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Range expansion and retraction along a moving contact zone has no effect on the genetic diversity of two passerine birds

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Disentangling the factors shaping species distributions remains a central goal in biogeography, ecology and evolutionary biology. The extrinsic pressures that may facilitate range shifts, such as climatic factors or biotic interactions are well known. However, in contrast, the possible intrinsic factors are manifold and hard to generalize across taxa. Recently, several theoretical studies have investigated the consequences of moving range borders on genetic diversity. However, empirical studies that support or refute these theoretical predictions are scarce. Moving contact zones between parapatric sister species are suitable models to test these hypotheses. Changes in genetic diversity can be tested simultaneously along the expanding and receding edges of two species of the contact zone while accounting for intra-specific effects (e.g. introgression). The two Old World warblers *Hippolais polyglotta* and *H. icterina* form a narrow moving contact zone, where interspecific interactions are suspected to be the main factor shaping this zone. We investigated the population genetic structure of both species along a transect ranging from the core range of the expanding *H. polyglotta* across the contact zone and far into the range of the receding *H. icterina*. The theoretical predictions of changes in genetic diversity at the range edges were tested. No gradual change in genetic diversity was detected for both the expanding and the receding range margin. Furthermore, no genetic structure was found in either species supporting the hypothesis that long distance dispersal (LDD) occurs frequently due to the high mobility of these long-distance migrants. The results suggest that when dispersal propensity is high and accompanied by frequent LDD events, then neither an enrichment nor a depletion of alleles along moving range edges would be detected. This these species as the probability to retain genetic diversity during exogenous induced range shifts is high in such mobile species.

Fluctuations in climatic conditions are known to induce shifts in the location and shape of species ranges (reviewed by Gaston 2003). Historically, these shifts occurred in concert to glacial-interglacial cycles. However, current anthropogenic climate change may affect ranges more rapidly than ever before in the past (Thomas and Lennon 1999, Parmesan and Yohe 2003). In combination with other factors, such as habitat fragmentation or pollution, current climate change occurs at a pace that species and communities are often unable to follow (Loarie et al. 2009, Devictor et al. 2012), resulting in species extinction and a loss of global biodiversity (Thomas et al. 2004, Bellard et al. 2012). The ecological and evolutionary consequences of range shifts for populations along expanding and receding range edges might be manifold, ranging from changes in niche preferences and selection on phenotypes to erosion of genetic diversity (Thomas et al. 2001, Hampe and Petit 2005). In the current context of global change, understanding and predicting the consequences of range shifts on the genetic diversity and structure of species is crucial. In this regard, the analysis of the genetic changes at the margins of shifting ranges may help give insight into the ongoing processes leading to range shifts.

Recently, a series of theoretical studies have simulated the effects on genetic diversity at expanding (Fayard et al. 2009, Ray and Excoffier 2010, Travis et al. 2010, Münkemüller et al. 2011) and receding (Leblois et al. 2006, Arenas et al. 2012) range edges. At expanding range edges the propensity of individuals to disperse may have contrasting effects on the genetic structure. Under a short distance dispersal scenario, neutral mutations forming at the range edge can either stay near their place of origin or 'surf' along with the expansion front, resulting in genetic differentiation. This hypothesized concept of 'allele surfing' (Edmonds et al. 2004, Klopfstein et al. 2006, Travis et al. 2010, Münkemüller et al. 2011) was confirmed by lab experiments on prokaryotes (Hallatschek et al. 2007) as well as by empirical genetic studies (Gassert et al. 2013). While short distance dispersal and allele surfing can lead to a depletion of genetic diversity at the expansion front, long-distance-dispersal (LDD) might lead to

the opposite phenomenon, i.e. maintaining or even increasing genetic diversity towards the expansive range edge and an elimination of any allele surfing effect (Fayard et al. 2009, Ray and Excoffier 2010). In contrast to the comparatively high number of studies investigating the genetic effects on expanding range edges, only a few analyzed the consequence on receding edges (Hampe and Petit 2005, Leblois et al. 2006, Arenas et al. 2012). Those revealed a loss of genetic diversity (Leblois et al. 2006, Arenas et al. 2012) although the degree of preserved genetic diversity depends strongly on the speed of range contraction (Arenas et al. 2012).

In addition to the intra-specific effects as described above, inter-specific effects may occur in species forming a moving hybrid zone (Buggs 2007, Excoffier et al. 2009). Asymmetrical introgression from the receding species into the range of the expanding species may occur as a result of the zone movement (Dasmahapatra et al. 2002, Buggs 2007). Introgression might eventually increase genetic diversity in populations of the expanding species within or bordering the contact zone (Excoffier et al. 2009). For these reasons, moving contact zones of parapatric species pairs represent interesting study systems for investigating the inter- and intra-specific genetic consequences of moving range margins. Opposite range dynamics (expansion vs contraction) and genetic interactions between species allow to test simultaneously hypotheses on changes in genetic diversity at both the expanding and receding margins.

The two Old World warblers *Hippolais polyglott*a (HP) and *H. icterina* (HI) are small migrating passerines (Passeriformes: Acrocephalidae), and sister species breeding in the Western Palearctic and overwintering south of the Sahara (Cramp 1988). They occur parapatrically in their breeding ranges and form a narrow contact zone crossing western central Europe, where HP occurs southwest of this zone and HI northeast of it (Fig. 1). Both species are morphologically similar, but clearly differentiated for wing characteristics (Faivre et al. 1999), vocalization (Secondi et al. 2003), migration behavior (Cramp 1988) and genetics (Helbig and Seibold 1999, Fregin et al. 2009). Both species came in secondary contact after postglacial range expansion from separated glacial refugia (Voous 1960, Glutz von Blotzheim 1991) as for many Western Palearctic taxa (Taberlet et al. 1998, Aliabadian et al. 2005).

For at least 70 yr HP has expanded its north-eastern range edge while the western edge of HI has been contracting, resulting in a north-eastward shift of the contact zone. Several authors attributed this observation to climate change (Bauer and Berthold 1996, Bijlsma et al. 2001). However, recent findings supported the hypothesis that location and movement of the contact zone are also strongly affected by the interactions between the two species rather than by climate alone (Engler et al. 2013). Long-term studies in the eastern part of the contact zone revealed that mixed pairing regularly occurred and became more frequent during the population decline of HI, the receding species (Faivre et al. 1999). Furthermore, morphological changes and bilateral song convergence suggested ongoing asymmetric introgression in that area (Faivre et al. 1999, Secondi et al. 2003), which was confirmed genetically using amplified fragment length polymorphisms (AFLP markers; Secondi et al. 2006, 2011). In contrast to dominant AFLP markers, co-dominant genetic markers such as microsatellites are generally assumed to be more informative and allow measurement of genetic differentiation or demographic histories (Freeland 2005). Furthermore, such marker systems may give a more accurate estimate of genetic diversity as they focus on neutral genetic variation, whereas AFLP markers also cover coding regions that might be under selection. For these reasons, microsatellites will complement previous studies performed using AFLP markers and will complete the picture of genetic effects along the moving contact zone in these two *Hippolais* warblers.

As both species are highly mobile long-distance migrants, we expect 1) intraspecific genetic differentiation between populations to be low, due to high admixture as a consequence of frequent LDD. Natal dispersal is hereby a key component in birds, which is assumed to be generally larger in migratory than in resident species, and lower in later life stages (i.e. breeding dispersal; see Paradis et al. 1998 and references therein). Given the observed levels of asymmetrical introgression in AFLP markers (Secondi et al. 2006), we expect 2) that neutral genetic diversity increases towards the expanding range edge in *H. polyglotta* accompanied by a heterozygote excess. For the receding edge of *H. icterina*, 3) we expect a depletion of genetic diversity together with genetic bottlenecks due to the ongoing decrease in population size (Arenas et al. 2012). To test these hypotheses, populations of both species were sampled and genotyped using microsatellites along a transect ranging from the core of HP to the contact zone with HI and further far into the range of HI.

Material and methods

Sampling and DNA extraction

In total, 310 individuals from 13 sampling sites were analyzed (192 *H. polyglotta* individuals from nine sites and 118 *H. icterina* individuals from five sites, Supplementary material Appendix 1, Table A1, Fig. 1). These samples were collected between 2001 and 2003 and originated from a previous study (Secondi et al. 2006). They were here genotyped using microsatellites. HP samples were taken along a transect from localities in the core range in the Spain and France to edge populations at the contact zone with HI in Belgium, France, and Germany. Sample locations for HI ranged from the contact zone to the Baltic Sea (ca 1000 km NE away from the contact zone). Blood was taken from the brachial vein of each individual (10–50 µl) and added to 500 µl of buffer (0.15 mM NaCl, 0.05 mM Tris, 0.001 mM EDTA, pH 8.0) in a screw-topped rubber-sealed microfuge tube. Samples were kept refrigerated (4°C) during field work and then transferred to the laboratory where they were stored frozen at –20°C. Genomic DNA was extracted using a phenol-chloroform procedure (Sambrook et al. 1987).

Genotyping

Fourteen microsatellite loci that amplify in both species (Engler et al. 2014) were used to genotype the individuals in this study (Supplementary material Appendix 1, Table A2).

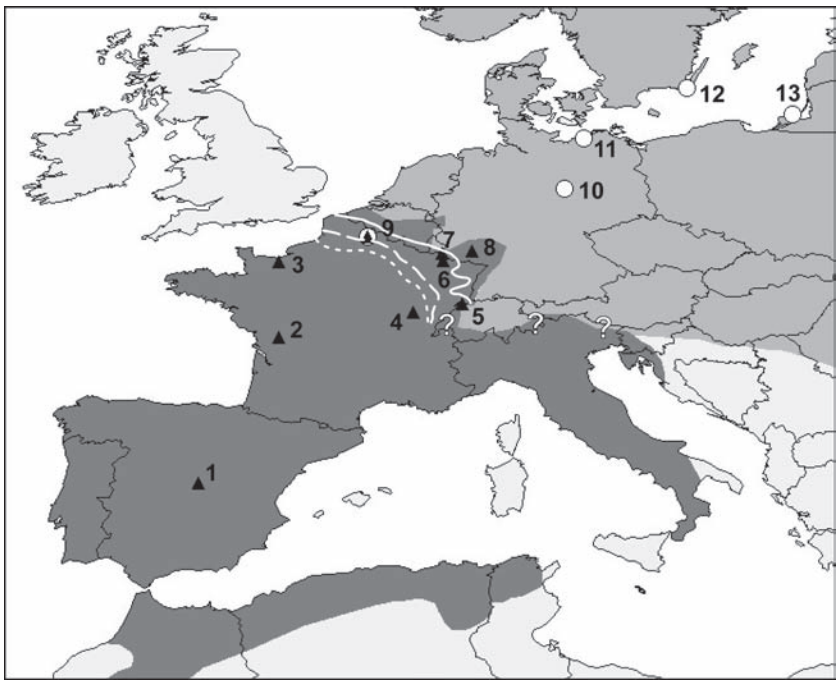

Figure 1. Current distributions as redrawn from Parkin et al. (2004) and location of study sites sampled for population genetic analyses in *Hippolais polyglotta* (dark grey shaded area and black triangles) and *Hippolais icterina* (light grey shaded area and white circles). Numbers correspond to those given in Supplementary material Appendix 1, Table A1. White lines indicate the previous northeastern range limits of *H. polyglotta* (fine dashed = 1935, Jouard (1935); coarse dashed = 1970–1975, Yeatman (1976); solid = 1984–1989, Yeatman-Berthelot and Jarry (1994); question mark = edge movement unknown).

Markers were combined into four multiplex sets according to their annealing temperature (T_a), allele size and dye label (Supplementary material Appendix 1, Table A2). PCR was performed using the Qiagen Multiplex PCR Kit. The PCR conditions followed the manufacturers' protocol with an initial hot start step of 95°C for 15 min, followed by 37 cycles of 30 s at 94°C, 90 s at 54–65°C depending on the primer set used (Supplementary material Appendix 1, Table A2) and 60 s at 72°C, with a final extension of 30 min at 60°C (for further details see Engler et al. 2014). Genotyping was conducted using a MegaBACE 1000 automated DNA sequencer (GE Healthcare). Amplicon lengths were scored using Fragment Profiler ver. 1.2 (Amersham Biosciences).

The program Microchecker ver. 2.2.3 (van Oosterhout et al. 2004) was used to check all loci for possible genotyping errors including identifying large allele dropout and stutter bands and estimating null allele frequencies. Fstat ver. 2.9.3.2 (Goudet 2001) was used to check for linkage disequilibria among loci. No groups of loci displayed linkage disequilibrium in any of the populations belonging to either species (assessed at the 1% nominal level). Furthermore, no large allele dropout was detected at any loci in any population. However, the presence of null alleles was suggested at five loci (DkiB119, Ase9, Ase56, TG04-004, and TG06-009) due to a significant excess of homozygotes across several populations (Supplementary material Appendix 1, Table A2). The presence of null alleles was apparent in both species for four of the five loci (DkiB119, Ase56, TG04-004 and TG06-009). Furthermore, stuttering may have affected the accuracy of allele scoring for two of these loci: TG04-004 and TG06-009. Therefore, these four loci were excluded from subsequent analyses. Two other markers had high null allele estimates in single populations (Ase46 in Chizé – HP; Ase19 in Rybachy – HI). However, because there was no suggestion that any of the other populations were affected by a high null allele frequency, it was decided to retain these two markers for further analyses. Not all loci were polymorphic in both species (Supplementary material Appendix 1, Table A2, Engler et al. 2014) and because there were species-specific genotyping errors associated with some markers (as suggested by Microchecker), we selected a final set of nine loci for HP and eight loci were used for HI, seven loci were shared between both sets (Supplementary material Appendix 1, Table A2).

Analysis of within-species effects

Allelic richness (AR) and inbreeding coefficients (F_{IS}) were calculated in Fstat. We calculated the AR of individuals for each site based on the site with the lowest number of individuals sampled (i.e. 12 in HP and 17 in HI) using a rarefaction method as implemented in Fstat. Unbiased expected (H_e) and observed (H_o) heterozygosities were calculated using GenAlEx ver. 6.4 (Peakall and Smouse 2006). Analysis of genetic differentiation between populations was conducted for either species using AMOVAs as well as pairwise F_{ST} and R_{ST} as implemented in GenAlEx by using a permutation approach with 999 iterations to test for statistical significance. AMOVAs were performed twice, based on either an infinite allele model (Kimura and Crow 1964) or a stepwise mutation model (Ohta and Kimura 1973). Furthermore,

two different Bayesian clustering analyses were used to infer spatial genetic structure separately for each species. Structure ver. 2.3.3 (Pritchard et al. 2000, Falush et al. 2003) was used as it represents the most widely used approach for such analyses. The most likely number of groups, *K,* was estimated on ten independent chains ranging from $K = 1$ to the maximum number of locations samples (5 in HI and 9 in HP) each with 1 000 000 iterations and a burn-in period of 500 000 iterations. The model assumed correlated allele frequencies and admixture. The initial value for alpha, the Dirichlet parameter for degree of admixture, was remained at the default value of 1.0. To infer *K* using the method by Pritchard et al. (2000) and Evanno et al. (2005), the program Structure Harvester (Earl and von Holdt 2011) was used.

In addition to Structure, we used Geneland ver. 4.0 (Guillot et al. 2008, 2012, Guillot and Santos 2009), a clustering model that incorporates spatial information of the sampled individuals (sample locations). Geneland clusters individuals of different populations and maximizes Hardy–Weinberg-Equilibrium and Linkage-Equilibrium for each cluster. The main advantage over alternative spatial clustering algorithms as implemented in Geneclust (Ancelet and Guillot 2006, François et al. 2006), Tess (Chen et al. 2007) or Baps (Corander et al. 2006) is that Geneland is based on a free Voronoi tessellation (for a discussion see Guillot et al. 2009) making the underlying spatial domain used for analysis independent from the sampling sites. A recent comparison shows that Geneland frequently outperforms other spatial clustering models (Safner et al. 2011). However, as typical for clustering algorithms, the 'true' number of panmictic clusters (*K*) is often overestimated (reviewed by Guillot et al. 2009, but see Kalinowski 2011), especially when isolation-by-distance (IBD) becomes a prominent aspect in the dataset (Frantz et al. 2009). Due to a lack of available methods accounting for this issue, results have to be checked for IBD patterns and each cluster therein has to be carefully checked for its biological relevance (Guillot et al. 2009). IBD for each species was estimated by Mantel tests performed with the 'ecodist' package (Goslee and Urban 2007) in R ver. 2.14.1 (R Development Core Team) between the linearized pairwise F_{ST} (Fst/(1 – Fst)) (sensu Rousset 1997) and the geographic distance between the study sites. In order to infer *K,* ten independent chains each with 1 000 000 iterations were calculated. *K* was allowed to vary between one and the maximum number of sampled populations of either species (five in HI, nine in HP). Every 100th iteration was sampled and the first 10% were discarded as burn-in. From the ten chains, the run with the maximum average log posterior probability after burn-in was used for results presentation.

To test for recent bottlenecks (heterozygote excess) along the receding range of HI as well as for expansion (heterozygote deficit) in the expansive populations of HP, we used the program Bottleneck ver. 1.2.02 (Piry et al. 1999). The basic assumption of the program is that recent changes in populations lead to faster changes in allele numbers than in the level of heterozygosities. For declining populations along a receding range edge this would mean an excess of heterozygotes (bottleneck), while a heterozygote deficit can be assumed for newly founded populations along an expansive range edge. Bottleneck estimates the distribution of the expected heterozygosity under mutation-drift equilibrium for each locus and population. These expected values were compared against the observed heterozygosity calculated from observed allele frequencies using Wilcoxon's signed rank tests (Cornuet and Luikart 1996, Piry et al. 1999) where significance was corrected for repeated testing of multiple sites (here the five sites in HP considered as sympatric or close allopatric, Fig. 2) using the Bonferroni correction. Since the mutation model underlying microsatellites is often unknown, we used the stepwise-mutation model (SMM) as well as the two-phase model (TPM) for the analysis. For the TPM, we used combinations of 95% single-step mutations and 5% multi-step mutations with a variance of 30 among multi-step mutations and 1000 replications (Piry et al. 1999, Husemann et al. 2015).

Analysis of between-species effects

To measure possible effects of allele transfer along the contact zone via hybridisation and asymmetrical introgression as shown in Secondi et al. (2006), we calculated a principal coordinate analysis (PCoA) based on an individual genetic distance matrix in GenAlEx subsequently followed by linear discriminant analysis (LDA). The individual genetic distance matrix was calculated following the methods from Peakall et al. (1995) and Smouse and Peakall (1999) in GenAlEx as well. In addition to the marker sets used before, we included two loci that were monomorphic in HI (TG11-011 and Ase46). Both loci consist of species-specific alleles which make them highly suitable for detecting hybrid individuals in this analysis (Engler et al. 2014). We performed the LDA in SPSS 14 for assessing the separation between species and between allopatric and sympatric (together with recent allopatric) sites as defined in Secondi et al. (2006) based on all PCoA axis scores. This was done under the assumption that, next to species-level differences, potential hybridisation will lead to an admixture of genotypes in areas that were currently (sympatry) or recently (close allopatry) part or the contact zone (see Secondi et al. 2006 for details). To test for clinal spatial genetic structuring, we used linear regression with the two main PCoA axes as explanatory variables, and the geographic distance to the contact zone location (see Fig. 2 for distance values) as predictor. Analyses were conducted in R 2.14.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c4k68> (Engler et al. 2015b).

Results

Genetic diversity did not vary significantly among most of the populations within both species when considering allelic richness (Supplementary material Appendix 1, Table A1, Fig. 2). Differences between unbiased expected (H_e) and observed heterozygosities (H_o) were non-significant among populations for each species (Supplementary material Appendix 1, Table A1, Fig. 2) and F_{IS} values were generally close to zero (Supplementary material Appendix 1, Table A1). Accordingly, there was also no spatial cline in genetic diversity parameters along transects from the contact zone to the range core (Fig. 2). Comparisons of

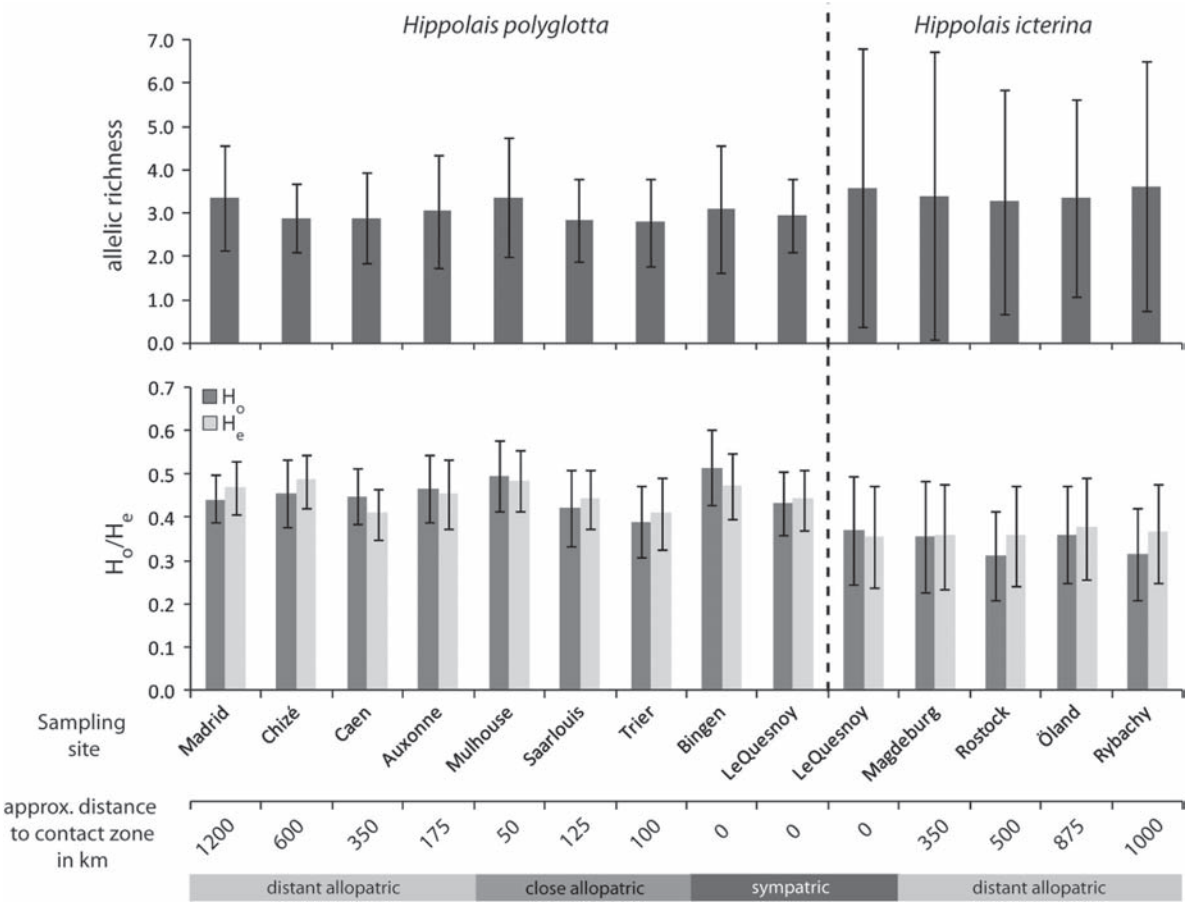

Figure 2. Average allelic richness (upper panel) and observed vs unbiased expected heterozygosities (lower panel) for each sampling site of *Hippolais polyglotta* (left) and *H. icterina* (right). Error bars represent standard errors. The minimum distance (in kilometers) from each sampling site to the moving range edge (contact zone) is shown on the bottom axis.

PCoA scores of the two main axes with the distance from the respective site to the contact zone were non-significant (linear regression – $PCo1_{HP}$: $F_{1,190} = 0.215$, $r^2 = 0.001$, $p = 0.643$; $PCo2_{HP}$: $F_{1,190} = 0.053$, $r^2 < 0.001$, $p = 0.819$; $PCo1_{HI}$: $F_{1,190} = 0.099$, $r^2 < 0.001$, $p = 0.754$; $PCo2_{HI}$: $F_{1,190} = 1.022$, $r^2 = 0.009$, $p = 0.314$).

There was no sign of heterozygote excess (bottleneck) at the receding range edge population of HI under both mutation models (LeQuesnoy p_{SMM} and $p_{TPM} = 0.988$). In four of the five populations of HP what were either sympatric or close allopatric (i.e. founded during the range expansion in recent times, cf. Secondi et al. 2006, Fig. 2) no heterozygote deficit could be detected irrespective of the mutation model used (all $p > 0.01$ after Bonferroni correction). A significant heterozygote deficit was only found in Mulhouse (close allopatric, $p_{SMM} = 0.01$; $p_{TPM} = 0.007$).

The posterior density and log-likelihood levels of the ten replicate chains derived from Geneland stabilized long before the end of the Markov Chains, indicating that convergence was reached. For each species, K converged in all ten chains to one (support of 60.74% and 59.47% for $K = 1$ in HP and HI respectively). The same result was revealed by the Structure analysis, where $K = 1$ showed the largest likelihood among all possible solutions (Supplementary material Appendix 1, results not shown). Pairwise genetic distances (F_{ST} and R_{ST} respectively) within each species were rather low (Table 1 and 2). Species-specific AMOVAs revealed no significant amount of variance explained among populations for both the infinite allele model (0.44% in HP, $F_{ST} = 0.004$, $p = 0.094$; 0% in HI, $F_{ST} = -0.001$, $p = 0.537$) as well as for the stepwise mutation model (0.45% in HP, $R_{ST} = 0.004$, $p = 0.207$; 0% in HI, $R_{ST} = -0.007$, $p = 0.922$). There was a tendency of IBD in HP (Mantel $r = 0.33$; $p = 0.057$; 95% CI = 0.06 to 0.58) but not in HI (Mantel $r = -0.31$; $p = 0.751$; 95%; CI = –0.71 to –0.29).

The discriminant analysis based on principal coordinates revealed a 100% distinction between the species and a high admixture between core and edge locations within each species (Fig. 3). Here, the first principal coordinate axis explained 63.13% of the total genetic variance (separating the two species) whereas the second explained additionally 10.64%. Consequently, there was no case of hybridization detected in the sample using this set of markers. This was confirmed with a Structure analysis as well, pooling the samples of both species and setting $K = 2$ (Supplementary material Appendix 1, data not shown)

Table 1. Pairwise F_{ST} (below diagonal) and R_{ST} values (above diagonal) among sample sites for *Hippolais polyglotta*. *indicates significance at $p < 0.05$.

	Madrid	Chizé	Caen	Auxonne	Mulhouse	Saarlouis	Trier	Bingen	Le Quesnoy
Madrid		0.007	0.079*	0.000	0.000	0.000	0.000	0.000	0.007
Chizé	0.003		0.062*	0.000	0.000	0.000	0.022	0.000	0.021
Caen	0.010	0.011		0.000	0.116*	0.097*	0.097*	0.034	0.191*
Auxonne	0.016*	0.001	0.009		0.000	0.000	0.000	0.000	0.017
Mulhouse	0.000	0.000	0.000	0.000		0.000	0.044	0.000	0.001
Saarlouis	0.026*	0.014	0.007	0.007	0.000		0.035	0.000	0.005
Trier	0.007	0.004	0.011	0.000	0.000	0.003		0.000	0.086*
Bingen	0.000	0.000	0.012	0.000	0.000	0.020*	0.001		0.018
Le Quesnoy	0.017*	0.006	0.011	0.000	0.000	0.000	0.000	0.012	

Discussion

Theoretical studies investigating changes in genetic patterns along shifting range edges assume strong clines of genetic diversity from the range center and link these changes to different degrees of mobility in dispersing individuals along the range edges. Here, we give empirical evidence of a lack of genetic changes in a mobile passerine sister species complex sharing a moving contact zone. In accordance to our first hypothesis, genetic differentiation was low in both species. However, in contrast to hypotheses two and three, we observed neither an increase of genetic diversity along the expanding range edge in *Hippolais polyglotta*, nor a depletion of genetic diversity along the receding range edge of its sister species *H. icterina*. In the following, we compare our results to the published theoretical literature and discuss the role of high mobility in migrating birds and link this outcome to range shifts under environmental change. Furthermore, we compare the contrasting conclusions based on the data based on microsatellite genotyping and AFLP markers and give recommendations for future studies.

Is high admixture the norm in migrating passerines?

Theory predicts a strong dependency of the expansion rate of a species on dispersal distance (Fisher 1937, Skellam 1951). As dispersal directly affects gene flow at large spatial scales (Wright 1969, Saccheri et al. 1998), the proportion of dispersing individuals is an inherent factor influencing the level of genetic differentiation between populations of the range periphery and populations of the core of the range (Vucetich and Waite 2003) that also affects genetic diversity (Ray and Excoffier 2010). The low genetic population differentiation and very weak spatial genetic structures in the two *Hippolais* warblers (Table 1 and 2) suggest extensive gene flow caused by a high dispersal propensity and long dispersal distances (i.e. frequent LDD; Paradis et al. 1998). This has been documented in other migratory passerines before (Lovette et al. 1998, Procházka et al. 2011). These genetic patterns underpin the role of dispersal on the spatial genetic structure of highly mobile species emigrating from different source populations (Exeler et al. 2008, Swaegers et al. 2013) to the range edge. Because of their higher dispersal capability (Weatherhead and Forbes 1994, Paradis et al. 1998), migratory birds are expected to show markedly higher levels of gene flow as compared to sedentary bird species, resulting in a generally lower genetic differentiation (Rockwell and Barrowclough 1987, Gill et al. 1993, Lovette et al. 1998, Arguedas and Parker 2000). Therefore, a high admixture can be considered as the norm rather than the exception in migrating passerines. In this regard, populations of HP at the expanding range edge were often isolated from each other by tens of kilometers, and single pairs or singing males have been found up to ca 150 km apart from the next larger population (Engler and Twietmeyer unpubl.). Such a scattered population structure during range expansion can only persist if the average dispersal distance is very large as recently founded range edge populations are unlikely to become source populations in a short period of time. This high admixture will also explain the spatial genetic patterns for the last remnants of HI along the receding range edge, where no bottleneck could be observed.

Table 2. Pairwise F_{ST} (below diagonal) and R_{ST} values (above diagonal) among sample sites for *Hippolais icterina*. No value was significant at $p < 0.05$.

	Le Quesnoy	Magdeburg	Rostock	Öland	Rybachy
Le Quesnoy		0.004	0.007	0.000	0.000
Magdeburg	0.000		0.062	0.000	0.001
Rostock	0.015	0.003		0.000	0.011
Öland	0.003	0.000	0.008		0.000
Rybachy	0.000	0.000	0.001	0.000	

Discordance of the introgression pattern between different marker systems

One surprising result of our study was the lack of any signs of introgression in microsatellite data although such a signal was distinct in the AFLP analysis carried out on the same DNA samples (Secondi et al. 2006). Even if methodological issues could cause genotyping errors in either method, we are confident of the validity in the results of both studies. In the AFLP analysis, introgressed individuals were all located close to the contact zone (Secondi et al. 2006). Errors due to false scoring or homologies should appear randomly throughout the sampled range but should not cluster spatially along the range edge. In microsatellites, on the other hand, we have used loci with private alleles in either species (Engler et al. 2014) and were able to detect hybrid offspring in a nest with an HI mother and a HP father (unpublished dataa). So, if we can rule out methodological issues, what kind of biological explanation could exist? First, many comparative studies have found contrasting results when using AFLPs and

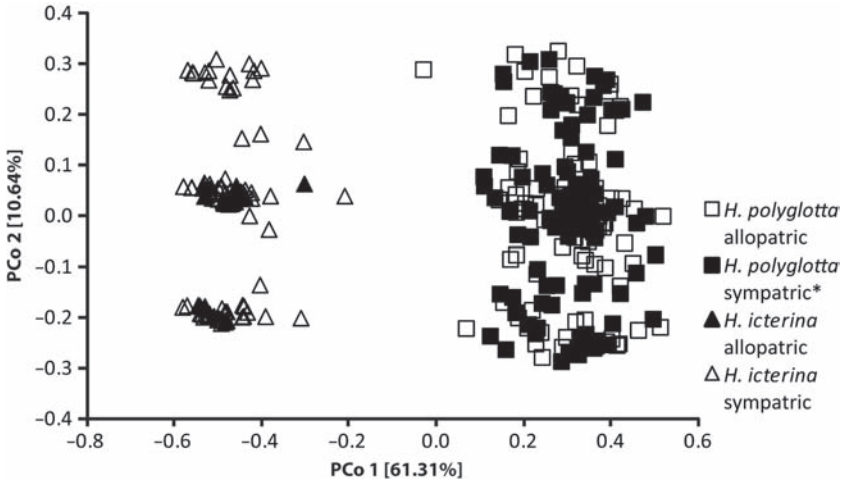

Figure 3. Principal coordinate analysis of the genetic structure between *Hippolais polyglotta* (squares) and *H. icterina* (triangles), separated for allopatric (white) and sympatric populations (black) respectively. Axis labels represent the first two coordinate axes with their respective explained variance. * in *H. polyglotta* the populations that have become classified as close allopatric (following the definition in Secondi et al. 2006) were merged to the sympatric group.

microsatellites. Sometimes microsatellites showed a higher differentiation (Maguire et al. 2002, Alacs et al. 2010), but often they did not (Mariette et al. 2002, Mock et al. 2002, Gaudeul et al. 2004, Nybom 2004). In this respect, Alacs et al. (2010) mentioned differences in evolutionary histories between the marker systems as one possible reason. Not only the faster rate of evolution in microsatellites (Brinkmann et al. 1998) could play a role here but also the adaptive nature of AFLP markers as compared to neutral microsatellites is an important aspect. It has been shown that a high percentage of AFLP markers are located within gene sequences in different eukaryotic species (Caballero et al. 2013).

For our results that could mean two things. First, the lack of hybrids detected by microsatellites highlights hybrids or rare events in general (see also Secondi et al. 2006a). Second, over a longer evolutionary timescale, hybridization may have favored the introgression of genes from HI to HP beneficial for populations expanding northwards and their manifestation in the sympatric and close allopatric range. If the AFLP included a single locus with a HI allele that may be adaptive in the expanding area of HP, it might be positively selected ('adaptive introgression') and promote the detection of hybrids. Even if the signature of neutral introgression is expected to disappear rapidly, e.g. due to density dependent priority effects (Waters et al. 2013), alien genes could persist in the gene-pool as long as they are beneficial (Kraus et al. 2012). As AFLP markers could involve all types of genes within its fragment (Caballero et al. 2013) they are likely to detect signals which have disappeared in microsatellites.

No changes in genetic diversity at moving range edges

As a consequence of restricted dispersal, depleted genetic diversity seems to be a rather common pattern at the edges of expanding ranges (Hewitt 1993, 2000). It has been reported for a wide range of taxa, such as plants (Schnabel and Hamrick 1990), insects (Cooper et al. 1995, Leotard et al. 2009, but see Hochkirch and Damerau 2009) and vertebrates (Santucci et al. 1998, Howes and Lougheed 2008, Garroway et al. 2011, Gassert et al. 2013). In contrast, an increase in genetic diversity, as predicted by theory when taking LDD events into account (Ray and Excoffier 2010), has received limited empirical support so far. For example, Hochkirch and Damerau (2009) detected an increase of allelic richness in expansive populations of the bush-cricket *Metrioptera roeselii*. These newly founded populations are dominated by highly mobile long-winged forms performing frequent LDD from a much larger source area as compared to populations in the centre of the species range, where flightless forms prevail. This observation fully matches the predictions by Ray and Excoffier (2010), who found that an increase of genetic diversity is highest when LDD events occurred directly at the expansion front during colonization of previously empty patches. This extreme bimodal distribution of dispersal distance, probably strongly influenced by wing dimorphism, may be common in some insect taxa, but cannot be transferred to monomorphic species. In many species, the distribution of dispersal distance is unimodal and slightly skewed towards long distances (Kot et al. 1996) which favours allele surfing and the depletion of genetic diversity at the range edge (Travis et al. 2010). However, in species where dispersal propensity is high, a high frequency of LDD events probably counteracts genetic drift at the expanding, or receding, range margins (cf. Vucetich and Waite 2003, Arenas et al. 2012) and result in a uniform range wide genetic diversity.

This has strong implications for specific responses to climate change and habitat fragmentation (Hof et al. 2011). Under a scenario of rapid climate change, species with a high dispersal propensity and capable of long distance dispersal may experience range shifts without much alteration of their genetic diversity even in a highly fragmented landscape. Extinction risk is thus strongly reduced compared to species that lose genetic diversity due to multiple founder events at the expanding edge, or experience strong drift at the receding edge of their distribution. However, according to Arenas et al. (2012), the speed of the range shift may not

indicate the capacity of a species to retain genetic diversity. Rapid range expansions would mainly be driven by individuals originating from the range edge if dispersal propensity is low, and from individuals originating from a much wider area if dispersal propensity is high. In the latter case, dispersal events are likely to generate exchanges of propagules and contribute to further homogenize the genetic structure of edge populations. This probably occurred for both *Hippolais* warblers. Range edges shifted during the past ca 70 yr up to 300–450 km in both species. The short generation time of one year and an average life span of 3–5 yr (Faivre et al. 2002) might promote the fast mixing of the gene pool in such highly mobile species.

As recently shown for several bird communities, many species fail to track the speed of changing climatic conditions in Europe (Devictor et al. 2012). This may in part be a consequence of biotic interactions that thwart species in their ability to shift their ranges in response to the changing environmental conditions. In this regard, species distribution models suggested that interspecific interactions with HI may slow the expansion of HP down (Engler et al. 2013). However, from a genetic perspective, species with high dispersal propensity such as HP and HI are likely to retain their genetic diversity and maintain the potential for adaptation to novel environmental conditions in a fast changing world.

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Supplementary material (Appendix ECOG-01520 at <www.ecography.org/readers/appendix>). Appendix 1.

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