ORIGINAL PAPER

Ecology predicts parapatric distributions in two closely related *Antirrhinum majus* subspecies

A. Khimoun · J. Cornuault · M. Burrus · B. Pujol · C. Thebaud · C. Andalo

Abstract Using a species distribution model, we reconstructed the environmental niches of *Antirrhinum majus pseudomajus* and *Antirrhinum majus striatum*, two closely related species with parapatric distributions. We tested whether retention of ancestral environmental niche (i.e. niche conservatism) or adaptation to different ecological conditions (i.e. niche divergence) could explain the maintenance of their non-overlapping geographic ranges. We found that the environmental niche of *A. m. pseudomajus* is almost twice as large as that of *A. m. striatum,* with substantial overlap indicating that *A. m. pseudomajus* and *A. m. striatum* should co-occur frequently within the geographic range of *A. m. striatum*. By analysing contact zones where both subspecies are geographically close, we found that the presence of one subspecies instead of the other was significantly influenced by particular combinations of climatic factors. Since independent genetic evidence indicates that the two subspecies have experienced phases of range overlap at or near contact zones over the course of their evolutionary history, we propose that ecological niche displacement might be an important factor in explaining the absence of current range overlap between *A. majus* subspecies.

Keywords *Antirrhinum majus* · Parapatry · Niche modeling · Niche divergence · Ecological character displacement

A. Khimoun and J. Cornuault have contributed equally to this work and should be considered sharing first authorship.

A. Khimoun (✉) · J. Cornuault · M. Burrus · B. Pujol · C. Thebaud · C. Andalo
Laboratoire Evolution et Diversité Biologique (EDB), UMR5174, Université de Toulouse (UPS),
118 route de Narbonne, 31062 Toulouse cedex 9, France
e-mail: aurelie.khimoun@gmail.com

A. Khimoun · J. Cornuault · M. Burrus · B. Pujol · C. Thebaud · C. Andalo
Laboratoire Evolution et Diversité Biologique (EDB), UMR5174, CNRS, 31062 Toulouse cedex 9,
France

 Springer

Introduction

Parapatry (i.e. geographically separated ranges abutting along common boundaries) is widespread among closely related species of plants and animals (Anderson and Evensen 1978; King 1993). Yet, it often remains a challenge to identify the mechanisms that prevent range overlap between parapatric species. It has long been hypothesized that parapatric distributions may be associated with spatial changes in environmental factors, species interactions in areas of contact, or dispersal limitation even in the absence of physical barriers (Bull 1991). When environmental factors produce spatial segregation, parapatric distributions are often found to match sharp or gradual environmental transitions (e.g. temperature, precipitation). In such cases of ecotonal changes, closely related species may be specifically adapted to the environmental conditions defining their respective habitats across their parapatric boundary. If so, geographic isolation of the two species may be maintained through local adaptation, which could drive divergence, reproductive isolation, and ultimately speciation between parapatric incipient species (Dobzhansky 1951; Funk 1998; Schluter 2001; Rundle and Nosil 2005; Schluter 2009). Under such an ecological divergence scenario, parapatric species should occupy different environmental niches both in regions where they are found to be completely isolated from each other (i.e. allopatry) and in regions where they are found in contact on each side of their common boundary (i.e. contact zone).

Competitive exclusion between closely related species is thought to prevent range overlap and therefore shape instances of parapatric distributions (Hutchinson 1953; Connor and Bowers 1987). This is expected when species have diverged when isolated geographically (i.e. allopatry) but retained the same environmental niche (Peterson et al. 1999; Wiens 2004; Wiens and Graham 2005). Under such an allopatric divergence scenario, both species should conserve their ancestral environmental niche in allopatry albeit they diverged (i.e. niche conservatism). However, when they meet secondarily after range expansion, ecological character displacement may occur in the area of sympatry, which could result in a partitioning of their environmental niche on each side of their common boundary (Ricklefs 2010). Thus, if competition plays a role in the parapatric distributions of closely related species, one might expect greater differences in environmental niches in sympatry than in allopatry (Brown and Wilson 1956; Dayan and Simberloff 2005).

In addition to niche divergence and competition, dispersal limitation has also the potential to shape parapatric distributions (Garcia-Ramos et al. 2000). This is because limited dispersal can prevent range overlap between geographically isolated populations of closely related species, thereby maintaining them distributed in parapatry. As a consequence, niche differences between species might be observed that are caused by environmental differences associated to their separated distribution ranges, due to spatial autocorrelation in environmental variables between the regions over which the species are distributed, rather than actual niche divergence between species (McCormack et al. 2010).

Species distribution models (SDMs) provide a powerful tool to investigate the role of environmental conditions in shaping spatial patterns of biodiversity (Cicero 2004; Guisan and Thuiller 2005; Elith et al. 2006). Because they can predict habitat suitability in unsampled areas and help to track species range shift in response to climate change (Wiens et al. 2009), SDMs are extensively used in the context of biodiversity inventories and conservation planning (Kremen et al. 2008). More recently, SDMs have been used in another context at the interface of ecology and evolutionary biology, to assess environmental niche differentiation among species (Kozak et al. 2008; Warren et al. 2008) and explore divergence mechanisms at the origin of species formation (titmice, Cicero 2004;

dendrobatid frogs, Graham et al. 2004; wild tomatoes, Nakazato et al. 2008; Mexican jays, McCormack et al. 2010).

In this study, we investigated the role of environmental conditions in the maintenance of geographic isolation between two subspecies of snapdragon plants, *Antirrhinum majus pseudomajus* and *Antirrhinum majus striatum*, by conducting an analysis of the geographic distribution of their environmental niche. Our aim was to examine whether niche divergence may explain parapatric distributions in this system, and infer indirectly from our results whether ecological processes might also be involved. *A. majus* provides an ideal study system to assess niche differentiation in a species divergence context since the two subspecies used in this study are endemic to the Pyrenean mountains and surrounding Mediterranean plains. However, while they both cover a large range of environmental conditions, their geographic distribution remains parapatric throughout their range.

Materials and methods

Study system

Antirrhinum majus (Scrophulariaceae) is an herbaceous short-lived perennial plant characterised by a patchy distribution centred over the Pyrenees, between north-eastern Spain and south-western France. The geographic range of *A. m. striatum* is surrounded by the range of *A. m. pseudomajus* (Fig. 1), which do not overlap. *A. m. striatum* and *A. m. pseudomajus* come into contact at the margins of their ranges. In the contact zones between
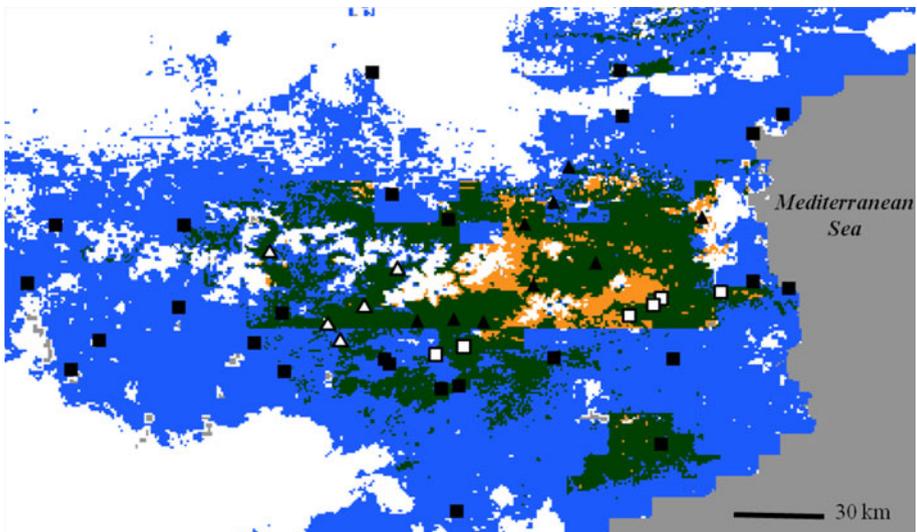

Fig. 1 Sampled localities and predicted potential niches of *A. m. pseudomajus* and *A. m. striatum. Black symbols* represent allopatric populations and *white symbols* represent introgressed populations of the contact zones. *Squares* and *triangles* represent respectively *A. m. pseudomajus* and *A. m. striatum* populations. *Blue* and *orange* regions represent the potential niches of *A. m. pseudomajus* and *A. m. striatum* respectively, as predicted using only allopatric populations. Areas of niche overlap are represented in *green*. (Color figure online)

those two subspecies, introgressive hybridization occurs and local replacement of *A. m. pseudomajus* by *A. m. striatum* is observed in the west part of the contact zone and conversely in the east part (Khimoun et al. 2011).

Environmental data

A total of 31 environmental variables were used to construct the SDMs: 15 climatic variables (including annual trends, seasonality, extreme climatic parameters; Hijmans et al. 2005), eight soil variables and four vegetation variables (Table 1). Previous studies have shown that vegetation indices could improve niche models when used in combination with climatic variables (Buermann et al. 2008). In particular, we used the mean normalized difference vegetation index (NDVI, average of the monthly NDVI values) that measures the density of vegetation and is therefore a good proxy of biotic competitive environment (Nakazato et al. 2008).

Environmental niche modeling

Antirrhinum majus occurrence records

We first characterized the environmental niches of *A. m. pseudomajus* and *A. m. striatum* from allopatric populations, where interspecific interactions do not operate. Genetic analyses of chloroplast and nuclear genes revealed the absence of genetic introgression between these populations (Khimoun et al. 2011), indicating that they have remained in allopatry for a long time. Consequently, we considered that the two subspecies niches cannot differ as a result of inter-specific competition when only these allopatric populations are taken into account. In total, we used occurrence data of 26 *A. m. pseudomajus* populations and 9 *A. m. striatum* populations. The small number of *A. m. striatum* allopatric populations is inherent to the system since *A. m. striatum* has a spatially restricted range compared to *A. m. pseudomajus*.

Preliminary models

The MaxEnt approach (Phillips et al. 2006) was used to predict each subspecies occurrence outside its sampled range. This method is appropriate for presence-only species records and has been shown to perform well in comparison with alternative approaches (Elith et al. 2006). We did not perform an a priori procedure of variable selection and we included the 31 environmental variables to construct the models. We used default values for the convergence threshold (10^{-5}) and the minimum number of iterations (500). Following Phillips et al. (2006), we constructed five types of model that included different features: (1) only linear features (raw environmental variables); (2) linear and quadratic features (including the square of environmental variables); (3) linear, quadratic and product features (adding the products of pairs of environmental variables); (4) threshold features (using binary thresholds on environmental variables) and (5) hinge features (like a linear feature but constant beyond a threshold). The suitability scores obtained from the five models were then averaged to give a single model called the average model. It has been previously shown that the averaging of different model predictions (ensemble modeling) should outperform single model predictions, even when some of the models perform badly (Grenouillet et al. 2010).

Table 1 Summary of environmental variables used in the study

Environmental variable	Abbreviation	Resolution	Source
Mean normalized vegetative index	NDVI	30 × 30 s	MODIS (Justice et al. 1998) (http://modis.gsfc.nasa.gov/)
Productivity	PRO	30 × 30 s	MODIS
Annual mean temperature	BIO1	30 × 30 s	WorldClim (Hijmans et al. 2005) (http://www.worldclim.org/)
Mean diurnal temperature range	BIO2	30 × 30 s	WorldClim
Isothermality	BIO3	30 × 30 s	WorldClim
Temperature seasonality (coefficient of variation)	BIO4	30 × 30 s	WorldClim
Maximal temperature of the warmest month	BIO5	30 × 30 s	WorldClim
Minimal temperature of the coldest month	BIO6	30 × 30 s	WorldClim
Temperature annual range	BIO7	30 × 30 s	WorldClim
Mean temperature of the wettest quarter	BIO8	30 × 30 s	WorldClim
Mean temperature of the driest quarter	BIO9	30 × 30 s	WorldClim
Mean temperature of the warmest quarter	BIO10	30 × 30 s	WorldClim
Mean temperature of the coldest quarter	BIO11	30 × 30 s	WorldClim
Annual precipitation	BIO12	30 × 30 s	WorldClim
Precipitation of the wettest month	BIO13	30 × 30 s	WorldClim
Precipitation of the driest month	BIO14	30 × 30 s	WorldClim
Precipitation seasonality (coefficient of variation)	BIO15	30 × 30 s	WorldClim
Precipitation of the wettest quarter	BIO16	30 × 30 s	WorldClim
Precipitation of the driest quarter	BIO17	30 × 30 s	WorldClim
Precipitation of the warmest quarter	BIO18	30 × 30 s	WorldClim
Precipitation of the coldest quarter	BIO19	30 × 30 s	WorldClim
Forest land	FOR	5 × 5 min	Harmonized World Soil Database, Land Use and Land Cover (http://www.iiasa.ac.at/Research/LUC/External-World-soildatabase/HTML/LandUseShares.html?sb=9)
Grass, scrub or woodland	GRA	5 × 5 min	Harmonized World Soil Database, Land Use and Land Cover

Table 1 continued

Environmental variable	Abbreviation	Resolution	Source
Rooting conditions	ROO	5 × 5 min	Harmonized World Soil Database, Soil Qualities For Crop Production (http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/SoilQualityData.html?sb=11)
Bulk density data	BUL	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=569
Field capacity data	FIE	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics
Profile available water capacity data	WAT	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics
Soil carbon density data	SOI	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics
Thermal capacity data	THE	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics
Total nitrogen density data	NIT	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics
Wilting point data	WIL	5 × 5 min	Distributed Active Archive Center for Biogeochemical Dynamics

Average prediction assessment and decision threshold

Model predictive performance is generally assessed by randomly dividing occurrence data into training (75 %) and testing (25 %) datasets (Fielding and Bell 1997; Araujo et al. 2005). However, this approach is not appropriate with limited occurrence records because the training dataset may be too small to calibrate the model correctly. Instead, we used a jack knife procedure thought to perform well with relatively small datasets (Pearson et al. 2007). This approach consists in alternately removing each locality from the training dataset, and calibrating the model with the $N - 1$ remaining localities. For each of the N constructed models, MaxEnt suitability scores were converted into presence/absence (Pearson et al. 2004) by using the "lowest training presence score" as a decision threshold. Model predictive performance was then evaluated as the model's capacity to successfully predict presence at the left-out localities, taking into account the estimated prevalence (i.e. the proportion of the study area occupied by the subspecies). This procedure was carried out as described in Pearson et al. (2007), except that in our study, both successes and failures were weighted by prevalence. Thus, failures to predict an observed presence when the species is present in most of the study area (high prevalence) receive a high penalty in our analyses. This procedure has been implemented in a script (available upon author's request) used with R software (R Development Core Team 2008). Further details on this test are provided in the supplementary online material (see supplementary online material, Appendix 1).

Tests for environmental niche divergence between the two subspecies

Niche identity

This procedure allowed us to test whether there was a difference between the two subspecies' niches, regardless of the environmental conditions available in their respective backgrounds. Niche overlap was quantified using the Schoener's D metric (Schoener 1968). Significance was assessed using randomization tests which consisted in creating a series of SDMs from randomized datasets of occurrences (pseudoreplicates) and computing the Schoener's D metric for each pseudoreplicate. This procedure permitted to build a null hypothesis that we compared with the observed D values (Warren et al. 2008). We used MaxEnt in batch mode to construct the SDMs from 1,000 pseudoreplicates following the procedure described above, i.e. using ensemble modeling. We then used the R software (R Development Core Team 2008) to average the predictions of these models and compute the significance of the Schoener's D metric.

Background test

Because differences in environmental niches can be due to spatial autocorrelation, the background test (see Warren et al. 2008) was performed to assess whether the potential environmental niches of *A. m. pseudomajus* and *A. m. striatum* were more similar or divergent than would be expected given the environmental conditions available in the regions they occupy (i.e. their backgrounds). For this procedure, pseudoreplicates were generated through randomization of the occurrence locations of one subspecies by randomly sampling the same number of points within its background. The test was carried out in both directions (randomization of *A. m. pseudomajus* and *A. m. striatum* occurrences). The background test is two-tailed because the observed values of the Schoener's D metric can be greater (niche conservatism) or lower (niche divergence) than the null hypothesis. We also adapted this test to average modeling. Both niche identity and niche background

tests are described in more detail in the supplementary online material (see supplementary online material, Appendix 2).

Test for niche divergence between the two subspecies in contact zones

First, we produced a graphical representation of the set of environmental variables that were suitable for each subspecies, both when they were in contact and in allopatry. To this aim, we conducted a Principal Component Analysis on environmental variables for introgressed populations of the contact zones and non-introgressed allopatric populations. Second, we tested if *A. m. pseudomajus* and *A. m. striatum* occupy different niches in sympatry and focussed on genetically introgressed populations at or near contact zones ($n = 5$ for *A. m. striatum* and $n = 6$ for *A. m. pseudomajus*; see Khimoun et al. 2011). Since introgression reveals evolutionary interactions between subspecies during phases of geographic contact (Khimoun et al. 2011), we considered that the absence of current records for one or the other subspecies in the area of introgression might therefore reflect the influence of biotic and/or abiotic factors rather than dispersal limitation. We performed a logistic regression with quasi-binomial error to analyze the effect of climatic variables on presence/absence data of the two subspecies throughout the introgression area. Environmental variables were standardized to mean 0 and unit variance and summarized into principal coordinates to avoid multicollinearity between climatic, soil and vegetation variables. Because differences in environmental conditions generally increased with geographic distance, residuals were considered to be spatially autocorrelated. Autocorrelation was assumed to decrease exponentially with geographic distance. All statistical analyses were performed using R software (R Development Core Team 2008).

Results

Environmental niches

The average models predicted occurrences at the test localities better than chance ($P < 0.001$ for *A. m. pseudomajus* and *A. m. striatum* models). The SDM built with *A. m. striatum* allopatric populations yielded a projected distribution restricted to the Pyrenees Mountains and surrounding valleys whereas the SDM built with *A. m. pseudomajus* allopatric populations predicted that its range should extend beyond the Pyrenees to the Mediterranean coast and surrounding plains (Fig. 1). The environmental niche of *A. m. pseudomajus* is almost twice as large as that of *A. m. striatum* (prevalence of 0.47 and 0.26, respectively). The predicted overlap of the two subspecies distributions is 0.19 (Schoener's D). This overlap reveals that environmental conditions should be suitable for the establishment of both subspecies over a large area within the actual range of *A. m. striatum* (Fig. 1). In particular, both subspecies should be present at every sampled locality of the contact zones. Thus, based on the distribution of environmental conditions that are suitable for both subspecies, *A. m. pseudomajus* and *A. m. striatum* are expected to be frequently found in sympatry (Fig. 1).

Niche divergence in allopatry

The niche identity test indicated that the current niche overlap between the two *Antirrhinum* subspecies is significantly lower than expected by chance, when considering

allopatric populations only ($P = 0.05$; see Fig. 2). The background test, which takes into account background differences in environmental conditions, indicated divergence between the potential niches of *A. m. striatum* and *A. m. pseudomajus* when the occurrence randomisation procedure was applied for *A. m. striatum* ($P = 0.02$ for Schoener's D metric). Such divergence was not found when the randomisation procedure was applied to *A. m. pseudomajus* ($P = 0.56$ for Schoener's D metric; see Fig. 3). Because the observed difference between subspecies niches was greater than the expected difference under the hypothesis that *A. m. striatum* was randomly distributed within its background, our results imply that *A. m. striatum* occurs in a part of its environmental background where conditions are particularly dissimilar to the environmental niche of *A. m. pseudomajus*.

Niche divergence in contact zones

The first three principal components from the PCA explained 75 % of the total variance (47, 18 and 10 % for PC1, PC2 and PC3, respectively). PC1 was mostly correlated with annual mean temperatures, extreme values of temperature and precipitation, PC2 was correlated with variables describing temperature variation, and PC3 was correlated with soil structure, soil nutrient and water availability. Vegetation variables were poorly correlated to the first three PCA axes (see supplementary online material, Appendix 3). According to the logistic regression analysis, the presence of one subspecies instead of the other was significantly affected by all pairwise interactions between PC1, PC2 and PC3 (Table 2). The association of higher precipitation with lower temperatures, higher thermal amplitudes and wetter, more compact and nutrient-deprived soils significantly increased the probability of observing *A. m. striatum* instead of *A. m. pseudomajus* (Fig. 4). Although the two subspecies were expected to co-occur in contact zones on the basis of environmental factors, they show significant ecological niche divergence throughout the area of
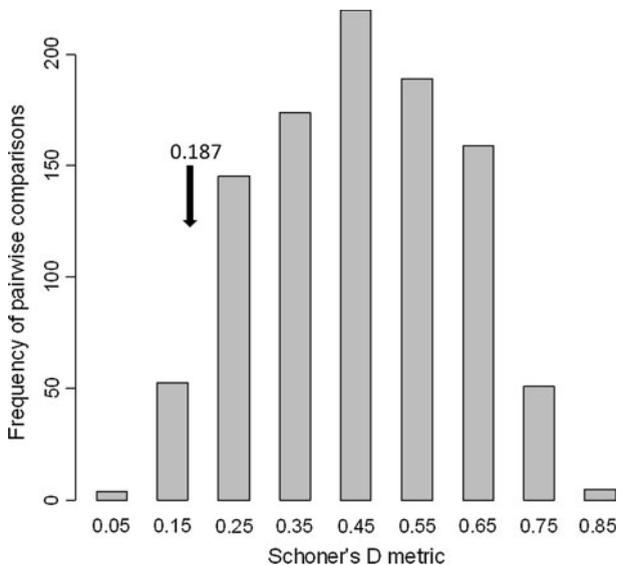

Fig. 2 Niche identity test of *A. m. pseudomajus* and *A. m. striatum*. The *histograms* represent the null distributions of niche overlap values from 1,000 pseudoreplicates. The *arrow* indicates the observed value of the potential niche overlap of *A. m. pseudomajus* and *A. m. striatum*
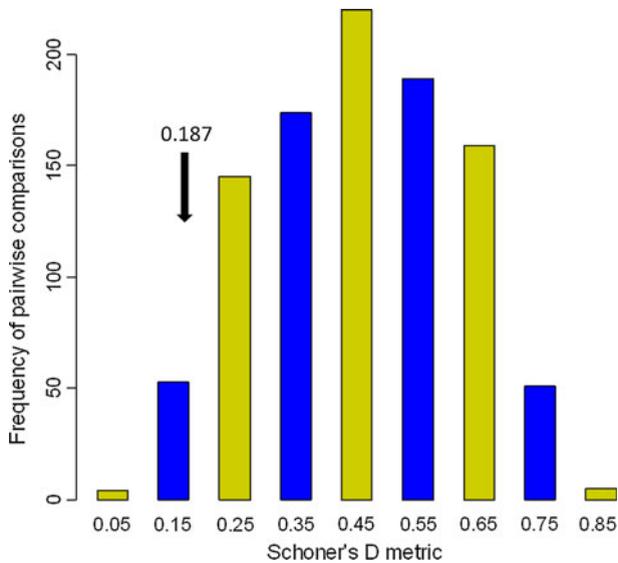
Fig. 3 Test of niche divergence between *A. m. pseudomajus* and *A. m. striatum* (background test). The *blue histogram* represents the null hypothesis when occurrences of *A. m. pseudomajus* are randomized within its background and the *yellow histogram* represents the null hypothesis when occurrences of *A. m. striatum* are randomized within its background. The *arrow* indicates the observed overlap values between *A. m. pseudomajus* and *A. m. striatum*. (Color figure online)

	Variables	Estimates	SE	*df*	*P*
Table 2 Results of the GLM analysing the effects of environmental variables on the distribution of *A. m. pseudomajus* and *A. m. striatum* in contact zones	PC1	−2.75	0.20	1	<0.001
	PC2	−15.52	0.03	1	<0.001
	PC3	38.03	0.06	1	<0.001
	PC1 × PC2	−0.48	0.18	1	<0.001
	PC1 × PC3	0.81	0.02	1	<0.001
	PC2 × PC3	−1.67	0.04	1	<0.001

introgression. Moreover, the contact zone populations of the two subspecies were found in a subset of the environmental niche which only partly overlapped the environmental niche of allopatric populations.

Discussion

Geographic segregation is not predicted by environmental niche modelling

Niche models based on environmental factors indicate that the predicted geographic range of both subspecies is larger than their actual range, with both subspecies occupying only partly the geographic range where environmental conditions are suitable for their establishment (Fig. 1). They also show that the geographic range of *A. m. pseudomajus* should be larger than the predicted range of *A. m. striatum* and include part of it on the basis of
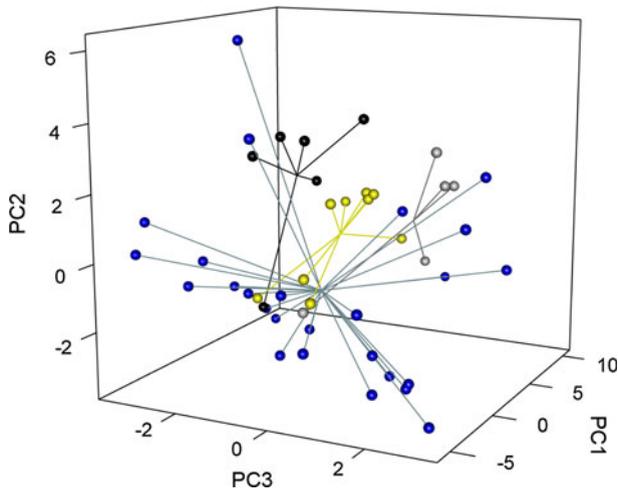
Fig. 4 3-D-display of introgressed and allopatric *A. m. pseudomajus* and *A. m. striatum* populations along principal components 1, 2 and 3. *Blue* and *yellow spheres* represent allopatric populations of *A. m. pseudomajus* and *A. m. striatum* respectively. *Black spheres* represent *A. m. pseudomajus* introgressed populations and *grey spheres* represent introgressed *A. m. striatum* populations. (Color figure online)

their predicted environmental niches (Fig. 1). Thus, on the basis of environmental conditions alone, *A. m. pseudomajus* and *A. m. striatum* should co-occur frequently within the *A. m. striatum* geographic range. Such co-occurrence is however not observed in nature. Even in localities where populations bear the signature of gene exchange between subspecies, populations of the two subspecies remain geographically separated. The predicted co-occurence of the two subspecies in the area of introgression and over most of *A. m. striatum* range could be due to the poor resolution of the environmental grids used for calibrating the models and/or the small number of occurrence records. Although the number of *A. m. striatum* populations that we used is relatively small, these populations cover the entire geographic range of the subspecies. Furthermore, the model predictive performances were good, suggesting that the set of environmental variables considered (31 variables) is sufficient for correctly representing both subspecies niches. This suggests that factors besides environmental factors, such as dispersal limitation and biotic interactions, could have important effects in explaining the absence of range overlap between taxa where they may share similar environmental requirements (Sillero 2011).

Dispersal limitation can prevent organisms from colonizing an area of suitable habitat in its entirety (Holt 2003). This seems likely in *Antirrhinum* since seeds are mostly dispersed over short distances from maternal plants, even though their small size and weight (<15 mg) may allow occasional long-distance dispersal (Andalo et al. 2010). While dispersal limitation might therefore explain the global pattern of subspecies geographic segregation, it can hardly explain the complete absence of sympatry where the two subspecies were once geographically close enough to exchange genes (Khimoun et al. 2011). Thus, it is possible that biotic interactions (e.g. competition, predation or parasitism), possibly in interaction with environmental factors, prevent the two subspecies from occupying the whole common area that is suitable to their establishment (Miller 1967).

Niche divergence in contact zones

In contact zones, the presence of one or the other subspecies was correlated with environmental conditions. Our results suggest that *A. m. striatum* populations are ecologically distinct from *A. m. pseudomajus* populations wherever they could occur in sympatry (see Fig. 4). Evidence for recent gene flow among subspecies populations in the contact zones suggests that differences in the environmental niche cannot be explained by dispersal limitation (Khimoun et al. 2011). Expansion processes might generate a geographically structured distribution of genetically introgressed populations (Currat et al. 2008). Under such scenario, the fact that *A. m. striatum* invaded the previous range of *A. m. pseudomajus* in the west part of the contact zone whereas *A. m. pseudomajus* reciprocally invaded *A. m. striatum* range in the east part of the contact zone could therefore be related to neutral demographic processes (Khimoun et al. 2011). However, our results show that such replacement is highly correlated to environmental conditions (Fig. 4). Thus, it seems possible that adaptation of each subspecies to different local conditions could explain the local asymmetry of subspecies replacement in the area of introgression. The two subspecies parapatric distribution could then reflect differential abilities to survive and reproduce in varying local environmental conditions. It is also possible that, depending upon environmental conditions, one subspecies has a superior ability over the other one to take up and/or use water and nutrient resources when they become available in a competitive environment. Although we do not have direct evidence to support this hypothesis, the observed pattern of niche displacement between the two subspecies in contact zones compared to allopatry suggests that competition between subspecies may be a major factor explaining why *A. m. pseudomajus* and *A. m. striatum* are prevented from occupying their entire potential niche, thereby maintaining their parapatric distributions.

To conclude, our results revealed that environmental factors alone could not be responsible for *Antirrhinum* subspecies parapatric distributions. We found that differences in environmental niches between subspecies in areas of contact were greater than expected by chance and related to possible differences in resource use, in particular water and soil nutrients that are often limiting in Mediterranean mountains. Thus, we argue that range overlap might be prevented in our study system by ecological niche displacement driven by competition, recognizing that more comprehensive geographic sampling and a functional characterization of differences in resource use between subspecies are required before any firm conclusion can be reached (Losos 2000).

References

Andalo C, Cruzan MB, Cazettes C et al (2010) Post-pollination barriers do not explain the persistence of two distinct *Antirrhinum* subspecies with parapatric distribution. Plant Syst Evol 286:223–234

Anderson S, Evensen MK (1978) Randomness in allopatric speciation. Syst Zool 27:421–430

Araujo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Glob Chang Biol 11:1504–1513

Brown WL, Wilson EO (1956) Character displacement. Syst Zool 5:49–64

Buermann W, Saatchi S, Smith TB et al (2008) Predicting species distributions across the Amazonian and Andean regions using remote sensing data. J Biogeogr 35:1160–1176

Bull CM (1991) Ecology of parapatric distributions. Annu Rev Ecol Syst 22:19–36

Cicero C (2004) Barriers to sympatry between avian sibling species (Paridae: Baeolophus) in local secondary contact. Evolution 58:1573–1587

Connor EF, Bowers MA (1987) The spatial consequences of interspecific competition. Ann Zool Fennici 24:213–226

Currat M, Ruedi M, Petit RJ, Excoffier L (2008) The hidden side of invasions: massive introgression by local genes. Evolution 62:1908–1920

Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. Ecol Lett 8:875–894

Dobzhansky T (1951) Genetics and the origin of species. Columbia University Press, New York

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Funk DJ (1998) Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. Evolution 52:1744–1759

Garcia-Ramos G, Sanchez-Garduno F, Maini PK (2000) Dispersal can sharpen parapatric boundaries on a spatially varying environment. Ecology 81:749–760

Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58:1781–1793

Grenouillet G, Buisson L, Casajus N, Lek S (2010) Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34:9–17

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Holt RD (2003) On the evolutionary ecology of species'' ranges. Evol Ecol Res 5:159–178

Hutchinson GE (1953) The concept of pattern of ecology. Proc Acad Nat Sci Phila 105:1–12

Justice CO, Vermote E, Townshend JRG et al (1998) The moderate resolution imaging spectroradiometer (MODIS): land remote sensing for global change research. IEEE Transact Geosci Remote 36:1228–1249

Khimoun A, Burrus M, Andalo C et al (2011) Locally asymmetric introgressions between subspecies suggest circular range expansion at the *Antirrhinum majus* global scale. J Evol Biol 24:1433–1441

King M (1993) Species evolution: the role of chromosome change. Cambridge University Press, Cambridge

Kozak KH, Graham CH, Wiens JJ (2008) Integrating GIS-based environmental data into evolutionary biology. Trends Ecol Evol 23:141–148

Kremen C, Cameron A, Moilanen A et al (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320:222–226

Losos JB (2000) Ecological character displacement and the study of adaptation. Proc Natl Acad Sci USA 97:5693–5695

McCormack JE, Zellmer AJ, Knowles LL (2010) Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? insights from tests with niche models. Evolution 64:1231–1244

Miller RS (1967) Pattern and process in competition. Adv Ecol Res 4:1–74

Nakazato T, Bogonovich M, Moyle LC (2008) Environmental factors predict adaptive phenotypic differentiation within and between two wild Andean tomatoes. Evolution 62:774–792

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27:285–298

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117

Peterson AT, Soberon J, Sanchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ricklefs RE (2010) Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. Proc Natl Acad Sci USA 107:1265–1272

Rundle HD, Nosil P (2005) Ecological speciation. Ecol Lett 8:336–352

Schluter D (2001) Ecology and the origin of species. Trends Ecol Evol 16:372–380

Schluter D (2009) Evidence for ecological speciation and its alternative. Science 323:737–741

Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726

Sillero N (2011) What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecol Model 222:1343–1346

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883

Wiens JJ (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annu Rev Ecol Evol Syst 36:519–539

Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci USA 106:19729–19736