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Antoine Guisan, Blaise Petitpierre, Olivier Broennimann, Curtis C. Daehler ...+1 more authors

Institutions: University of Lausanne, University of Hawaii at Manoa, ETH Zurich

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Unifying niche shift studies: insights from biological invasions

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5 Antoine Guisan[1], Blaise Petitpierre[1], Olivier Broennimann[1], Curtis Daehler[2] & Christoph

6 Kueffer[3]

7

8 [1] Department of Ecology & Evolution, University of Lausanne, 1015 Lausanne,

9 Switzerland

10 [2] 3Department of Botany, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, HI

11 96822, USA

12 [3] Institute of Integrative Biology, ETH Zürich, Universitätstrasse 16, 8092 Zürich,

13 Switzerland

14

15 *Corresponding author*: Antoine Guisan (antoine.guisan@unil.ch)

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26

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*

54 *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*

5

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 ≠ 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 envelop 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 envelops) 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

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

Range unfilling in the native range

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

Biased or incomplete sampling of species distributions

Another issue relates to the type and quality of species distribution data. Although it is important to cover an entire species' niche to assess niche change without bias, its complete native and exotic distribution ranges need not necessarily be considered. Because of the niche-biotope duality (Colwell & Rangel, 2009; Soberón & Nakamura, 2009) (Box 2), the climatic niche of a species might well be fully captured even if only a part of its geographical distribution is sampled. However, and similarly to the issue of range unfilling, when geographic truncation leads to environmental truncation (Raes, 2012), niche change studies based on both ordinations and ENMs (Fig. 3) should be considered with care, because their conclusions will only be applicable to the climate space investigated and within analog climatic combinations between the two ranges. In these situations, approaches based on ecological niche models (ENMs (Guisan & 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

10

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 $\underline{u}$nfilling and $\underline{e}$xpansion in complement to $\underline{c}$entroid shift and $\underline{o}$verlap 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 artic-alpine) (Pellissier *et al.*, 2013) or across time in response to global change

391 (Maiorano *et al.*, 2012).

392

401

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572

573

Boxes

Glossary box

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

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

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

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

Exotic niche: The niche measured based on a species' distribution in the exotic range. Synonyms: 'naturalized niche', 'adventive niche', 'invaded niche' or 'invasive niche' (for invasive species).

Exotic range: The geographic range where a species is not native. Synonyms: 'naturalized range', 'adventive range', 'invaded range' (for invasive species)

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

Fundamental niche: The envelope of environmental (abiotic) conditions allowing populations to sustain themselves in an n-dimensional environmental space. It depicts the eco-physiological requirements of species (Soberon, 2007). Synonyms: '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;
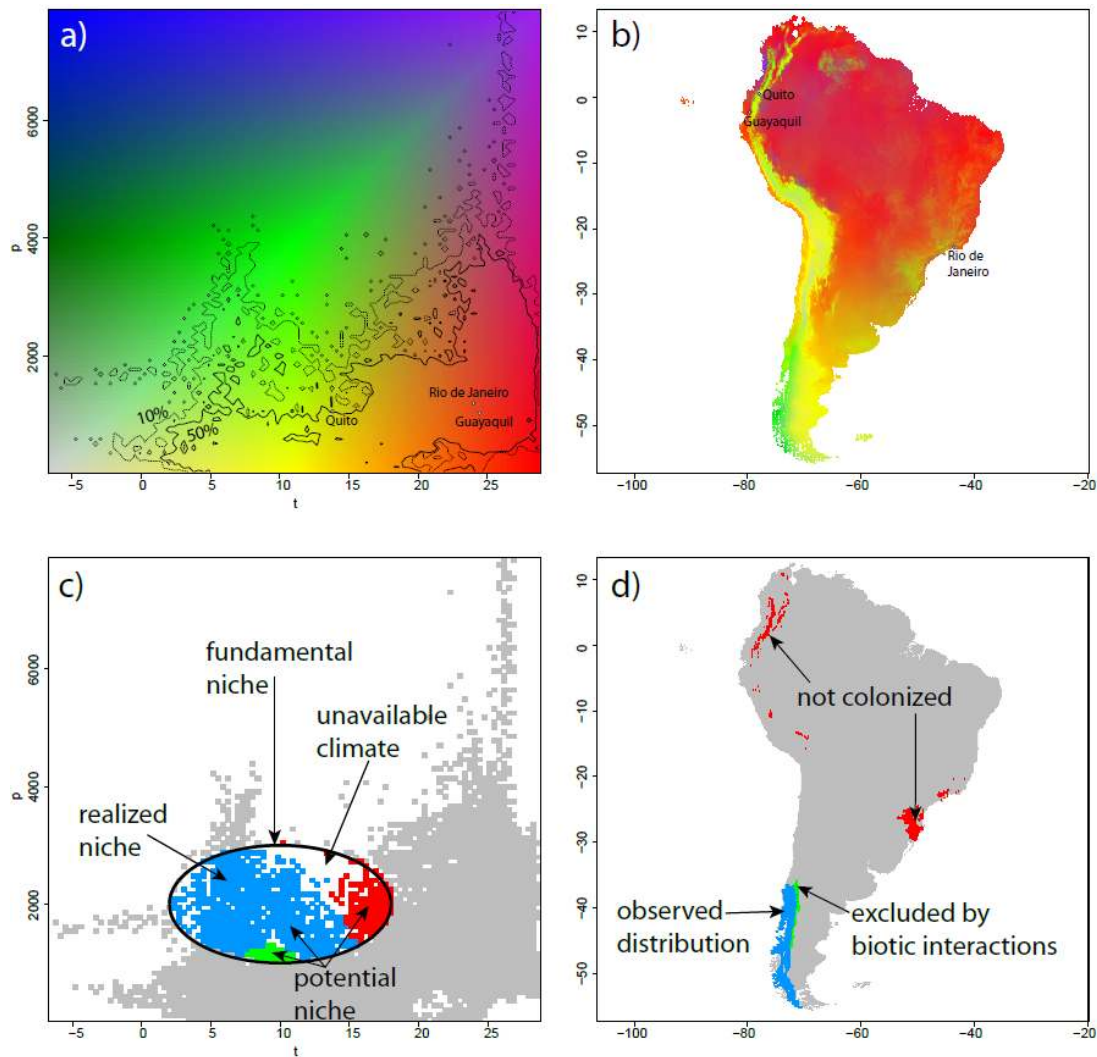
655 Soberón & Nakamura, 2009).

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

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

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

Box 3: Metrics to quantify and decompose niche changes – The COUE scheme

The niche space of an exotic species can be classified into three categories: niche space occurring only in the exotic range (i.e. expansion, ε), in both exotic and native range (i.e. stability, σ) and only in the native range (i.e. unfilling, υ). Niche comparisons can then be made at two levels: (i) relative to the entire niche of the species, pooled from the two ranges (pooled ranges approach); or (ii) relative to the native or exotic ranges separately (range-specific approach). The table below presents a unified terminology (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 (≈ 0)	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

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

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

752

753

756 **Figure captions**

757

758 <u>**Figure 1**</u>: 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 symetric 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 <u>**Figure 2**</u>: 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.

787

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
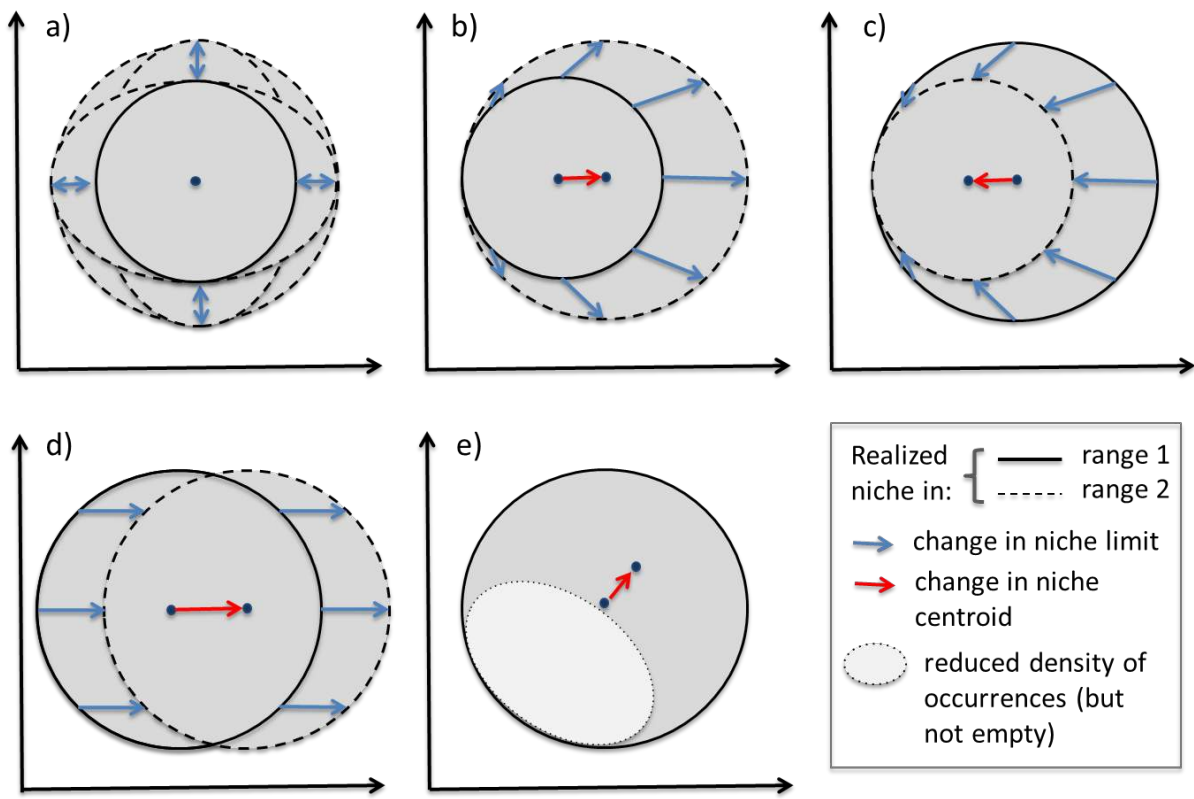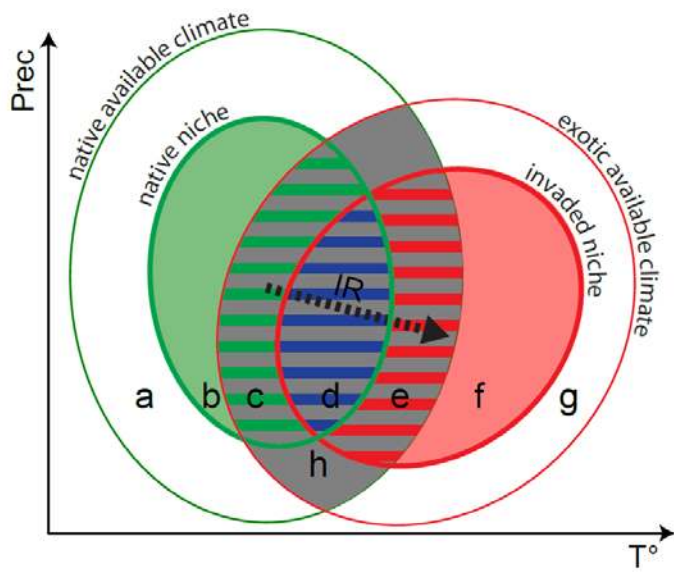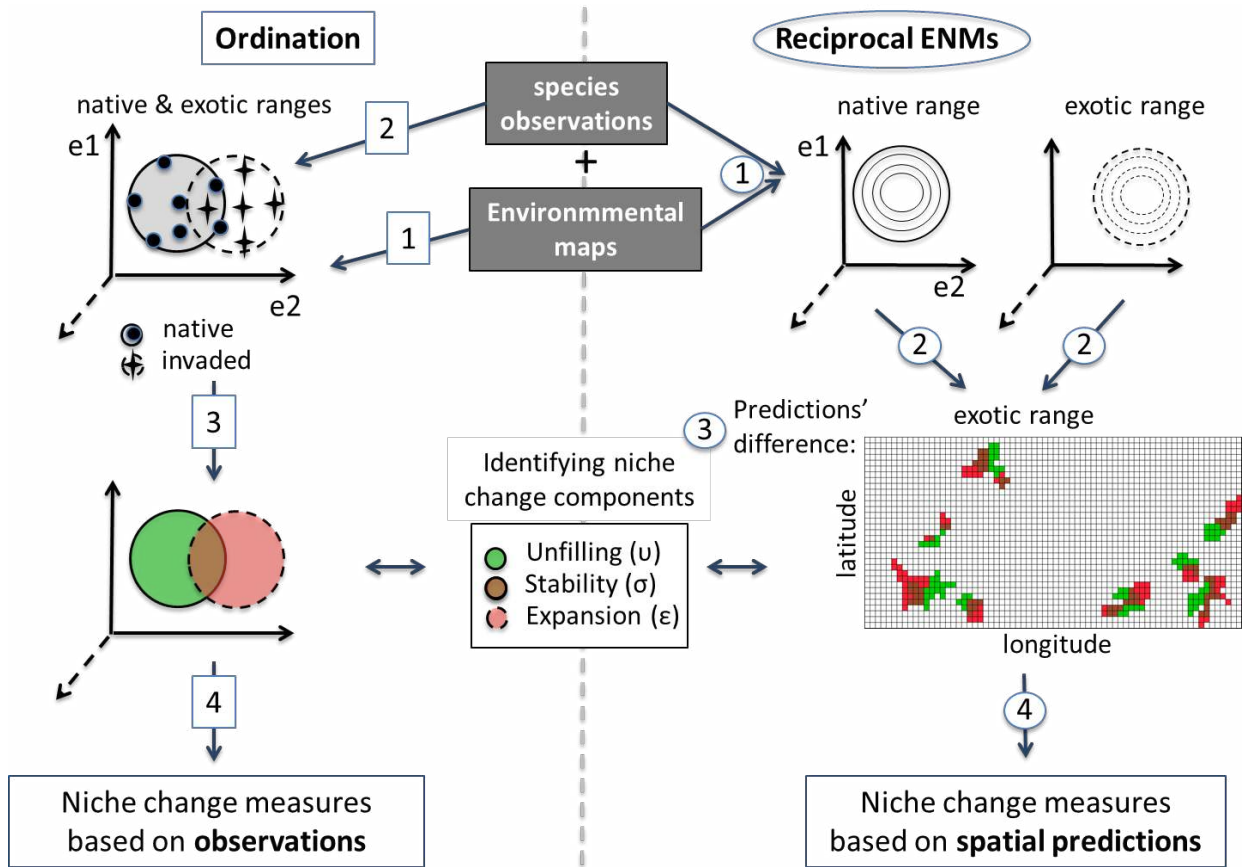

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809 Figure 2

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818   Figure 3

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