA*, **105**, 11549–11555.
- 12
13
14 534 Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian Phylogenetics with
15
16 535 BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–73.
- 17
18 536 Duputié, A., Zimmermann, N.E. & Chuine, I. (2014) Where are the wild things? Why we need
19
20 537 better data on species distribution. *Global Ecology and Biogeography*, **23**, 457–467.
- 21
22
23 538 Early, R. & Sax, D.F. (2014) Climatic niche shifts between species' native and naturalized
24
25 539 ranges raise concern for ecological forecasts during invasions and climate change.
26
27 540 *Global Ecology and Biogeography*, **23**, 1356–1365.
- 28
29
30 541 Elton, C.S. (1927) *Animal Ecology*. Sidgwick and Jackson, London.
- 31
32 542 Francisco-Ortega, F., Jansen, R.K., Santos-Guerra, A. (1996). Chloroplast DNA evidence of
33
34 543 colonization, adaptive radiation, and hybridization in the evolution of the
35
36 544 Macaronesian flora. *Proceedings of the National Academy of Sciences USA*, **93**,
37
38 545 4085–4090.
- 39
40
41 546 García-Maroto, F., Mañas-Fernández A., Garrido-Cárdenas, J.A., Alonso, D.L., Guil-
42
43 547 Guerrero, J.L., Guzmán, B. & Vargas P. (2009) Delta 6-desaturase sequence
44
45 548 evidence for explosive Pliocene radiations within the adaptive radiation of
46
47 549 Macaronesian *Echium* (Boraginaceae). *Molecular Phylogenetics and Evolution*, **52**,
48
49 550 563–574.
- 50
51 551 Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.T. & Wang, G. (2006) Are mountain
52
53 552 passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and*
54
55 553 *Comparative Biology*, **46**, 5–17.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 554 Gobierno de Canarias (2015) *Catálogo Climático de Gran Canaria y Tenerife*. Data available
555 at climainpacto.eu/efectos/catalogos-climaticos, accessed on January 5th 2015.
- 556 Goodson, B.E., Santos-Guerra, A. & Jansen, R.K. (2006) Molecular systematics of
557 *Descurainia* (Brassicaceae) in the Canary Islands: biogeographic and taxonomic
558 implications. *Taxon*, **55**, 671–682.
- 559 Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's finches.
560 *Science*, **313**, 224–226.
- 561 Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004) Integrating
562 phylogenetics and environmental niche models to explore speciation mechanisms in
563 dendrobatid frogs. *Evolution*, **58**, 1781–1793.
- 564 Grinnell, J. (1917) The niche-relationships of the California thrasher. *The Auk*, **34**, 427–433.
- 565 Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton
566 University Press, Princeton.
- 567 Hutchinson, G. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative
568 Biology*, **22**, 415–427.
- 569 Instituto de Meteorologia de Portugal (2012) *Climate Atlas of the Archipelagos of the Canary
570 Islands, Madeira and the Azores – Air temperature and Precipitation (1971–2000)*.
571 Ministerio de Agricultura, Alimentación y Medio Ambiente.
- 572 Irl S.D.H., Harter, D., Steinbauer, M.J., Puyol Gallego, D., Fernández-Palacios, J.M.,
573 Jentsch, A. & Beierkuhnlein, C. (2015) Climate vs. topography – spatial patterns of
574 plant species diversity and endemism on a high-elevation island. *Journal of Ecology*,
575 **103**, 1621–1633.
- 576 Kozak, J.H. & Wiens, J.J. (2006) Does niche conservatism promote speciation? A case study
577 in North American salamanders. *Evolution*, **60**, 2604–2621.

- 1
2
3 578 Lee, C., Kim, S.C., Lundy, K. & Santos-Guerra, A. (2005) Chloroplast DNA phylogeny of the
4
5 579 woody *Sonchus* alliance (Asteraceae: Sonchinae) in the Macaronesian Islands.
6
7 580 *American Journal of Botany*, **92**, 2072–2085.
8
9
10 581 Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship
11
12 582 between phylogenetic relatedness and ecological similarity among species. *Ecology*
13
14 583 *Letters*, **11**, 995–1003.
15
16 584 Lynch, J.D. (1989) The gauge of speciation: on the frequency of modes of speciation.
17
18 585 Speciation and its consequences (ed. by D. Otte and J.A. Endler), pp. 527–553,
19
20 586 Sinauer Associates, Sunderland.
21
22
23 587 Mort, M., Soltis, D.E., Soltis, P.S., Francisco-Ortega, J. & Santos-Guerra, A. (2002)
24
25 588 Phylogenetics and evolution of the Macaronesian clade of Crassulaceae inferred from
26
27 589 nuclear and chloroplast sequence data. *Systematic Botany*, **27**, 271–288.
28
29
30 590 Normand, S., Ricklefs, R.E., Skov, F., Bladt, J., Tackenberg, O. & Svenning, J.-C. (2011)
31
32 591 Postglacial migration supplements climate in determining plant species ranges in
33
34 592 Europe. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3644–3653.
35
36 593 Ojeda, I., Santos-Guerra, A., Jaén-Molina, R., Oliva-Tejera, F., Caujapé-Castells, J., Cronk,
37
38 594 Q. (2011) The origin of bird pollination in Macaronesian *Lotus* (Loteae, Leguminosae).
39
40 595 *Molecular Phylogenetics and Evolution*, **62**, 306–318.
41
42
43 596 Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the
44
45 597 distribution of species: are bioclimate envelope models useful? *Global Ecology and*
46
47 598 *Biogeography*, **12**, 361–371.
48
49 599 Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward.
50
51 600 *Ecology Letters*, **9**, 741–758.
52
53
54 601 Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches
55
56 602 in evolutionary time, *Science*, **285**, 1265–1267.
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 603 Prinzing, A. (2001) The niche of higher plants: evidence for phylogenetic conservatism.
604 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**,
605 2383–2389.
- 606 Rambaut, A., Drummond, A.J., 2010. Tracer v1.5. <<http://beast.bio.ed.ac.uk/Tracer>>.
- 607 Ricklefs, R.E. & Bermingham, E. (2002) The concept of the taxon cycle in biogeography.
608 *Global Ecology and Biogeography*, **11**, 353–361.
- 609 Santana, B. & Martín, J.L. (2013) *Catálogo de mapas climáticos de Gran Canaria y Tenerife*
610 – Tomo 2. Proyecto Clima-Impacto (MAC/3/C159). Viceconsejería de Medio
611 Ambiente del Gobierno de Canarias (135 páginas).
- 612 Schluter, D. & McPhail, J.D. (1992) Ecological character displacement and speciation in
613 sticklebacks. *The American Naturalist*, **140**, 85–108.
- 614 Stoecklin, J. (2011) Evolution der Gattung *Echium* auf den Kanarischen Inseln: vom Kraut
615 zum Strauch zum Rosettenbaum (Evolution of the Genus *Echium* on the Canary
616 Islands: from Herb to Shrub to Rosette Tree). *Bauhinia*, **23**, 57–66.
- 617 Whittaker, R.J. & Fernandez-Palacios, J.M. (2007) *Island Biogeography: Ecology, Evolution,*
618 *and Conservation*. 2nd edition. Oxford University Press, Oxford.
- 619 Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic
620 island biogeography. *Journal of Biogeography*, **35**, 977–994. □
- 621 Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness.
622 *Trends in Ecology and Evolution*, **19**, 639–644.
- 623 Wiens, J.J., & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and
624 conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**,
625 519–539.
- 626 Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V.,
627 Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D.,

628 McCain, C.M. & Stephens, P.R. (2010) Niche conservatism as an emerging principle
629 in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.

630 Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The*
631 *American Naturalist*, **95**, 169–193.

632 Yu, D.W. & Wilson, H.B. (2001) The competition-colonization trade-off is dead; long live the
633 competition-colonization trade-off. *The American Naturalist*, **158**, 49–63.

634

635 **Biosketches & author contributions**

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

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

641 Author contributions: MS and RF conceived the research, developed the methodology and
642 wrote the manuscript. MS analysed the data. HS calculated the phylogenies. All authors
643 contributed to the research design and commented on the results and the manuscript.

644

645 **Supplementary material**

646 S1 – Supplemental material on phylogenetic data

647 S2 – Summary statistics per species

648 S3 – Niche differentiation–phylogenetic distance relationships for all species pairs

649 S4 – Results using unconstrained niches

650 S5 – Niche fill and overlap/potential overlap for four-dimensional niche space

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

651 S6 –Data quality and species distribution maps

652

For Peer Review

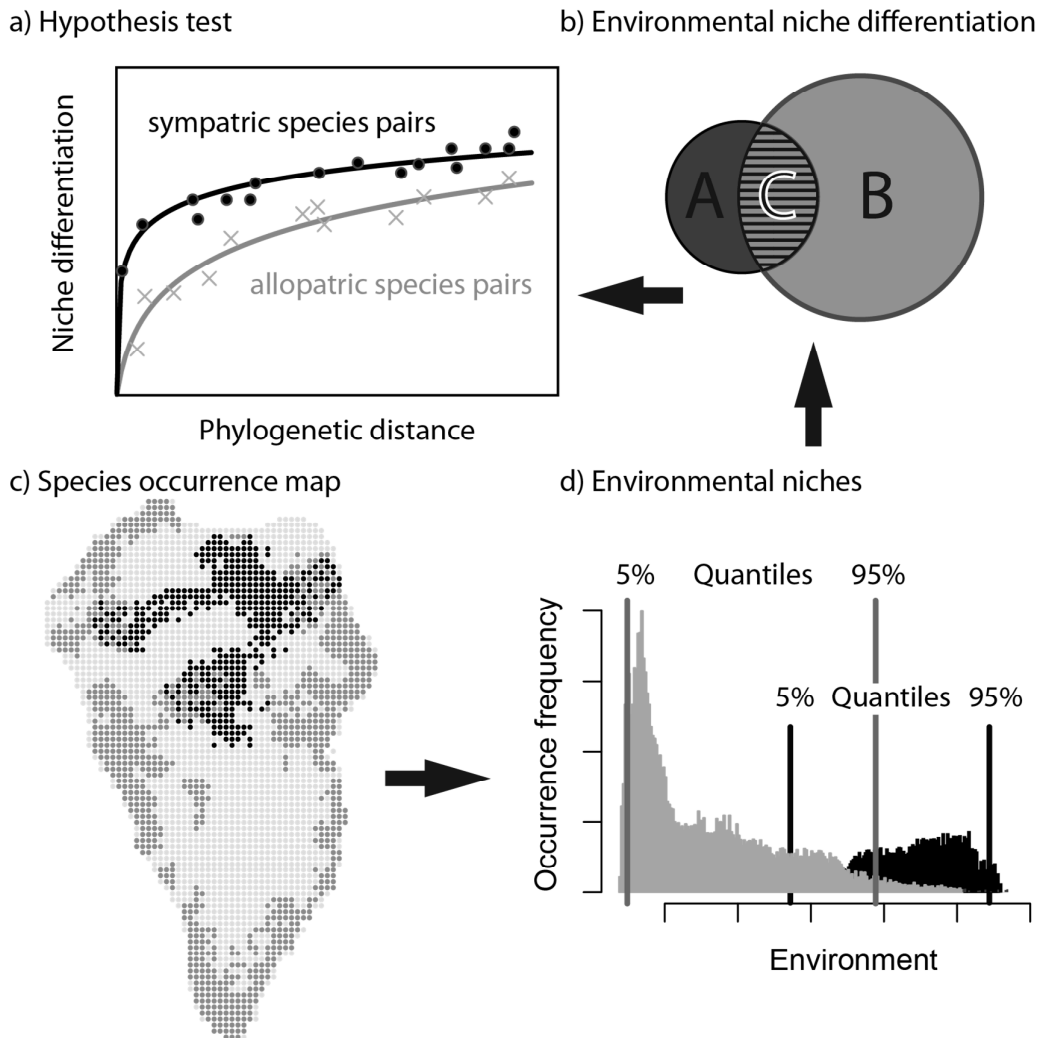
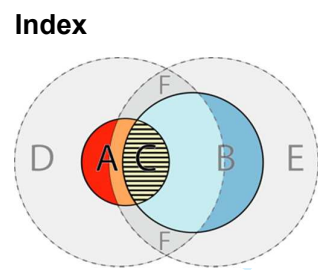
653
654**Figures**

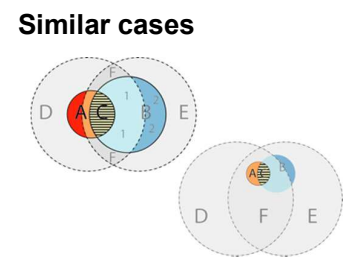
Figure 1: Predictions of the niche conservatism (NC) and competitive displacement (CD) hypotheses for climatic niche differentiation in radiating plant clades in the Canary Islands. NC predicts a positive relationship between phylogenetic distance and climatic niche differentiation, while CD predicts 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 500m x 500m 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 500m x 500m 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.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49

Name
Niche differentiation (unconstrained)

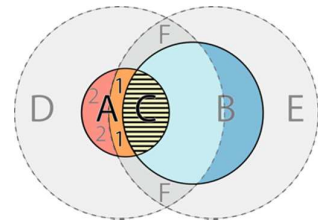


Formula
 $A / A+C$

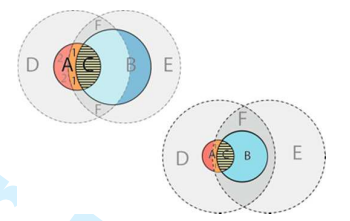


Notes
Measures the degree to which species A has differentiated from species B (species with the larger niche). It is independent of the overall size of the species' niche.

Niche differentiation (constrained)

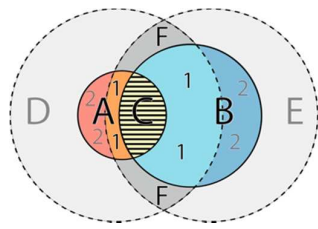


$A1 / A1+C$

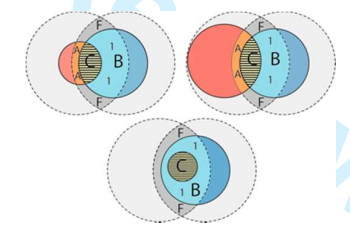


The constrained niche differentiation index is likely to be more reliable than the unconstrained one (especially if D and E are not too large). This index was chosen as the main response variable in the analyses.

Overlap/potential overlap

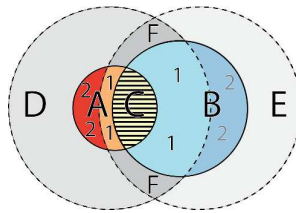


$C / A1+B1+C+F$



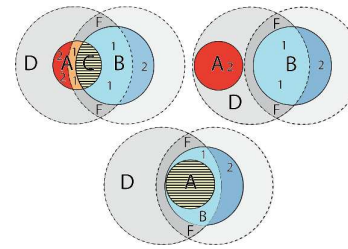
Quantifies the overlap of a species pair in relation to its potential overlap. Index is independent of the degree of nesting.

Niche fill



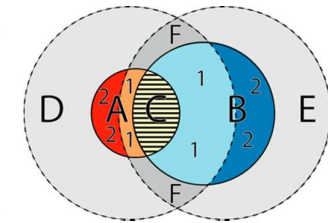
$$A+C/A+C+B1+F+D$$

$$(or B+C/B+C+A1+F+E)$$



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. The grey parts (D,E, F; see overview graph on the right) 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).



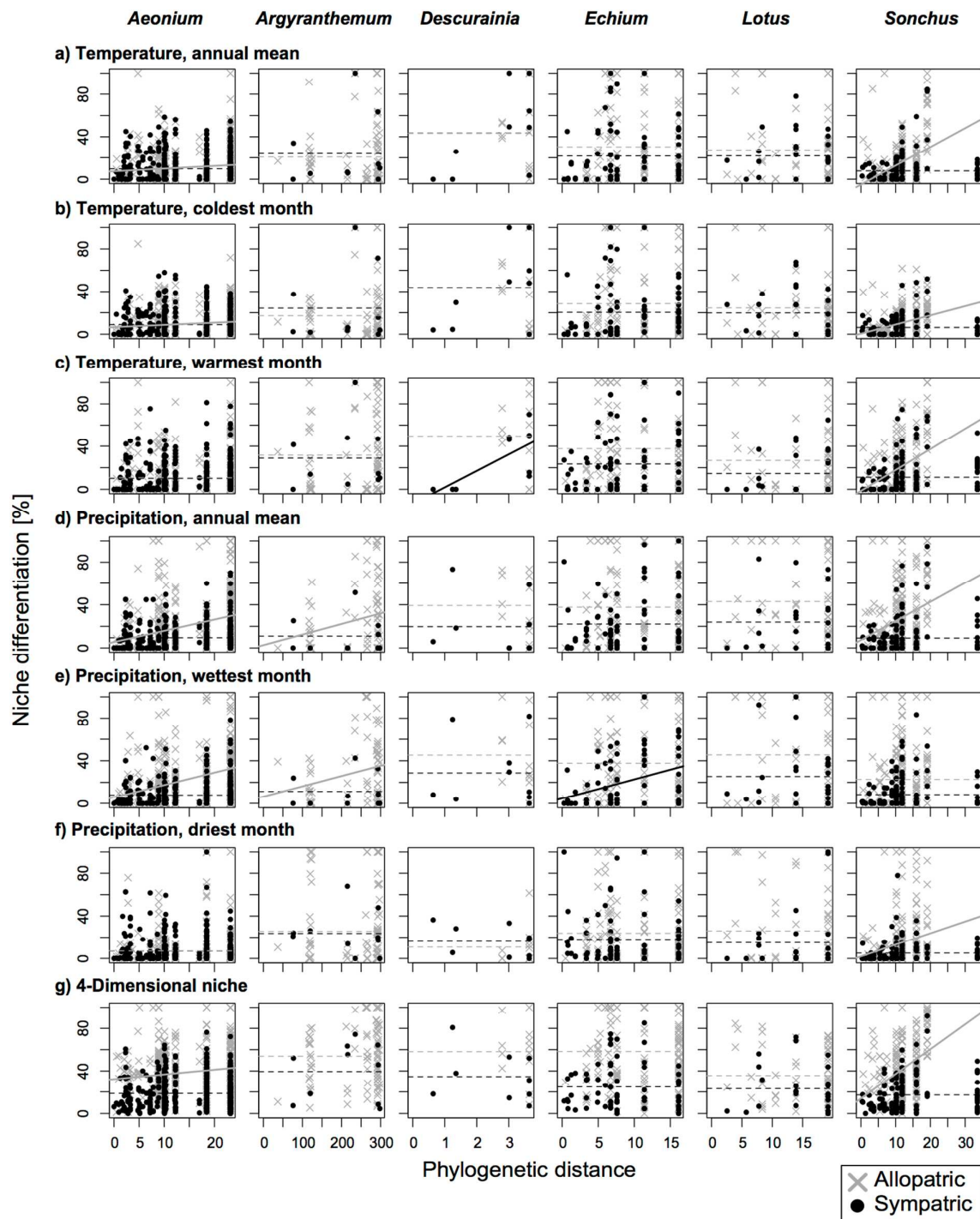


Figure 3: Niche differentiation vs. phylogenetic distance for all pairwise comparisons of species within each clade, for each climatic variable. Allopatric (grey crosses, grey lines) species pairs are distinguished from sympatric (black circles, black lines) species pairs, *sensu lato* (see Methods). 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.

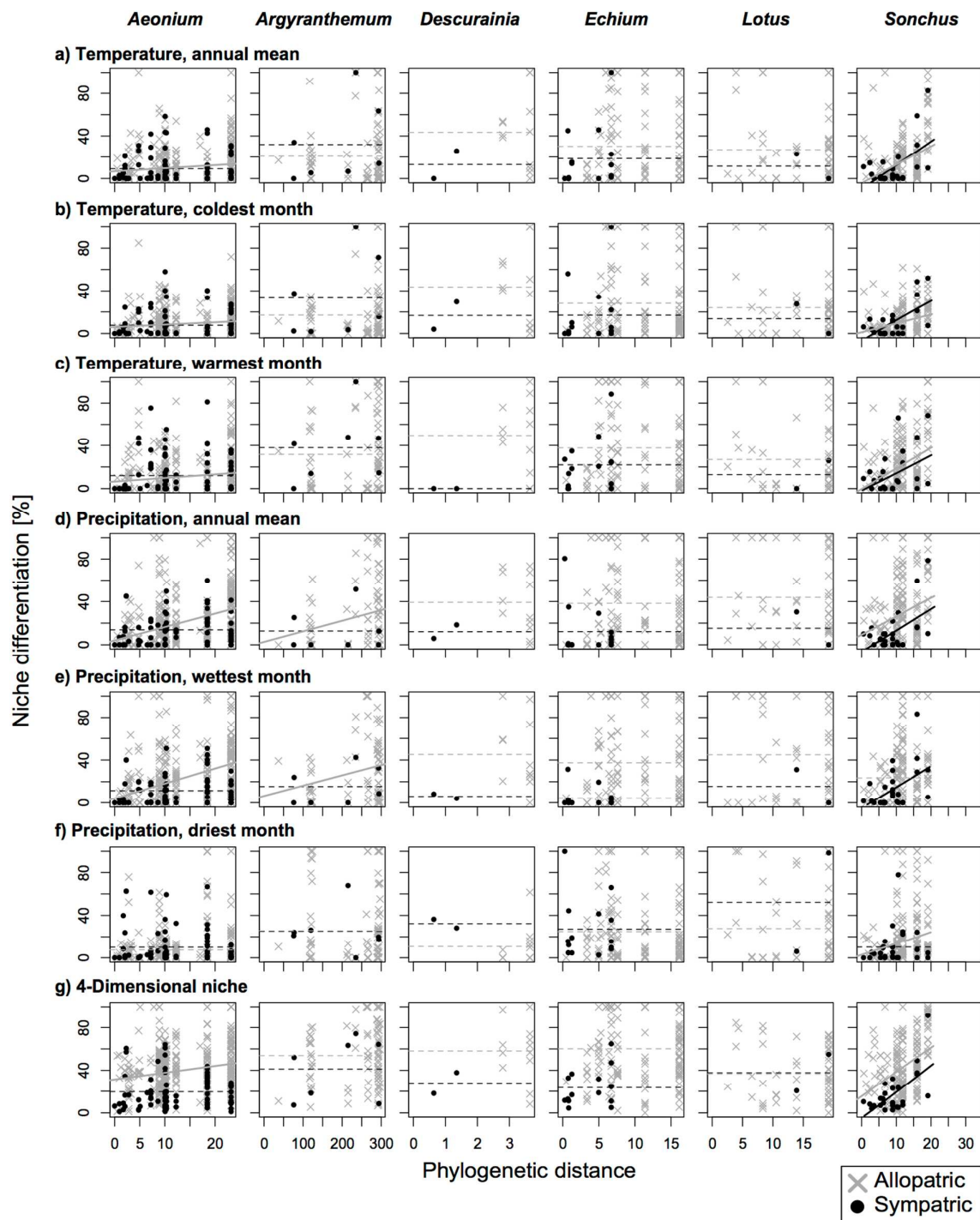


Figure 4: Niche differentiation vs. phylogenetic distance for all pairwise comparisons of species within each clade, for each climatic variable. Allopatric (grey crosses, grey lines) species pairs are distinguished from sympatric (black circles, black lines) species pairs, *sensu stricto* (see Methods). 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 not run for sympatric comparisons for *Descurainia* and *Lotus* because sample size = 2).

Tables

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 0 are indicated with asterisks ($*0.01 < P < 0.05$; $**0.001 < P < 0.01$); none of the values is significantly greater than 1.

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

Table 2: Niche fill (see Figure 2 for definitions and formulae) for the six climatic variables and the 4-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 is given after 'N='. Values shown are mean \pm standard error of the mean (range).

Clade	Mean temp.	Mean precip.	4-D niche	
<i>Aeonium</i> N=41	41.6 \pm 2.3 (19-74)	50.8 \pm 1.9 (23-77)	39.8 \pm 3.2 (7-86)	
<i>Argyranthemum</i> N=15	44.7 \pm 5.1 (13-74)	46.9 \pm 5.3 (26-92)	29.2 \pm 5.4 (3-65)	
<i>Descurainia</i> N=7	40.6 \pm 5.0 (22-62)	41.2 \pm 5.2 (16-55)	26.2 \pm 6.1 (12-50)	
<i>Echium</i> N=22	40.2 \pm 4.2 (14-81)	45.5 \pm 4.3 (13-80)	33.6 \pm 4.8 (2-79)	
<i>Lotus</i> N=14	36.8 \pm 5.3 (6-71)	38.8 \pm 5.2 (2-63)	26.7 \pm 6.9 (2-83)	
<i>Sonchus</i> N=27	39.6 \pm 2.4 (17-66)	49.6 \pm 2.9 (21-75)	34.9 \pm 4.4 (7-77)	
	Warmest	Coldest	Wettest	Driest
<i>Aeonium</i> N=41	40.7 \pm 2.2 (18-79)	41.4 \pm 2.5 (17-76)	47.5 \pm 2.0 (25-69)	30.9 \pm 2.6 (3-63)
<i>Argyranthemum</i> N=15	36.7 \pm 4.1 (18-66)	46.3 \pm 5.4 (12-73)	46.1 \pm 4.6 (20-85)	25.5 \pm 5.6 (5-77)
<i>Descurainia</i> N=7	38.1 \pm 4.8 (26-61)	40.4 \pm 5.0 (19-59)	43.1 \pm 4.0 (30-60)	13.5 \pm 2.6 (3-23)
<i>Echium</i> N=22	38.7 \pm 3.9 (11-78)	40.5 \pm 4.3 (13-81)	44.4 \pm 3.5 (15-75)	26.7 \pm 3.8 (1-65)
<i>Lotus</i> N=14	34.6 \pm 5.3 (8-78)	36.5 \pm 5.6 (4-70)	39.1 \pm 5.1 (10-70)	22.0 \pm 5.4 (3-60)
<i>Sonchus</i> N=27	41.7 \pm 2.6 (15-70)	40.1 \pm 2.7 (16-66)	46.8 \pm 2.8 (26-72)	34.0 \pm 3.9 (3-76)

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 two sample permutation test (function *permTs* in R-package *perm* version 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 with bold font; 'ns' indicates $P > 0.10$ (note: all ns 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 (Figures 3–4). "N" indicates the number of sympatric/the number of allopatric species pairs. Results are for constrained analyses; see Table S4.1 for results of unconstrained analyses.

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

Supplementary material

For Steinbauer *et al.*, Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Global Ecology and Biogeography*

S1 – Details of phylogenetic methods

Table S1.1: Plastic and nuclear markers used for calculating phylogenetic distance, with details of calibration points

Clade	Nuclear DNA regions	Plastid DNA regions	Calibration points
<i>Aeonium</i>	ITS1-5.8S-ITS2 (Mort et al. 2002)	matK, trnL-trnF, trnH-psbA (Mort et al. 2002)	1) <i>Aeonium</i> alliance stem node (split from <i>Umbilicus</i>): 19 +/- 1 Mio years, normal prior distribution; 2) crown node of <i>Aeonium</i> alliance: 10 +/- 2, normal prior distribution
<i>Echium</i>	delta-6 desaturase (García-Maroto et al. 2009)	--	Macaronesian <i>Echium</i> stem node: 20.6 +/- 1 Mio years, normal prior distribution
<i>Descurainia</i>	ITS1-5.8S-ITS2 (Goodson et al. 2006)	cytB, ndhC, ndhF-rpl32, psbC, rps16, trnC, trnD, trnE-trnT (Goodson et al. 2006)	stem node (split <i>Descurainia</i> - <i>Robeschia</i>): 14 +/- 1 Mio years, normal prior distribution
<i>Lotus</i>	ITS1-5.8S-ITS2 (Ojeda et al. 2011)	matK, trnH-psbA, rbcL, rpoB, RpoC1 (Ojeda et al. 2011)	1) Madeira/Azores <i>Lotus</i> crown node: 2.5 +/- 1 Mio years, normal prior distribution 2) Macaronesian <i>Lotus</i> crown node: 12 +/- 1 Mio years, normal prior distribution
<i>Sonchus</i>	ITS1, ITS2 (Lee et al. 2005)	matK, trnH-psbA, trnT-trnL, trnL-trnF (Lee et al. 2005)	1) <i>Sonchus</i> s.l. stem node (split <i>Reichardia</i> - <i>Sonchus</i>): 25 +/- 2 Mio years, normal prior distribution

S2 – Summary statistics per species

Table S2.1: Number of occurrence records (presences in 500m x 500m grid cells) for each species ('N'). Also given are the mean and standard deviation ('SD') of mean annual temperature and precipitation for those grid cells in which each species occurs. Note: temperature and precipitation are not evenly distributed within islands; there are many more lowland (high temperature, low precipitation) than high-elevation cells. Therefore, mean values do not necessarily represent the centre of a species' environmental niche.

Name	N	Mean Temp.	SD Temp.	Mean Prec.	SD Prec.
Aeonium clade					
<i>Aeonium balsamiferum</i>	281	19,3	0,6	173	24
<i>Aeonium canariense</i>	5045	18,0	1,9	441	189
<i>Aeonium castello-paivae</i>	723	17,7	1,7	404	119
<i>Aeonium ciliatum</i>	1018	18,6	1,4	435	135
<i>Aeonium cuneatum</i>	356	18,0	1,3	507	150
<i>Aeonium davidbramwellii</i>	516	17,6	1,8	585	232
<i>Aeonium decorum</i>	905	18,6	1,7	318	104
<i>Aeonium gomerense</i>	62	16,8	0,9	478	64
<i>Aeonium goochiae</i>	822	17,0	1,8	668	240
<i>Aeonium haworthii</i>	984	18,3	1,6	419	144
<i>Aeonium hierrense</i>	621	18,3	1,9	459	190
<i>Aeonium lancerottense</i>	556	19,7	0,9	164	30
<i>Aeonium lindleyi</i>	1956	18,5	1,5	408	131
<i>Aeonium nobile</i>	639	17,3	2,3	549	192
<i>Aeonium percarneum</i>	2608	18,4	1,8	309	135
<i>Aeonium pseudourbicum</i>	305	17,2	1,4	325	87
<i>Aeonium saundersii</i>	290	17,6	1,6	393	131
<i>Aeonium sedifolium</i>	770	18,4	1,7	379	141
<i>Aeonium simsii</i>	1396	17,1	2,3	391	161
<i>Aeonium smithii</i>	1031	14,6	3,1	410	118
<i>Aeonium spathulatum</i>	3725	14,8	2,7	568	228
<i>Aeonium tabulaeforme</i>	1264	18,1	1,6	431	128
<i>Aeonium undulatum</i>	841	16,4	1,7	503	119
<i>Aeonium urbicum</i>	2790	18,1	1,6	366	136
<i>Aeonium volkerii</i>	136	20,0	1,1	312	67
<i>Aichryson laxum</i>	3452	17,0	1,8	509	183
<i>Aichryson palmense</i>	883	15,0	2,2	864	226
<i>Aichryson parlatorei</i>	1595	17,2	2,0	474	233
<i>Aichryson porphyrogennetos</i>	237	16,3	1,7	469	116
<i>Aichryson punctatum</i>	1894	17,1	2,0	517	191
<i>Aichryson tortuosum</i>	783	19,7	0,8	163	28
<i>Greenovia aizoon</i>	548	14,0	2,5	549	153
<i>Greenovia aurea</i>	2665	16,0	2,5	503	202
<i>Greenovia diplocycla</i>	2122	16,5	2,2	543	247
<i>Greenovia dodrentalis</i>	349	18,3	1,4	405	131
<i>Monanthes anagensis</i>	282	18,0	1,3	547	148

1						
2	<i>Monanthes brachycaulos</i>	4076	17,4	2,6	397	164
3	<i>Monanthes icterica</i>	404	18,0	1,3	353	89
4	<i>Monanthes laxiflora</i>	1942	18,2	1,5	397	152
5	<i>Monanthes minima</i>	321	18,8	2,1	305	115
6	<i>Monanthes polyphylla</i>	1862	18,1	1,8	428	162
7						
8						
9	Argyranthemum clade					
10	<i>Argyranthemum callichrysum</i>	393	17,3	1,5	391	104
11	<i>Argyranthemum</i>					
12	<i>coronopifolium</i>	305	19,3	1,2	338	124
13	<i>Argyranthemum escarrei</i>	323	19,1	1,6	210	94
14	<i>Argyranthemum filifolium</i>	803	20,7	0,9	143	59
15	<i>Argyranthemum</i>					
16	<i>foeniculaceum</i>	861	16,7	2,5	433	180
17	<i>Argyranthemum gracile</i>	1251	19,2	1,6	224	78
18	<i>Argyranthemum hierrense</i>	353	18,8	1,6	359	107
19	<i>Argyranthemum lemsii</i>	53	19,7	0,9	321	74
20	<i>Argyranthemum lidii</i>	112	19,1	1,2	217	67
21	<i>Argyranthemum maderense</i>	224	19,2	0,6	180	26
22	<i>Argyranthemum sundingii</i>	30	19,7	0,7	413	75
23	<i>Argyranthemum sventenii</i>	124	18,8	1,9	345	162
24	<i>Argyranthemum tenerifae</i>	1078	11,3	1,8	396	86
25	<i>Argyranthemum webbii</i>	589	14,8	2,6	879	266
26	<i>Argyranthemum winteri</i>	62	19,0	0,6	179	20
27						
28						
29	Descurainia clade					
30	<i>Descurainia artemisioides</i>	132	18,7	1,5	251	104
31	<i>Descurainia bourgeauana</i>	1254	11,3	1,8	412	117
32	<i>Descurainia gilva</i>	387	12,7	2,1	913	197
33	<i>Descurainia gonzalesii</i>	566	11,4	1,1	394	47
34	<i>Descurainia lemsii</i>	337	13,0	1,8	513	127
35	<i>Descurainia millefolia</i>	3041	17,4	2,0	433	180
36	<i>Descurainia preauxiana</i>	1322	18,0	1,8	304	108
37						
38						
39	Echium clade					
40	<i>Echium acanthocarpum</i>	115	16,3	1,2	522	102
41	<i>Echium aculeatum</i>	2406	18,3	1,9	349	140
42	<i>Echium auberianum</i>	272	9,8	1,4	335	86
43	<i>Echium bethencourtii</i>	33	18,1	0,6	556	68
44	<i>Echium bonnetii</i>	1342	20,0	1,3	179	74
45	<i>Echium brevirame</i>	1005	18,4	1,9	502	207
46	<i>Echium callithyrsum</i>	276	17,0	2,7	412	184
47	<i>Echium decaisnei</i>	3245	19,4	1,6	231	100
48	<i>Echium gentianoides</i>	171	10,9	1,3	993	94
49	<i>Echium giganteum</i>	946	17,4	2,2	457	134
50	<i>Echium handiense</i>	17	18,3	0,4	202	15
51	<i>Echium hierrense</i>	389	18,0	2,0	420	130

1						
2	<i>Echium lancerottense</i>	936	19,9	0,8	148	37
3	<i>Echium leucophaeum</i>	488	18,8	1,3	428	125
4	<i>Echium onosmifolium</i>	1392	18,4	1,8	281	110
5	<i>Echium simplex</i>	417	18,7	1,3	457	152
6	<i>Echium strictum</i>	2960	18,4	1,6	381	161
7	<i>Echium sventenii</i>	19	18,3	1,1	215	37
8	<i>Echium triste</i>	477	20,5	1,1	153	54
9	<i>Echium virescens</i>	2056	16,6	2,4	409	158
10	<i>Echium webbii</i>	1008	14,7	2,5	802	240
11	<i>Echium wildpretii</i>	1386	11,9	1,8	555	263
12						
13						
14						
15						
16	Lotus clade					
17	<i>Lotus arinagensis</i>	53	21,4	0,2	132	5
18	<i>Lotus berthelotii</i>	135	15,3	2,2	344	97
19	<i>Lotus callis-viridis</i>	54	19,3	0,8	153	30
20	<i>Lotus campylocladus</i>	2921	14,4	2,8	532	214
21	<i>Lotus dumetorum</i>	279	18,3	1,5	516	163
22	<i>Lotus emeroides</i>	531	18,3	1,3	358	91
23	<i>Lotus glaucus</i>	1702	19,7	1,4	278	140
24	<i>Lotus holosericeus</i>	334	18,2	1,9	295	98
25	<i>Lotus kunkelii</i>	28	20,3	0,8	214	45
26	<i>Lotus lancerottensis</i>	2178	20,2	0,9	140	35
27	<i>Lotus mascaensis</i>	66	17,9	1,2	350	78
28	<i>Lotus sessilifolius</i>	1138	19,5	1,6	283	123
29	<i>Lotus spartioides</i>	597	16,3	2,1	403	131
30	<i>Lotus tenellus</i>	217	20,4	0,9	200	72
31						
32						
33						
34						
35						
36	Sonchus clade					
37	<i>Atalanthus arboreus</i>	411	18,7	1,4	374	145
38	<i>Atalanthus capillaris</i>	377	18,5	2,1	335	183
39	<i>Atalanthus microcarpus</i>	338	19,2	1,8	262	80
40	<i>Atalanthus pinnatus</i>	5126	18,5	1,7	324	139
41	<i>Atalanthus regis-jubae</i>	161	18,3	0,8	378	90
42	<i>Babcockia platylepis</i>	1177	16,8	2,0	383	153
43	<i>Chrysoprenanthes pendula</i>	735	18,6	1,5	270	84
44	<i>Lactucosonchus webbii</i>	107	14,6	1,5	943	197
45	<i>Sonchus acaulis</i>	3875	17,5	2,0	411	164
46	<i>Sonchus asper</i>	1620	17,2	2,4	488	249
47	<i>Sonchus bornmuelleri</i>	149	18,7	1,1	518	113
48	<i>Sonchus brachylobus</i>	507	19,7	1,1	187	61
49	<i>Sonchus canariensis</i>	1137	16,9	2,4	357	157
50	<i>Sonchus congestus</i>	2366	17,7	1,7	457	147
51	<i>Sonchus fauces-orci</i>	197	17,9	1,3	299	89
52	<i>Sonchus gandogerii</i>	93	19,2	1,1	367	76
53	<i>Sonchus gomerensis</i>	690	18,0	1,6	375	119
54	<i>Sonchus gummifer</i>	1038	18,5	2,1	388	156
55	<i>Sonchus hierrensis</i>	2137	17,2	1,8	511	211
56						
57						
58						
59						
60						

1						
2	<i>Sonchus ortunoi</i>	261	17,5	1,5	407	122
3	<i>Sonchus palmensis</i>	772	16,5	2,1	773	255
4	<i>Sonchus pinnatifidus</i>	366	19,6	0,8	169	31
5	<i>Sonchus radicans</i>	683	18,6	1,4	395	128
6	<i>Sonchus tectifolius</i>	134	19,0	1,4	425	134
7	<i>Sonchus tuberifer</i>	170	17,8	1,4	353	82
8	<i>Sonchus wildpretii</i>	29	16,7	0,9	488	66
9	<i>Sventenia bupleuroides</i>	45	17,2	1,3	345	108
10						
11						
12						
13						
14						
15						
16						
17						
18						
19						
20						
21						
22						
23						
24						
25						
26						
27						
28						
29						
30						
31						
32						
33						
34						
35						
36						
37						
38						
39						
40						
41						
42						
43						
44						
45						
46						
47						
48						
49						
50						
51						
52						
53						
54						
55						
56						
57						
58						
59						
60						

For Peer Review

S3 – Additional results using constrained niches

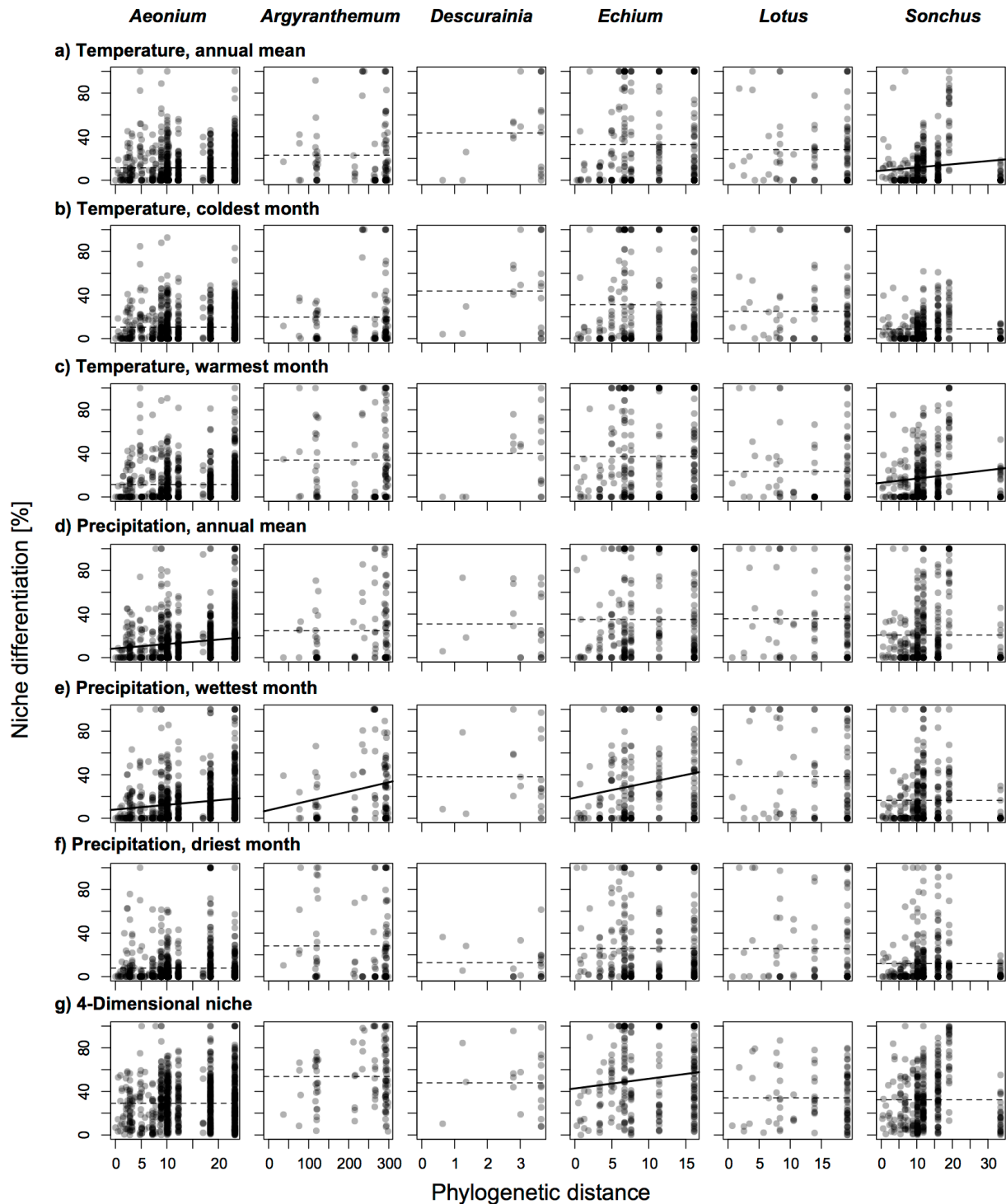


Figure S3.1: Niche differentiation vs. phylogenetic distance for each climatic variable, for all species pairs in each clade (constrained analysis, i.e. calculation of niche differentiation was restricted to the niche space shared between islands occupied by the two species being compared; see Figure 2). Points are all grey and semi-transparent, so darker shades indicate overlapping points. 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.

S4 – Results using unconstrained niches

Table S4.1: Whether sympatric or allopatric species pairs showed higher average niche differentiation within clades (column headed 'Unconstrained niches'), for the six climatic variables and the combined four-dimensional climatic niche. Where $P < 0.10$, as judged by two sample permutation test (function *permTs* in R-package *perm* version 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 with bold font; 'ns' indicates $P > 0.10$ (note: all ns were also $P > 0.20$). Phylogenetic distance between pairs was not accounted for because it is largely uncorrelated with the niche differentiation indices. 'N' indicates the number of sympatric/the number of allopatric species pairs. This is the unconstrained equivalent of Table 3.

Variable	Clade	Unconstrained niches
Temperature, mean annual	<i>Aeonium</i> (N=41/800)	Allopatric, P = 0.005
	<i>Argyranthemum</i> (N=15/95)	ns
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	ns
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	Allopatric, P = 0.095
Temperature, coldest month	<i>Aeonium</i> (N=41/800)	Allopatric, P = 0.008
	<i>Argyranthemum</i> (N=15/95)	ns
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	ns
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	ns
Temperature, warmest month	<i>Aeonium</i> (N=41/800)	ns
	<i>Argyranthemum</i> (N=15/95)	ns
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	Allopatric, P = 0.043
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	Allopatric, P=0.063
Precipitation, mean annual	<i>Aeonium</i> (N=41/800)	Allopatric, P = 0.062
	<i>Argyranthemum</i> (N=15/95)	ns
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	Allopatric, P = 0.01
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	Allopatric, P < 0.001
Precipitation, wettest month	<i>Aeonium</i> (N=41/800)	Allopatric, P < 0.001
	<i>Argyranthemum</i> (N=15/95)	ns
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	Allopatric, P = 0.002
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	Allopatric, P = 0.006
Precipitation, driest month	<i>Aeonium</i> (N=41/800)	ns
	<i>Argyranthemum</i> (N=15/95)	ns
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	ns
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	ns
4-dimensional niche (summer and winter precipitation and temperature)	<i>Aeonium</i> (N=41/800)	Allopatric, P<0.001
	<i>Argyranthemum</i> (N=15/95)	Allopatric, P=0.094
	<i>Descurainia</i> (N=7/21)	ns
	<i>Echium</i> (N=22/206)	Allopatric, P<0.001
	<i>Lotus</i> (N=14/73)	ns
	<i>Sonchus</i> (N=27/333)	Allopatric, P<0.001

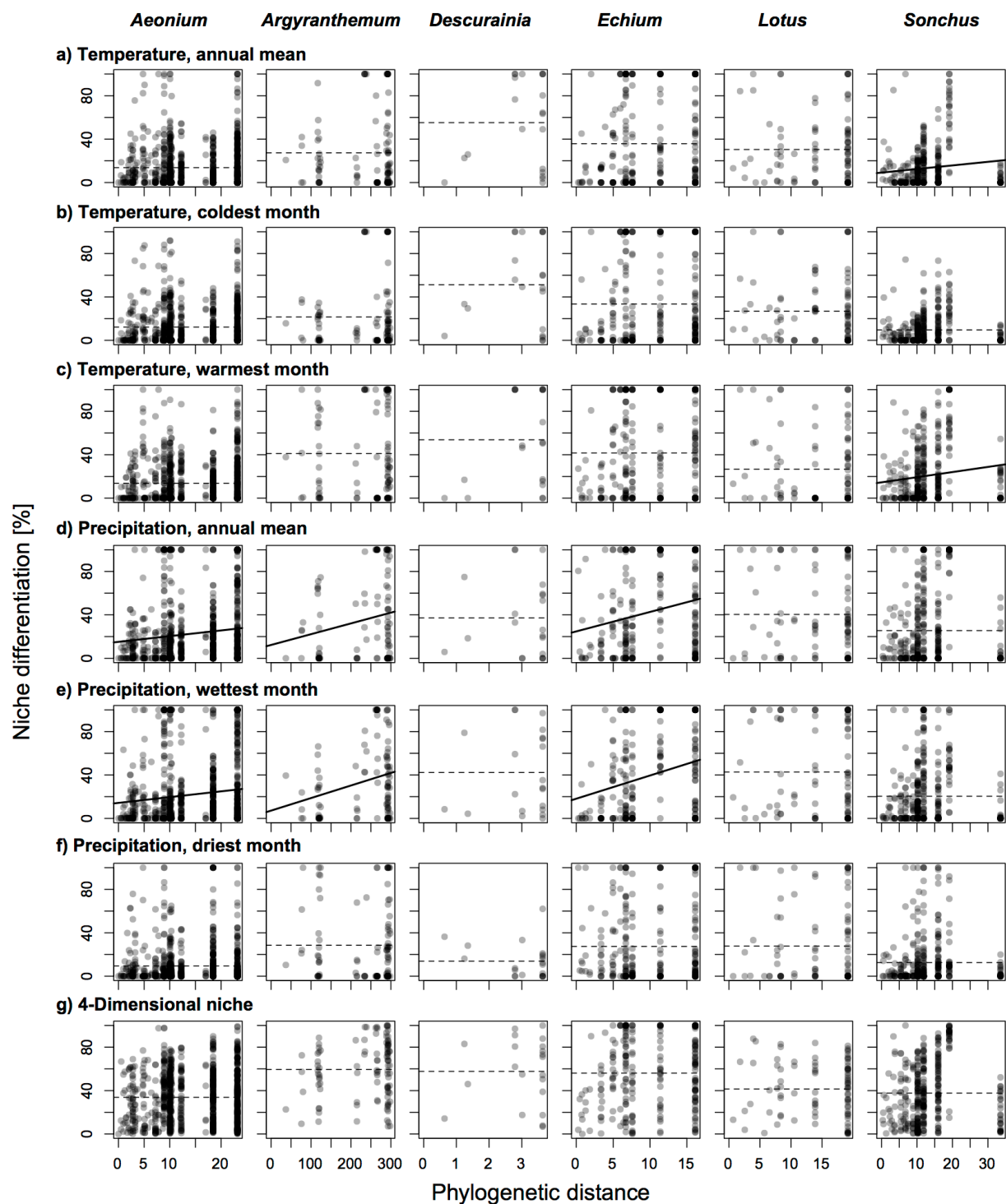
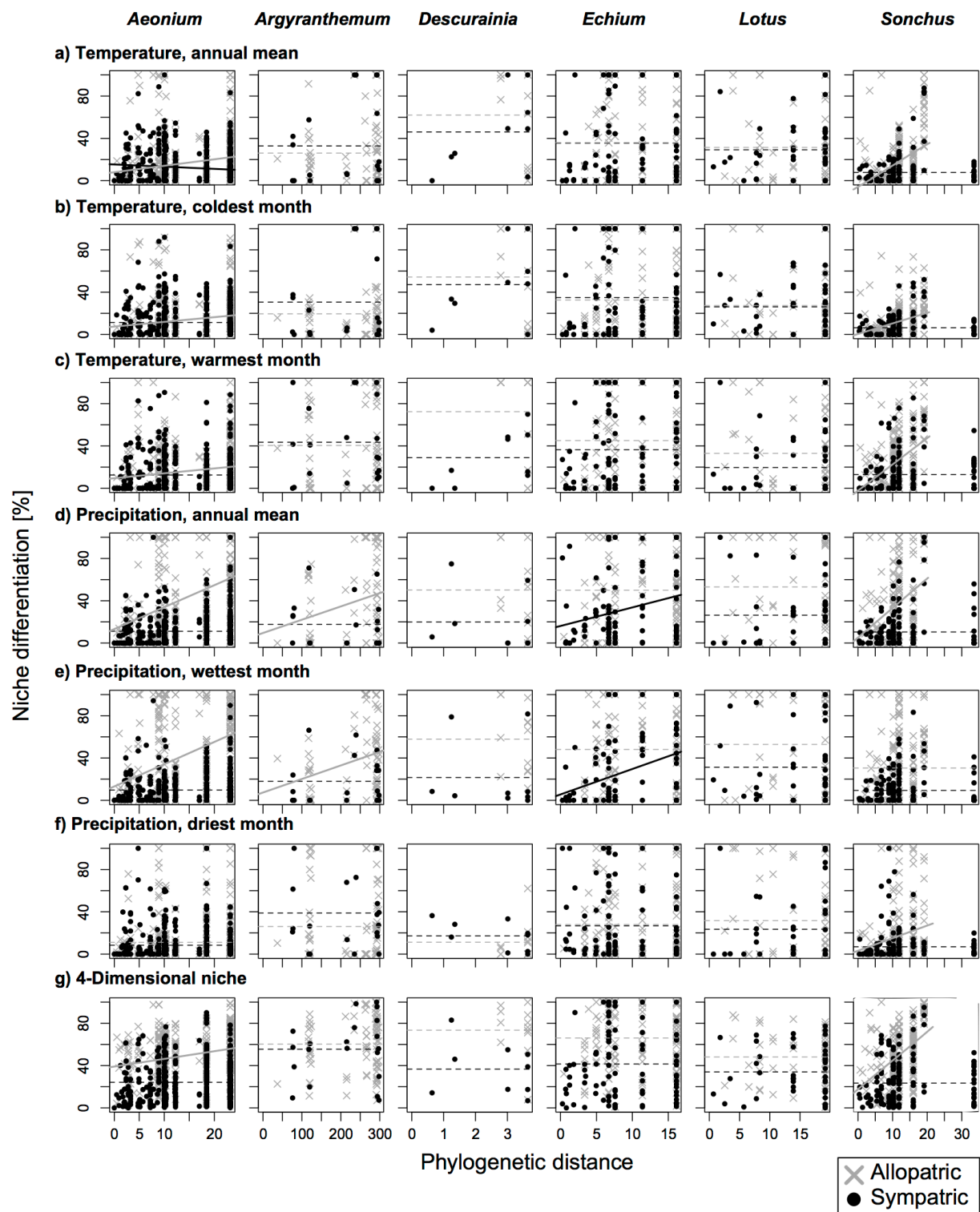


Figure S4.1: Niche differentiation vs. phylogenetic distance for each climatic variable, for all species pairs in each clade (unconstrained analysis, i.e. calculation of niche differentiation not restricted to the niche space shared between islands occupied by the two species being compared; see Figure 2). Points are all grey and semi-transparent, so darker shades indicate overlapping points. 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. This is the unconstrained equivalent of Figure S3.1.



51 **Figure S4.2:** Niche differentiation vs. phylogenetic distance for all pairwise comparisons of
 52 species within each clade, for each climatic variable. Allopatric (grey crosses, grey lines)
 53 species pairs are distinguished from sympatric (black circles, black lines) species pairs,
 54 *sensu lato* (see Methods). Solid regression lines indicate significant relationships between
 55 niche differentiation and phylogenetic distance ($P < 0.05$); dashed lines are flat and show
 56 non-significant relationships as the mean niche differentiation value. This is the
 57 unconstrained equivalent of Figure 3.
 58
 59
 60

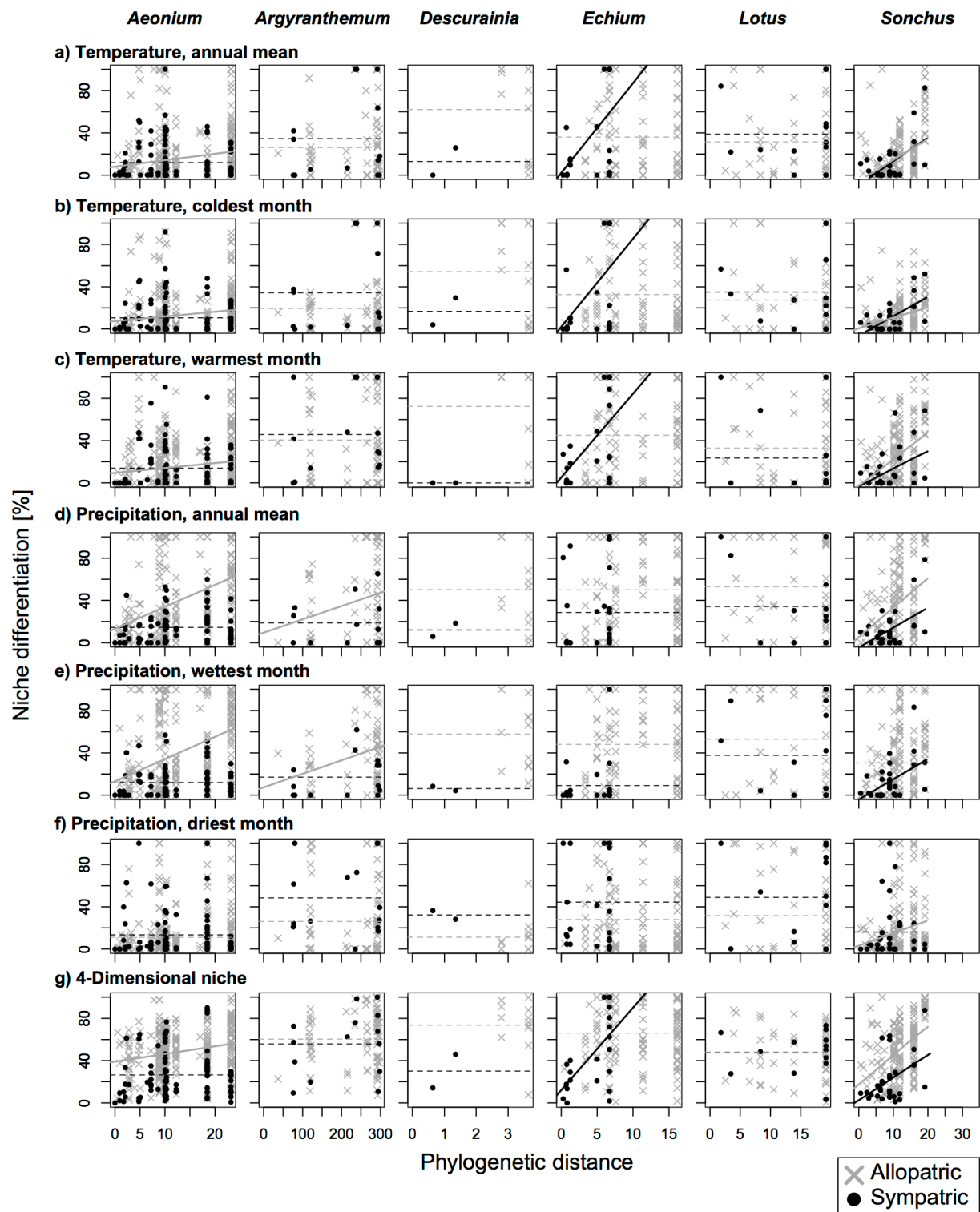


Figure S4.3: Niche differentiation vs. phylogenetic distance for all pairwise comparisons of species within each clade, for each climatic variable. Allopatric (grey crosses, grey lines) species pairs are distinguished from sympatric (black circles, black lines) species pairs, *sensu stricto* (see Methods). 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 not run for sympatric comparisons for *Descurainia* because sample size = 2). This is the unconstrained equivalent of Figure 4.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

S5 – Niche overlap/potential overlap

Table S5.1: Niche overlap/potential overlap (see Figure 2 of the main paper for definitions and formulae) for the six climatic variables and the 4-dimensional niche measure. Each datapoint represents a pair of species within the clade; the number of these datapoints is given after 'N='. Values shown are mean \pm standard error of the mean (range).

Clade	Mean temp.	Mean precip.	4-D niche	
<i>Aeonium</i> N=861	36.4 \pm 0.5 (0-74)	41.2 \pm 0.5 (0-77)	13.1 \pm 0.3 (0-46)	
<i>Argyranthemum</i> N=105	33.2 \pm 1.9 (0-69)	32.7 \pm 1.9 (0-85)	5.4 \pm 0.5 (0-21)	
<i>Descurainia</i> N=21	23.4 \pm 3.5 (0-57)	25.2 \pm 2.7 (5-46)	4.9 \pm 0.7 (0-12)	
<i>Echium</i> N=231	25.9 \pm 1.4 (0-80)	28.2 \pm 1.4 (0-79)	7.1 \pm 0.5 (0-35)	
<i>Lotus</i> N=91	26.5 \pm 1.9 (0-66)	23.2 \pm 1.9 (0-62)	6.1 \pm 0.8 (0-36)	
<i>Sonchus</i> N=351	34.7 \pm 0.7 (0-66)	36.8 \pm 1 (0-73)	9.5 \pm 0.4 (0-47)	
	Warmest	Coldest	Wettest	Driest
<i>Aeonium</i> N=861	34.7 \pm 0.5 (0-80)	37.5 \pm 0.6 (1-75)	37.0 \pm 0.5 (0-68)	26.6 \pm 0.6 (0-63)
<i>Argyranthemum</i> N=105	24.1 \pm 1.6 (0-66)	36.7 \pm 2.0 (0-70)	30.2 \pm 1.6 (0-63)	19.1 \pm 1.7 (0-58)
<i>Descurainia</i> N=21	22.1 \pm 2.5 (0-42)	23.3 \pm 3.6 (0-56)	27.0 \pm 3.4 (0-53)	9.9 \pm 1.3 (2-19)
<i>Echium</i> N=231	22.7 \pm 1.2 (0-70)	27.0 \pm 1.4 (0-74)	27.8 \pm 1.2 (0-72)	19.4 \pm 1.1 (0-65)
<i>Lotus</i> N=91	23.7 \pm 1.7 (0-68)	27.4 \pm 2.1 (0-70)	23.3 \pm 2.0 (0-69)	14.1 \pm 1.7 (0-60)
<i>Sonchus</i> N=351	34.0 \pm 0.8 (0-76)	37.5 \pm 0.8 (11-66)	35.6 \pm 0.7 (0-68)	27.7 \pm 1.0 (0-66)

S6 – Data quality and species distribution maps

The Canary Islands are among the world's botanically best-studied archipelagos, with European botanists surveying the islands frequently, and often intensively, since the beginning of the 18th century. The data used here originate from a long-term governmental initiative (BIOTAS/ATLANTIS). This initiative pulled together these sampling efforts over the centuries by gathering all available occurrence information for each species. More than 1,000,000 literature-based and herbarium records were digitized and geo-referenced on the Canary Islands, an area of less than 7500 km² (Hortal *et al.*, 2007). Following its success, the government initiative was extended to other Macaronesian archipelagos with the support of the EU project ATLANTICO – INTERREG III B (2000-2006).

The main initial aim of the BIOTAS/ATLANTIS project was supporting governmental decisions with empirical data; scientific interest arose later on. Despite the huge sampling effort, the database is not exhaustive enough to provide reliable presence–absence records for all species occurring on the Canary Islands. We thus agree with earlier publications that claim that the data provided are not suitable for direct analyses of spatial species richness patterns (Aranda & Lobo, 2011). Indeed, it is obvious that any richness map directly generated from the data reflects sampling intensity (Hortal *et al.*, 2007).

The occurrence information reflects true occurrence records of species, but does have problems, particularly that for some taxa occurrence information at coarser resolution may have been downscaled to fit the 500x500m resolution of the data base. By integrating across the data collections of botanists across several decades of sampling, however, the data base provides very reliable information on the particular species in which botanists have been most interested for centuries – species endemic to the Canary Islands. Hortal *et al.* (2007) showed that richness patterns in the data are very biased by sampling intensity, quantifying sampling intensity by the number of occurrence records. Endemic species have more than twice the number of occurrence records, compared with non-endemic native species (mean number of records per species = 1750 for Canarian endemics, vs. 840 for non-endemic natives), indicating that the data base is most appropriate for characterizing the distributions of endemic species. Sampling has been primarily focused on locations where the endemics occur. From our personal observations over decades on the islands, we similarly perceive sampling to have been most intensive in less disturbed natural environments (often protected areas), and the distributions of endemic species, as mapped from the ATLANTIS database, to be realistic. We thus believe that the data provide good approximations of the distributions of endemic species, while many non-endemic species (particularly small, unattractive ruderal plants) are clearly under-sampled.

One big advantage of the data provided in the ATLANTIS data base is that the information integrates historic occurrence information. This is of particular advantage for niche modelling as applied in this manuscript because it includes species' occurrence information from times when human population densities were much lower than today and some invasive ungulates that have had devastating effects on vegetation (*Ovis gmelini*, *Ammotragus lervia*) had not yet been introduced. In tandem with the stability of the climate of the Canary Islands over the last few centuries, this allows us to better quantify the climatic niche of species than if only using current distribution data. A nice example of the advantage of integrating historic data is provided by *Aeonium nobile*, one of the iconic endemics from La Palma. The occurrence pattern generated from ATLANTIS shows a distinct and large

1
2 occurrence area in the eastern part of La Palma, where it is virtually absent today. However,
3 small fragments of this presumably once large population were still found four decades ago
4 by Voggenreiter (1973), and it is known that this population was much larger in the past. It is
5 likely that local extinction occurred as a result of the proximity to the island's capital, leaving
6 no record that would be traceable by present-day botanical surveys (e.g. Irl *et al.*, 2015).
7 Without the historical surveys, this would leave a gap in the measured climatic niche of the
8 species, even though this species is actually adapted to east-coast climates of La Palma.
9

10
11 The integration of historic presences limits the possibility for comparisons between
12 ATLANTIS and present day surveys, which are biased by land use-induced changes in
13 vegetation patterns that have occurred within the last few decades. Despite this limitation, we
14 have assessed data quality using one of the most intensive vegetation records available in
15 the study area. Irl and colleagues sampled 1921 vegetation plots, each of c. 7850 m²,
16 covering the island of La Palma, with a particular focus on the endemic flora. This represents
17 2.7 plots (2.1 ha) per km²; 900 of those plots also contain information on overall richness and
18 were used in Irl *et al.* 2015). Their data were not included in the ATLANTIS database and
19 therefore represent an independent distribution dataset for the flora of La Palma. Despite La
20 Palma only being 706 km² in size, this huge sampling effort was not enough to cover the
21 distribution of some rare endemic species. The ATLANTIS database, despite covering the
22 whole archipelago, provides almost six times more occurrence information for the species
23 sampled in both datasets, and includes rare species that are missing in Irl *et al.* (2015).
24
25

26
27 The resolution of Irl *et al.* (2015) differs from the one provided in ATLANTIS (500m x
28 500m grid cells that span the entire Canary Islands). Still, niche ranges estimated from 5%
29 and 95% quantiles (as done in the current manuscript) are highly correlated between the two
30 data sets across all 22 endemic species that occur in sufficient numbers in Irl *et al.* 2015
31 (N>5; upper limit mean annual temperature correlation $r = 0.92$, lower limit mean annual
32 temperature correlation $r = 0.73$, upper limit mean annual precipitation correlation $r = 0.83$,
33 lower limit mean annual precipitation correlation $r = 0.84$) indicating that niche estimates
34 based on both data sets are comparable. Notable differences do occur in some species, but
35 can be explained by larger historic than present distributions (e.g. *Aeonium nobile*) or rare
36 occurrences beyond the climatic ranges occupied by most individuals (e.g. *Echium*
37 *wildpretii*). *Echium wildpretii* is mainly found in the summit scrub, but it occasionally (but
38 repeatedly) occurs below 1000m meters within the Caldera de Taburiente, probably because
39 winds blow seeds from the caldera rim into the lowlands, where they occasionally establish
40 and persist for some decades of favourable climate. This distribution is reflected in
41 ATLANTIS but absent in Irl *et al.* (2015). It was thus reasonably common for us to find that
42 the ranges of climates represented by the Irl *et al.* occurrence records of the endemics in the
43 six radiations were nested within the climatic ranges represented by the ATLANTIS
44 occurrence records of the same species on La Palma. On the other hand it was very rare to
45 find that the Irl *et al.* records extended the climatic ranges beyond those represented by the
46 ATLANTIS records (this only happened for *Descurainia millefolia*, *Aichryson punctatum* [both
47 temperature only] and *Echium bethencourtii* [temperature and precipitation]). These findings
48 give us confidence that the ATLANTIS data are fit for the purpose for which we use them in
49 this paper.
50
51
52
53
54
55
56
57
58

59 Our study focuses on well-studied endemic species: 123 out of our 126 species are
60 archipelago endemics and 86 are single island endemics. The ATLANTIS data provide

1
2 reliable long-term presence-only occurrence information for Canary endemic species
3 generally, and the species analyzed in this paper in particular. As described above, the
4 climatic niche estimates derived from these data compare well with the best available
5 vegetation data for La Palma. In addition, the ATLANTIS data produce distributions for
6 endemics that match well with known distributions on El Hierro, as derived from the sampling
7 by Christian Stierstorfer and Markus von Gaisberg (Otto *et al.*, 2015). In sum, ATLANTIS
8 provides remarkable sampling density, far exceeding that of almost all other studies using
9 species distribution modelling or niche estimation, and producing good estimates of the
10 distributions of Canary endemic species (see Figure S6.1, which starts on the next page).
11
12
13
14
15

16 References

- 17 Aranda, S. C. & Lobo, J. M. (2011), How well does presence-only-based species distribution modelling
18 predict assemblage diversity? A case study of the Tenerife flora. *Ecography*, 34: 31–38.
19
20 Hortal, J., Lobo, J. M. & Jiménez-Valverde, A. (2007), Limitations of Biodiversity Databases: Case
21 Study on Seed-Plant Diversity in Tenerife, Canary Islands. *Conservation Biology*, 21: 853–863.
22
23 Irl S.D.H., Harter, D., Steinbauer, M.J., Puyol Gallego, D., Fernández-Palacios, J.M., Jentsch, A.,
24 Beierkuhnlein, C. (2015) Climate vs. topography – spatial patterns of plant species diversity and
25 endemism on a high-elevation island. *Journal of Ecology*, doi:10.1111/1365-2745.12463
26
27 Otto, R., Whittaker, R.J., von Gaisberg, M., Stierstorfer, C., Naranjo-Cigala, A., Steinbauer, M.J.,
28 Borregaard, M.K., Arévalo, J.R., Garzón-Machado, V., Del Arco, M., Fernández-Palacios, J.M.
29 (2015) Transferring and implementing the general dynamic model of oceanic island biogeography
30 at the scale of island fragments: the role of geological age and topography in plant diversification in
31 the Canaries. *Journal of Biogeography*, accepted.
32
33 Voggenreiter, V. (1973) Pflanzenverbreitungstypen auf La Palma. Geobotanisch-arealkundliche
34 Untersuchungen I. Aeonium. *Cuadernos de Botánica Canaria* 18/19: 43–48.
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure S6.1: Distribution maps for all species used in this study. Black grid cells (500x500m) indicate presence records, grey grid cells absence records. The maps represent presence-only data from the ATLANTIS database. Incorrect absences, which may occasionally occur, are not problematic for environmental niche calculations as long as the presence records represent the species' environmental niches reasonably well.

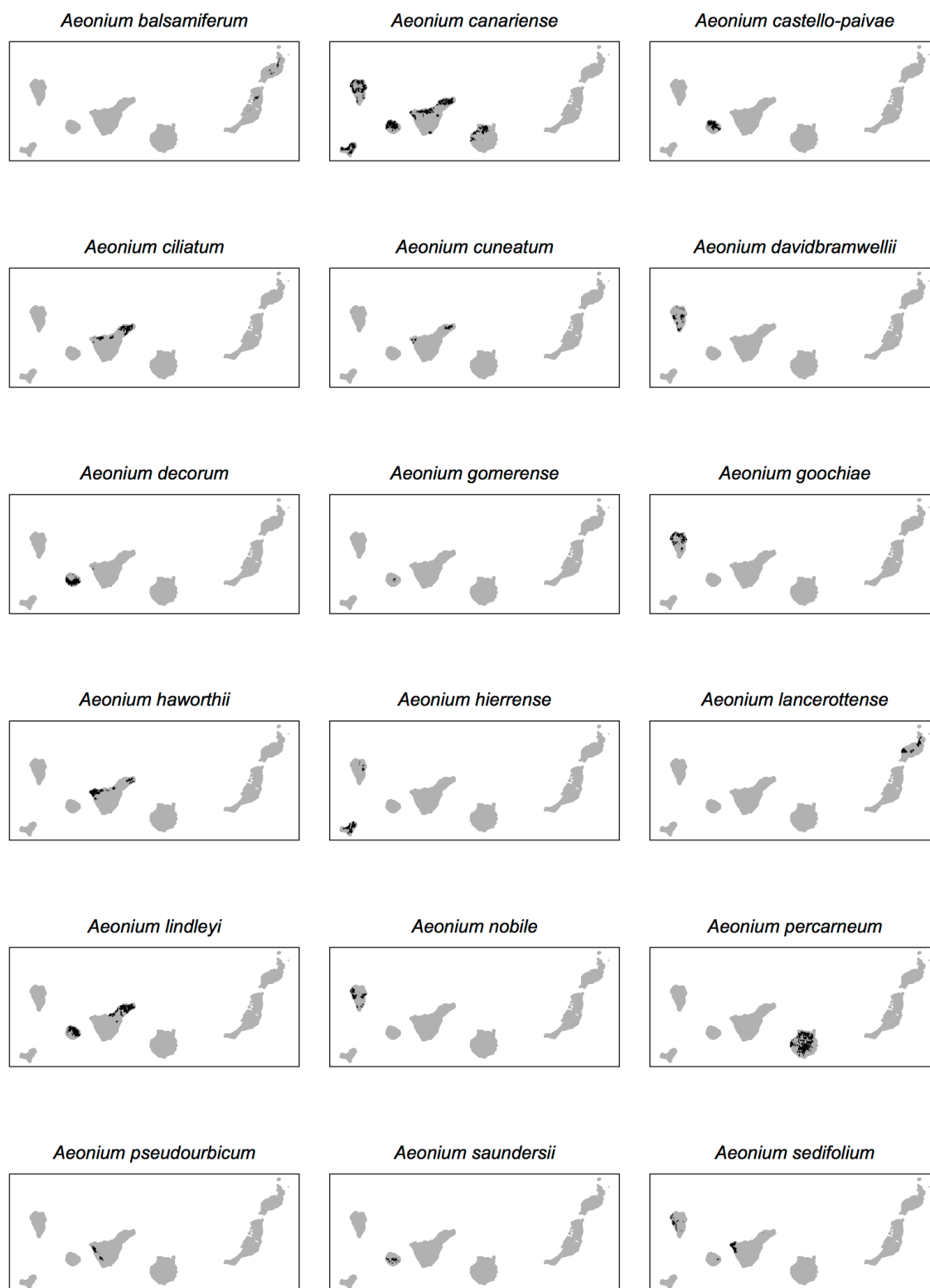


Table S6.1 continued (2 of 7)

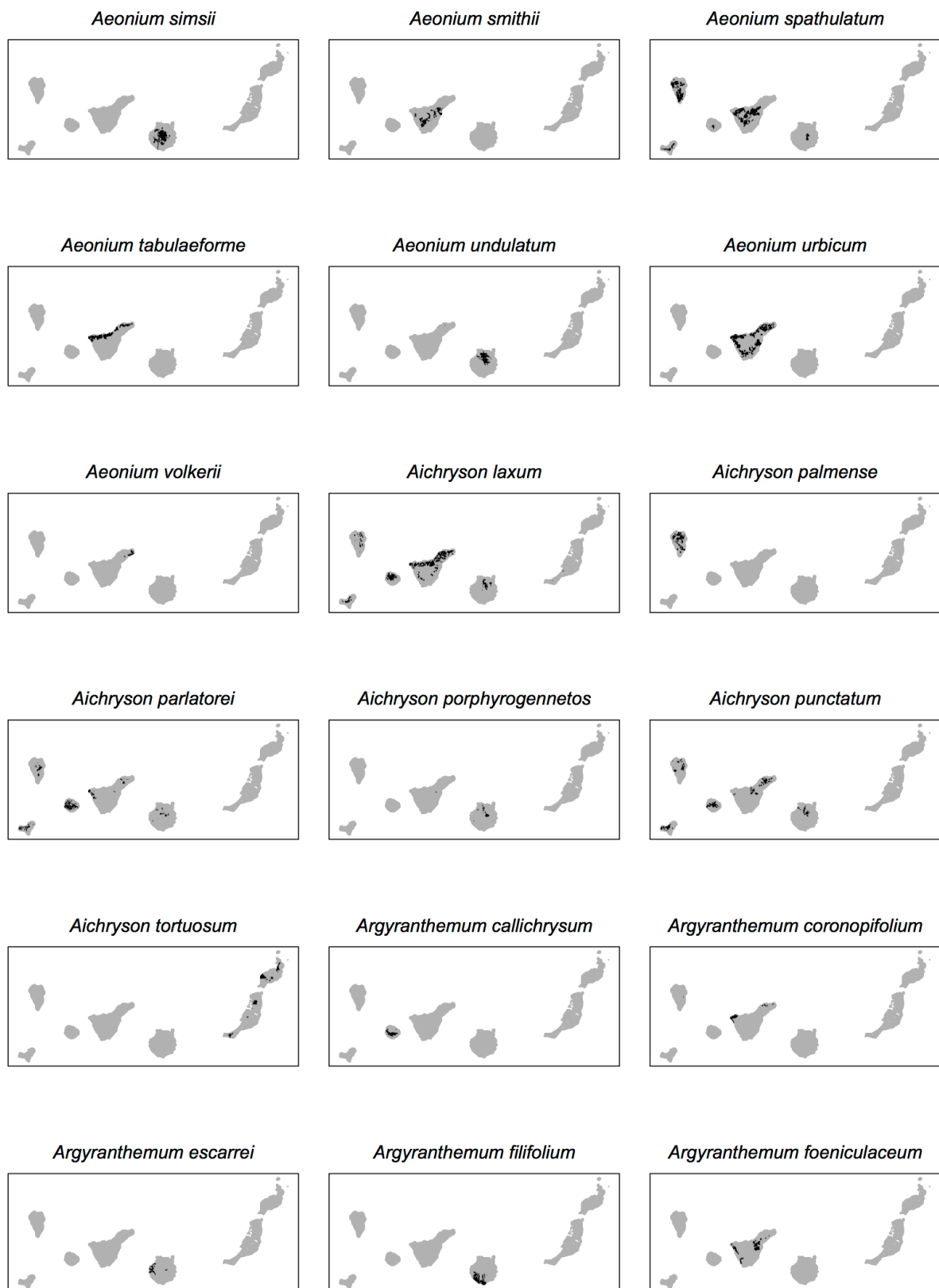


Table S6.1 continued (3 of 7)

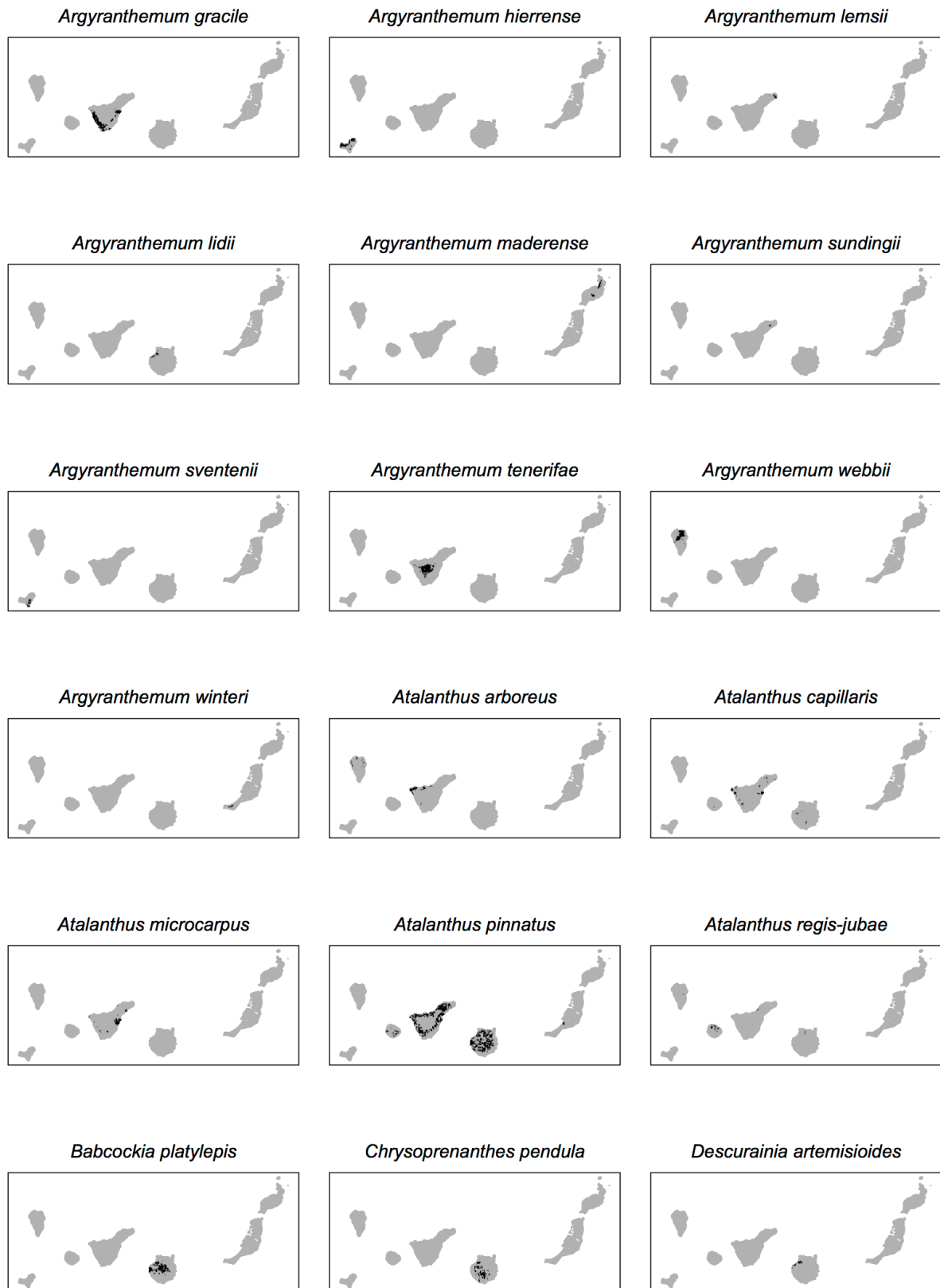


Table S6.1 continued (4 of 7)

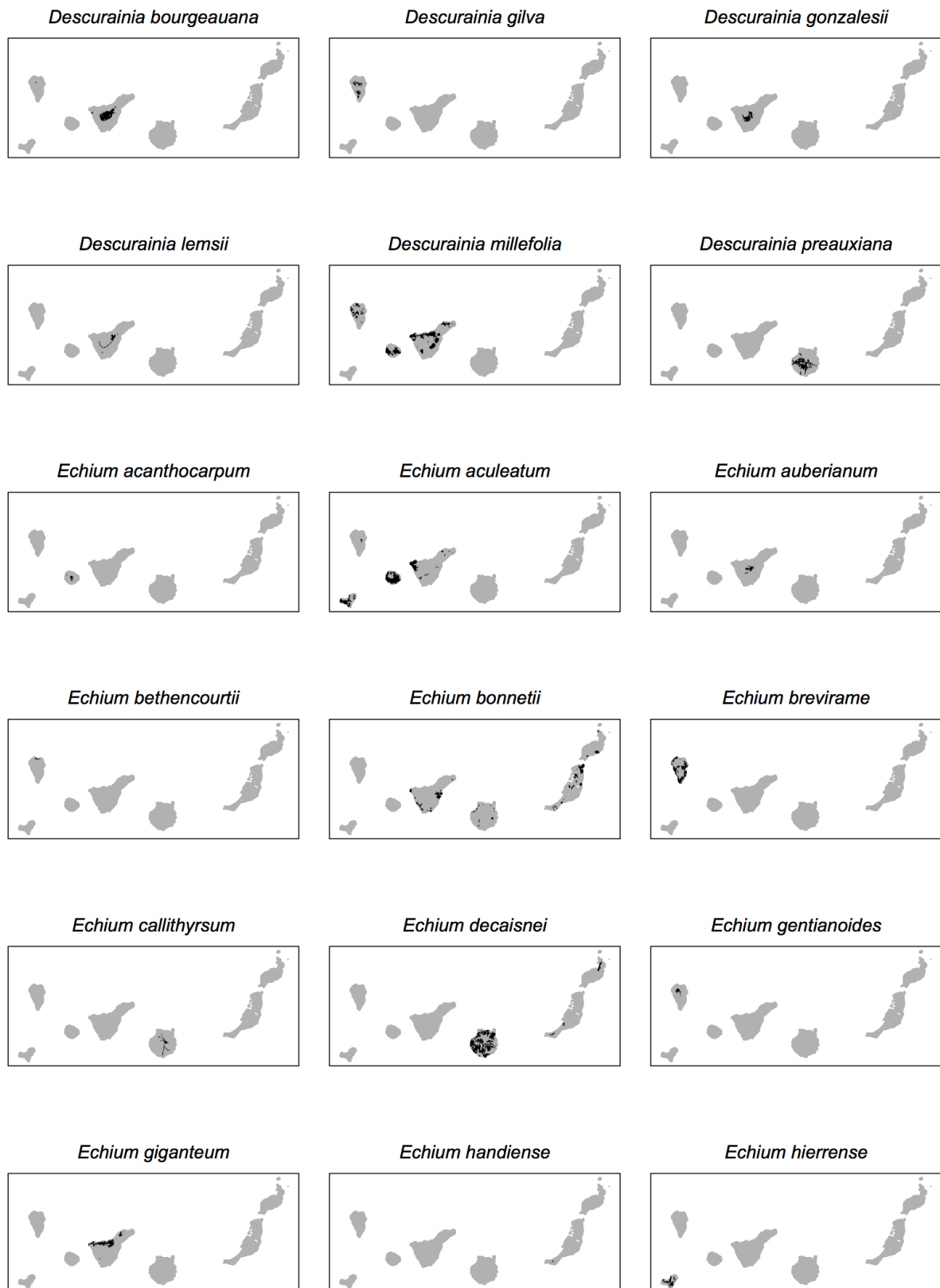


Table S6.1 continued (5 of 7)

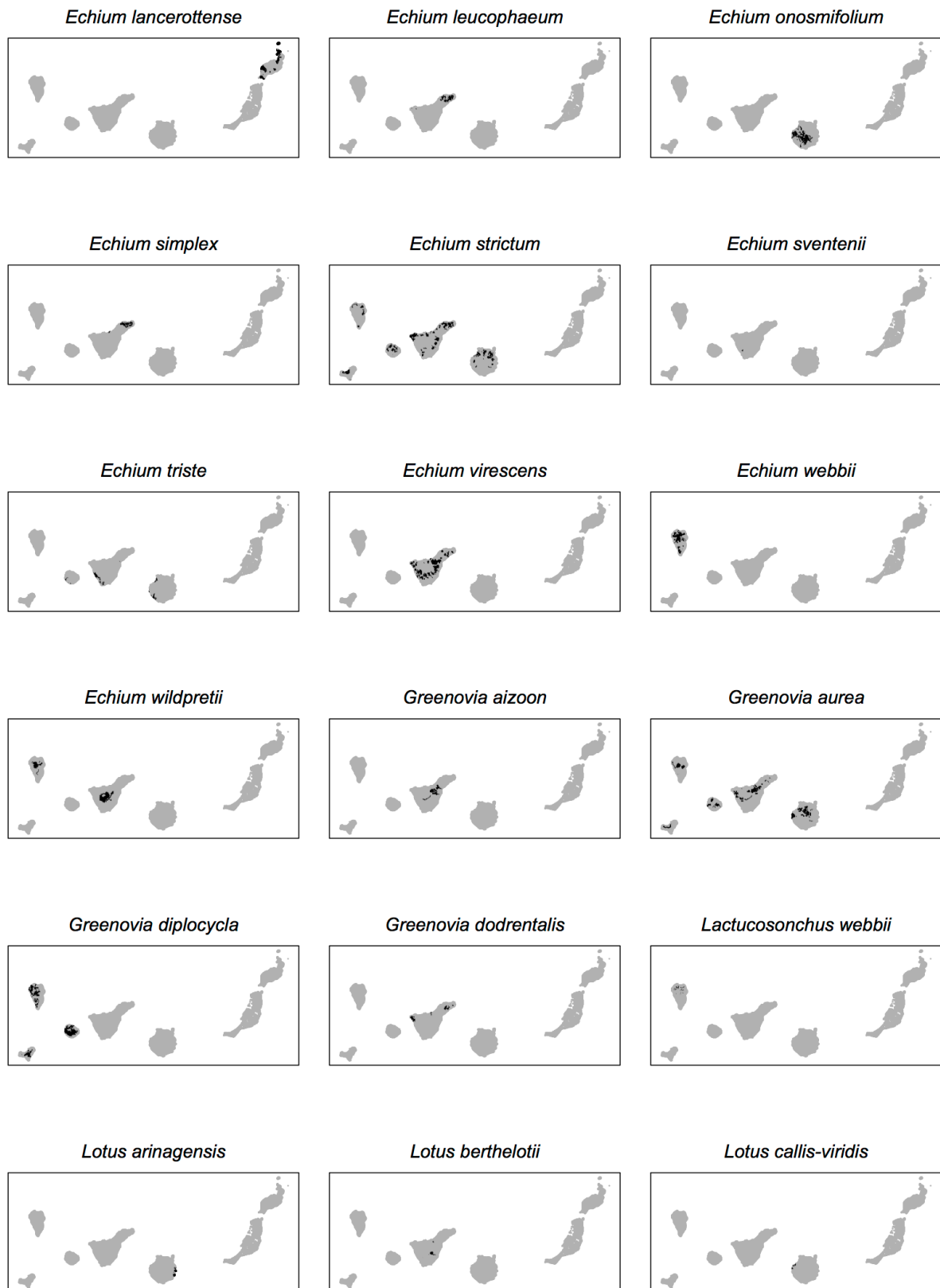


Table S6.1 continued (6 of 7)

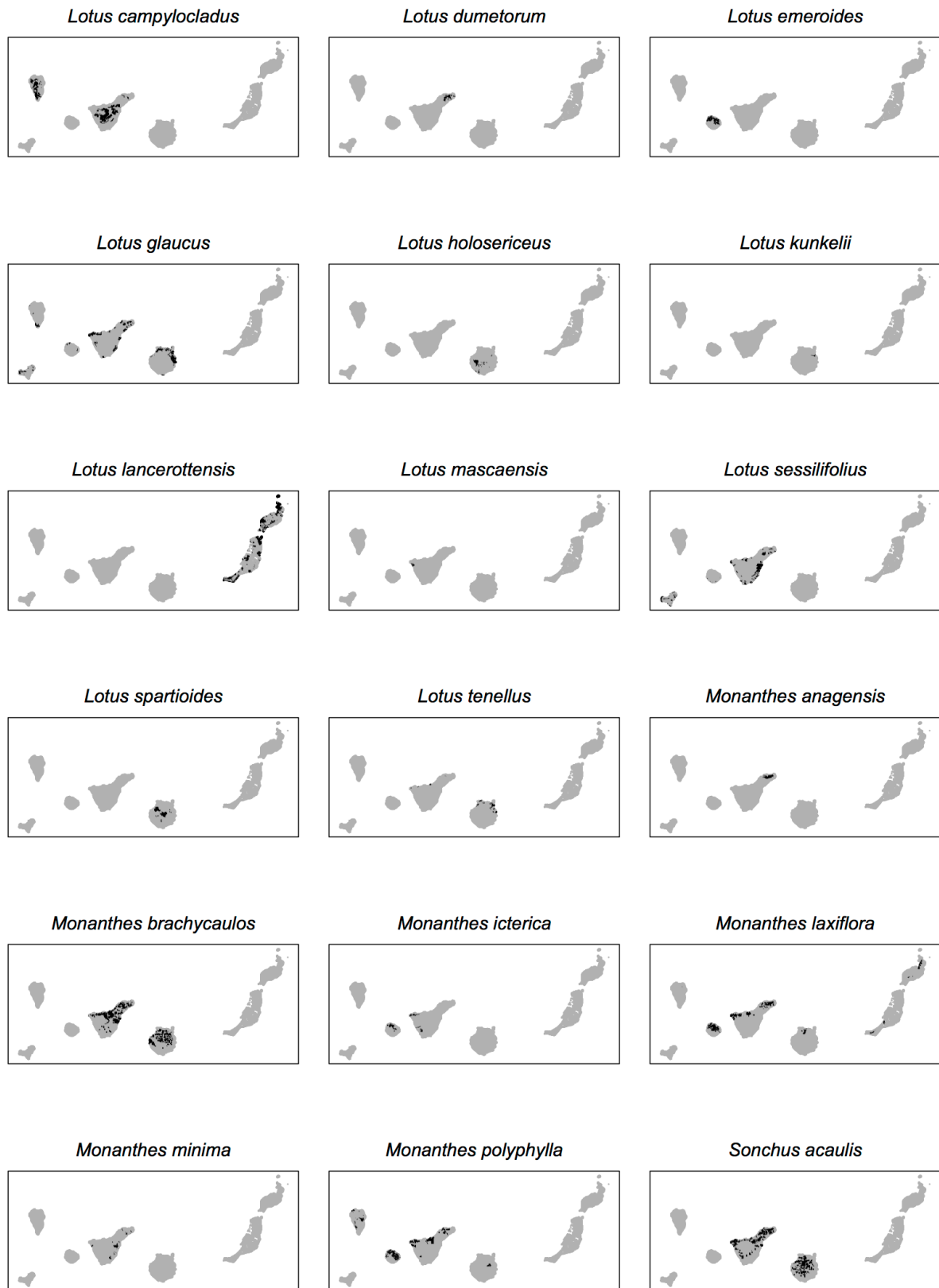


Table S6.1 continued (7 of 7)

