

1 **Global analysis of ecological niche conservation and niche shift in exotic populations of**  
2 **monkeyflowers (*Mimulus guttatus*, *M. luteus*) and their hybrid (*M.* × *robertsii*)**

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11 **Glossary**

12 **Climatic envelope:** Climatic factors that are an important component of a species' environmental  
13 tolerances and preferences across its geographic range (Banta et al., 2012).

14 **Ecological niche** (*sensu* Grinnel): The environmental space where “the abiotic conditions constraining the  
15 species' existence at a given location, potentially restricting its distribution” (Grinnel, 1917)

16 **Exotic:** Non-native.

17 **Invasive:** Non-native, exotic, with potential deleterious effects to the local environment.

18 **Invasion:** Expansion of a species' range outside its native distribution.

19 **Niche expansion:** In the exotic range, the species occurs in novel environmental conditions which are not  
20 found in its native one, as a result from adaptation to novel local conditions.

21 **Niche unfilling:** When despite having environmental conditions in the exotic range that are similar to  
22 those in its native one in a given area, a species does not occupy it.

23

24

25 **Abstract**

26 **Background:** Hybridisation associated with biological invasions may generate new  
27 phenotypic combinations, allowing hybrids to occupy new ecological niches. To date, few  
28 studies have assessed niche shifts associated with hybridisation in recently introduced  
29 populations while simultaneously characterising the niche of parental species in both native  
30 and introduced ranges

31 **Aims:** Here, we compared (1) the ecological niche of a novel hybrid monkeyflower, *M. ×*  
32 *robertsii*, with the niches of its two parental taxa (*M. guttatus*, *M. luteus*), and (2) the  
33 ecological niches of native (Americas) and introduced parental populations (Europe and  
34 New Zealand).

35 **Methods:** We assembled >13,000 geo-referenced occurrence records and eight  
36 environmental variables and conducted an ecological niche model analysis using maximum  
37 entropy, principal component and niche dynamics analysis.

38 **Results:** We found no evidence of niche shift in the hybrid, which may result in potential  
39 competition between parental and derived taxa in the introduced range. *M. guttatus* showed  
40 niche conservatism in introduced populations in Europe, but a niche shift in New Zealand,  
41 while *M. luteus* showed a niche shift in Europe.

42 **Conclusions:** The comparison of native and non-native populations of parental taxa,  
43 suggests that whether invasions result in niche shifts or not depends on both taxon and  
44 geographic region, highlighting the idiosyncratic nature of biological invasions

45 **Keywords:** *Erythranthe*, global change, hybridisation, invasive species, *Mimulus*, niche  
46 conservatism, niche modelling, polyploidy.  
47

48

## 49 **Introduction**

50 Human trade and travel have helped disperse species beyond their native range, sometimes  
51 connecting previously isolated taxa. Some non-native species represent a threat to native  
52 biodiversity, human health and the economy (Mack et al. 2000; Simberloff et al. 2013; Pyšek et al.  
53 2017). Understanding the ecology of non-native species and the potential differences between  
54 populations in their native and exotic ranges can help understanding the processes that contribute  
55 to biological invasion and to develop effective management strategies. A powerful tool to  
56 characterise the broad-scale environmental conditions in which native and non-native populations  
57 occur is niche modelling (Guisan et al. 2017). Ecological niche models (ENMs; Anderson 2012)  
58 are correlative statistical techniques which estimate the relationships between geo-referenced  
59 occurrences of taxa and environmental variables, allowing the characterisation of habitat  
60 suitability and the projection of their geographic distribution (Peterson et al. 2003). ENMs are  
61 widely used in invasion ecology, projecting fitted models of exotic/invasive species onto the  
62 empirically defined distribution of native species (Guisan et al. 2017). ENMs can also be used to  
63 quantify changes in the niche of a taxon e.g., between its native and introduced range, by comparing  
64 differences in the environmental space defined by occurrences (Warren et al. 2008; Broennimann  
65 et al. 2012). Assuming that a species occupies all the environmentally suitable habitat in its native  
66 range, Petitpierre et al. (2012) have described two processes that could differentiate the niches of  
67 native and non-native populations: (1) niche expansion (i.e., species occur in novel environmental  
68 conditions in their exotic range - not found in their native ranges - resulting from adaptation to  
69 novel local conditions) and (2) niche unfilling (i.e. a partial filling of the niche in the invaded range  
70 that has environmental conditions identical to those in its native range). Assessing whether these  
71 processes lead to a significant realised niche differentiation between native and non-native

72 populations entails testing two different hypotheses, namely niche equivalency (native and non-  
73 native niches are indistinguishable and interchangeable) and niche similarity (whether niches are  
74 more similar than expected by chance; Warren et al. 2008). Comparisons between introduced and  
75 native populations allow testing the extent to which local adaptation (niche expansion) or niche  
76 matching (niche unfilling) help explaining the realised niche of non-native populations.

77 In addition to the potential occupation of new ecological spaces, biological invasions may  
78 result in hybridisation, as previously isolated taxa come into secondary contact. Hybridisation can  
79 produce organisms that are genetically more diverse than their parental taxa and, in some cases,  
80 result in novel taxa (Dietz and Edwards 2006; Marchant et al. 2016; Parisod and Broennimann  
81 2016; Vallejo-Marín and Hiscock 2016; Visger et al. 2016; Molina-Henao and Hopkins 2019).  
82 Well-known examples of novel hybrid taxa arising through hybridisation with at least one non-  
83 native parent include taxa in the genera *Spartina* (Ainouche et al. 2004) and *Tragopogon* (Soltis et  
84 al. 2004). The new genotypes and phenotypes created through hybridisation can potentially enable  
85 hybrid taxa to exploit new environmental conditions compared to their parental taxa (Sheth and  
86 Anger 2014), thus potentially shifting their fundamental niche (Marchant et al. 2016; Parisod and  
87 Broennimann 2016). However, to date only a few studies have investigated the extent to which  
88 hybridisation *vs.* range expansion is associated with shifts in niche occupancy (e.g. Mukherjee et  
89 al. 2012; Thornton and Murray 2014, Visger et al. 2016; Molina-Henao and Hopkins 2019).

90 Some species of monkeyflowers (*Mimulus* spp.) are prime examples of recent plant  
91 invasion and hybridisation events that have yielded widespread, novel hybrids that exist only in the  
92 non-native range of the parents (Stace 2010; Stace et al. 2015). Among these hybrid taxa, probably  
93 the best-studied case is the triploid hybrid *M. × robertsii* Silverside in the British Isles. The hybrid  
94 monkeyflower, *M. × robertsii* is the product of crosses between two non-native species that are

95 allopatric in their native range: the tetraploid *M. luteus* L. from South America (Chile and  
96 Argentina, hereafter *M. luteus* (Nat.)), and the mostly diploid *M. guttatus* DC. from western North  
97 America (Mexico to Alaska, hereafter *M. guttatus* (Nat.)). In this study, we followed Lowry et al.  
98 (2019) and used the classical taxonomical definition of *Mimulus* (Grant 1924), rather than the  
99 recent nomenclature proposed by Nesom (2012, 2014), which renames *Mimulus* Section *Simiolus*  
100 to a new genus (*Erythranthe*), and divides *M. guttatus* into a number of different taxa (e.g.,  
101 *Erythranthe guttata*, *E. grandis* and *E. microphylla*). Both *M. guttatus* and *M. luteus* were  
102 introduced in Europe in the nineteenth century (hereafter *M. guttatus* (Inv.) and *M. luteus* (Inv.)),  
103 and were used in the horticultural trade probably due to their striking yellow and red flowers. In  
104 the British Isles, *M. guttatus* was introduced in 1812, after which it became naturalised and is  
105 currently widely distributed throughout Great Britain and Northern Ireland, where the diploid  
106 cytotype is by far the most common (Simon-Porcar et al. 2017). *M. guttatus* has also been  
107 introduced into New Zealand and eastern North America. The introduction of *M. guttatus* to New  
108 Zealand appears to date back at least to 1878 (Owen 1996), while the introduction history in other  
109 regions is less well known. The South American *M. luteus* appears to have arrived in the British  
110 Isles around the 1830s. Historical records suggest that *M. luteus* has been found across the British  
111 Isles and in other areas of Europe and New Zealand. At present, naturalised populations of *M.*  
112 *luteus* are very rare compared to other non-native monkeyflowers and are mainly restricted to the  
113 UK (Vallejo-Marín and Lye 2013). The origin and exact parentage of *M. × robertsii* is unknown,  
114 but naturalised populations of these hybrids became established by 1844 and since then, this taxon  
115 has become widely distributed in the UK (Stace et al. 2015), with about 40% monkeyflower  
116 populations being composed partially or entirely of hybrids (Vallejo-Marín and Lye 2013). Both  
117 hybrid and parental taxa occupy mainly wet habitats such as banks of streams and rivers, bogs and

118 other wet places (Truscott et al. 2006). To date, no study has been conducted to characterise the  
119 ecological niche of non-native and hybrid populations of monkeyflowers.

120 In this study we compared ecological niches between the non-native European populations  
121 of parental and hybrid monkeyflowers and among native and non-native populations of the parental  
122 taxa. Specifically, we addressed the following questions: (1) Does the ecological niche of parental  
123 taxa shift during the invasion process, and, if so, to what extent? (2) Which regions in the native  
124 range have the highest ecological niche similarity to the conditions in which introduced populations  
125 grow? (3) Does the fundamental niche of the hybrid differ from those of the native and exotic  
126 fundamental niches of the parent species?

## 127 **Materials and methods**

### 128 *Georeferenced occurrences*

129 Georeferenced occurrence data of the three taxa and their subordinates taxonomic ranks  
130 were downloaded from the Global Biodiversity Information Facility (GBIF 2016; [www.gbif.org](http://www.gbif.org)),  
131 the Nodo Nacional de Información de Biodiversidad (GBIF Spain 2016; [www.gbif.es](http://www.gbif.es)), the GBIF  
132 France (GBIF France 2016; [www.gbif.fr](http://www.gbif.fr)), the Botanical Society of Britain and Ireland (BSBI 2016;  
133 [www.bsbi.org](http://www.bsbi.org)), the NBN gateway (NBN 2016; <https://data.nbn.org.uk>), the FloraWeb (FloraWeb  
134 2016; [www.floraweb.de](http://www.floraweb.de)), the Integrated Digitized Biocollections (iDigBio 2016; [www.idigbio.org](http://www.idigbio.org)  
135 ) and the Kasviatlas (Lampien and Lahti 2016; <http://www.luomus.fi/kasviatlas>). In addition to  
136 these sources, records of *M. guttatus* from its native range were included from Oneal (2014).

137 Records with erroneous coordinates (e.g., records located in sea), expressed with different  
138 geographic coordinates than latitude and longitude decimal degrees and with a coordinate accuracy

139 less than 1 km were excluded. In order to make sure that the species occurrences were encompassed  
140 in the time span of the environmental variables, only data collected after 1950 were considered.

#### 141 *Environmental variables*

142 Bioclimatic variables describing the current environmental conditions (1950 - 1990 year  
143 span) were downloaded from the WorldClim database (Hijman et al. 2005; www.worldclim.org)  
144 at a spatial resolution of 30 arc-second and manipulated using R v3.4.0 (R Core Team 2019).  
145 Following previous studies on native populations of monkeyflowers (Grossenbacher et al. 2014;  
146 Sobel 2014), eight of the most important bioclimatic variables for characterising the niches of  
147 *Mimulus* ssp. were chosen for the analysis. These bioclimatic variables were cropped to the  
148 distribution of the outermost records of each taxon plus a buffer of 2 ° (Table 1; cf. Sobel 2014).

#### 149 *Niche analysis*

150 Since niche differentiation in environmental space may or may not translate into occupation  
151 of different geographic spaces (Warren et al. 2008), all of the analyses were computed in the  
152 environmental space of the three species in both native and invasive range using the *ecospat* R  
153 package. The ecological niche space occupied by each species in each native/exotic range was  
154 studied using environmental PCA (PCA-env, Broennimann et al. 2012). PCA-env is an ordination  
155 technique calibrated on the whole environmental space of both the native and the exotic range,  
156 which allows plotting a kernel-smoothed density of occurrences for each species in the principal  
157 component space (Di Cola et al. 2017). In order to avoid projecting a model in non-analogous  
158 climatic conditions (a combination of climatic conditions which are not found in the climatic  
159 envelope of the space and time where the model is trained), we computed a PCA of the  
160 environmental predictors between each range to check if analogous climatic conditions were  
161 present (Guisan et al. 2017).



162           The overlap between two different niches in the ecological space was quantified using  
163 Schoener's D metric (Warren et al. 2008), which ranges from no overlap ( $D = 0$ ) to complete  
164 overlap ( $D = 1$ ). Additionally, the niche overlap can be decomposed into niche unfilling and niche  
165 expansion. Niche unfilling represents the partial filling in the exotic range of the potential niche  
166 estimated in the native niche. In contrast, niche expansion represents the proportion of non-native  
167 occurrences having environmental conditions different from the native ones, thus describing a  
168 species colonising novel environmental conditions in its exotic range. This decomposition provides  
169 additional information about the drivers of the niche dynamic between native and invaded ranges  
170 (Petitpierre et al. 2012; Guisan et al. 2014), or about how two sister species have evolved different  
171 niches. Each index was computed using the 90th percentile of the available environmental  
172 conditions which were common to both ranges, in order to remove the marginal environments and  
173 avoid the bias due to the density function artefacts (Petitpierre et al. 2012; Di Cola et al. 2017;  
174 Villaverde et al. 2017).

175           In addition, we computed niche equivalency and niche similarity tests (Warren et al. 2008)  
176 to assess if the difference between estimated realised niches was statistically significant. We tested  
177 niche divergence (alternative = 'lower') for both analyses, and we randomly shifted the exotic niche  
178 only in the comparisons between native and exotic niche (`rand.type = 2`) (see Di Cola et al. 2017  
179 for further information on choosing parameter settings). Niche equivalence tests assess whether the  
180 realised ecological niches of two taxa are environmentally identical and interchangeable. For each  
181 taxa, it tests whether the observed D derived from the occurrences of the taxa is constant when the  
182 occurrences of both taxa are randomly reallocated and compared to a null distribution generated  
183 by 100 pseudoreplicate datasets (Warren et al. 2008; Broennimann et al. 2012). The hypothesis of  
184 niche equivalency is rejected when observed values of D are significantly different ( $P < 0.05$ ) from  
185 the simulated values and so the taxa do not have equivalent realised niches. The niche equivalency

186 test is often rejected because it uses only occurrences of species and does not consider the  
187 environmental conditions available in the occurrences surrounding space. For these reasons, some  
188 authors (e.g. Hu et al. 2016) suggested that this test should be used for evaluating the transferability  
189 of niche models in space and time only and to assess biogeographical hypotheses using the niche  
190 similarity test (Peterson 2011). In fact, the niche similarity test assesses if the ecological niches  
191 of two taxa are more similar than expected by chance, accounting for the differences in the  
192 surrounding environmental conditions in the geographic areas where both species are distributed  
193 (Warren et al. 2010). It evaluates whether the overlap between observed niches in two ranges is  
194 different from the overlap between the observed niche in one range and randomly selected niches  
195 from the other range (Warren et al. 2008; Broennimann et al. 2012). The niche similarity test  
196 indicates niche similarity while accounting for the similarity in background environmental  
197 conditions.

### 198 ***Ecological niche modelling (ENM)***

199 Ecological niche models were constructed using Maxent v3.4 (Phillips et al. 2017) in the  
200 R package *dismo* (Hijmans et al. 2017). To reduce the effects of sampling bias and thus to avoid a  
201 possible source of model inaccuracy (Phillips et al. 2006; Phillips et al. 2009; Syfert et al. 2013),  
202 spatial filtering with a thinning distance of 2 km was applied to the final dataset of the three  
203 species using the R package *spThin* (Aiello-Lammens et al. 2015), while in order to avoid  
204 overfitting, species-specific tuning of the settings of the Maxent models we used AICc values in  
205 the R package *ENMeval* (Muscarella et al. 2014). The models were built and evaluated for the  
206 geographic space where occurrence data were available plus for an additional buffer of 2° for  
207 each species (Sobel 2014; Soberón 2018), and then were re-projected into the environmental  
208 conditions of their respective native/exotic population or vice-versa. Nevertheless, to restrict the

209 modelling to the conditions encountered in the original range, extrapolation was not applied, and  
210 clamping was done when projecting. Models were set up to obtain a logistic response of the  
211 predicted distribution and were evaluated using the area under the curve (AUC) provided for the  
212 test data (Phillips, Anderson and Schapire 2006; Ward 2007). AUC values range from 0 to 1.  
213 According to the classification of Swets (1988), model with AUC = 0.5 do not discriminate  
214 between suitable and unsuitable cells better than a random model, an AUC score >0.7 shows a  
215 “useful” discrimination ability, >0.8 shows a “good” model performance and >0.9 a “very good”  
216 model performance. Recently, some authors (e.g. Breiner et al. 2015; Cola et al. 2017) have  
217 suggested the use of the Boyce index, a presence-only and threshold-independent evaluator of  
218 the predictions of ENMs (Hirzel et al. 2006), in addition to AUC. The Boyce index, computed  
219 through the *ecospat* R package (Di Cola et al. 2017), ranges between -1 (the model predicts areas  
220 where presences are more frequent as being highly suitable for the species) and +1 (the model  
221 predictions are consistent with the distribution of presences in the evaluation data set). Values  
222 close to zero mean that the model is not different from a random model (Hirzel et al. 2006).

### 223 ***ENMs projections***

224 The ENMs were trained in the native and invaded ranges of each species and then projected  
225 two ways (1) projecting the native range onto the exotic range (prospective modelling) and (2)  
226 projecting the exotic range onto the native range (retrospective niche modelling). (1) Prospective  
227 niche modelling. The western North American occurrences of *M. guttatus* were used to train the  
228 native niche model and then projected it into its exotic ranges (Europe and New Zealand). Western  
229 South American occurrences were used to train the *M. luteus* model in the native range of the  
230 species and then projected into Europe only. (2) Retrospective niche modelling. We used the  
231 occurrence records from the exotic range (Europe and New Zealand for *M. guttatus*, Europe only

232 for *M. luteus*), and projected it back into western North America and South America, respectively.  
233 These analyses show the predicted niche suitability of the native range, based on the estimated  
234 ecological niche inferred from a given invasive region.

235 Finally, the hybrid niche model was projected onto the native range of the two parental taxa,  
236 in order to assess the overlap of the predicted niche suitability of the hybrid in the native regions  
237 of the parental taxa.

## 238 **Results**

239 A total of 13,326 records were retained after curating the data. Spatial filtering yielded a  
240 final number of 9,079 records across all taxa and geographic regions (Table 2). The number of  
241 spatially filtered records per taxon and region varied widely. The taxon with the largest number of  
242 records across all regions was *M. guttatus* (6,648) with ca. 73% of records found in the introduced  
243 European range, mostly in Britain and Ireland, and 25% (1,763) in its native North American range.  
244 We obtained only 19 records (<1%) in its introduced range in New Zealand. There were  
245 considerably fewer records of *M. luteus*, with most of them found in its introduced range (625 or  
246 95% of the total), and only 30 records in its native South American range. There was a relatively  
247 large number of records of the hybrid *M* × *robertsii* (1,776), all restricted to Britain and Ireland.

248 Only the models trained in South America and New Zealand used exclusively linear and  
249 quadratic features, suggesting that the model complexity increased as the sample size increased  
250 (Table 2). The AUC metrics were also influenced by the sample size and higher scores were  
251 obtained for the models which had larger sample size (Table 2). The Boyce index values were  
252 always > 0.7, confirming good model performances.

253 ***Principal component analysis and niche similarity***

254         The PCA made on the climatic conditions present in the ranges of *M. guttatus* showed  
255 analogous climate conditions for its North American and European ranges (SM1a). On the  
256 contrary, non-analogous climate and divergent patterns were observed for its North American and  
257 New Zealand ranges and for its European and New Zealand ranges (Figure S1b, c). For *M. luteus*,  
258 non-analogous climate and divergent patterns were observed between the native range of *M.*  
259 *luteus* its European range, thus no reprojection was made for this species (Figure S2a).  
260 Analogous conditions were found for the native ranges of *M. luteus* and *M. guttatus* (Figure S2b).  
261 Following these findings, only the reciprocal reprojection of *M. guttatus* between its native and  
262 European ranges was possible.

263         *M. guttatus* showed a relatively low niche overlap between its native North American and  
264 exotic ranges ( $D = 0.190$  and  $D = 0.203$ , for Europe and New Zealand, respectively). Similarly,  
265 the niche overlap between the two exotic ranges (Europe and New Zealand) was very low ( $D =$   
266  $0.043$ ) (Table 3). Low niche overlap was related to niche unfilling in the native and introduced  
267 regions, while, between Europe and New Zealand was associated with niche expansion as  
268 indicated by the niche dynamics statistics (Table 3). Evidence of niche conservatism (niches  
269 equivalent and more similar than by chance) did not emerge from equivalency and similarity test  
270 results between the native niche and the two invasive niches (Table 3). In fact, the *M. guttatus*  
271 (Nat.) niche was equivalent but similar by chance to the European populations' niche and the  
272 native niche was not equivalent and similar by chance to the New Zealand one. When the two  
273 exotic niches were compared, they were found to be not equivalent and similar by chance. Low  
274 niche overlap ( $D = 0.309$ ) was observed in the comparison between *M. luteus* (Nat.) and its  
275 European exotic niche. As evidence of low niche overlap and lack of niche conservatism, both

276 niche unfilling and expansion were observed and the niche equivalency and similarity test  
277 resulted in not equivalent and similar by chance niches (Table 3). In the European range, *M.*  
278 *guttatus* (Inv.) showed high niche similarity ( $D = 0.734$ ) and niche conservatism with *M. luteus*  
279 (Inv.), having the two niches equivalent and more similar than by chance (Table 3). In contrast,  
280 the niche of *M. luteus* (Nat.) showed low niche overlap ( $D = 0.384$ ) and niche expansion when  
281 compared to that of *M. guttatus* (Nat.). Evidence of niche conservatism arose from comparisons  
282 between the parental taxa and the hybrid in their exotic ranges in Europe. European *M. guttatus*  
283 (Inv.) showed high niche similarity ( $D = 0.606$ ) and non-equivalent, but more similar than by  
284 chance, niche (Table 3). *M. luteus* (Inv.) showed higher niche overlap with *M. × robertsii* ( $D =$   
285  $0.705$ ) and niche conservatism, with both niches equivalent and more similar than by chance  
286 (Table 3).

### 287 ***Environmental niche modelling***

288 *M. guttatus* trained in its native range in North America showed high niche suitability in  
289 south-western United States, north-western Mexico and the along the Alaskan coast (Figure 1a),  
290 consistent with its current distribution. In particular, this model predicted suitable areas close to  
291 Haida Gwaii (Queen Charlotte) and Prince of Wales islands and further north and east in Alaska  
292 from the south-east of Kodiak Island and onto the Aleutian Islands range from around Unalaska in  
293 the east to Attu in the west. The Alaskan coast is one of the few geographic regions with relatively  
294 high niche suitability predicted by the ENM for *M. guttatus* trained in its European exotic range  
295 and re-projected onto its native range (Figure 1b). When the ENM for native populations was re-  
296 projected onto their exotic range in Europe, it showed high niche suitability in almost all of the  
297 current distribution of *M. guttatus* in western Europe (Figure 2a). However, the predicted suitable  
298 area was larger than the one predicted using the known distribution of *M. guttatus* in Europe,

299 which showed the highest suitability in the British Isles, the north coast of France, parts of Belgium  
300 and the Netherlands, and central Germany (Figure 2b). The ENM for New Zealand populations of  
301 *M. guttatus*, predicted suitable areas mainly along the coast and on North Island (Figure 2c).

302 The ENM for *M. luteus* (Nat.) predicted suitable conditions in the southern central Andean  
303 region of Chile (Figure 3a). In Europe, the model trained on exotic populations predicted suitable  
304 areas mainly in the British Isles, except for south-east England and the Scottish Highlands (Figure  
305 3b), which fits its current distribution. The ENM for *M. × robertsii* showed highly suitable areas  
306 mainly in the British Isles (Figure 4c). The predicted distribution of *M. × robertsii* resembled the  
307 distribution of *M. luteus* (Figure 4b), both of which are geographically more restricted than *M.*  
308 *guttatus*, which has a wider predicted distribution extending outside of the British Isles (Figure 4c).  
309 In general, the ecological niche of the hybrid *M. × robertsii* appeared similar to both parental taxa,  
310 showing a high overlap in the environmental space (Figure 5).

## 311 **Discussion**

312 In this study, we modelled and compared the ecological niche of *M. guttatus* and *M. luteus* in their  
313 native and invasive ranges, as well as the ecological niche of their hybrid, *M. × robertsii*. While  
314 previous studies have analysed the niche of *M. guttatus* using either a correlative (Ferris et al. 2014;  
315 Grossenbacher et al. 2014) or a mechanistic approach (Sheth and Angert 2014), our study is the  
316 first to model the ecological niche and spatial distribution of the South American taxon *M. luteus*  
317 and the hybrid *M. × robertsii*. Furthermore, our study allowed us to compare the ecological niches  
318 of these three closely related taxa using and measuring niche differences in a gridded environmental  
319 space built choosing ecologically relevant variables (Early and Sax 2014). Below, we discuss how  
320 the niche models produced here can be used to understand potential shifts in ecological niche

321 following hybridisation, as well as the niche changes associated with range expansion and  
322 biological invasions.

### 323 *The ecological niche of the hybrid*

324 One of the objectives of our study was to determine if a novel hybrid occupied a new ecological  
325 niche different from its parents. We found that, generally, *M. × robertsii* shows high niche overlap  
326 compared to the environmental niche of its parents. However, the comparison of the ecological  
327 niche between the hybrid and each parental taxon suggests that the niche of *M. × robertsii* is  
328 equivalent and more similar to that of *M. luteus* than to the niche of *M. guttatus*. The asymmetry  
329 of niche similarity between the hybrid and the two parental taxa may translate in different  
330 probabilities of co-occurrence and competition (Costa and Schlupp 2012; Mukherjee et al. 2012;  
331 Molina-Henao and Hopkins 2019). The co-occurrence of *M. luteus* and the hybrid may provide  
332 more opportunities for competition between these two taxa. If the hybrid were a more aggressive  
333 competitor than the South American parent, it is possible that competitive interactions may help to  
334 explain the apparent historical decline in the occurrence of *M. luteus* compared to that of the hybrid.  
335 Biotic interactions are important in the successful establishment of hybrids in the same  
336 environment as their parental taxa (Gaskin 2016; Marchant et al. 2016) and may also be responsible  
337 in shaping the ecological sorting of invasive monkeyflowers.

### 338 *The ecological niches of parental taxa: relationship between exotic and native* 339 *populations*

340 *Mimulus guttatus* Although our results indicate that the ecological niche of invasive  
341 populations of *M. guttatus* in Europe is similar to that of the native populations, we found  
342 that there was an overall low niche overlap among them. The low overlap is associated with



343 a large amount (61%) of niche unfilling, meaning that the niche in the exotic ranges covers  
344 only a fraction of the environmental variability present in the native niche (Figure S4a),  
345 which is consistent with niche conservatism for introduced populations of *M. guttatus* in  
346 Europe. Accordingly, previous studies on *Mimulus* species showed that native *M. guttatus*  
347 populations occur in a broad climatic niche (Ferris et al. 2014; Grossenbacher et al. 2014;  
348 Sheth and Angert 2014). Previous work on other systems have also found that niche  
349 unfilling is more common than niche shifts in terrestrial plants because the populations in  
350 the new environment occupy only a subset of the native environmental range (Petipierre et  
351 al. 2012; Strubbe et al. 2013; Guisan et al. 2014). Consistent with the idea that exotic  
352 populations in Europe do not presently occupy the full range of environments covered in  
353 their native range, the projection of the native population niche into Europe shows highly  
354 suitable niche areas outside its current distribution in its exotic range (Figure 2a), whereas  
355 the species occurs mainly in the north-western Europe and the British Isles. Future studies  
356 should also investigate if there are other biotic (e.g., herbivores, pathogens) or abiotic  
357 factors (soil chemistry) that prevent *M. guttatus* to spread to other parts of Europe.

358         The re-projection of the exotic niche of *M. guttatus* modelled in Europe into its the  
359 geographic regions of its origin identifies as environmentally suitable only a portion of the north-  
360 west of the American continent, in particular the Aleutian Islands. Recent genetic analyses of the  
361 populations of *M. guttatus* that occur in the British Isles have suggested the North Pacific region  
362 of North America as the geographic area of origin of the introduced populations (Puzey and  
363 Vallejo-Marín 2014; Pantoja et al. 2018). Our niche analyses are consistent with this inference, as  
364 well as with historical records indicating that one of the first *M. guttatus* specimens recorded in  
365 the British Isles originated from material collected in the Aleutian Islands in Alaska (Sims 1812;

366 Pennell 1935, p. 116). The PCA (Figure S3) made on the climatic data for three sets of *M.*  
367 *guttatus* populations (British Isles, north of Haida Gwaii, south of Haida Gwaii), showed that the  
368 populations of the British Isles are closely related to the northern North American populations.  
369 Our findings support niche conservatism of *M. guttatus* in its exotic range in Europe, and are  
370 consistent with previous genetic analyses that identify the North Pacific as the source of the  
371 origin of European populations. The use of ENM to predict the geographic origin of invasive  
372 populations assuming the conservation of the realised niche and using records from the exotic  
373 range has rarely been done. Hardion et al. (2014) have used the distribution of invasive  
374 populations of *Arundo donax* (giant cane) in the Mediterranean region to identify the source of  
375 origin of this global invasive plant to the Middle East, refining the hypothesised sources of origin  
376 as southern Iran and the Indus Valley.

377         The ecological niche of the exotic populations of *M. guttatus* in New Zealand is not  
378 equivalent or similar by chance when compared to those in its native and European ranges. These  
379 findings, coupled to (1) low D scores, (2) niche dynamics suggesting niche unfilling (61%) when  
380 comparing North America vs. New Zealand, and (3) both niche unfilling (24%) and expansion  
381 (48%) in comparing Europe vs. New Zealand, suggest that the invasive populations have shifted  
382 their niches compared to the source populations (Figures S4b, 5). The difference in ecological niche  
383 detected between European and New Zealand populations could arise due to the small number of  
384 occurrences sampled in New Zealand. However, this difference might reflect different source  
385 populations adapted to slightly different climatic characteristics, or be caused by post-colonisation  
386 evolution, allowing the fine-tuning of niche evolution. The timing of the naturalisation of *M.*  
387 *guttatus* in New Zealand in 1878 (Owen 1996) is compatible with a colonisation event from British  
388 sources, which had become widespread in the UK by the mid 1800s. Alternatively, New Zealand

389 could have been independently colonised directly from the native range or from other populations,  
390 perhaps as part of the horticultural trade or seed exchange between botanic gardens. These  
391 inferences should be carefully interpreted considering (1) the small size of the *M. guttatus*  
392 population in New Zealand (19 occurrences), (2) that both niche dynamics analyses reported niche  
393 unfilling, and (3) that the PCA made on the environmental predictors highlighted non-analogous  
394 conditions in the exotic range. However, there is an indication from ongoing genetic analyses that  
395 at least some of the populations in New Zealand can be traced back to the UK (Vallejo-Marín et  
396 al. unpublished).

#### 397 *Mimulus luteus*

398 The ENM of the non-native populations of *M. luteus* indicated suitable areas mainly in the  
399 British Isles, which is consistent with the current distribution of this taxon. The projected  
400 niche in the exotic range is similar but non-equivalent to the native one, with evidence of  
401 both niche unfilling (35%) and expansion (16%; Figure S6a). While these findings  
402 statistically reject a niche conservation hypothesis, it is important to consider that the niche  
403 in its native range was estimated on the basis of a relatively small sample size. Therefore,  
404 observed differences found between niches in the native and exotic ranges of *M. luteus*  
405 could reflect variation in subsampling of the environmental niche among populations in the  
406 native range due to small sample size. Additional sampling in the native range of *M. luteus*  
407 would be required to confirm the conclusions reached in our study. In its native range, *M.*  
408 *luteus* presents different morphological varieties, which are partly geographically  
409 structured, and it is unknown whether these varieties occupy different ecological niches  
410 (Carvallo and Ginocchio 2004). To date, there has been no genetic evidence for the source  
411 of the origin of non-native populations of *M. luteus*. Based purely on niche similarity, we

412 would predict that the source of the exotic populations of *M. luteus* in Europe - if there to  
413 be a single one - might be northern Patagonia, characterised as highly suitable area in our  
414 ENM. However, we acknowledge that our conclusions should be interpreted with caution  
415 due to the small number of native *M. luteus* occurrences included in our study.

416 *Comparison between M. guttatus and M. luteus* The comparison between the niches of the  
417 parental taxa in both their native and European ranges, showed niche equivalency between  
418 the two species and niches more similar than expected by chance. The two species seemed  
419 to grow in similar environmental conditions in both ranges, although the niche overlap  
420 between *M. guttatus* and *M. luteus* is lower in their allopatric American range than in the  
421 shared exotic range in Europe one ( $D = 0.384$  and  $D = 0.734$ , respectively). In fact, the  
422 niches of these taxa do not fully overlap in their native ranges. Closely related species often  
423 show similar but not equivalent niches (e.g. Aguirre-Gutiérrez et al. 2015; Dagnino et al.  
424 2017) and our findings suggest that these two species have colonised similar habitats in the  
425 exotic range in Europe.

## 426 **Conclusions**

427 This study provided the first ENMs and niche comparisons of these three closely related  
428 monkeyflower taxa in their native American and exotic ranges in Europe and New Zealand. Niche  
429 conservation was supported for comparisons between native and exotic *M. guttatus* populations in  
430 Europe as well as for the comparison between exotic populations of *M. luteus* the hybrid *M. ×*  
431 *robertsii*. In contrast, we found evidence of a niche shift in New Zealand populations of *M. guttatus*  
432 compared to both its native North American and introduced European populations. Similarly,  
433 introduced populations of *M. luteus* in Europe showed a niche shift compared to native populations  
434 in South America. Nevertheless, the evidence of niche shift in both taxa must be interpreted with

435 caution due to (a) non-analogous climatic conditions between ranges (Guisan et al. 2012); (b) niche  
436 unfilling dynamics and (c) the small size of both native and exotic populations (*M. guttatus* in New  
437 Zealand and *M. luteus* in South America).

438         Retrospective ecological niche modelling allowed us to predict the geographic origin of  
439 European populations of *M. guttatus*, supporting the Aleutian Islands as the potential source of  
440 origin of this taxon in Europe. However, the effectiveness of retrospective ENM strongly depends  
441 on the equivalency of both niches, and on the presence of analogous environmental condition in  
442 both ranges. The ecological (climatic) niche of *M. × robertsii* showed a high degree of overlap  
443 with both of its progenitors, although it was more similar to *M. luteus* than to that of *M. guttatus*.  
444 Large similarity in niches may intensify competitive interactions between closely related taxa  
445 resulting in one of them being outcompeted, resulting it becoming locally extinct. The outcome of  
446 potentially competitive interactions occupying similar environmental niches in the invasive range  
447 might be affected by biotic factors, which were not included here, such as differential herbivory or  
448 pathogen susceptibility. It remains to be established how climate change (e.g. drier summers or  
449 milder winters) may affect the distribution of monkeyflowers in both their native and introduced  
450 ranges. Future analyses of ecological niches incorporating biotic interactions and other non-  
451 climatic factors are required to better understand how hybridisation and invasion shape the  
452 distribution of closely related and potentially competing taxa.

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463 pollination.

#### 464 **Disclosure statement**

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641 **Tables**

642 Table 1. List of the Worldclim variables (Hijman et al. 2005) used to model *Mimulus* spp.  
643 environmental niches.

<b>Variables</b>	<b>Abbreviation</b>
Annual mean temperature	Bio1
Temperature seasonality	Bio4
Maximum temperature of warmest month	Bio5
Minimum temperature of coldest month	Bio6
Annual mean precipitation	Bio12
Precipitation seasonality	Bio15
Precipitation of wettest quarter	Bio16
Precipitation of driest quarter	Bio17

644

645 Table 2. Models with the lowest Akaike Information Criteria corrected for small sample size (AICc) and selected for each species and  
 646 their characteristics. All models' Area Under the Curve (AUC) and Boyce index scores have been shown to be robust (Swets JA. 1988;  
 647 Di Cola et al. 2017). L: linear features; Q: quadratic features, P: product features; H: hinge features.

<b>Species</b>	<b>Training region</b>	<b>n° of records</b>	<b>Model features</b>	<b>Beta multiplier</b>	<b>AUC (± SD)</b>	<b>Boyce Index</b>
<i>M. guttatus</i>	NA	1763	LQP	1	0.819 ± 0.006	0.999
	EU	4866	LQPH	0.5	0.807 ± 0.002	0.998
	NZ	19	LQ	1	0.650 ± 0.062	0.783
<i>M. luteus</i>	SA	30	L	0.5	0.867 ± 0.082	0.924
	EU	625	LQPH	2	0.902 ± 0.012	0.994
<i>M. × robertsii</i>	EU	1776	LQPH	2	0.792 ± 0.009	0.985

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650 Table 3. Results of the niche equivalency and similarity test carried in the environmental space. \*\* =  $p < 0.01$ ; \* =  $p < 0.05$ ; ns =  $p >$   
 651 0.05. Nat. = Native; Inv. = Invasive (non-native); NA = North America; SA = South America; EU = Europe; NZ = New Zealand.

Species pair	Populations	rand.type	Schoener's <i>D</i>	Equivalency	Similarity	Unfilling	Expansion	Interpretation
<i>M. guttatus</i> - <i>M. guttatus</i>	Nat. (NA) - Inv. (EU)	2	0,190	ns	ns	<b>0,612</b>	0,000	Equivalent but similar by chance
	Nat. (NA) - Inv. (NZ)	2	0,203	**	ns	<b>0,616</b>	0,006	Not equivalent and similar by chance, supposed niche divergence
	Inv. (EU) - Inv. (NZ)	1	0,043	**	ns	<b>0,243</b>	<b>0,483</b>	Not equivalent and similar by chance, supposed niche divergence
<i>M. luteus</i> - <i>M. luteus</i>	Nat. (SA) - Inv. (EU)	2	0,309	*	ns	<b>0,348</b>	<b>0,162</b>	Not equivalent and similar by chance, supposed niche divergence
<i>M. luteus</i> - <i>M. guttatus</i>	Nat. (SA) - Nat. (NA)	1	0,384	ns	**	0,001	<b>0,340</b>	Equivalent and more similar than by chance, evidences of niche conservatism
	Inv. (EU) - Inv. (EU)	1	0,734	ns	**	0,013	0,027	Equivalent and more similar than by chance, evidences of niche conservatism



<i>M. × robertsii</i> - <i>M. guttatus</i>	Nat. (EU) - Inv. (EU)	1	0,606	**	**	0,049	0,000	Not equivalent but more similar than by chance, there is no niche conservatism but there are similarities
<i>M. × robertsii</i> - <i>M. luteus</i>	Nat. (EU) - Inv. (EU)	1	0,705	ns	**	0,055	0,000	Equivalent and more similar than by chance, evidences of niche conservatism

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655 **Figures**

656 **Figure 1 a, b.** ENM trained on a) the current *M. guttatus* native distribution in North America and b) the current *M. guttatus* European  
657 invasive distribution projected into the native geographical area. The suitability index ranges from 0 (unsuitable areas, in blue) to 1  
658 (suitable areas, in red).

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660 **Figure 2 a, b, c.** ENM trained on a) the current *M. guttatus* native distribution in North America and projected into Europe, b) the  
661 current *M. guttatus* invasive distribution in Europe, c) the current *M. guttatus* invasive distribution in New Zealand. The suitability  
662 index ranges from 0 (unsuitable areas, in blue) to 1 (suitable areas, in red).

663 **Figure 3 a, b.** ENM trained on a) the current *M. luteus* native distribution in South America and b) the current *M. guttatus* invasive  
664 distribution in Europe. The suitability index ranges from 0 (unsuitable areas, in blue) to 1 (suitable areas, in red).

665 **Figure 4 a, b, c.** ENM trained on the current distribution of the three species in Europe: a) *M. guttatus*, b) *M. luteus*, c) *M. × robertsii*.  
666 The suitability index ranges from 0 (unsuitable areas, in blue) to 1 (suitable areas, in red).

667 **Figure 5 a, b, c.** *Mimulus* niches in the European environmental space: a) *M. luteus* (light blue) and *M. guttatus* (orange), b) *M.*  
668 *guttatus* (light blue) and *M. × robertsii* (orange), c) *M. luteus* (light blue) and *M. × robertsii* (orange). The continuous line represents  
669 the 100% of the available environmental background and the dashed line represents the 90% of most common conditions. The purple  
670 area represents the environmental space where the two niches overlap. The arrows allow visualising the centroids shift of the native  
671 and invasive distribution.

672 **Supplementary Materials**

673 **SM1.** PCA on the climatic predictors for *M. guttatus* in a) Blue = North America, Red = Europe; b)  
674 Blue = North America, Red = New Zealand; c) Blue = Europe, Red = New Zealand.

675 **SM2.** PCA on the climatic predictors for a) *M. lutes* in Blue = South America, Red = Europe; b)  
676 Blue = *M. guttatus* in North America, Red = *M. luteus* in South America.

677 **SM3.** the PCA made on the climatic data for three *M. guttatus* population: UK, occurrences further  
678 north than Queen Charlotte Island and occurrences further south than Queen Charlotte Island.

679 a) Individuals plot, b) variables plot. UK (green): *M. guttatus* occurrences in UK; NAN (blue): *M.*  
680 *guttatus* occurrences further north than Queen Charlotte Island; NAS: *M. guttatus* occurrences  
681 further south than Queen Charlotte Island (red).

682 **SM4.** *M. guttatus* niches in the environmental space: a) Native niche (light blue) and Invasive  
683 European niche (orange), b) Native niche (light blue) and Invasive New Zealand niche (orange).  
684 The continuous line represents the 100% of the available environmental background and the dashed  
685 line represents the 90% of most common conditions. The purple area represents the environmental  
686 space where the two niches overlap. The arrows allow visualising the centroids shift of the native  
687 and invasive distribution.

688 **SM5.** *M. guttatus* invasive niches in the environmental space: European (light blue) and New  
689 Zealand niche (orange). The continuous line represents the 100% of the available environmental  
690 background and the dashed line represents the 90% of most common conditions. The purple area  
691 represents the environmental space where the two niches overlap. The arrows allow visualising the  
692 centroids shift of the native and invasive distribution.

693 **SM6.** *M. luteus* niches in the environmental space: a) Native niche (light blue) and Invasive  
694 European niche (orange), b) Native niche (light blue) and *M. guttatus* native niche (orange). The  
695 continuous line represents the 100% of the available environmental background and the dashed line  
696 represents the 90% of most common conditions. The purple area represents the environmental space  
697 where the two niches overlap. The arrows allow visualising the centroids shift of the native and  
698 invasive distribution.

699 **Online supplementary materials:**

- 700 • The webmap showing the ENMs results and the occurrences used to train the models is  
701 available at <http://mimulusmap.plant-evolution.org/>

702 • The R codes used in this study are available in the GitLab  
703 repository [https://gitlab.com/danidr/mimulus\\_enm](https://gitlab.com/danidr/mimulus_enm)

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