2020, available online: https://doi.org/10.1080/17550874.2020.1750721

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

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Glossary

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

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

Exotic: Non-native.

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

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

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

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

Abstract

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

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

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

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

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

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

Introduction

Human trade and travel have helped disperse species beyond their native range, sometimes connecting previously isolated taxa. Some non-native species represent a threat to native biodiversity, human health and the economy (Mack et al. 2000; Simberloff et al. 2013; Pyšek et al. 2017). Understanding the ecology of non-native species and the potential differences between populations in their native and exotic ranges can help understanding the processes that contribute to biological invasion and to develop effective management strategies. A powerful tool to characterise the broad-scale environmental conditions in which native and non-native populations occur is niche modelling (Guisan et al. 2017). Ecological niche models (ENMs; Anderson 2012) are correlative statistical techniques which estimate the relationships between geo-referenced occurrences of taxa and environmental variables, allowing the characterisation of habitat suitability and the projection of their geographic distribution (Peterson et al. 2003). ENMs are widely used in invasion ecology, projecting fitted models of exotic/invasive species onto the empirically defined distribution of native species (Guisan et al. 2017). ENMs can also be used to quantify changes in the niche of a taxon e.g., between its native and introduced range, by comparing differences in the environmental space defined by occurrences (Warren et al. 2008; Broennimann et al. 2012). Assuming that a species occupies all the environmentally suitable habitat in its native range, Petitpierre et al. (2012) have described two processes that could differentiate the niches of native and non-native populations: (1) niche expansion (i.e., species occur in novel environmental conditions in their exotic range - not found in their native ranges - resulting from adaptation to novel local conditions) and (2) niche unfilling (i.e. a partial filling of the niche in the invaded range that has environmental conditions identical to those in its native range). Assessing whether these processes lead to a significant realised niche differentiation between native and non-native populations entails testing two different hypotheses, namely niche equivalency (native and non-native niches are indistinguishable and interchangeable) and niche similarity (whether niches are more similar than expected by chance; Warren et al. 2008). Comparisons between introduced and native populations allow testing the extent to which local adaptation (niche expansion) or niche matching (niche unfilling) help explaining the realised niche of non-native populations.

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

Some species of monkeyflowers (*Mimulus* spp.) are prime examples of recent plant invasion and hybridisation events that have yielded widespread, novel hybrids that exist only in the non-native range of the parents (Stace 2010; Stace et al. 2015). Among these hybrid taxa, probably the best-studied case is the triploid hybrid *M.* × *robertsii* Silverside in the British Isles. The hybrid monkeyflower, *M.* × *robertsii* is the product of crosses between two non-native species that are allopatric in their native range: the tetraploid *M. luteus* L. from South America (Chile and Argentina, hereafter *M. luteus* (Nat.)), and the mostly diploid *M. guttatus* DC. from western North America (Mexico to Alaska, hereafter *M. guttatus* (Nat.)). In this study, we followed Lowry et al. (2019) and used the classical taxonomical definition of *Mimulus* (Grant 1924), rather than the recent nomenclature proposed by Nesom (2012, 2014), which renames *Mimulus* Section *Simiolus* to a new genus (*Erythranthe*), and divides *M. guttatus* into a number of different taxa (e.g., *Erythranthe guttata*, *E. grandis* and *E. microphylla*). Both *M. guttatus* and *M. luteus* were introduced in Europe in the nineteenth century (hereafter *M. guttatus* (Inv.) and *M. luteus* (Inv.)), and were used in the horticultural trade probably due to their striking yellow and red flowers. In the British Isles, *M. guttatus* was introduced in 1812, after which it became naturalised and is currently widely distributed throughout Great Britain and Northern Ireland, where the diploid cytotype is by far the most common (Simon-Porcar et al. 2017). *M. guttatus* has also been introduced into New Zealand and eastern North America. The introduction of *M. guttatus* to New Zealand appears to date back at least to 1878 (Owen 1996), while the introduction history in other regions is less well known. The South American *M. luteus* appears to have arrived in the British Isles around the 1830s. Historical records suggest that *M. luteus* has been found across the British Isles and in other areas of Europe and New Zealand. At present, naturalised populations of *M. luteus* are very rare compared to other non-native monkeyflowers and are mainly restricted to the UK (Vallejo-Marín and Lye 2013). The origin and exact parentage of *M.* × *robertsii* is unknown, but naturalised populations of these hybrids became established by 1844 and since then, this taxon has become widely distributed in the UK (Stace et al. 2015), with about 40% monkeyflower populations being composed partially or entirely of hybrids (Vallejo-Marín and Lye 2013). Both hybrid and parental taxa occupy mainly wet habitats such as banks of streams and rivers, bogs and other wet places (Truscott et al. 2006). To date, no study has been conducted to characterise the ecological niche of non-native and hybrid populations of monkeyflowers.

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

Materials and methods

Georeferenced occurrences

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

Records with erroneous coordinates (e.g., records located in sea), expressed with different geographic coordinates than latitude and longitude decimal degrees and with a coordinate accuracy less than 1 km were excluded. In order to make sure that the species occurrences were encompassed in the time span of the environmental variables, only data collected after 1950 were considered.

Environmental variables

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

Niche analysis

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

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

In addition, we computed niche equivalency and niche similarity tests (Warren et al. 2008) to assess if the difference between estimated realised niches was statistically significant. We tested niche divergence (alternative = 'lower') for both analyses, and we randomly shifted the exotic niche only in the comparisons between native and exotic niche (rand.type = 2) (see Di Cola et al. 2017 for further information on choosing parameter settings). Niche equivalence tests assess whether the realised ecological niches of two taxa are environmentally identical and interchangeable. For each taxa, it tests whether the observed D derived from the occurrences of the taxa is constant when the occurrences of both taxa are randomly reallocated and compared to a null distribution generated by 100 pseudoreplicate datasets (Warren et al. 2008; Broennimann et al. 2012). The hypothesis of niche equivalency is rejected when observed values of D are significantly different ($P < 0.05$) from the simulated values and so the taxa do not have equivalent realised niches. The niche equivalency test is often rejected because it uses only occurrences of species and does not consider the environmental conditions available in the occurrences surrounding space. For these reasons, some authors (e.g. Hu et al. 2016) suggested that this test should be used for evaluating the transferability of niche models in space and time only and to assess biogeographical hypotheses using the niche similarity test (Peterson 2011). In fact, the niche similarity test assesses if the ecological niches of two taxa are more similar than expected by chance, accounting for the differences in the surrounding environmental conditions in the geographic areas where both species are distributed (Warren et al. 2010). It evaluates whether the overlap between observed niches in two ranges is different from the overlap between the observed niche in one range and randomly selected niches from the other range (Warren et al. 2008; Broennimann et al. 2012). The niche similarity test indicates niche similarity while accounting for the similarity in background environmental conditions.

Ecological niche modelling (ENM)

Ecological niche models were constructed using Maxent v3.4 (Phillips et al. 2017) in the R package *dismo* (Hijmans et al. 2017). To reduce the effects of sampling bias and thus to avoid a possible source of model inaccuracy (Phillips et al. 2006; Phillips et al. 2009; Syfert et al. 2013), spatial filtering with a thinning distance of 2 km was applied to the final dataset of the three species using the R package *spThin* (Aiello-Lammens et al. 2015), while in order to avoid overfitting, species-specific tuning of the settings of the Maxent models we used AICc values in the R package *ENMeval* (Muscarella et al. 2014). The models were built and evaluated for the geographic space where occurrence data were available plus for an additional buffer of 2º for each species (Sobel 2014; Soberón 2018), and then were re-projected into the environmental conditions of their respective native/exotic population or vice-versa. Nevertheless, to restrict the modelling to the conditions encountered in the original range, extrapolation was not applied, and clamping was done when projecting. Models were set up to obtain a logistic response of the predicted distribution and were evaluated using the area under the curve (AUC) provided for the test data (Phillips, Anderson and Schapire 2006; Ward 2007). AUC values range from 0 to 1. According to the classification of Swets (1988), model with AUC = 0.5 do not discriminate between suitable and unsuitable cells better than a random model, an AUC score >0.7 shows a "useful" discrimination ability, >0.8 shows a "good" model performance and >0.9 a "very good" model performance. Recently, some authors (e.g. Breiner et al. 2015; Cola et al. 2017) have suggested the use of the Boyce index, a presence-only and threshold-independent evaluator of the predictions of ENMs (Hirzel et al. 2006), in addition to AUC. The Boyce index, computed through the *ecospat* R package (Di Cola et al. 2017), ranges between –1 (the model predicts areas where presences are more frequent as being highly suitable for the species) and +1 (the model predictions are consistent with the distribution of presences in the evaluation data set). Values close to zero mean that the model is not different from a random model (Hirzel et al. 2006).

ENMs projections

The ENMs were trained in the native and invaded ranges of each species and then projected two ways (1) projecting the native range onto the exotic range (prospective modelling) and (2) projecting the exotic rage onto the native range (retrospective niche modelling). (1) Prospective niche modelling. The western North American occurrences of *M. guttatus* were used to train the native niche model and then projected it into its exotic ranges (Europe and New Zealand). Western South American occurrences were used to train the *M. luteus* model in the native range of the species and then projected into Europe only. (2) Retrospective niche modelling. We used the occurrence records from the exotic range (Europe and New Zealand for *M. guttatus*, Europe only for *M. luteus*), and projected it back into western North America and South America, respectively. These analyses show the predicted niche suitability of the native range, based on the estimated ecological niche inferred from a given invasive region.

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

Results

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

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

Principal component analysis and niche similarity

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

M. guttatus showed a relatively low niche overlap between its native North American and exotic ranges (D = 0.190 and D = 0.203, for Europe and New Zealand, respectively). Similarly, the niche overlap between the two exotic ranges (Europe and New Zealand) was very low (D = 0.043) (Table 3). Low niche overlap was related to niche unfilling in the native and introduced regions, while, between Europe and New Zealand was associated with niche expansion as indicated by the niche dynamics statistics (Table 3). Evidence of niche conservatism (niches equivalent and more similar than by chance) did not emerge from equivalency and similarity test results between the native niche and the two invasive niches (Table 3). In fact, the *M. guttatus* (Nat.) niche was equivalent but similar by chance to the European populations' niche and the native niche was not equivalent and similar by chance to the New Zealand one. When the two exotic niches were compared, they were found to be not equivalent and similar by chance. Low niche overlap (D = 0.309) was observed in the comparison between *M. luteus* (Nat.) and its European exotic niche. As evidence of low niche overlap and lack of niche conservatism, both niche unfilling and expansion were observed and the niche equivalency and similarity test resulted in not equivalent and similar by chance niches (Table 3). In the European range, *M. guttatus* (Inv.) showed high niche similarity (D = 0.734) and niche conservatism with *M. luteus* (Inv.), having the two niches equivalent and more similar than by chance (Table 3). In contrast, the niche of *M. luteus* (Nat.) showed low niche overlap (D = 0.384) and niche expansion when compared to that of *M. guttatus* (Nat.). Evidence of niche conservatism arose from comparisons between the parental taxa and the hybrid in their exotic ranges in Europe. European *M. guttatus* (Inv.) showed high niche similarity (D = 0.606) and non-equivalent, but more similar than by chance, niche (Table 3). *M. luteus* (Inv.) showed higher niche overlap with *M.* × *robertsii* (D = 0.705) and niche conservatism, with both niches equivalent and more similar than by chance (Table 3).

Environmental niche modelling

M. guttatus trained in its native range in North America showed high niche suitability in south-western United States, north-western Mexico and the along the Alaskan coast (Figureure 1a), consistent with its current distribution. In particular, this model predicted suitable areas close to Haida Gwaii (Queen Charlotte) and Prince of Wales islands and further north and east in Alaska from the south-east of Kodiak Island and onto the Aleutian Islands range from around Unalaska in the east to Attu in the west. The Alaskan coast is one of the few geographic regions with relatively high niche suitability predicted by the ENM for *M. guttatus* trained in its European exotic range and re-projected onto its native range (Figure 1b). When the ENM for native populations was re-projected onto their exotic range in Europe, it showed high niche suitability in almost all of the current distribution of *M. guttatus* in western Europe (Figure 2a). However, the predicted suitable area was larger than the one predicted using the known distribution of *M. guttatus* in Europe, which showed the highest suitability in the British Isles, the north coast of France, parts of Belgium and the Netherlands, and central Germany (Figure 2b). The ENM for New Zealand populations of *M. guttatus*, predicted suitable areas mainly along the coast and on North Island (Figure 2c).

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

Discussion

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

The ecological niche of the hybrid

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

The ecological niches of parental taxa: relationship between exotic and native populations

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

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

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

The ecological niche of the exotic populations of *M. guttatus* in New Zealand is not equivalent or similar by chance when compared to those in its native and European ranges. These findings, coupled to (1) low D scores, (2) niche dynamics suggesting niche unfilling (61%) when comparing North America vs. New Zealand, and (3) both niche unfilling (24%) and expansion (48%) in comparing Europe vs. New Zealand, suggest that the invasive populations have shifted their niches compared to the source populations (Figures S4b, 5). The difference in ecological niche detected between European and New Zealand populations could arise due to the small number of occurrences sampled in New Zealand. However, this difference might reflect different source populations adapted to slightly different climatic characteristics, or be caused by post-colonisation evolution, allowing the fine-tuning of niche evolution. The timing of the naturalisation of *M. guttatus* in New Zealand in 1878 (Owen 1996) is compatible with a colonisation event from British sources, which had become widespread in the UK by the mid 1800s. Alternatively, New Zealand could have been independently colonised directly from the native range or from other populations, perhaps as part of the horticultural trade or seed exchange between botanic gardens. These inferences should be carefully interpreted considering (1) the small size of the *M. guttatus* population in New Zealand (19 occurrences), (2) that both niche dynamics analyses reported niche unfilling, and (3) that the PCA made on the environmental predictors highlighted non-analogous conditions in the exotic range. However, there is an indication from ongoing genetic analyses that at least some of the populations in New Zealand can be traced back to the UK (Vallejo-Marín et al. unpublished).

Mimulus luteus

The ENM of the non-native populations of *M. luteus* indicated suitable areas mainly in the British Isles, which is consistent with the current distribution of this taxon. The projected niche in the exotic range is similar but non-equivalent to the native one, with evidence of both niche unfilling (35%) and expansion (16%; Figure S6a). While these findings statistically reject a niche conservation hypothesis, it is important to consider that the niche in its native range was estimated on the basis of a relatively small sample size. Therefore, observed differences found between niches in the native and exotic ranges of *M. luteus* could reflect variation in subsampling of the environmental niche among populations in the native range due to small sample size. Additional sampling in the native range of *M. luteus* would be required to confirm the conclusions reached in our study. In its native range, *M. luteus* presents different morphological varieties, which are partly geographically structured, and it is unknown whether these varieties occupy different ecological niches (Carvallo and Ginocchio 2004). To date, there has been no genetic evidence for the source of the origin of non-native populations of *M. luteus*. Based purely on niche similarity, we would predict that the source of the exotic populations of *M. luteus* in Europe - if there to be a single one - might be northern Patagonia, characterised as highly suitable area in our ENM. However, we acknowledge that our conclusions should be interpreted with caution due to the small number of native *M. luteus* occurences included in our study.

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

Conclusions

This study provided the first ENMs and niche comparisons of these three closely related monkeyflower taxa in their native American and exotic ranges in Europe and New Zealand. Niche conservation was supported for comparisons between native and exotic *M. guttatus* populations in Europe as well as for the comparison between exotic populations of *M. luteus* the hybrid *M. × robertsii*. In contrast, we found evidence of a niche shift in New Zealand populations of *M. guttatus* compared to both its native North American and introduced European populations. Similarly, introduced populations of *M. luteus* in Europe showed a niche shift compared to native populations in South America. Nevertheless, the evidence of niche shift in both taxa must be interpreted with caution due to (a) non-analogous climatic conditions between ranges (Guisan et al. 2012); (b) niche unfilling dynamics and (c) the small size of both native and exotic populations (*M. guttatus* in New Zealand and *M. luteus* in South America).

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

Acknowledgements

We are extremely grateful to the Botanical Society of the Britain and Ireland (BSBI) for providing access to their monkeyflower records. We thank all reviewers for their comments on previous versions of this manuscript.

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Disclosure statement

No potential conflict of interest was reported by the authors

Funding

Daniele Da Re was supported by an ERASMUS+ 2016-2017 grant provided by the European Commission. Mario Vallejo-Marin was supported by the University of Stirling.

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Tables

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

Variables	**Abbreviation**
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

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

Species	**Training region**	**n° of records**	**Model features**	**Beta multiplier**	**AUC (± SD)**	**Boyce Index**
M. guttatus	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
M. luteus	SA	30	L	0.5	0.867 ± 0.082	0.924
	EU	625	LQPH	2	0.902 ± 0.012	0.994
M. × *robertsii*	EU	1776	LQPH	2	0.792 ± 0.009	0.985

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

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

M. × *robertsii* - *M. guttatus*	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
M. × *robertsii* - *M. luteus*	Nat. (EU) - Inv. (EU)	1	0,705	ns	**	0,055	0,000	Equivalent and more similar than by chance, evidences of niche conservatism

Figures

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

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

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

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*. The suitability index ranges from 0 (unsuitable areas, in blue) to 1 (suitable areas, in red).

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

Supplementary Materials

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

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

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

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

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

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

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

Online supplementary materials:

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

- The R codes used in this study are available in the GitLab repository https://gitlab.com/danidr/mimulus_enm