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Species distribution models contribute to determine the effect of climate and interspecific interactions in moving hybrid zones

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Abstract

Climate is a major factor delimiting species' distributions. However, biotic interactions may also be prominent in shaping geographical ranges, especially for parapatric species forming hybrid zones. Determining the relative effect of each factor and their interaction of the contact zone location has been difficult due to the lack of broad scale environmental data. Recent developments in species distribution modelling (SDM) now allow disentangling the relative contributions of climate and species' interactions in hybrid zones and their responses to future climate change. We investigated the moving hybrid zone between the breeding ranges of two parapatric passerines in Europe. We conducted SDMs representing the climatic conditions during the breeding season. Our results show a large mismatch between the realized and potential distributions of the two species, suggesting that interspecific interactions, not climate, account for the present location of the contact zone. The SDM scenarios show that the southerly distributed species, *Hippolais polyglotta*, might lose large parts of its southern distribution under climate change, but a similar gain of novel habitat along the hybrid zone seems unlikely, because interactions with the other species (*H. icterina*) constrain its range expansion. Thus, whenever biotic interactions limit range expansion, species may become 'trapped' if range loss due to climate change is faster than the movement of the contact zone. An increasing number of moving hybrid zones are being reported, but the proximate causes of movement often remain unclear. In a global context of climate change, we call for more interest in their interactions with climate change.

Introduction

Climate is a major factor shaping species distributions (Hutchinson, 1918; MacArthur, 1958; Gaston, 2003). However, not all climatically suitable regions are available to a species. Ecological barriers, either abiotic or biotic, impede dispersal and colonization of new areas. Among biotic factors, interspecific interactions can drastically reduce population growth and dispersal beyond a contact zone with natural enemies (DeWalt *et al.*, 2004), competitors (Hairston, 1980; Cunningham *et al.*, 2009) or sexually interacting species (Barton & Hewitt, 1985; Gröning & Hochkirch, 2008). Evidence comes from empirical data (Letcher *et al.*, 1994; Bullock *et al.*, 2000; Hochkirch & Lemke, 2011), experiments (Hairston, 1980; Davis *et al.*, 1998; Hochkirch *et al.*, 2007) and modelling (Cunningham *et al.*, 2009). However, little work has attempted to quantify how much of the potential range of a species is left unoccupied because of negative interspecific interactions on a species' range. Analysing this gap between the potential and realized distributions may provide insights into the relative contribution of abiotic factors and interspecific interactions, at least for indigenous taxa. Recent developments in species distribution modelling (SDM) allow estimating the size of the suitable area not colonized by a species and match the observed movements of species distributions

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with predicted global changes (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Soberón & Nakamura, 2009).

Parapatric pairs of hybridizing species are ideal study systems in this regard. The location of a hybrid zone between parapatric taxa is primarily determined by extrinsic factors such as climate or habitat (Moore & Price, 1993; MacCallum *et al.*, 1998; Bridle *et al.*, 2001; Walls, 2009; Scriber, 2011). However, in dynamic systems such as moving zones, intrinsic factors (relative hybrid fitness, dispersal) contribute to determine the zone position at a given time (Barton & Hewitt, 1985; Parsons *et al.*, 1993; Swenson, 2006; Buggs, 2007). If extrinsic factors are the major drivers of zone location, parapatric species will meet at ecotones (which can be steplike (Kruuk *et al.*, 1999) or wide (Moore, 1977)), specific locations along environmental gradients (Endler, 1977) or any environmental barriers to gene flow (Barton & Hewitt, 1985). Hybrid fitness is expected to be lower than the fitness of both parental forms in these areas (Barton & Hewitt, 1985), but it may equal or higher under some conditions (hybrid bounded superiority, Moore, 1977). Further, extrinsic factors might also promote spatial clustering of hybrid zones, for example, in mountain systems ('suture zones'; Hewitt, 1996; Aliabadian *et al.*, 2005; Swenson & Howard, 2004). A zone whose existence is maintained by intrinsic factors is a tension zone, where zone width is a balance between dispersal and selection. Tension zones tend to move towards, and become trapped at, barriers to gene flow and 'density troughs' caused by environmental gradients (i.e. extrinsic factors; Barton & Hewitt, 1985).

Different predictions can be compared to determine which mechanisms underlie the dynamics of a hybrid zone (Swenson, 2006). If extrinsic factors such as temperature or precipitation clines determine the location of a hybrid zone (environmental gradient model; Endler, 1977), the predicted range of a species should closely match its realized range. In contrast, in a zone maintained mainly by intrinsic factors (a tension zone), the predicted range should extend beyond the contact zone. Both types of factor may interact although as exemplified by the trapping of hybrid zones in areas of low density (Barton & Hewitt, 1985). Swenson (2006) also found a mixture of these two patterns in four avian species pairs hybridizing in the Great Plains of North America. He observed a close match between the predicted and realized range in the oriental species, but a strong mismatch in all occidental species for which the predicted ranges extended further east beyond the contact zones. Climate parameters such as temperature and precipitation seem to constrain the ranges of the eastern taxa, but not of the western taxa (Rising, 1969; Moore, 1977; Swenson, 2006).

Due to the strong influence of climatic parameters on species ranges (e.g. Parmesan, 2006), climate change is expected to change the relative fitness of two interacting species in a contact zone and potentially displace hybrid zones. Zone movement towards density troughs and barriers to gene flow is predicted by the tension zone hypothesis even under stable environmental conditions (Barton & Hewitt, 1985). However, under climate change, one would expect the zone to track density changes in both species, illustrating the close interaction of extrinsic and intrinsic factors, which might impede the identification of the relative contribution of each. Nevertheless, if climate change is likely to shift the location of the zone, it should not fundamentally modify the mismatch between the potential and the realized distribution.

So far, SDMs have been little used to unravel the factors driving hybrid zone dynamics (Swenson, 2008). We used this approach here to determine whether intrinsic or extrinsic factors determine the movement dynamics of a hybrid zone between the breeding ranges of two passerines: the Melodious warbler, *Hippolais polyglotta*, and the Icterine warbler, *H. icterina* (Fig. 1). These two parapatric species hybridize in Western Europe (Faivre *et al.*, 1999; Secondi *et al.*, 2006). During the breeding season, no obvious climatic barriers exist, so that we predict a strong mismatch between predicted and realized distributions in both species. The hybrid zone of these two species shifted north-eastwards during the last decades (Jouard, 1935; Yeatman, 1976; Yeatman-Berthelot & Jarry, 1994) possibly in response to climate change. We modelled (i) the potential current breeding range of each species based on climatic parameters during the respective time span as well as (ii) their expected breeding ranges under two climate change scenarios to determine whether predicted changes are consistent with observed changes. By combining these two approaches, we may gain insight into the dynamics of hybrid zone movement.

Materials and methods

Data acquisition

Both species are long distance migrants wintering in sub-Saharan Africa and remaining at breeding sites in Europe from May until August (Cramp, 1988). Following Hutchinson's niche concept (Hutchinson, 1957, 1978), which is the theoretical basis for interpreting SDM results (Soberón, 2007; Godsoe, 2010), a species physically responds only to conditions it is actually exposed to and which determine its realized niche. Because our study species both inhabit their breeding range only from May to August, we used climate data of the breeding season for modelling and extracted monthly temperature and precipitation min/max values obtained in 2.5-arc-min resolution from Worldclim data base (Vers. 1.4, www.worldclim.org, Hijmans *et al.*, 2005). To avoid multicollinearity that might lead to an overfitting during modelling (Heikkinen & Luoto, 2006), we used the mean temperature and precipitation, as well as the temperature range computed across the 4-month time period.

Presence localities from the breeding ranges were compiled from multiple sources (Table S1), resulting in 4577 and 24 815 localities for *H. polyglotta* and *H. icterina*, respectively (Fig. S1). Because of the large number of samples and their strongly biased nature (e.g. 77.68% of all *H. icterina* records derived from Sweden), we conducted a cluster analysis based on Euclidean distances as suggested by Rödder *et al.* (2009). The cluster analysis was based on the climatic variables, wherein the resulting dendrogram was blunted and only one randomly selected record per class was used for further processing. This approach reduces the aggregation of observations in the environmental space which generates spatial autocorrelation and affects the reliability of SDM predictions (Dormann *et al.*, 2007; Phillips, 2008; Phillips *et al.*, 2009). Subsequently, the remaining localities ($n = 150$ for each species) were visually checked for additional clumping in geographical space. While the spatial distribution of the remaining localities for *H. polyglotta* was homogenously distributed in space and therefore well suited for further modelling, we detected spatial clumping in a few regions in the western part of the distribution of *H. icterina*. This might be caused by uneven sampling effort or data accessibility between western and eastern European countries. Uneven sampling across different regions (such as countries) may underestimate the species' niche in some parts of the environmental space, which might cause biased predicted ranges for interpreting model results (Barbet-Massin *et al.*, 2010). To account for this sampling bias, we ran an additional cluster analysis in the same way as for *H. icterina* before, but used just the geographical coordinates of each locality as explanatory variables. We obtained a more homogeneous distribution based on 100 localities that better met the assumptions of SDM. Finally, 150 localities for *H. polyglotta* and 100 localities for *H. icterina* remained for modelling.

Species distribution modelling

To model distributions, we used Maxent vers. 3.3.3a (Phillips *et al.*, 2004; Phillips & Dudík, 2008; Elith *et al.*, 2011) and applied the standard settings. For model testing, a bootstrap approach was applied in 100 model runs which iteratively omitted 30% of the records from the training model data set. Despite recent criticisms (Lobo *et al.*, 2008; Jiménez-Valverde, 2012), but lacking alternatives (e.g. Baldwin, 2009), the AUC statistic (Swets, 1988; Fielding & Bell, 1997) was used for model evaluation. However, AUC scores should always be interpreted with caution as a stand-alone validation procedure. As we chose the logistic output in Maxent, model predictions ranged between 0 (not suitable) and 1 (fully suitable). We used the nonfixed 10 percentile threshold for each species derived from Maxent to cut off biologically irrelevant noise from model prediction maps as recommended by Liu *et al.* (2005). Furthermore, a jackknife-based approach was used to test for each variables' explanative power.

A more thorough analysis of model outputs was conducted using ENM Tools 1.3. (Warren *et al.*, 2010). First, we computed niche overlap using the *Schoener's D* metric (Warren *et al.*, 2008; Rödder & Engler, 2011), which allows a direct comparison of niche overlap. Thereafter, we carried out niche similarity tests to determine whether observed niche overlap differed significantly from random expectations (Warren *et al.*, 2008). For this purpose, records of both warblers were pooled and randomly reassigned to one species keeping the initial sample sizes constant. For each randomly reassigned subsets, a Maxent SDM was run and niche overlaps among the model outputs were calculated. This procedure was repeated 100 times to create a null distribution of overlap values which was compared to the actual observed niche overlap to assess its significance.

To assess the geographical shifts in potential distributions of both species under presumed anthropogenic climate change, SDMs were projected onto A2a and B2a emission scenarios for the year 2080 derived from the Intergovernmental Panel on Climate Change (IPCC). These emission scenarios represent two possible future economic, political and environmental developments resulting in different CO_2 emissions. The A2a scenario represents a rather pessimistic future, whereas B2a is more optimistic, with lower ground temperature rise as compared to A2a. Further, each emission scenario was represented by three global circulation models (GCMs) to cope with uncertainties that are prone to a single GCM (Beaumont *et al.*, 2009). We choose CCCMA, CSIRO and HadCM3 GCMs for our modelling (also available from www.worldclim.org).

Results

Our results suggest a large mismatch between the realized and potential distribution of the two *Hippolais* warblers. The potential breeding distribution of *H. polyglotta* extended eastwards beyond the contact zone and far into the realized distribution of *H. icterina* (Fig. 2a). Reciprocally, the potential distribution of *H. icterina* extended westwards and included large parts of the realized distribution of *H. polyglotta* in Western Europe (Fig. 2b).

SDM performance was 'fair' in *H. polyglotta* ($AUC_{mean} = 0.791$, $AUC_{SD} \pm 0.027$) and 'excellent' in *H. icterina* ($AUC_{mean} = 0.925$, $AUC_{SD} \pm 0.0184$) according to the classification from Swets (1988; modified by Araújo *et al.*, 2005). The 10 percentile threshold pro-

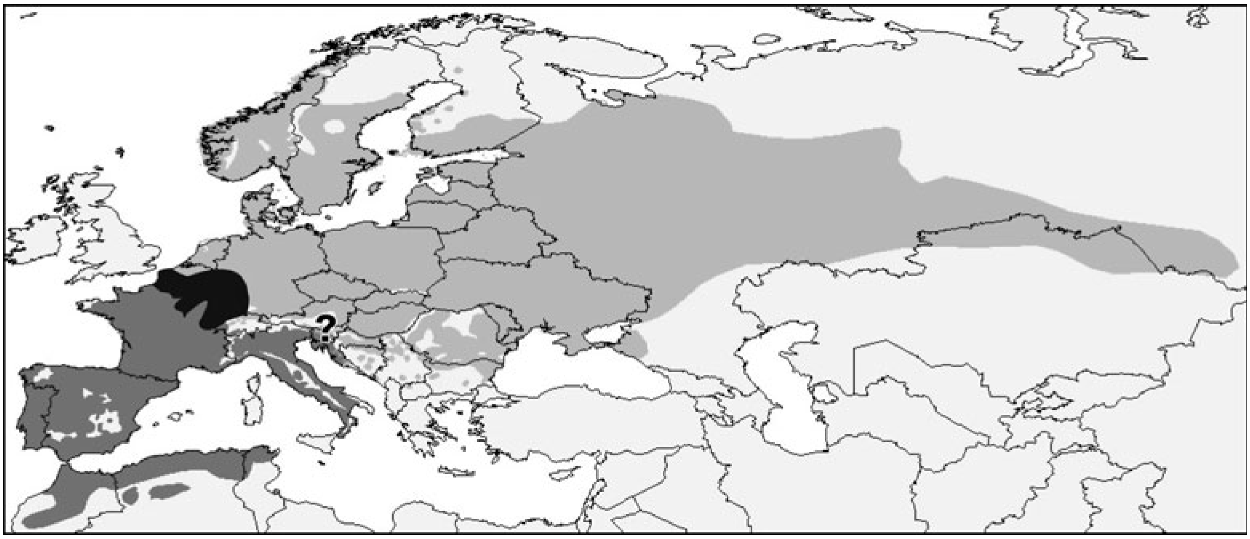

Fig. 1 Current breeding range of *Hippolais polyglotta* (dark grey) and *H. icterina* (grey, BirdLife International & Natureserve, 2011) as well as the location of their hybrid zone (black). The question mark highlights the unclear situation of the contact zone in Croatia.

vided by Maxent was 0.382 for *H. polyglotta* and 0.275 for *H. icterina*. Variable contributions differed markedly between species (Fig. 3). In *H. polyglotta*, mean temperature followed by mean precipitation contributed most (median: 63.34% and 25.65% respectively), whereas temperature range was rather unimportant (median: 11.26%). For *H. icterina*, the temperature range was by far the most important variable (median: 81.06%). Differences in variable contributions between both species were significant for all climate variables (Mann–Whitney *U*: P_{mean}: $Z = -8.523$, $P < 0.0001$, T_{mean}: $Z = -12.217$, $P < 0.0001$, T_{range}: $Z = -12.217$, $P < 0.0001$). Overlap in the potential niches of both species was classified as 'moderate' ($D = 0.52$) according to the categorization proposed by Rödder & Engler (2011). However, the observed overlap was significantly lower than expected from the null distribution (mean: 0.859, 95%-CI: 0.855–0.863, $P < 0.0001$).

Potential distributions of both species shifted in response to projected climate changes under the A2a and B2a emission scenarios for 2080 (Fig. 4). Large parts of the Mediterranean range of *H. polyglotta* lost climatic suitability, whereas other parts of the potential distribution north-east of its current range increased in suitability. These areas of potential distribution gain were situated at the north-eastern range margin of *H. polyglotta*. A strong response to changing climate was also expected in *H. icterina* (Fig. 4). Interestingly and in contrast to *H. polyglotta*, the response of *H. icterina* strongly depended on the emission scenario. Whereas losses in the realized range were mainly expected in south-eastern Europe under B2a, additional areas in large parts of Central Europe and eastern France became unsuitable under A2a. Furthermore, most of its potential distribution extending into the range of *H. polyglotta* became unsuitable under A2a. Northward range extension seems very likely in *H. icterina*, because large regions in Scandinavia and north-western Russia became climatically suitable under both emission scenarios. However, realized niche overlap between both species increased with predicted 2080 climate warming (*Schoener's D*: A2a = 0.60, B2a = 0.62).

Discussion

Interspecific interactions as a driver of breeding ranges

Model outputs showed a high overlap in the potential distributions of both *Hippolais* warblers (Fig. 2), although niche overlap was significantly lower than expected by chance and the SDMs of both species were determined by different climate variables (Fig. 3). The large longitudinal overlap of the SDMs suggests that suitable climatic conditions for breeding of both species occur across nearly the entire Western Palearctic and that Grinnellian niches between the sister species remain rather conservative. Thus, the results were consistent with the hypothesis that the breeding ranges of the two species are limited by interspecific interactions rather than by a climatic gradient during the breeding season. In contrast to the pattern found by Swenson (2006), the potential ranges of both species extended far beyond the contact zone. In *Hippolais* warblers, no climatic barriers seem to limit dispersal and the colonization of new areas. Thus, the observed pattern is better explained by the tension zone hypothesis than by the environmental gradient hypothesis (Endler, 1977).

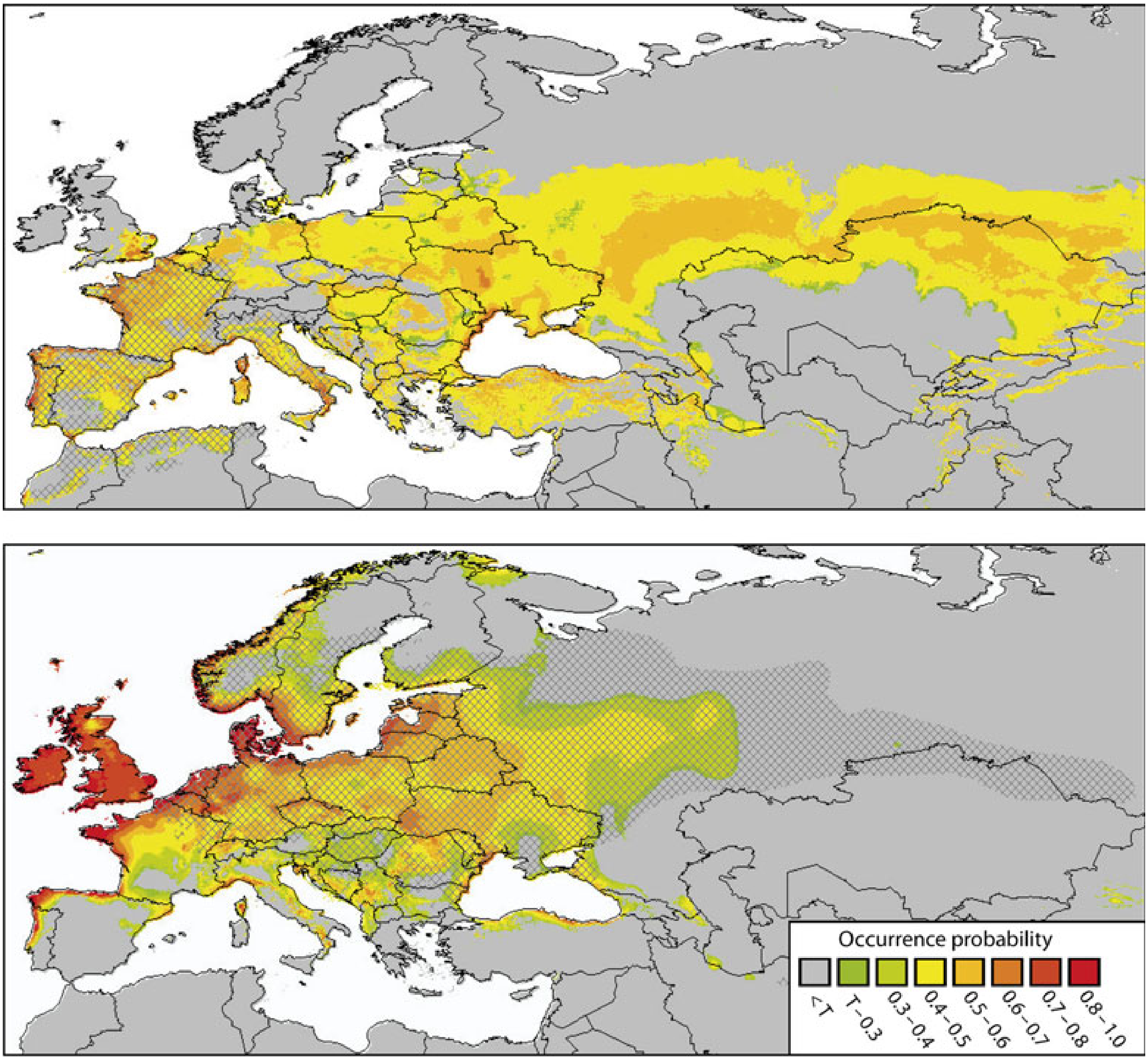

Fig. 2 Potential distribution of *H. polyglotta* (upper panel) and *H. icterina* (lower panel). '*T*' indicates the 10 percentile threshold for either species. Predictions below this threshold were coloured as light grey. For direct comparison, realized ranges were also visualized (grey cross-hatches, BirdLife International & Natureserve, 2011).

Besides hybridization, other types of interactions (e.g. competition or pathogens) may influence population growth and account for the current location of the contact zone. *Hippolais* warblers tend to form heterospecific territorial clusters in sympatry, where nest predation is higher than in monospecific clusters at least in *H. icterina* (Faivre, 1993). In addition, the contact zone is paralleled by a contact zone between two main malaria lineages each hosted by one warbler. Cross-species transmission is asymmetric (more frequent in *H. icterina*) and has been found only within or in close vicinity of the contact zone (Reullier *et al.*, 2006). This suggests that the spatial proximity between individuals may generate fitness costs additional to the hybridization costs that may eventually impair range expansion beyond the contact zone.

Geographical shift of the contact zone under climate change

Species distribution models suggest that the *Hippolais* contact zone is mainly maintained by interactions between the two species and not by bioclimatic factors. The zone has been moving north-east during the last

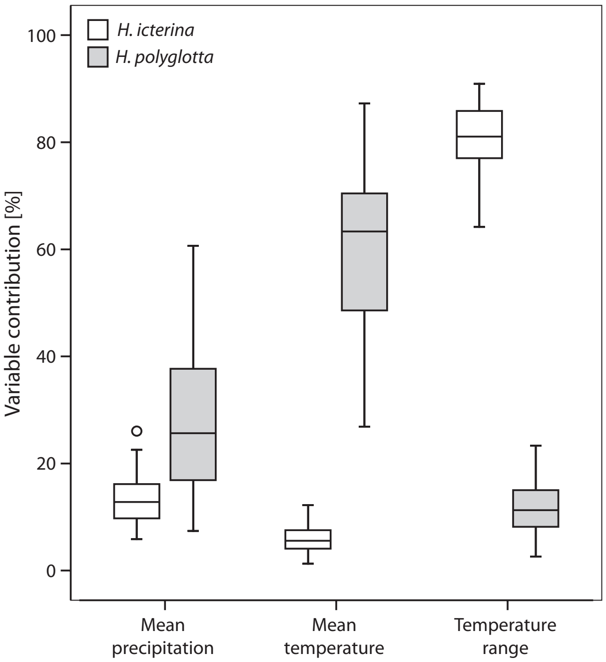

Fig. 3 Contributions of the three bioclimatic variables chosen for modelling in Maxent for the SDMs of both species based on 100 replications for each species (white: *Hippolais icterina*, grey: *H. polyglotta*).

decades (Secondi *et al.*, 2003). Such a movement is predicted by theory, if the dispersal-selection equilibrium depends on environmental conditions (Barton & Hewitt, 1985). It is well documented that climate change causes range shifts of species (e.g. Parmesan, 1999). Because of its effect on environmental gradients, it is also expected to shift the location of tension zones (Bull & Burzacott, 2001; Buggs, 2007). New climatic conditions might induce opposite demographic trends in sympatric populations of each species (as suggested by the SDMs) and ultimately affect the position and the extent of the zone. Consistently, an increase in population growth is expected in *H. polyglotta*, whereas a decrease is expected in *H. icterina* in their contact zone. This process should generate unbalanced densities and dispersal asymmetries between species, that is, factors known to favour zone movements (Barton & Hewitt, 1985).

Based upon the different emission scenarios for the future, it is likely that both species will face strong range retractions at their south-western range margin and range expansions in the north-east. No sharp climatic discontinuity during the breeding season is observed in the contact zone region. Instead, climate varies gradually here. Thus, observed demographic trends may be expected to continue in the future. However, in species where nonclimatic factors hamper range expansion at one margin, the consequences of climate change on the future distribution are difficult to forecast. For Mediterranean species such as *H. polyglotta*, new climate conditions may render large areas suitable, but colonization may be impaired by interspecific interactions. Indeed, the Melodious warbler is currently expanding its range, but is expected to lose large parts of its southern range. Thus, its breeding area may eventually shrink if the losses at the southern margins occur at a faster rate than the gains at the northern margins. This might have dramatic consequences for many other hybridizing species distributed parapatrically. Thermophilous species might experience net range reduction if the range margin at lower latitudes moves faster than the poleward margin. In extreme cases, such species might be brought to the verge of extinction by being squeezed between two boundaries moving at different speeds. For the polewards distributed species, the change in breeding range will partly depend on the rate of climate change, the size of the suitable bioclimatic area available at its poleward (or uppermost in mountainous areas) margin, and the presence of uncrossable barriers like mountain tops and coastlines.

Interestingly, the additional constraints caused by extrinsic factors on population growth are likely to increase loss rate at the contact zone border for the northern species and thus reduce the strength of the interspecific factors affecting the southern species. Accordingly, it is difficult to predict the fate of the contact zone itself. Although it is possible to build a distribution model of a current zone (Swenson, 2006), forecasting the amount of changes in location and width to come in the future is far more challenging than for single species cases and strongly depends on the contribution of extrinsic environmental factors to hybrid zone formation. The evolutionary dynamics of a species' niche is also a key element to consider. Whether the niche of a species remains stable over time or whether adjustments occur that dampen the effects of climate change is currently being debated (Peterson *et al.*, 1999; Pearman *et al.*, 2008; Rödder & Lötters, 2010).

The numbers of studies reporting range expansions and moving contact zones have both increased during recent decades (e.g. Parmesan, 1999; Buggs, 2007; Hochkirch & Damerau, 2009; Price, 2009; Chen *et al.*, 2011). However, in contrast to simple range expansions, evidence for climate effects on moving contact zones remains scarce (but see Hillis & Simmons, 1986; Shaw *et al.*, 1990; Hersteinsson & MacDonald, 1992; Ruedi *et al.*, 1997; Britch *et al.*, 2001) and movement opposite to the expected direction has been observed (Sorjonen, 1986). The frequencies of expected vs. non-expected shifts must be reported for more species before identifying climate change as a major driver of contact zone movements (Buggs, 2007). In this regard, Price (2009) listed many examples of hybrid zones, where still no information on movement is available, suggesting that much research is still needed in this context.

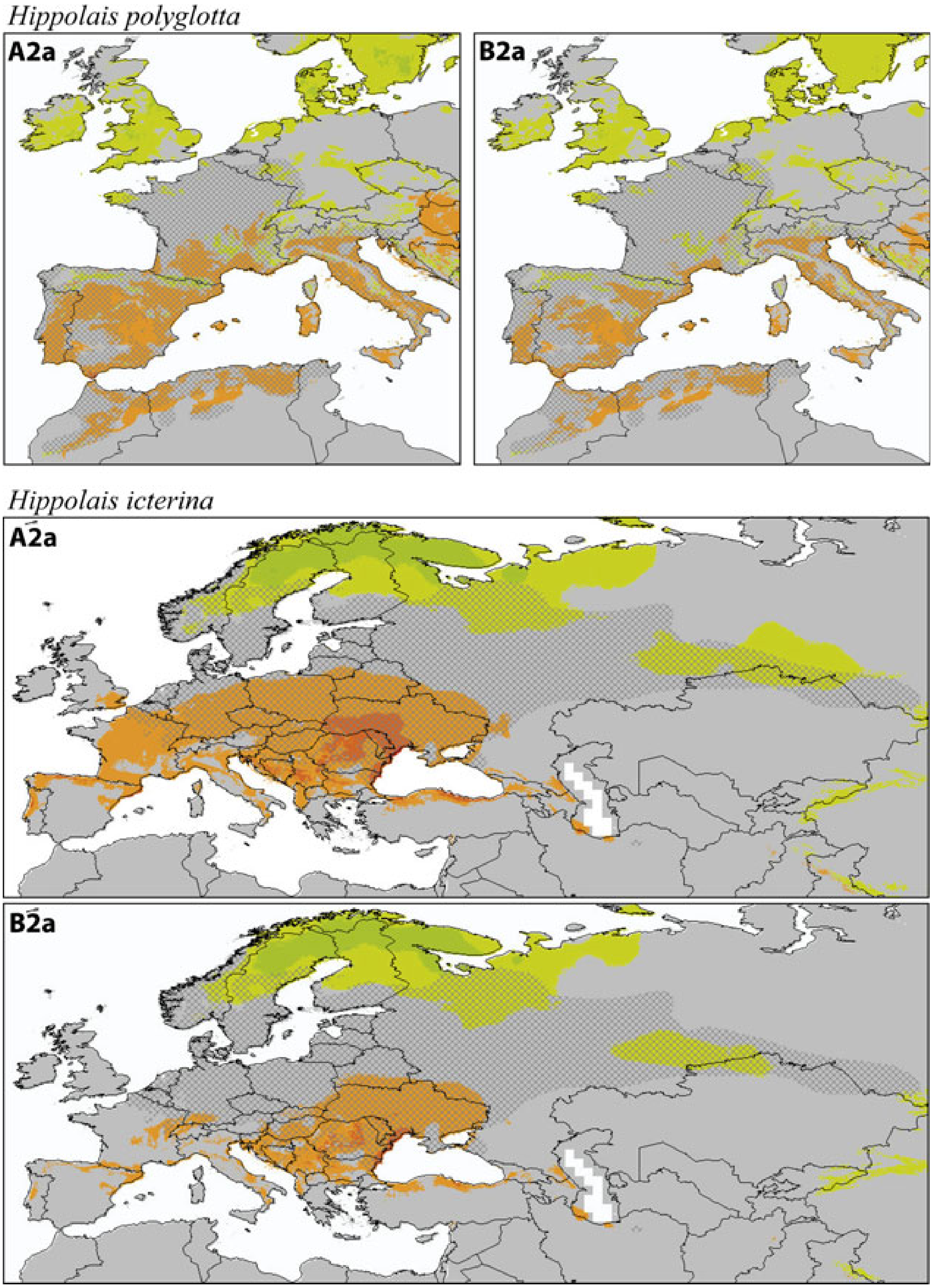

Fig. 4 Gains (green/grey) and losses (orange/dark grey) of the potential distribution of *H. polyglotta* and *H. icterina* for the 2080 A2a and B2a emission scenario family, respectively. Each colour is represented in two intensities. The lighter colouration represents 20–40%, the darker 40–60% change compared with current predictions, respectively. Marginal changes of up to 20% are shown in light grey. Current breeding distributions are shown as cross-hatched overlay.

The present study demonstrates the effect of interspecific interactions on species range dynamics using recent modelling techniques. It highlights the need to consider the relative strengths of intrinsic and extrinsic factors on the dynamics of contact zones. To this regard, integrating scenarios of climate change into the spatio-temporal dynamics of hybrid zones is a challenging but promising issue.

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References

Aliabadian, M., Roselaar, C.S., Nijman, V., Sluys, R. & Vences, M. 2005. Identifying contact zone hotspots of passerine birds in the Palaearctic region. *Biol. Lett.* **1**: 21–23.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. 2005. Validation of species-climate impact models under climate change. *Global Change Biol.* **11**: 1504–1513.

Baldwin, R.A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* **11**: 854–866.

Barbet-Massin, M., Thuiller, W. & Jiguet, F. 2010. How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography* **33**: 878–886.

Barton, N.H. & Hewitt, G.M. 1985. Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* **16**: 113–148.

Beaumont, L.J., Gallagher, R.V., Thuiller, W., Downey, P.O., Leishman, M.R. & Hughes, L. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers. Distrib.* **15**: 409–420.

BirdLife International & Natureserve 2011. Bird species distribution maps of the world. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2.

Bridle, J.R., Baird, S.J.E. & Butlin, R.K. 2001. Spatial structure and habitat variation in a grasshopper hybrid zone. *Evolution* **55**: 1832–1843.

Britch, S.C., Cain, M.L. & Howard, D.J. 2001. Spatio-temporal dynamics of the *Allonemobius fasciatus - A. socius* mosaic hybrid zone: a 14-year perspective. *Mol. Ecol.* **10**: 627–638.

Buggs, R.J.A. 2007. Empirical study of hybrid zone movement. *Heredity* **99**: 301–312.

Bull, C.M. & Burzacott, D. 2001. Temporal and spatial dynamics of parapatric boundary between two Australian reptile ticks. *Mol. Ecol.* **10**: 639–648.

Bullock, J.M., Edwards, R.J., Carey, R.D. & Rose, R.J. 2000. Geographic separation of two Ulex species at three spatial scales: does competition limit species' ranges? *Ecography* **23**: 257–271.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of global warming. *Science* **333**: 1024–1026.

Cramp, S. 1988. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic*. Oxford University Press, Oxford.

Cunningham, H.R., Rissler, L.J. & Apodaca, J.J. 2009. Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. *J. Anim. Ecol.* **78**: 52–62.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**: 783–786.

DeWalt, S.J., Denslow, J.S. & Ickes, K. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* **85**: 471–483.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G. *et al.* 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**: 609–628.

Elith, J. & Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Ann. Rev. Ecol. Evol. Syst.* **40**: 677–697.

Elith, J., Phillips, S., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**: 1–15.

Endler, J.A. 1977. *Geographic Variation, Speciation, and Clines. Monographs in Population Biology 10*. Princeton University Press, Princeton.

Faivre, B. 1993. Could predation play a role in the population decline of the Icterine warbler *Hippolais icterina*? *Rev. Ecol. Ter. et Vie* **48**: 399–420.

Faivre, B., Secondi, J., Ferry, C., Chastragnat, L. & Cezilly, F. 1999. Morphological variation and the recent evolution of wing length in the Icterine Warbler: a case of unidirectional introgression? *J. Avian Biol.* **30**: 152–158.

Fielding, A.H. & Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**: 38–49.

Gaston, K.J. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.

Godsoe, W. 2010. I can't define the niche but I know it when I see it: a formal link between statistical theory and the ecological niche. *Oikos* **119**: 53–60.

Gröning, J. & Hochkirch, A. 2008. Reproductive interference between animal species. *Q. Rev. Biol.* **83**: 257–282.

Guisan, A. & Thuiller, W. 2005. Predicting species distributions: offering more than simple habitat models. *Ecol. Lett.* **8**: 993–1009.

Hairston, N.G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* **6**: 817–826.

Heikkinen, R.K. & Luoto, M. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog. Phys. Geogr.* **6**: 751–777.

Hersteinsson, P. & MacDonald, D.W. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**: 505–515.

Hewitt, G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* **58**: 247–276.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**: 1965–1978.

Hillis, D. & Simmons, J. 1986. Dynamic change of a zone of parapatry between two species of *Pholidobolus* (Sauria: Gymnophthalmidae). *J. Herpetol.* **20**: 85–87.

Hochkirch, A. & Damerau, M. 2009. Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. *Biol. J. Linn. Soc.* **97**: 118–127.

Hochkirch, A. & Lemke, I. 2011. Asymmetric mate choice and hybrid fitness in two sympatric grasshopper species. *Behav. Ecol. Sociobiol.* **65**: 1637–1645.

Hochkirch, A., Gröning, J. & Bücker, A. 2007. Sympatry with the devil – Reproductive interference could hamper species coexistence. *J. Anim. Ecol.* **76**: 633–642.

Hutchinson, G.E. 1918. Limiting factors in relation to specific ranges of tolerance of forest trees. *Bot. Gaz.* **66**: 465–493.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* **22**: 415–427.

Hutchinson, G.E. 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven, CT.

Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Glob. Ecol. Biogeogr.* **21**: 498–507.

Jouard, H. 1935. Sur la distribution en France des deux espèces d'Hypolaïs, et sur quelques-uns des caractères propres à les faire distinguer sûrement. *Alauda* **7**: 85–99.

Kruuk, L.E.B., Baird, S.J.E., Gale, K.S. & Barton, N.H. 1999. A comparison of multilocus clines maintained by environmental adaptation or by selection against hybrids. *Genetics* **153**: 1959–1971.

Letcher, A.J., Purvis, A., Nee, S. & Harvey, P.H. 1994. Patterns of overlap in the geographic ranges of Palearctic and British mammals. *J. Anim. Ecol.* **63**: 871–879.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**: 385–393.

Lobo, J.M., Jiménez-Valverde, A. & Real, R. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* **17**: 145–151.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**: 599–619.

MacCallum, C.J., Nurnberger, B., Barton, N.H. & Szymura, J.M. 1998. Habitat preference in the *Bombina* hybrid zone in Croatia. *Evolution* **52**: 227–239.

Moore, W.S. 1977. An evaluation of narrow hybrid zones in vertebrates. *Q. Rev. Biol.* **52**: 263–277.

Moore, W.S. & Price, J.T. 1993. Nature of selection in the northern flicker hybrid zone and its implication for speciation theory. In: *Hybrid Zones and the Evolutionary Process* (R.G. Harrison, ed.), pp. 196–225. Oxford University Press, New York.

Parmesan, C. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.

Parsons, T.J., Olson, S.L. & Braun, M.J. 1993. Unidirectional spread of secondary sexual plumage traits across an avian hybrid zone. *Science* **260**: 1643–1646.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. 2008. Niche dynamics in space and time. *Trends Ecol. Evol.* **23**: 149–158.

Peterson, A., Soberón, J. & Sánchez-Cordero, V. 1999. Conservatism of ecological niches in evolutionary time. *Science* **285**: 1265–1267.

Phillips, S.J. 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). *Ecography* **31**: 272–278.

Phillips, S.J. & Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.

Phillips, S.J., Dudík, M. & Schapire, R.E. 2004. A maximum entropy approach to species distribution modeling. In: Proceedings of the 21th International Conference on Machine Learning, pp. 83. ACM Press, Banff, Canada.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. *et al.* 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**: 181–197.

Price, T. 2009. *Speciation in Birds*. Roberts and Company, USA.

Reullier, J., Pérez-Tris, J., Bensch, S. & Secondi, J. 2006. Diversity, distribution and exchange of blood parasites meeting at an avian moving contact zone. *Mol. Ecol.* **15**: 753–763.

Rising, J.D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comp. Biochem. Physiol.* **31**: 915–925.

Rödder, D. & Engler, J.O. 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Glob. Ecol. Biogeogr.* **20**: 915–927.

Rödder, D. & Lötters, S. 2010. Explanative power of variables used in species distribution modeling: an issue of general model transferability or niche shift in the invasive greenhouse frog (*Eleutherodactylus planirostris*). *Naturwiss.* **97**: 781–796.

Rödder, D., Schmidtlein, S., Veith, M. & Lötters, S. 2009. Alien invasive slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied? *PLoS ONE* **4**: e7843.

Ruedi, M., Smith, M.F. & Patton, J.L. 1997. Phylogenetic evidence of mitochondrial DNA introgression among pocket gophers in New Mexico (family Geomyidae). *Mol. Ecol.* **6**: 453–462.

Scriber, J.M. 2011. Impacts of climate warming on hybrid zone movement: geographically diffuse and biologically porous "species borders". *Insect Sci.* **18**: 121–159.

Secondi, J., Bretagnolle, B., Compagnon, C. & Faivre, B. 2003. Species-specific song convergence in a moving hybrid zone between two passerines. *Biol. J. Linn. Soc.* **80**: 507–517.

Secondi, J., Faivre, B. & Bensch, S. 2006. Spreading introgression in the wake of a moving contact zone. *Mol. Ecol.* **15**: 2463–2475.

Shaw, D.D., Marchant, A.D., Arnold, M.L., Contreras, N. & Kohlmann, B. 1990. The control of gene flow across a narrow hybrid zone: a selective role for a chromosomal rearrangement? *Can. J. Zool.* **68**: 1761–1769.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**: 1115–1123.

Soberón, J. & Nakamura, M. 2009. Niches and distributional areas: concepts, methods, and assumptions. *PNAS* **106**: 19644–19650.

Sorjonen, J. 1986. Mixed singing and interspecific territoriality-consequences of secondary contact of two ecologically and morphologically similar nightingale species in Europe. *Ornis Scand.* **17**: 53–67.

Swenson, N.G. 2006. Gis-based niche models reveal unifying climatic mechanisms that maintain the location of acian hybrid zones in a North American suture zone. *J. Evol. Biol.* **19**: 717–725.

Swenson, N.G. 2008. The past and future influence of geographic information systems on hybrid zone, phylogeographic and speciation research. *J. Evol. Biol.* **21**: 421–434.

Swenson, N.G. & Howard, D.J. 2004. Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. *Am. Nat.* **166**: 581–591.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* **240**: 1285–1293.

Walls, S.C. 2009. The role of climate in the dynamics of a hybrid zone in Appalachian salamanders. *Global Change Biol.* **15**: 1903–1910.

Warren, D.L., Glor, R.E. & Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**: 2868–2883.

Warren, D.L., Glor, R.E. & Turelli, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33**: 607–611.

Yeatman, L. 1976. *Atlas des oiseaux nicheurs de France*. SOF, Paris.

Yeatman-Berthelot, D. & Jarry, G. 1994. *Nouvel atlas des oiseaux nicheurs de France*. SOF, Paris.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of sources for occurrence locations in *Hippolais polyglotta* and *H. icterina* respectively.

Figure S1 Distribution of the raw samples depending on Table S1 for *H. polyglotta* (black) and *H. icterina* (white) respectively (upper panel) as well as sampling distribution after filtering (see methods for details).

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