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1 *Reviews for Trends in Ecology & Evolution*

2

3 **Unifying niche shift studies: insights from biological invasions**

4

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25

26

27

28 **Abstract**

29 Assessing whether the climatic niche of a species may change between different
30 geographic areas or time periods has become increasingly important in the context of
31 ongoing global change. However, approaches and findings have remained largely
32 controversial so far, calling for a unification of methods. Here, we build on a review of
33 empirical studies of invasion to formalize a unifying framework that decomposes niche
34 change into unfilling, stability and expansion situations, taking both a pooled-range and
35 range-specific perspective on the niche, while accounting for climatic availability and
36 climatic analogy. This framework provides new insights into the nature of climate niche
37 shifts and our ability to anticipate invasions, and may help guiding the design of
38 experiments for assessing causes of niche changes.

39

40

41 **Niche shifts during invasions: setting the scene**

42 How climate determines the distribution of species is a classic question in ecology,
43 closely tied to Hutchinson's (1957) concept of the environmental niche, and still a major
44 research topic (Soberón & Nakamura, 2009; Peterson *et al.*, 2011). Although, for some
45 species, it has become possible to determine the fundamental climatic niche based on
46 physiological information and a mechanistic understanding (e.g. (Kearney & Porter,
47 2009)), for most species only the realized climate niche can realistically be estimated
48 through empirical studies (Guisan & Thuiller, 2005). With global change, it has become
49 increasingly important not only to describe species' climate niches but also to
50 understand whether these can change rapidly (niche shifts) or not (niche conservatism)
51 between different geographic areas or time periods (Peterson, 2011) (Fig. 1). The
52 primary approach to investigating climatic niches in space and time has been to analyse
53 climatic conditions across a species' distributional ranges and/or over time (Pearman *et al.*, 2008a).

55 As already understood by Charles Elton (1958), biological invasions offer a unique
56 opportunity to study how species colonize new environments (Sax *et al.*, 2007;
57 Richardson & Pysek, 2008; Kueffer *et al.*, 2013), and whether they retain their climatic

58 niche in a new range (Pearman *et al.*, 2008a). Addressing this question has proved
59 important in recent years as a test of our capacity to use climate matching to assess
60 invasion risks by exotic species at transnational scales (Venette *et al.*, 2010; Guisan *et al.*,
61 2013), in particular when using ecological niche models (ENMs), which rely heavily on
62 climatic niche conservation between native and exotic ranges (Pearman *et al.*, 2008a;
63 Colwell & Rangel, 2009; Peterson, 2011). Do a majority of species retain their native
64 climatic niche when introduced elsewhere? The answer to this question is fundamental
65 because it informs both theoretical and applied ecology, but approaches have diverged
66 and findings have remained largely controversial so far (Table S1, supplementary
67 material) (Pearman *et al.*, 2008a; Peterson, 2011).

68 Evidence exists both for and against climatic niche conservatism during invasions. A
69 recent large-scale survey of 50 Holarctic terrestrial plant invaders concluded that
70 climatic niche shifts are rare overall between the native and invaded ranges, and
71 therefore models can usefully predict invasion in the exotic range (Petitpierre *et al.*,
72 2012.) The same conclusions were reached for birds (Strubbe *et al.*, 2013) and other
73 groups (see (Peterson, 2011); Table S1, suppl. mat.). But the assumption of niche
74 conservatism was also challenged by evidence of climatic niches shifting during
75 invasions (e.g. (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Rödder & Lötters,
76 2009; Medley, 2010; Lauzeral *et al.*, 2011); Table S1), potentially hampering predictions
77 in the new range. Contrasting evidence of niche dynamics during invasions, and
78 particularly of the frequency of niche shifts (i.e. of centroid and/or limits; see Fig. 1)
79 among various taxonomic groups, thus coexist in the literature (about 50% shifts/42%
80 no-shifts and 8% no-conclusion in Table S1). This contrasting evidence may, however,
81 correspond to different types of niche changes, biological and/or methodological study
82 contexts, data types, species characteristics or methods being used (Peterson &
83 Nakazawa, 2008; Mandle *et al.*, 2010; Peterson, 2011; Soberon & Peterson, 2011;
84 Broennimann *et al.*, 2012) (Table S1), which confounding effects prevent sound
85 interpretation of the possible mechanisms behind niche changes. Unification of the
86 analytic context and metrics used, and a well-balanced comparison across different
87 species, taxonomic groups, environmental spaces and geographic areas (Pearman *et al.*,
88 2008a; Kueffer *et al.*, 2013), may contribute to reconcile conflicting evidence in
89 observational studies of biological invasions requires.

90 Here, we build on a review of niche changes reported in empirical invasion studies
91 (Table S1) to formalize a new framework that unifies the analytical context (Box 1, Figs
92 1 and 2), clarifies the role of the niche-biotope duality (Box 2) (Colwell & Rangel, 2009;
93 Soberón & Nakamura, 2009), and helps to identify potential factors influencing niche
94 change between ranges. The central idea of this framework is to decompose a niche
95 comparison between native and exotic ranges into its three basic components: niche
96 unfilling, niche stability and niche expansion (Box 3, Fig. 2) (Petitpierre *et al.*, 2012). We
97 present these elements and discuss them along with the importance of taking into
98 account the available environment, distinguishing analog from non-analog climatic
99 conditions between ranges (Box 4), and accounting for niche factors and niche dynamics
100 at finer resolution. We conclude with recommendations on using the proposed
101 framework for future niche change studies.

102

103 **Niche changes and associated metrics**

104 *Which niche is measured from field observations?*

105 The realized climatic niche quantified from field observations is determined by biotic
106 constraints on the fundamental eco-physiological niche, population dynamics (e.g.
107 source-sink dynamics) and dispersal limitations (i.e. accessibility; Box 2) (Pulliam, 2000;
108 Soberon, 2007; Barve *et al.*, 2011), but it is also constrained by the availability of the
109 environment in the areas (Box 4) at the timescale considered in the study (i.e. some
110 conditions can be available at one time in one area, but not earlier or later) (Jackson &
111 Overpeck, 2000; Mandle *et al.*, 2010). A change in this realized niche can thus result
112 from adaptive evolution occurring in the colonized range (Sax *et al.*, 2007; Alexander &
113 Edwards, 2010) or from changes in biotic interactions, dispersal limitations, or from
114 pre-adaptation to conditions not (anymore) available in the initial range at the time of
115 the study but available in the colonized range (Pearman *et al.*, 2008a). Hereafter, we
116 consider a niche shift as any change of the realized niche, i.e. the niche as measured by
117 climatic characteristics at sites of species occurrence in the field. It thus includes
118 implicitly any potential change of the fundamental niche, although with such empirical
119 data, a change caused by evolution of physiological tolerance cannot be differentiated
120 from a change due to other factors (Broennimann *et al.*, 2007; Soberon & Peterson,
121 2011).

122 *Two main approaches to quantifying niche changes*

123 Two main approaches have been used so far to compare niches between ranges, based
124 on direct observations or on model predictions (Broennimann *et al.*, 2012) (Fig. 3, Table
125 S1, suppl. mat.). The first approach uses observations directly and compares the
126 difference in environmental attributes of the sites where the species occurs between the
127 native and exotic ranges in environmental space. This comparison can be done either
128 through univariate (e.g. (Lauzeral *et al.*, 2011)) or multivariate tests (e.g. in a reduced
129 PCA space (Broennimann *et al.*, 2007); Fig. 3a). Such a direct approach does not rely on
130 any underlying model that relates the occurrences to the environment. The approach
131 can be considerably improved by calculating smooth densities of species occurrences in
132 a gridded environmental space, as a way to avoid unrealistic 'holes' in a niche due to low
133 sampling effort (Broennimann *et al.*, 2012) (see also (Guisan *et al.*, 2012; Webber *et al.*,
134 2012)). The second approach relies instead on the outcomes of ecological niche models
135 (ENMs (Peterson *et al.*, 2011); also called species distribution models, SDMs (Guisan &
136 Thuiller, 2005)), and compares the overlap of reciprocal predictions of geographic
137 distributions (i.e. predicting the invaded distribution with the model fitted in the native
138 range, and vice-versa), usually comparing in the exotic range the two predictions by the
139 models fitted in each range (Fitzpatrick *et al.*, 2007; Warren *et al.*, 2008; Warren *et al.*,
140 2010) (Fig. 3b). Specialized software has been developed for niche comparisons based
141 on the ENM approach (ENMTool (Warren *et al.*, 2010)). Comparative analyses with
142 virtual species, for which distributions and niche overlap are known, showed that the
143 first approach (ordination) quantified niche overlap overall more accurately than the
144 second (ENM) (Broennimann *et al.*, 2012); however, the ordination approach provides a
145 mathematically less formalized representation of the niche and is less able to optimize
146 the weighting of the different environmental factors based on their relevance for a
147 species' ecology. The ENM approach is particularly useful to assess ENM transferability
148 between ranges (Randin *et al.*, 2006). Thus, although both approaches have strengths
149 and weaknesses (Broennimann *et al.*, 2012), comparisons of niche change results
150 between studies (meta-analyses) should include preferentially those based on
151 ordinations, and at least make clear which approach was used (see Table S1).

152 *Different components of niche change: centroid shift, overlap, expansion and unfilling*

153 From either of these approaches, different niche change metrics can be calculated, at
154 two levels of analyses – pooled ranges and range-specific (Box 3). The most commonly
155 used metrics so far measure either a shift of the niche centroid, C (mean position; e.g.
156 using Euclidean distance (Broennimann *et al.*, 2007)), or a change in the overlap, O,
157 between the two niches (e.g. using Schoener's D (Warren *et al.*, 2008) or minimum
158 convex polygons (Gallagher *et al.*, 2010)), and they are usually calculated in relation to
159 the entire realized niche between two ranges (i.e. pooled; Box 3). However, a niche
160 change detected in one of these two ways can result from multiple situations (Fig. 1):

161 (i) a change of the niche envelope (overlap $\neq 1$) due to symmetric niche expansion or
162 contraction (hereafter called 'unfilling' in the case of invasions, because it corresponds
163 to a part of the native niche that was not filled) in climatic space, thus not shifting the
164 niche centroid (Fig. 1a); a species may expand both to warmer and colder conditions in a
165 way that the average temperature-related niche position remains stable as it is observed
166 for common spotted knapweed invading North America (*Centaurea stoebe*, Fig. S1a,
167 suppl. mat.);

168 (ii) a change of the niche centroid with displacement of the niche envelope (Fig. 1b-d)
169 due to niche unfilling (e.g. black cherry tree invading Europe, *Prunus serotina*, Fig. S1b)
170 and/or expansion (e.g. desert false indigo invading Europe, *Amorpha fruticosa*, Fig. S1c)
171 in the invaded range; or

172 (iii) a change of the niche centroid only, without niche expansion or unfilling, due to a
173 change of the density of occurrences within the same niche envelope in climatic space
174 (Fig. 1e). The latter case can result from changes in competition, limited dispersal or
175 availability of environmental conditions in the exotic range that reduce the density of
176 species occurrences in some part of the niche space (Soberon & Peterson, 2011),
177 changing the position of the centroid with only a weak impact on the niche limits, as
178 shown for pinweed invading North America (*Erodium cicutarium*, Fig. S1d). Thus, a shift
179 of the niche centroid between the native and the exotic range (Fig. 1b-e) can provide a
180 first indication that a niche change occurred, but it is not sufficient to interpret its exact
181 nature. And, reciprocally, an absence of a shift of the niche centroid does not mean that
182 no niche shift occurred.

183 New indices were thus required to decompose niche comparisons to reveal two distinct
184 components of niche changes: *expansion* and *unfilling* (Box 3, Fig. S1) (Petitpierre *et al.*,

185 2012). *Unfilling* (U) most commonly corresponds to the proportion of the native niche
186 non-overlapping with the exotic niche, and *expansion* (E) refers to the proportion of the
187 exotic niche non-overlapping with the native niche. These indices, as just defined,
188 measure changes that are relative to one of the ranges (native or exotic), but they can
189 also be measured with regard to the entire species distribution, where native and exotic
190 ranges are pooled (Box 3). The pooled versions of E and U (E_p and U_p in Box 3) thus
191 inform us about the species niche dynamic at the global scale of the study, but convey
192 less information about our ability to predict species invasions from the native range
193 (Box 3). E and U (and equivalently E_p and U_p) are recently published indices (Petitpierre
194 *et al.*, 2012) that can easily be calculated from the same two main approaches previously
195 described (Broennimann *et al.*, 2012), but provide much more information than simple
196 overlap or centroid changes. Studies that found overall niche conservatism for invaders
197 relied consistently on such complete set of niche change metrics (Table S1, suppl. mat.).
198 Later, we will refer to the whole set of niche change metrics as the COUE scheme (Box
199 3).

200 *Dealing with available and non-analog climates between ranges*

201 The availability of climatic conditions in geographic space matters when quantifying
202 niche changes between ranges. Due to the niche-biotope duality (i.e. the correspondence
203 between environmental and geographic spaces; Box 2), some conditions common in the
204 exotic range may be rare in the native range (or the converse; Box 4) so that, without
205 correction, one may detect niche shifts (measured with centroid change or overlap of
206 percentile envelopes) only because these conditions are more or less available in one
207 range than in the other (Soberón & Nakamura, 2009; Soberon & Peterson, 2011).
208 Accounting for environmental availability is thus necessary and has been done so far in
209 two ways. First, niche change metrics can be corrected by the distribution of the
210 available environment, either by comparing the overlap between native and exotic
211 niches with the overlap between native and exotic ranges (Mandle *et al.*, 2010), or by
212 transforming species densities in the environmental space into species “occupancies”
213 (i.e. the ratio of density of species to the density of available environment (Broennimann
214 *et al.*, 2012); see also (Dormann *et al.*, 2010)). Second, niche metrics can be calculated
215 only within the most common environments shared between native and exotic ranges
216 (say within the shared portion of the 75th percentiles encompassing the prevailing

217 conditions in each range (Petitpierre *et al.*, 2012)). Removal of rare climates is however
218 likely to have a strong impact on the results (with either approach) when the two ranges
219 show important differences in climate availability. In this case we advise comparing
220 analyses across a range of percentiles (say 75, 80, 85, 90, 95 and 100%) in order to see
221 how the quantification of niche change can be affected by various levels of trimming (see
222 suppl. online mat. in (Petitpierre *et al.*, 2012)) and to understand the implications
223 (specific to each case study) for the interpretation of niche changes.

224 An extreme case of climate non-availability is when climate conditions exist only in one
225 of the two ranges (Box 4) (Williams & Jackson, 2007). These non-analog climates
226 represent a severe problem when calculating niche change metrics, because no insight
227 on the biology of the species in these non-analog climates can be learned from a
228 comparison between ranges. This is because colonization of portions of environmental
229 space not present in the native range cannot be considered unambiguously as resulting
230 from niche evolution in the exotic range, and the interpretation of these situations thus
231 remains speculative (Mandle *et al.*, 2010; Soberon & Peterson, 2011). A scientifically
232 more rigorous approach to assess niche expansion, therefore, is to restrict the analyses
233 to the shared, analog climatic conditions between the native and exotic ranges (e.g.
234 (Petitpierre *et al.*, 2012)), and to provide measures of expansion in non-analog
235 situations separately (Guisan *et al.*, 2012). Studies that restricted their analyses to
236 analog environments found niche conservatism to be dominant among invader species
237 (Table S1, suppl. mat.). Complementary experimental approaches would then be needed
238 to determine whether, for instance, expansions in non-analog conditions may represent
239 a change of the fundamental niche (Pearman *et al.*, 2008a). This issue is particularly
240 important because non-analog climates not only occur across space but will also occur
241 over time due to climate change (Williams & Jackson, 2007). This is also the reason why
242 projections of ecological models in non-analogous climates are considered unreliable
243 (Fitzpatrick & Hargrove, 2009; Mandle *et al.*, 2010). Still, colonization of non-analog
244 climates in the exotic range may represent relevant situations to consider from a
245 management perspective, calling for separate ENM projections in both analog and non-
246 analog climates in the invaded range (through fitting ENMs with pooled data from the
247 native and exotic range (Broennimann & Guisan, 2008)).

248

249 **What other factors could affect the quantification of climatic niche changes?**

250 *Range unfilling in the native range*

251 Geographic range unfilling (not to be confused with niche unfilling) – i.e. when a species
252 does not occupy all the geographic locations that have suitable conditions within its
253 climatic niche – can occur in the native range as a result of non-equilibrium situations,
254 such as ongoing post-glacial recolonization during the Holocene (Normand *et al.*, 2011),
255 and can potentially affect the quantification of niche change. This problem is also known
256 as the ‘accessible area’ issue (Barve *et al.*, 2011). But geographic range unfilling does not
257 necessarily lead to niche unfilling in environmental space. For instance, it was shown
258 that range unfilling can nonetheless translate into complete climatic niche filling for
259 some tree species in Europe (Randin *et al.*, 2013). Range unfilling particularly affects
260 niche quantification if the climates present in the unfilled geographic space are rare
261 and/or not well represented – or even absent – in other parts of the range. However,
262 published analyses generally calculate range filling based on a geographic projection of
263 the realized niche at the time of the study (e.g. (Normand *et al.*, 2011)), and thus these
264 documented cases of range unfilling cannot translate into niche unfilling. But range
265 unfilling measured in other ways - e.g. field common garden experiments located
266 beyond a species’ current geographic and climatic range (Alexander *et al.*, 2012;
267 Alexander, 2013; Hargreaves *et al.*, 2014) - may reveal niche unfilling.

268 *Biased or incomplete sampling of species distributions*

269 Another issue relates to the type and quality of species distribution data. Although it is
270 important to cover an entire species’ niche to assess niche change without bias, its
271 complete native and exotic distribution ranges need not necessarily be considered.
272 Because of the niche-biotope duality (Colwell & Rangel, 2009; Soberón & Nakamura,
273 2009) (Box 2), the climatic niche of a species might well be fully captured even if only a
274 part of its geographical distribution is sampled. However, and similarly to the issue of
275 range unfilling, when geographic truncation leads to environmental truncation (Raes,
276 2012), niche change studies based on both ordinations and ENMs (Fig. 3) should be
277 considered with care, because their conclusions will only be applicable to the climate
278 space investigated and within analog climatic combinations between the two ranges. In
279 these situations, approaches based on ecological niche models (ENMs (Guisan &
280 Thuiller, 2005; Peterson *et al.*, 2011); Fig. 3) may be less reliable for spatial predictions,

281 as they rely heavily on fitted species-environment response curves that could be biased
282 (Thuiller *et al.*, 2004; Raes, 2012). In addition to environmental truncation, bias or
283 errors in the geographic sampling of the distribution of a species may also bias
284 measures of niche change. For instance, coarse atlas distribution data may portray a
285 species in areas where it does not exist, while occurrence data (e.g. from herbaria) may
286 under-represent or omit areas where the species occurs, both possibly affecting niche
287 quantification.

288 *Beyond macroclimate: microclimate and non-climatic factors*

289 Climate is often seen as the main factor driving species distributions at large scales
290 (Guisan & Thuiller, 2005), and most global-scale studies of niche changes in native
291 (Pearman *et al.*, 2008b; Crisp *et al.*, 2009; Maiorano *et al.*, 2012) and exotic species
292 (Broennimann *et al.*, 2007; Gallagher *et al.*, 2010; Medley, 2010; Lauzeral *et al.*, 2011;
293 Petitpierre *et al.*, 2012) looked at changes in macroclimate (i.e. the coarse and large-
294 scale climate that usually determines biomes). This primary role of macroclimate does
295 not prevent finer climatic characteristics or other abiotic factors from affecting species
296 distributions, such as the restriction to specialized habitats (e.g. mountain
297 microclimates, stream banks or particular soil types) that must generally be
298 characterized at a finer spatial grain (e.g. 1 km x 1 km) than that typically used in
299 macroclimatic studies. Niche changes may be particularly observed in non-climatic
300 components (such as soils) of a species' niche. For instance, Bertrand *et al.* (2012)
301 showed that a shift of the climatic niche centroid can be observed when soil variables
302 are included in the analyses. When shaping the distribution in the native range, these
303 micro-scale factors could thus result in the detection of apparent macroclimatic niche
304 expansion in the exotic range for two reasons: (i) part of the native macroclimate might
305 not be occupied by the species due to spatial correlation with factors that hinder its
306 occurrence (Bertrand *et al.*, 2012); or (ii) a species might occur under conditions in the
307 native range that, within the coarse cells of macro-climatic maps, are scattered and
308 marginal (and thus smoothed and hindered in niche analyses based on mean values
309 within coarse cells), but are dominant in the exotic range and thus only revealed there in
310 the niche quantification, causing an apparent niche shift.

311 However, these factors will only modify measures of macroclimatic niche change if: (i)
312 their geographic distribution matches a restricted portion of the climatic niche in the

313 native or exotic range, and (ii) this restricted portion is the one that shows niche change.
314 In this regard, studies at a finer resolution (e.g. microclimate) and/or including non-
315 climatic factors would be useful for a more detailed understanding of niche dynamics in
316 invaded ranges. But to be complementary to the strict macroclimatic niche studies
317 conducted so far, findings based on macroclimate alone should be presented and
318 compared to findings when microclimatic and non-climatic components are added (as
319 for analog/non-analog climates), so that their relative effect can be properly assessed
320 (e.g. (Bertrand *et al.*, 2012)).

321

322 **Toward a unifying framework: conclusion and remaining challenges**

323 There has recently been a great diversity of studies examining climate niche change in
324 exotic species (Table S1, suppl. mat.), some reporting dramatic niche changes
325 (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Gallagher *et al.*, 2010; Medley, 2010).
326 However, how many shifts occur in analog versus in non-analog climates, and whether
327 these only occur in specific taxonomic groups or habitats, remains to be investigated.
328 Among 36 studies including ca. 180 species, about 50% of the species showed overall a
329 niche shift, with a higher prevalence among plants than animals, and a majority of the
330 studies reporting niche shifts included only one or a few species (Table S1). It might
331 therefore be that studies reporting a shift (rather than no shift) were preferentially
332 published, especially considering that the only two studies that concluded overall niche
333 conservatism among a large number of invader species used an ordination approach,
334 relied on the most complete set of niche change metrics, and accounted for
335 environmental availability (Table S1 in supplementary material). Therefore, conclusions
336 on niche shifts likely depend strongly on the organisms, methods and data used, and
337 generalization about the frequency and drivers of niche shifts can only be based on a
338 standardized and rigorous approach for quantifying niche shifts within each group. This
339 could ultimately allow concluding if there are identifiable trends among niche shifts, or if
340 niche changes are very idiosyncratic (i.e. species specific). In order to promote such
341 standardization in future studies, we recommend:

342 - Using at least ordination, rather than only ENM, approaches to quantify climatic niche
343 changes (see (Broennimann *et al.*, 2012));

344 –Using as much as possible, within a same taxonomic group, the same set of variables
345 used in previous studies on the same group, so that proper comparisons can be ensured;
346 this does not prevent additionally testing niche changes with other sets of variables, if
347 thought to be more meaningful to picture species’ niches in the group considered;

348 - Disentangling all possible situations of niche change through measures of niche
349 unfilling and expansion in complement to centriod shift and overlap metrics, at the two
350 possible analytical levels (COUE scheme; Box 3);

351 - Correcting these niche change metrics to account for the density of occurrences and
352 the available environment in both ranges (or time periods);

353 - Assessing whether niche metrics change when excluding rare climates along a range of
354 percentiles, and when considering analog and non-analog environments separately; this
355 will ensure retaining all the necessary information for further interpretation and
356 comparison of results from different studies.

357 We suggest three important remaining challenges for studies of realized niche changes
358 during biological invasions:

359 1) Assessing climatic niche changes at finer scales and in combination with other non-
360 climatic factors, such as differences in soils (Bertrand *et al.*, 2012), biota, and
361 disturbances between the native and exotic range. High-resolution data are becoming
362 increasingly available and standardized to be comparable across large spatial areas.
363 They constitute avenues to provide complementary answers to questions on
364 macroclimate niche changes, and to improve our ability to predict and anticipate
365 invasions.

366 2) Assessing invasions in non-analog environments has been poorly addressed so far. As
367 these situation cannot be predicted from the native range with static approaches, and
368 thus their interpretations remain speculative, they require mechanistic approaches (e.g.
369 (Kearney & Porter, 2009)) or experiments (see below). It is however a promising field of
370 investigation that may deliver invaluable insights on colonization processes in non-
371 analog situations while also improving assessments of biodiversity under future climate
372 changes (Williams & Jackson, 2007). Retrospective studies that examine the details of
373 invasion success and failure into particular non-analog climates, relative to the native

374 climatic niche, could inform us of possible predictors of invasion into non-analog
375 climates (e.g. for niche-based spatial predictions) (Guisan *et al.*, 2012).

376 3) Although correlative niche shift studies of exotic species may guide experimental
377 studies (Kueffer *et al.*, 2013), a dual approach has been rare so far (but see (Hill *et al.*,
378 2013)). Experimental studies on populations found in geographic areas where niche
379 expansion occurred in the exotic range are needed to rigorously identify the related
380 ecological or evolutionary causes, e.g. through rapid evolution (Sax *et al.*, 2007;
381 Alexander, 2013), increased phenotypic plasticity (Hahn *et al.*, 2012) or biotic
382 interactions (e.g. enemy-release) (Alexander & Edwards, 2010). Similarly, information
383 about unfilling can help identify interesting model systems (Kueffer *et al.*, 2013) for
384 studying why some habitats and landscapes are more resistant to invasions, e.g. due to
385 dispersal limitations (Barve *et al.*, 2011) or abiotic or biotic resistance (Richardson,
386 2011).

387 We expect that systematic use of this framework will substantially advance
388 generalization about niche change, not only in invasion studies (including pests and
389 diseases) but also in studies of niche conservatism between disjoint distributions (e.g.
390 arctic-alpine) (Pellissier *et al.*, 2013) or across time in response to global change
391 (Maiorano *et al.*, 2012).

392

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401

402

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571
572

573

574 **Boxes**

575 **Glossary box**

576 *Analog climate*: A combination of climate factors found in one area or time period that is
577 within the envelop of climatic conditions found in a different area or time period used
578 for comparison (Williams & Jackson, 2007). Contrary: ‘non-analog climate’.

579 *Accessible range*: The geographic locations within a given area that are accessible to a
580 species given its current distribution and the timescale considered in the study. It is thus
581 conditional upon spatial configuration and the species’ dispersal ability (Soberon, 2007;
582 Barve *et al.*, 2011).

583 *Available environment*: the set of environmental conditions that exist in a given area
584 (Jackson & Overpeck, 2000) (Box 3). Synonyms: ‘realized environment’ (whole range,
585 not species-specific), ‘background environment’.

586 *Ecological niche model* (ENM; also called species distribution or habitat suitability
587 models): multivariate models fitting the niche of species by relating distribution
588 observations with environmental variables measured at the same sites, and projected
589 over a whole study area (see (Guisan & Thuiller, 2005; Peterson *et al.*, 2011)).

590 *Exotic niche*: The niche measured based on a species’ distribution in the exotic range.
591 Synonyms: ‘naturalized niche’, ‘adventive niche’, ‘invaded niche’ or ‘invasive niche’ (for
592 invasive species).

593 *Exotic range*: The geographic range where a species is not native. Synonyms:
594 ‘naturalized range’, ‘adventive range’, ‘invaded range’ (for invasive species)

595 *Exotic species*: A species present in a region where it is not native, mostly due to human
596 actions that enabled it to overcome biogeographical barriers (Richardson, 2011).
597 Synonyms: ‘alien species’, ‘non-native species’, ‘non-indigenous species’, ‘introduced
598 species’.

599 *Fundamental niche*: The envelope of environmental (abiotic) conditions allowing
600 populations to sustain themselves in an n-dimensional environmental space. It depicts
601 the eco-physiological requirements of species (Soberon, 2007). Synonyms:
602 ‘Physiological niche’.

603 *Native niche*: The niche measured in the native range.

604 *Native range*: The complete geographic area where an exotic species is native.

605 *Niche-biotope duality*: The reciprocal correspondence between the niche conditions in
606 multidimensional environmental space and the physical locations that a species actually
607 occupies in geographical space (derived from (Colwell & Rangel, 2009)).

608 *Niche centroid*: the mean niche position in n-dimensional environmental space.

609 *Niche conservatism*: The tendency for species to retain their niche in space and time.
610 Synonyms: 'niche stability'.

611 *Niche envelope*: The envelope of conditions in multivariate environmental space defining
612 a species' niche. The boundary of the envelope can be defined in many different ways
613 (e.g. percentiles; see (Broennimann *et al.*, 2012)).

614 *Niche expansion*: Proportion of the exotic niche non-overlapping with the native niche.

615 *Niche overlap*: the intersection of two niches in n-dimensional environmental space.

616 *Niche shift*: A change in the centroid (see above) or limits of the niche envelop in
617 environmental space. Synonyms: niche change.

618 *Niche stability*: Proportion of the exotic niche overlapping with the native niche

619 *Niche unfilling*: Proportion of the native niche non-overlapping with the exotic niche.

620 *Non-analog climate*: See 'analog' climate.

621 *Ordination*: statistical approach used to represent the arrangement of a series of objects
622 described by multiple descriptor variables into a reduced multidimensional space which
623 axes represent combinations of the initial variables (see PCA).

624 *PCA*: Principal component analysis, a classical ordination approach (see above).

625 *Potential niche*: The intersection between the fundamental niche and the realized
626 environment (see (Jackson & Overpeck, 2000; Soberón & Nakamura, 2009)).

627 *Rare climate*: Climatic conditions poorly represented overall within an area during a
628 given time period.

629 *Realized niche*: The environmental (abiotic) niche of a species as quantified from field
630 observations, i.e. the fundamental niche modulated by biotic exclusions, population

631 dynamics (such as source-sink dynamics) and dispersal limitations (Soberon, 2007;
632 Colwell & Rangel, 2009). Synonyms: 'Ecological niche'.

633 *Schoener's D*: The most common measure of niche overlap (see (Warren *et al.*, 2008;
634 Broennimann *et al.*, 2012)).

635

636 **Box 1: The analytical context for quantifying niche shifts**

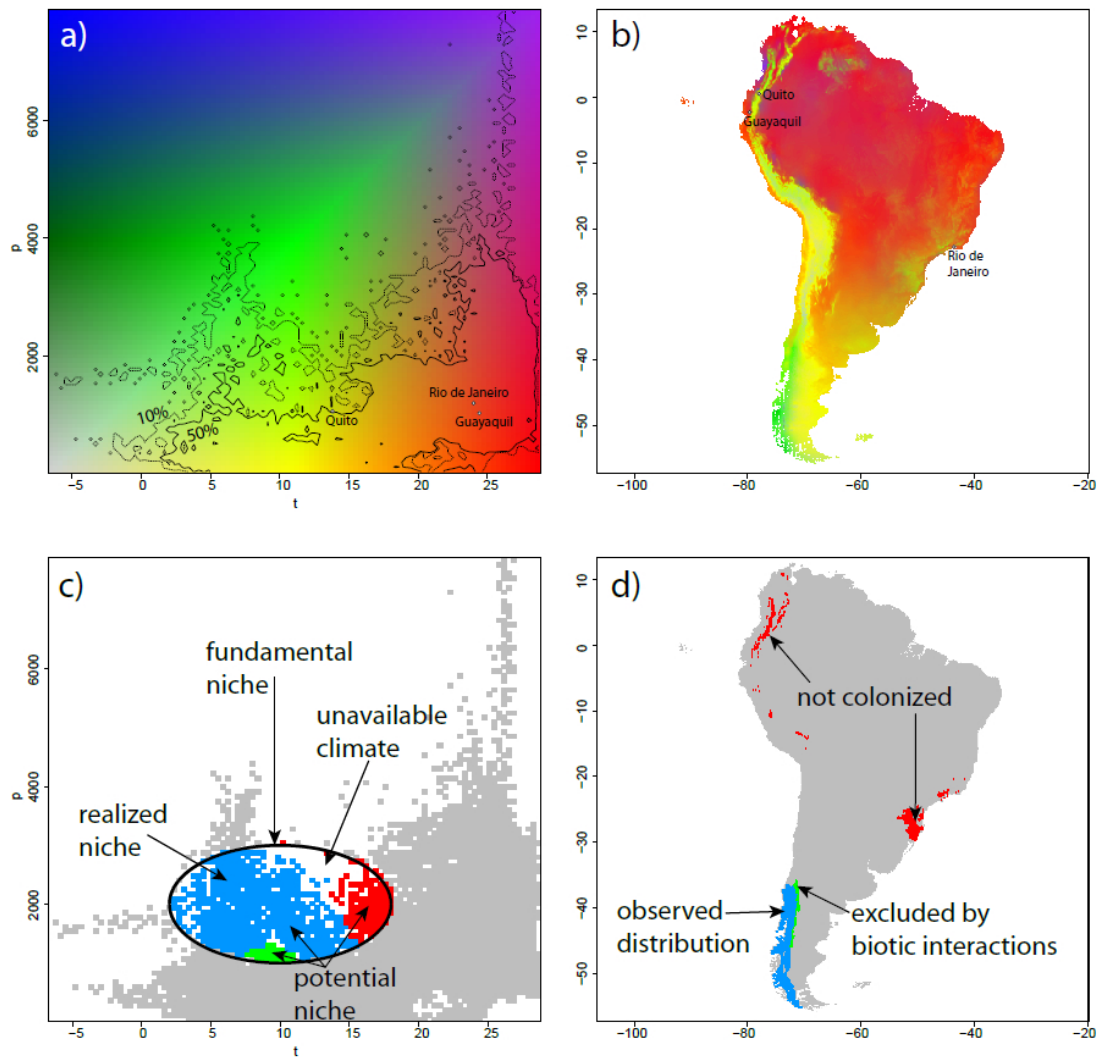
637 Assessing niche change between ranges is generally done by considering a species
638 native in one area (its native range) and invading another (or several other)
639 biogeographically separated area (the exotic range; e.g. (Petitpierre *et al.*, 2012)). This
640 context could similarly apply to the same species in two (or more) time periods (e.g.
641 (Maiorano *et al.*, 2012)). Regions large enough to include the entire (or large parts of)
642 the native and exotic species' geographic distributions are usually considered for
643 comparison. The choice of these areas will strongly condition the niche-biotope duality
644 (Box 2), and thus the available environments (Fig. 2, Box 3), and ultimately the
645 quantification of niche changes (Soberón & Nakamura, 2009; Soberon & Peterson,
646 2011). Optimally, the studied ranges should encompass the species' complete
647 geographic distribution in the native and introduced ranges that could potentially be
648 reached by a species given its dispersal ability, i.e. the accessible areas (Barve *et al.*,
649 2011). In practice we recommend defining areas with ecological relevance, such as
650 biomes or ecoregions, and using species data (atlas or occurrences) well representing
651 the focal species' range. The full multi-dimensional set of environmental conditions
652 observed in one area/time period is the realized environment (Box 3; Box 2) (Jackson &
653 Overpeck, 2000; Ackerly, 2003) and the envelop of conditions where the species is
654 observed represents its realized environmental niche (Box 2) (Araujo & Guisan, 2006;
655 Soberón & Nakamura, 2009).

656

657 **Box 2: Hutchinson's niche-biotope duality**

658 It is important to recall the niche (environmental space) versus biotope (geographic
659 space) duality framework described by G.E. Hutchinson (see (Colwell & Rangel, 2009),
660 Glossary). This duality means that there is no direct match between the topology of the
661 niche space and the geographic distribution of a species (see figure below). The same
662 combination of climate factors (colors in panel a of the figure) can occur in one or

663 several localities in geographic space (same colors in panel b), and locations close in
664 environmental space can be far apart geographically and vice versa (Soberón &
665 Nakamura, 2009). For instance, in South America, the cities of Quito and Guayaquil are
666 close to each other but climatically far away, whereas Guayaquil and Rio are
667 geographically far but climatically close (see figure below). Interpretation of niches and
668 distributions of species thus requires careful screening of both spaces jointly (see figure
669 a,c vs. b,d), with special attention to issues of dispersal limitations, biotic interactions
670 and available environmental conditions (Colwell & Rangel, 2009). Blank areas in panel c
671 of the figure below represent environments that are not available within the geographic
672 range considered (here South America). The intersection of the available environment
673 and the fundamental (i.e. physiological) limits of a species define its potential niche
674 (Jackson & Overpeck, 2000; Soberón & Nakamura, 2009). Parts of this potential niche
675 can be unoccupied by the species because of dispersal limitations (i.e. red areas in
676 panels c and d) or exclusion by biotic interactions (i.e. green parts in panels c and d). As
677 the potential niche rests on the hypothetical quantification of the fundamental niche
678 (see (Sax *et al.*, 2013)), whereas we focus mainly on the realized niche here, we do not
679 expand further on this concept. For a full theoretical development of the concepts and
680 definitions of niches and distributional areas, with formal abbreviations, see Soberon &
681 Nakamura (2009) and Peterson et al. (2011).



682

683 Hutchinson's duality framework, inspired by Soberon and Nakamura (2009) and
 684 Soberon & Peterson (2011). The fundamental niche ellipse pictured in panel c) is
 685 theoretical (artificially created) and could not be derived from field observations.

686

687

688 **Box 3: Metrics to quantify and decompose niche changes - The COUE scheme**

689

690 The niche space of an exotic species can be classified into three categories: niche space
 691 occurring only in the exotic range (i.e. expansion, ϵ), in both exotic and native range (i.e.
 692 stability, σ) and only in the native range (i.e. unfilling, υ). Niche comparisons can then be
 693 made at two levels: (i) relative to the entire niche of the species, pooled from the two
 694 ranges (pooled ranges approach); or (ii) relative to the native or exotic ranges
 695 separately (range-specific approach). The table below presents a unified terminology
 696 (COUE, an acronym based on its main components, centroid shift, overlap, unfilling and

697 expansion, as defined below) for niche comparisons and related metrics of niche
 698 changes.

699

Niche change component	Absolute component	Metric	
		Pooled ranges	Range-specific
Centroid shift	--	C	--
Expansion	ε	E_p	E
Stability	σ	$S_p (\approx O)$	S_n, S_e
Unfilling	υ	U_p	U

700

701 Centroid shift measures the change in mean niche position (and thus mean intensity) in
 702 the pooled ranges space, and thus no range-specific counterpart exists here. At the
 703 pooled-range level, niche stability (S_p) measures the proportion of niche assessed from
 704 the pooled native and exotic occurrences (possibly transformed into ENM predictions or
 705 densities in the environmental space, Fig. 3) present in both native and exotic ranges.
 706 This is similar to the niche overlap (O) assessed through Schoener's D or Hellinger's I
 707 (see (Warren *et al.*, 2008; Broennimann *et al.*, 2012)). The non-overlapping parts of the
 708 two niches ($1 - S_p$) can then be decomposed into global ratios of expansion (E_p) and
 709 unfilling (U_p) based on the pooled ranges. Decomposing niche changes relative to the
 710 pooled species distribution informs about the magnitude of niche changes at the global
 711 scale (i.e. relative to the entire realized niche of the species), but may not be informative
 712 about niche changes specific to either exotic or native ranges (as used e.g. in (Petitpierre
 713 *et al.*, 2012)). For example, the exotic niche can be very small relative to the entire
 714 pooled niche but entirely located in environments different from the native niche, in
 715 which case E_p would be very small although the entire invaded niche is distinct from the
 716 native niche and would hardly be predictable from the native range data. It is however
 717 possible to quantify a ratio of expansion (E) and unfilling (U) relatively to the exotic or
 718 native niches only, i.e. at the range-specific level. These inform us about the relative
 719 importance of changes in each exotic and native niche. In turn, niche stability can be
 720 assessed from the perspective of native or invaded niches separately, depending on
 721 whether it complements the relative expansion or relative unfilling ratios ($S_n = 1 - U$; S_e
 722 $= 1 - E$, respectively).

723

724

725 **Box 4: The available climate and the analog/non-analog issue**

726 The available environment is a subset of all possible environmental combinations (Box
727 2). The existence of non-available environments constrains niche shape and size
728 (Jackson & Overpeck, 2000). For instance, places with very warm summer temperature
729 (say >40°C) and very cold winter temperature (say <-20°C) do not currently exist on
730 Earth (see Figure 1 in (Jackson & Overpeck, 2000)). When comparing the available
731 environment in two areas, some habitats in one area (or time period) may be much
732 more frequent or rare than in the other area (or time period), or some specific
733 conditions found in one range may be totally absent from the other range. For instance,
734 some very dry conditions of Western North America are not found in Western Europe
735 (Broennimann *et al.*, 2007) and tropical conditions of the Tertiary in Europe are not
736 observed anymore (Willis & McElwain, 2002). Conditions similar in two ranges or two
737 time periods are called 'analog' and those differing 'non-analog' (Williams & Jackson,
738 2007; Fitzpatrick & Hargrove, 2009) (or 'non-overlapping backgrounds' in (Soberon &
739 Peterson, 2011)). Non-analog environments in an invaded range, or in the future,
740 typically represent situations outside the range of values considered to quantify the
741 native niche and not experienced by the species before invasion, and therefore lead to
742 difficulty in interpreting niche shifts (Petitpierre *et al.*, 2012) and predicting species
743 distributions (Fitzpatrick & Hargrove, 2009). Tools are available to define areas in the
744 exotic range with climates analog to the native range. The simplest approach is to define
745 a bounding box that encloses all the conditions present in the native range (e.g.
746 BIOCLIM; Busby 1991). Any pixel in the exotic range outside of the bounding box range
747 can be considered non-analogous. A more refined approach is the MESS analysis
748 (Multivariate Environmental Similarity Surfaces)(Elith *et al.*, 2010), an index of
749 similarity reporting the closeness of a point described by a set of climate attributes (e.g.
750 a pixel in the exotic range) to the distribution of these attributes within a population of
751 reference points (e.g. the native range).

752

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755

756 **Figure captions**

757

758 **Figure 1:** Theoretical scenarios of realized niche changes in space (e.g. following
759 invasions) or time (e.g. under climate change). Change of : (i) the niche envelop
760 (expansion or contraction) without change of the niche centroid, due to symmetric niche
761 change, i.e. in two opposite (a) or all directions in climatic space; (ii) the niche centroid
762 with expansion (b, c) or displacement (d) of part of or the whole niche envelop , or (iii)
763 the niche centroid only, due to a change of the density of occurrences within the same
764 niche envelop in climatic space (e). The latter case would result in stability (no change)
765 in figure 2. Observed changes are likely to be combinations of these cases.

766

767 **Figure 2:** Schematic 2-dimensional representation of the indices of niche change
768 (unfilling, stability and expansion) presented in (2012) (see definitions in Box 3). Solid
769 thin lines show the density of available environments (Box 4) in the native range (in
770 green) and in the invaded range (in red). The gray area shows the most frequent
771 environments common to both ranges (i.e. analog environments). The green and red
772 thick lines show respectively the native and the invaded niches. Niche unfilling (U),
773 stability (S_e) and expansion (E) are shown respectively with green, blue and red hatched
774 surfaces inside analog environments. The definition of a niche shift using the change of
775 niche centroid only (inertia ratio, IR) is shown with a thick dotted arrow. In this context,
776 the lower-case letters represent similar features in both graphs: a. available conditions
777 in the native range, outside of the native niche and non-analog to the invaded range.. b.
778 Conditions inside of the native niche but non-analog to the invaded range. c. Unfilling, i.e.
779 conditions inside of the native niche but outside the invaded niche , possibly due to
780 recent introduction combined with ongoing dispersal of the exotic species, which should
781 at term fill these conditions. d. Niche stability, i.e. conditions filled in both native and
782 invaded range. e. Niche expansion, i.e. conditions inside the invaded niche but outside
783 the native one, due to ecological or evolutionary change in the invaded range. f.
784 Conditions inside of the invasive niche but non-analog to the native range. g. Available

785 conditions in the invaded range but outside of the invasive niche and non-analog to the
786 native range. h. Analog conditions between the native and invaded ranges.

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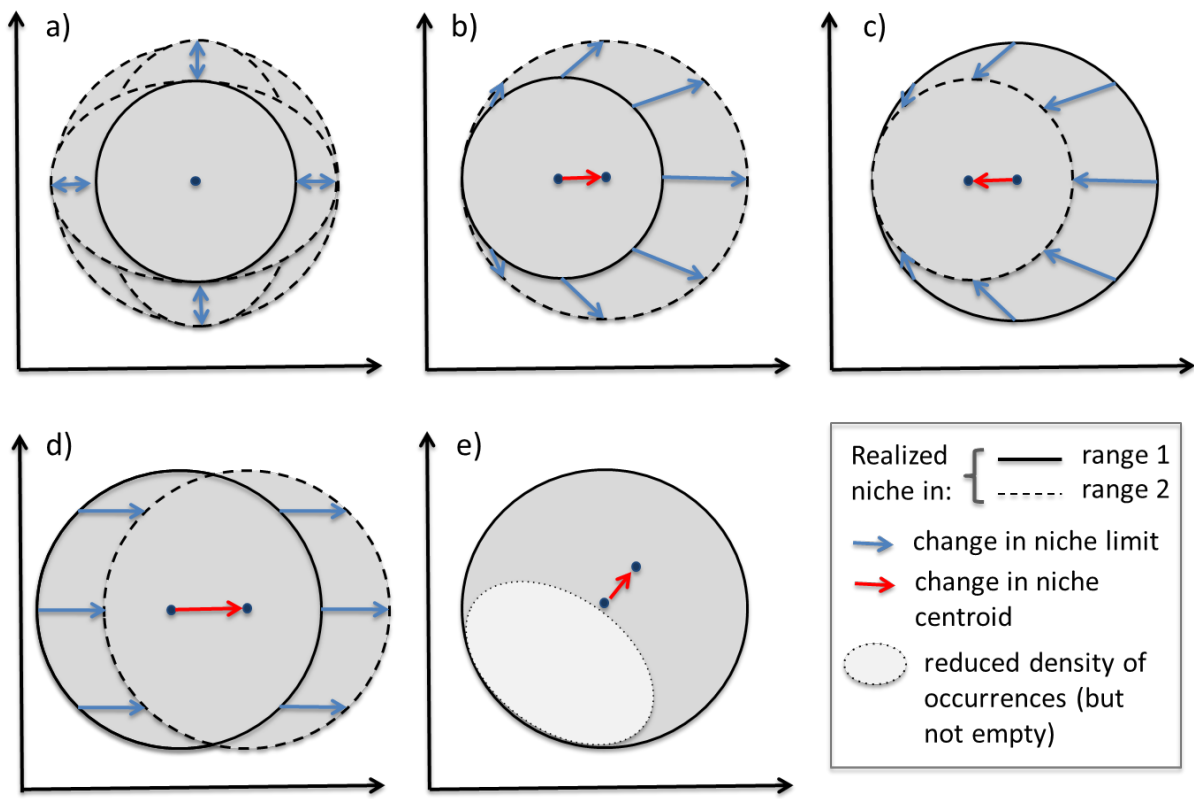
788 **Figure 3:** The two approaches commonly used to quantify niche changes between
789 ranges (Box 1). Ordination is based on the observations directly, whereas ENM is based
790 on predictions (see (Broennimann *et al.*, 2012), and Box 1). Steps for ordination are
791 (square numbers): 1. Definition of the reduced multidimensional environmental space;
792 2. Plot of the observations from each range in this space; 3. Comparison of the niche
793 defined from observations in each range; 4. Calculation of the niche change metrics (see
794 Box 3). Steps for ENMs are: 1. Fit of ENMs by relating field observations to
795 environmental variables; 2. Projections of the ENMs in geographic space; 3. Compute
796 difference in the projections; 4. Calculation of the niche change metrics (see Box 3). See
797 main text for discussion of the respective strengths and weaknesses of the two
798 approaches.

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802 Figure 1



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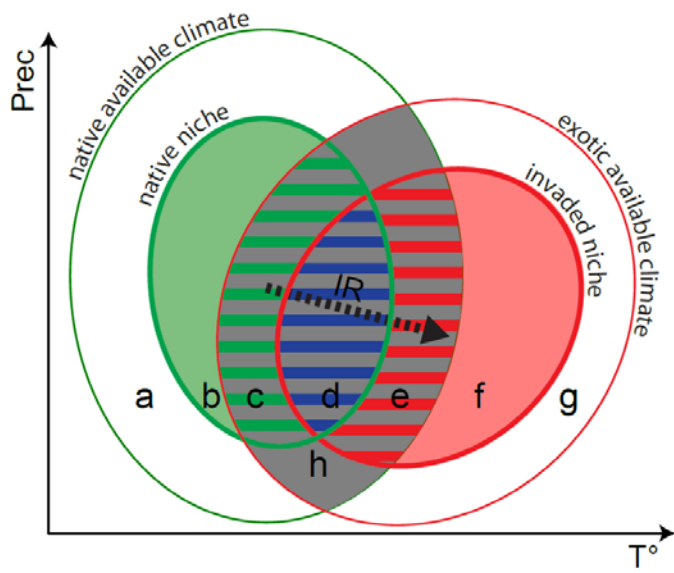
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809 Figure 2



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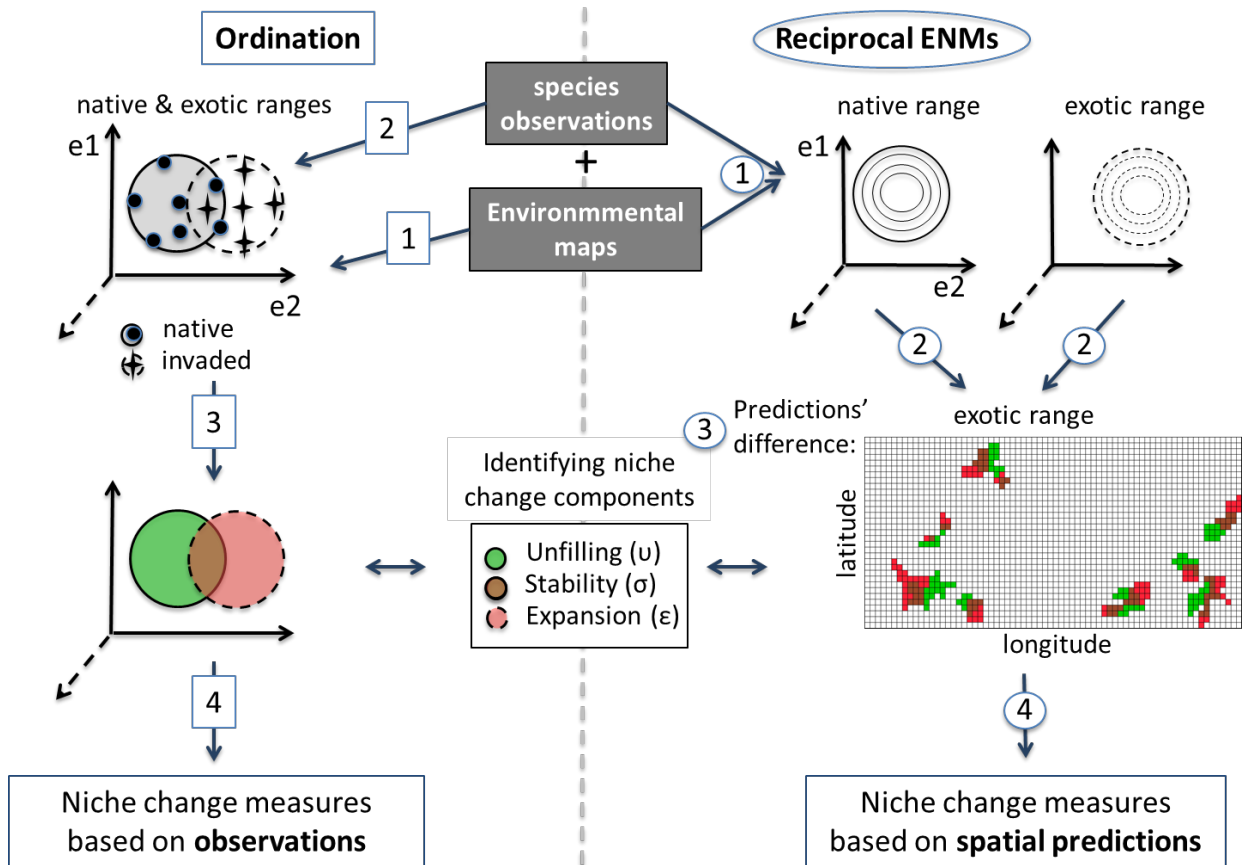
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818 Figure 3



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