

ORIGINAL
ARTICLENiche availability in space and time:
migration in *Sylvia* warblersIrina Laube^{1,3,*}, Catherine H. Graham² and Katrin Böhning-Gaese^{1,3}

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ABSTRACT

Aim The ecological niche of a species is dynamic at a variety of spatial and temporal scales; embracing this complexity is required for accurate assessment of species' niche requirements and to forecast how species will respond to novel and dynamic climates. In the context of recent advances in species distribution modelling, however, both the environment and the ecological niche of a species have often been treated and quantified as static entities. Here, our aim was to explore how species' realized niches and geographical ranges are dynamically shaped by the decoupled spatio-temporal availability of different environmental conditions, using the migration of *Sylvia* warblers as an example.

Location Palaearctic, Afrotropical and Indo-Malay ecozones.

Methods We used a species distribution modelling approach to evaluate the niche characteristics of *Sylvia* warblers under their actual migration strategies as well as null models assuming resident behaviour. We focused on climate and land cover as niche dimensions, taking into account the spatial availability of environmental conditions during the peak breeding and non-breeding season for each *Sylvia* species.

Results Migration did not increase the overlap between breeding and non-breeding niches compared with breeding and non-breeding niche overlap in resident null models. *Sylvia* warblers did not compensate for the costs of a longer migratory journey by tracking their climatic niche or land-cover niche more closely. Instead, *Sylvia* warblers migrated further than the closest available area with suitable climate and land cover.

Main conclusions Climatic niche tracking is unlikely to be the main driver of migration in *Sylvia* warblers. We suggest that taking dynamic environments into account and comparing actual niche characteristics to those resulting from alternative possible range dynamics enhances our understanding of the drivers behind organisms' movements and distributions.

Keywords

Birds, geographical range, migration, niche breadth, niche tracking, species distribution modelling, *Sylvia*, warblers.

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INTRODUCTION

If we are to make progress in understanding the factors that drive species' range dynamics we must grapple with what has been termed Hutchinson's duality, that is, we have to examine the environmental conditions of ecological niches as well as the distribution of these conditions in geographical space (Colwell & Rangel, 2009). The environmental conditions

available to organisms are highly dynamic in space and time at a variety of scales (e.g. days, seasons and decades). The tracking of such dynamic conditions in space and time has been linked to diverse phenomena such as the daily movements of zooplankton in the water column (Williamson *et al.*, 2011), annual migrations of birds, mammals, fish and insects (Milner-Gulland *et al.*, 2011), periods of dormancy in crustaceans, fungi and plants (Lubzens *et al.*, 2010), and

range shifts of organisms as a consequence of climate change (Barbet-Massin *et al.*, 2009; Doswald *et al.*, 2009). Seasonal changes in the environment have long been used to explain the regular movement of organisms across geographical regions (Lack, 1954; Milner-Gulland *et al.*, 2011).

To conceptualize these dynamics, we can distinguish between two extreme scenarios of how organisms might react to the dynamic nature of available niche space in their environment. First, organisms might move in geographical space to track their favoured environmental conditions, remaining in the specific subset of niche space they prefer (species 2 in Fig. 1). Alternatively, organisms may stay where they are and tolerate the local change in environmental conditions. The organism's niche then has to encompass the full range of environmental conditions available locally over time (Soberón, 2007; Pearman *et al.*, 2008) (species 1 in Fig. 1). Intermediate strategies between these two scenarios of perfect niche tracking and no niche tracking are conceivable and have been observed (Martínez-Meyer *et al.*, 2004). Species may be constrained in their ability to track their niche when their different required environmental conditions occur independently from one another in time and space. Here, we used migration in *Sylvia* warblers to explore how taking the spatio-temporal availability of environmental conditions into account can improve our understanding of niche and range dynamics.

There has been a renewed conceptual focus on the ecological niche (e.g. Soberón, 2007; Pearman *et al.*, 2008), sparked by recent developments in species distribution modelling (*sensu* Franklin, 2010). In this context, both the environment and the ecological niche of a species have often been treated and quantified as static entities (Fisher *et al.*, 2010; Franklin, 2010), for example by averaging environmental and occurrence data over long periods to estimate the realized niche of a species (e.g. Dormann *et al.*, 2010). Here, we used species distribution models to explore dynamics in the environment and the ecological niche, focusing on climate and land use as potential determinants of range limits. We considered niches in the Hutchinsonian tradition, in the sense that we regard the niche as an entity defined in an abstract hyperspace which can be limited by dispersal and biotic interactions (Hutchinson, 1957; Colwell & Rangel, 2009), while focusing on broad environmental conditions (Grinnell, 1917; Soberón, 2007). Thus, we focused on realized niches quantified from large-scale occurrence data, which also reflect dispersal limitations and biotic interactions (Soberón, 2007; Colwell & Rangel, 2009).

Species distribution models have previously been used to relate species' movements across regions to a potential niche-tracking strategy in studies focusing on migrating birds and butterflies and the overlap in environmental dimensions between their breeding and non-breeding niches

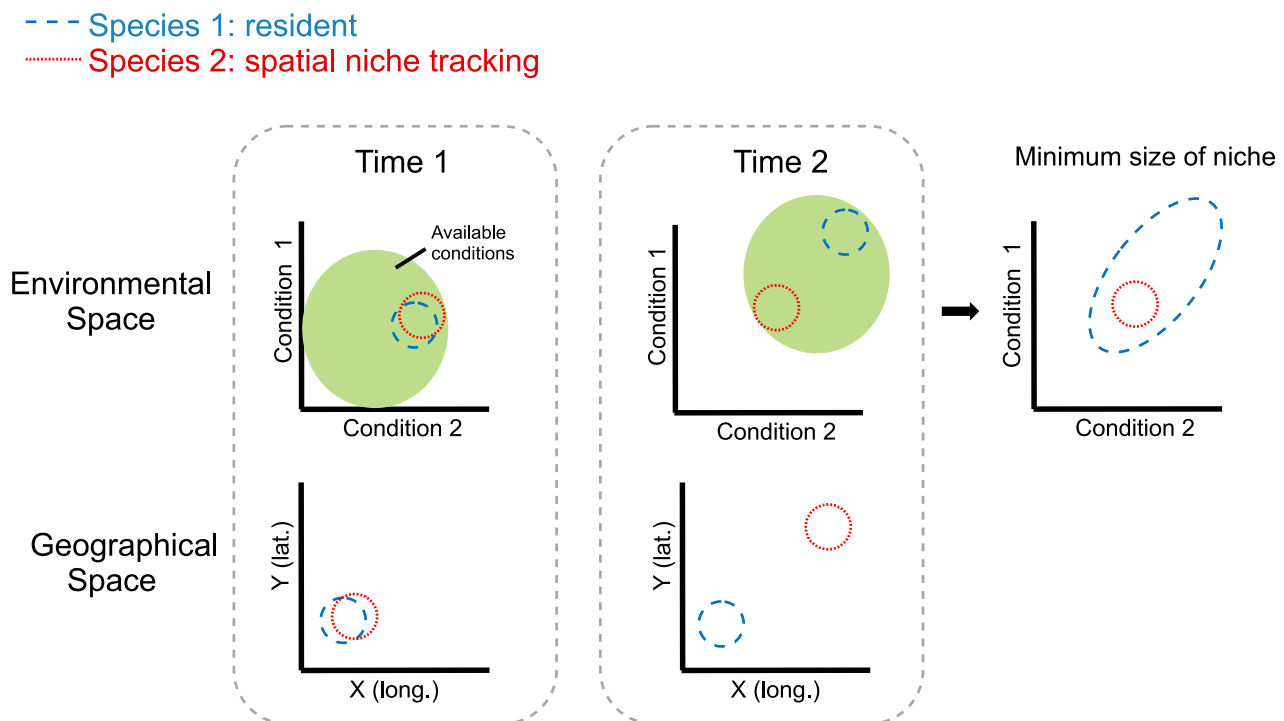


Figure 1 Organismal strategies to cope with dynamic environmental niche space availability. Two extreme scenarios of niche and range dynamics are shown for a geographical region at two points in time with different availability of environmental niche space (green circle). Species staying in one geographical location (species 1, blue niches and ranges) have to tolerate the change in available niche space. The species' niche has to be broad enough to encompass the range of environmental conditions available locally through time. Species moving in geographical space to track their favoured conditions ('spatial niche tracking'; species 2, red niches and ranges) always stay within their preferred subset of environmental niche space and can have narrow niches.

(Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Batalden *et al.*, 2007; Marini *et al.*, 2010) or on annual temperature tracking (Joseph & Stockwell, 2000). Patterns of extensive overlap between breeding and non-breeding niche ('niche trackers'; Joseph & Stockwell, 2000; Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Marini *et al.*, 2010) and of little overlap ('niche switchers'; Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004) have both been found. These studies have described spatio-temporal patterns in the realized niches of species, but they have not evaluated these against the niche characteristics that result from potential alternative range dynamics, and nor have they explicitly related the observed patterns to the dynamic availability of environmental conditions in space and time. These studies have also examined environmental dimensions (most often climate) that have similar spatio-temporal dynamics, although the availability of different niche dimensions is not necessarily synchronized in time and space (Jiménez-Valverde *et al.*, 2009). For example, across different seasons, the same climatic conditions may be available in locations with very different land cover.

Predictions on the relationship between environmental variation, movement and niche characteristics

We examine three predictions resulting from hypotheses on how environmental variation in space and time relates to the spatial movements and niche characteristics of organisms using migration behaviour in *Sylvia* warblers as a case study. The 26 species of *Sylvia* warblers evaluated here include temperate and tropical residents, as well as short-, middle- and long-distance migrants (Shirihai *et al.*, 2001). Extensive information is available on their ranges, ecology and phylogeny (e.g. Shirihai *et al.*, 2001; Böhning-Gaese *et al.*, 2003; Voelker & Light, 2011).

Trade-offs between niche breadth and migration distance

Under the niche-tracking scenario (species 2 in Fig. 1), organisms incur costs and require adaptation for high mobility, potentially over long distances (Alerstam *et al.*, 2003; Wikelski *et al.*, 2003) whereas, under the resident scenario (species 1 in Fig. 1), they incur costs and require adaptation for high environmental tolerance (DeWitt *et al.*, 1998). Hence, there might be a trade-off between the ability of organisms to track niches in space and their ability to tolerate a wide variety of conditions, such that it is less likely for a species to evolve to be both an excellent niche-tracker and have very high environmental tolerance. If such a trade-off exists, species that move long distances should have more constant niches throughout the year (i.e. greater niche overlap across seasons, *sensu* Broennimann *et al.*, 2012) than more resident species, particularly for niche dimensions that are highly temporally dynamic, such as climate. If niche dimensions are, however, spatially autocorrelated and temporally more static (e.g. land cover), then species that move

longer distances may experience larger changes in these dimensions, resulting in less niche overlap between different seasons. It follows that species that move long distances should have narrower total annual niches for the niche dimensions they are tracking (species 2 in Fig. 1) and broader total annual niches for niche dimensions that are more static in time but vary in space.

Based on these predictions, we evaluate the following specific questions. Do *Sylvia* warblers that migrate longer distances between breeding and non-breeding grounds show greater niche overlap between these areas for temporally dynamic climatic niche dimensions and lower overlap in static land-cover niche dimensions? Do *Sylvia* warblers that migrate longer distances show lower total annual climatic niche breadth and higher total annual land-cover niche breadth? To address these questions, we quantified climate and land-cover niche characteristics in both the breeding and the non-breeding areas for each species.

Niche tracking

If the reason for movement is niche-tracking, then movement should lead to greater niche overlap in the seasonal niches for the tracked niche dimension than a resident strategy (see the smaller size of minimum niche for species 2 in Fig. 1).

Specifically, we ask whether the climatic niche of migrant *Sylvia* warblers is more stable as a result of migration than if these same warblers had not migrated. To answer this question, we compared the climatic niche overlap between the breeding and non-breeding conditions which the species actually experience to the hypothetical climatic niche overlap resulting from staying either on the breeding or on the non-breeding grounds during the whole year.

Geographical proximity

If organisms that move in geographical space as a response to dynamic niche availability (species 2 in Fig. 1) minimize the cost of movement, they should move to the nearest available geographical location with suitable conditions.

Specifically, we ask whether migrant *Sylvia* warblers move to the closest place with suitable conditions. For this question, we projected environmental niche conditions onto geographical space, located the areas with similar climate and land cover to the observed breeding and non-breeding grounds and evaluated whether warblers move to the closest location with suitable conditions.

MATERIALS AND METHODS

Study species

Sylvia Scopoli, 1769 is a genus of 27 primarily insectivorous passerines, occurring in Europe, Africa and western Asia. Böhning-Gaese *et al.* (2003) have classified 14 of them as

residents, four as short-distance migrants and nine as long-distance migrants. *Sylvia dohrni*, an island endemic recently added to the genus (Voelker *et al.*, 2009), was not included in the analyses because its extremely small range precluded reliable quantification of niche characteristics. Migration distances in kilometres, based on the orthodrome distance between centres of gravity for breeding and non-breeding ranges, were taken from Böhning-Gaese *et al.* (2003). Phylogenetic information on the relationships of species within the genus was taken from Voelker & Light (2011).

Ranges

Information on breeding and non-breeding ranges of the *Sylvia* species was taken from Shirihai *et al.* (2001), except for *Sylvia abyssinica*, which was identified as a member of the genus more recently (Böhning-Gaese *et al.*, 2003) and whose range was taken from Fry *et al.* (2000). The range maps in Shirihai *et al.* (2001) combine expert knowledge with an extensive collation of point records and are the most comprehensive compilation of knowledge available about geographical distributions in *Sylvia*. The range maps are spatially detailed and were thus gridded at a resolution of 25 km × 25 km. Grids were converted into presences and absences based on a threshold of 10% (the minimum percentage overlap between the range and a grid cell for that grid cell to be classified as presence). To assess whether this threshold affects our results, we also conducted all analyses for a 50% gridding threshold, and both thresholds yielded very similar results (see Appendix S1 in Supporting Information).

Environmental variables

We used environmental data from all biogeographical realms currently inhabited by *Sylvia* warblers: Palearctic, Afrotropical and Indo-Malay. The data were resampled to the same 25 km × 25 km grid as the gridded range maps. We chose environmental variables based on our knowledge of *Sylvia* ecology and behaviour. We used mean monthly temperature and total precipitation to represent abiotic environmental conditions (over the period 1961–1990, CRU CL 2.0; available at http://www.cru.uea.ac.uk/~tim/grid/CRU_CL_2_0.html; New *et al.*, 2000) and the monthly normalized difference vegetation index (NDVI) to reflect plant productivity (1982–1999; Global Land Cover Facility; available at: <http://glcf.umd.edu/data/gimms/>; Tucker *et al.*, 2005), which influences the availability of bird food resources such as insects. We used the mean values of these variables for the three peak breeding and non-breeding months for each species (Heikkinen *et al.*, 2006) based on information in the literature (Urban *et al.*, 1997; Fry *et al.*, 2000; Shirihai *et al.*, 2001; see Appendix S2). Because the habitat choice of *Sylvia* warblers is determined by vegetation type and structure (Shirihai *et al.*, 2001), we used UMD Land Cover Classification data (available at: <http://glcf.umd.edu/data/landcover/>; 1-km pixel resolution, Hansen *et al.*, 2000) to reflect vegetation cover.

We distinguished between open shrubland, closed shrubland, wooded grassland, woodland and broad-leaved forest and calculated the proportion of each of these classes for each grid cell.

Niche characteristics

Ecologists have long debated how best to measure niche overlap and niche breadth (e.g. Colwell & Futuyma, 1971; Warren *et al.*, 2008; Dormann *et al.*, 2010). We based our approach on recommendations from Broennimann *et al.* (2012), who provide an up-to-date assessment of niche quantification methods. For each species, we conducted a principal components analysis (PCA) of the environmental variables described above for the whole study region (Palearctic, Afrotropical and Indo-Malay ecozones) including the data from both the breeding and non-breeding seasons. Depending on the question, we used either all environmental variables in the PCA or calculated separate PCAs for the three climate and five land-cover variables. The first two principal components of the PCA were used as the axes to describe the total annual environmental space, bounded by the minimum and maximum environmental values found in any of the two seasons in the whole study region (e.g. for *Sylvia atricapilla*, see axes in Fig. 2).

For further analysis, the environmental space described by the first two PCA axes was divided into 100 × 100 regularly spaced grid cells (v_{ij}), with each cell thus representing a unique set of environmental conditions. Next, we calculated the density of species occurrences (o_{ij}) and the density of available environments (e_{ij} : the number of grid cells with these environmental conditions in the whole study region during that season) in each grid cell in the environmental space for each species and for both breeding and non-breeding seasons. Both o_{ij} and e_{ij} were calculated using a kernel smoothing function to account for imperfect sampling of occurrences and to make the metrics independent of the number of grid cells in environmental space. Dividing o_{ij} by e_{ij} for each species and season then gave the occupancy of the environment (z_{ij}) in the grid cells in environmental space (e.g. for *S. atricapilla*, grey shading in Fig. 2). If the environmental conditions corresponding to a grid cell were unavailable in a particular season (i.e. $e_{ij} = 0$), z_{ij} was set to zero. This procedure corrects the observed occurrences for the availability of environmental conditions in each season to ensure unbiased comparisons (Broennimann *et al.*, 2012).

Niche overlap between seasonal ranges was calculated using the D metric (Schoener, 1970; Warren *et al.*, 2008) on the occupancy values in environmental space (z_{ij}). To calculate D , the absolute differences in occupancy values between the two ranges are summed, halved and then subtracted from one. D varies from 0 (no niche overlap) to 1 (complete niche overlap).

To calculate niche breadth, we converted the environmental occupancy values (z_{ij}) to proportions and then calculated the Shannon index (Colwell & Futuyma, 1971). This measure

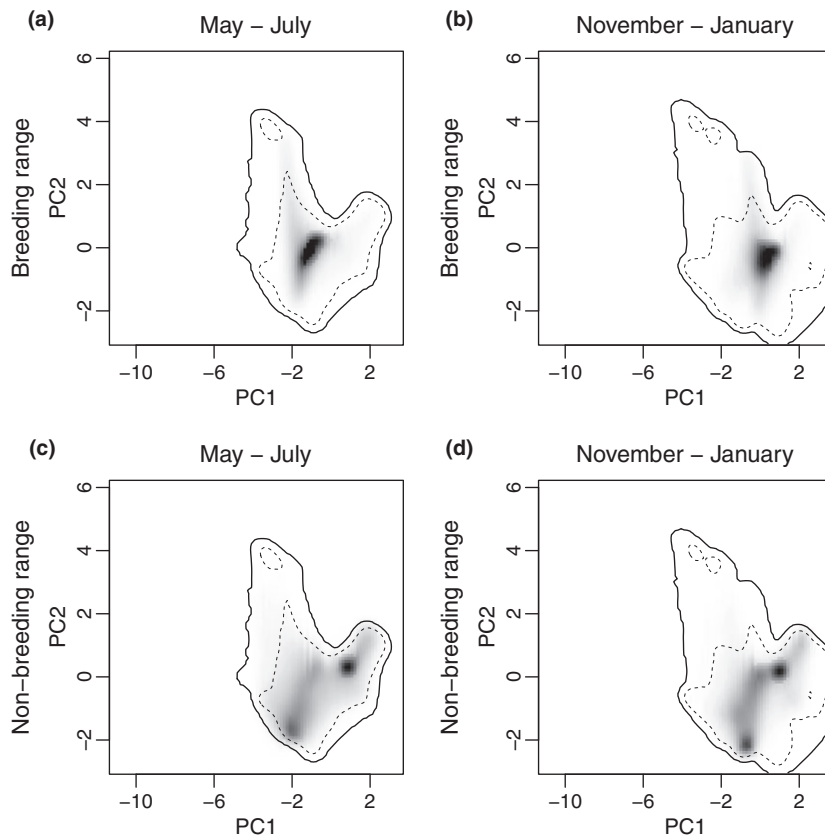


Figure 2 Visualization of occupied and available niche space for *Sylvia atricapilla*, based on the first two axes of a principal components analysis quantifying the variation in climate and land cover across the Palearctic, Afrotropical and Indo-Malay ecozones and in both breeding (May–July) and non-breeding seasons (November–January). Solid and dashed contour lines show 100% and 50% of available environment in the entire study area, respectively. Grey shading shows occupancy values in environmental space (z_{ij}), i.e. niche space for a particular range. (a) Occupied niche space during breeding season, (b) niche availability in breeding range during non-breeding season, (c) niche availability in non-breeding range during breeding season, (d) occupied niche space during non-breeding season.

of niche breadth thus takes into account both the number of occupied grid cells in environmental space and the evenness in the occupancy among those grid cells.

All analyses were conducted in R 2.13.2 (R Development Core Team, 2011) using published code and libraries (Baddeley & Turner, 2005; Broennimann *et al.*, 2012).

Movement distances

To determine whether a species moved during migration from its breeding range to the closest non-breeding range with suitable non-breeding environmental conditions, we conducted the following five steps. First, we projected the non-breeding occupancy values derived from each species' PCAs including both climate and land cover (e.g. for *Sylvia atricapilla*, Fig. 2d) onto geographical space to attribute a suitability value to each grid cell in geographical space. Second, to distinguish suitable from unsuitable areas, we applied a threshold to the suitability maps using the sensitivity-equals-specificity rule (Liu *et al.*, 2005). Third, we calculated the nearest-neighbour distances from all suitable non-breeding grid cells to all cells in the breeding range. Fourth, we selected the suitable non-breeding grid cells that had the shortest nearest-neighbour distances to the known breeding range. To avoid making assumptions about range sizes, we selected the same number of grid cells as the number of grid cells in the known non-breeding range. Fifth, we calculated the average of the pairwise distances between all grid cells in

the closest suitable non-breeding area and all grid cells in the known breeding range to obtain the minimum migration distance.

Analogously, we calculated whether a species moved from its non-breeding range to the closest breeding range with suitable breeding environmental conditions. To compare the minimum migration distances to the actual migration distances for each species, we calculated actual migration distance as the average of the pairwise distances between all breeding-range grid cells and all non-breeding-range grid cells ensuring consistency between the quantifications of minimum and actual migration distances for this question.

Statistical analysis

Trade-offs between niche breadth and migration distance

We calculated linear regressions between niche overlap and movement distances and between total annual niche breadth and movement distances separately for climate and land-cover niches for all *Sylvia* warblers. To take the phylogenetic relationship between *Sylvia* warblers into account, we checked the residuals from the linear regressions for phylogenetic autocorrelation. We tested for phylogenetic signal in the residuals using the Abouheif test with 999 randomizations, as implemented in the R package ADEPHYLO 1.1 (Jombart *et al.*, 2010), and by calculating Pagel's λ and testing for a significant difference to a λ of zero (no phylogenetic

structure), as implemented in the R package CAICR 1.0.4 (Freckleton, 2009).

Niche tracking

To determine whether variation between seasons in the climatic niche of migrant *Sylvia* warblers is reduced as a result of migration, we calculated the climatic niche overlap for the breeding or non-breeding grounds assuming a given warbler had not migrated [analogous to the intersection of Fig. 2(a,b), and the intersection of Fig. 2(c,d), but without land-cover variables] and compared this overlap to the climatic niche overlap the migrants actually experience between breeding and non-breeding grounds [analogous to the intersection of Fig. 2(a,d)] using paired *t*-tests. Additionally, to examine to what extent conditions in the non-breeding range differ from the conditions available in the breeding range during the non-breeding season, we calculated the climatic niche overlap between non-breeding grounds and the climate available on the breeding range during the non-breeding season [analogous to the intersection of Fig. 2(b,d)].

Geographical proximity

To evaluate whether migrant *Sylvia* warblers move to the closest place with suitable conditions based on niche quantifications incorporating both climate and land cover, we used

paired *t*-tests to compare the known migration distance with the distance from the breeding range to the closest suitable non-breeding area and the known migration distance with the distance from the non-breeding range to the closest suitable breeding area. We also divided the differences between known migration distance and the migration distances to the closest suitable area by the known migration distance to obtain species-specific estimates of potential reductions in distance from adopting the shortest possible migration distance. We examined all migration-distance variables for normality using Shapiro–Wilk tests and normal probability plots. Shapiro–Wilk tests did not indicate any deviation from normality in any of the migration-distance variables ($P > 0.09$).

RESULTS

Trade-offs between niche breadth and migration distance

Contrary to our prediction, movement distance between breeding and non-breeding grounds in *Sylvia* warblers was not significantly related to the overlap between breeding and non-breeding climatic niches ($\beta = 0.00001$, $t = -1.03$, $P = 0.31$, $r^2 = 0.04$, Fig. 3a) or to total annual climatic niche breadth ($\beta = -0.0000002$, $t = -0.04$, $P = 0.97$, $r^2 < 0.01$, Fig. 3c). Land-cover niches showed the expected relationship with migration distance: *Sylvia* warblers with greater

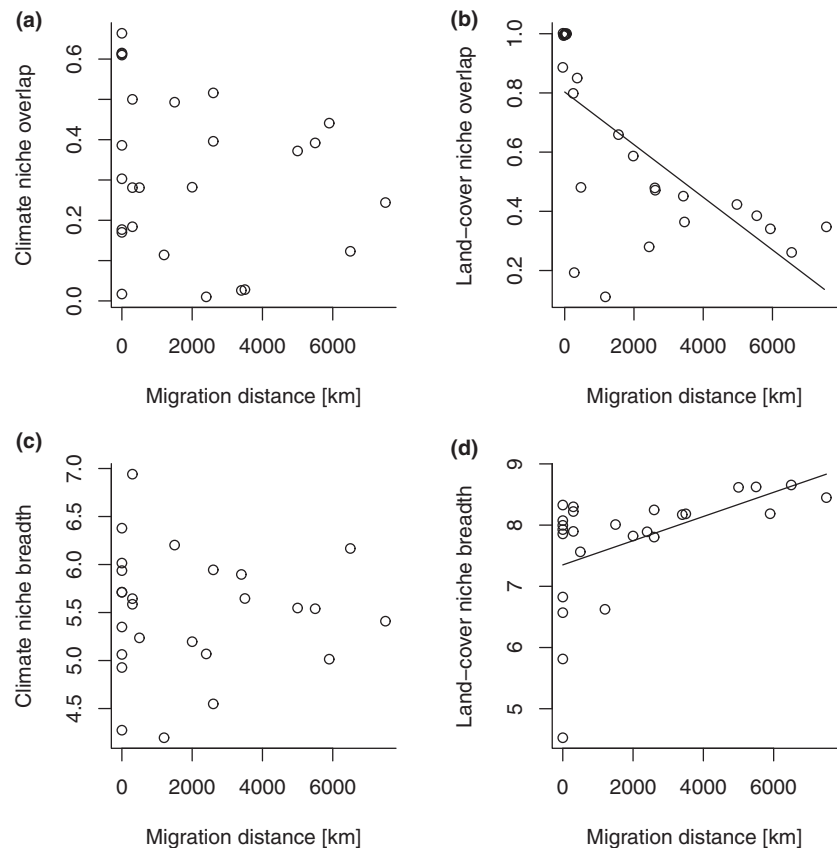


Figure 3 Relationship between migration distance and (a) climatic niche overlap between breeding and non-breeding season, (b) land-cover niche overlap between breeding and non-breeding season, (c) total annual climatic niche breadth, (d) total annual land-cover niche breadth, for 26 species of *Sylvia* warblers.

distances between breeding and non-breeding grounds did exhibit a significantly lower overlap in their land-cover niche ($\beta = -0.00008$, $t = -4.55$, $P = 0.0001$, $r^2 = 0.46$, Fig. 3b) and had significantly broader total annual land-cover niches ($\beta = 0.00019$, $t = 2.77$, $P = 0.01$, $r^2 = 0.24$, Fig. 3d). A few species that migrate short distances deviated slightly from this pattern due to the size difference between their very small breeding ranges and larger non-breeding ranges (Fig. 3b, scatter below regression line). There was no significant phylogenetic signal in any of the regression residuals (Abouheif tests, $P > 0.05$; likelihood-ratio tests for $\lambda = 0$, $P > 0.55$), indicating that our results are not affected by the phylogenetic relatedness of the species.

Niche tracking

The climatic niche overlap between breeding and non-breeding grounds for migrant *Sylvia* warblers was not significantly higher than if they had stayed year-round either on the breeding grounds ($t = 0.59$, d.f. = 12, $P = 0.56$) or on the non-breeding grounds ($t = -0.03$, d.f. = 12, $P = 0.97$) (Fig. 4). There was little climatic niche overlap between the conditions that migrant *Sylvia* warblers experience on the non-breeding grounds and the conditions available on their breeding grounds during the non-breeding season: $D = 0.15 \pm 0.25$ (mean \pm SD; $n = 13$).

Geographical proximity

When both climate and land cover were incorporated into niche quantifications, the known migration distances were significantly greater than the distances between the known breeding ranges and the closest suitable non-breeding area ($t = 4.55$, d.f. = 12, $P < 0.001$, Fig. 5). Migrant *Sylvia* warblers could migrate an average of $21\% \pm 20\%$ (mean \pm SD) less far by flying to the closest suitable non-breeding area. Similarly, known migration distances were significantly longer than the distances between the known non-breeding

range and the closest suitable breeding area ($t = 5.72$, d.f. = 12, $P < 0.001$, Fig. 5) with a potential reduction in distance of on average $23\% \pm 18\%$.

DISCUSSION

We have developed a new conceptual and methodological approach to explore how organisms respond to spatio-temporally dynamic niche space (Fig. 1) and applied it to seasonal migration in *Sylvia* warblers. Migration in *Sylvia* does not conform to a pattern of climatic or land-cover niche tracking, whereby a species' movement behaviour would limit the environmental conditions it experiences. Our results also highlight the decoupled spatio-temporal availability of climate and land cover to migrating *Sylvia* warblers. Future research should explore how migratory behaviour is influenced by and evolves under such complex constraints, and how climate and land cover translate into reproductive output and mortality (Wilson *et al.*, 2011).

Trade-offs between niche breadth and migration distance

Our results indicate that *Sylvia* warblers do not compensate for the costs of a long migratory journey by closely tracking their preferred climatic niche. We suggest three primary reasons for the absence of this predicted trade-off.

First, *Sylvia* warblers may move between environments that are optimal for different stages of their life cycles. In this case, the advantage of migration might not be climatic niche tracking but rather higher reproductive success and lower nest predation at higher latitudes, and lower winter mortality at tropical latitudes (Böhning-Gaese *et al.*, 2000; Alerstam *et al.*, 2003; McKinnon *et al.*, 2010). Thus, there may be seasonal differences in how climate and land cover translate into fitness benefits and costs. To avoid obscuring such seasonal shifts, species distribution models should be fitted with seasonal subsets of occurrence and environmental data (Heikki-

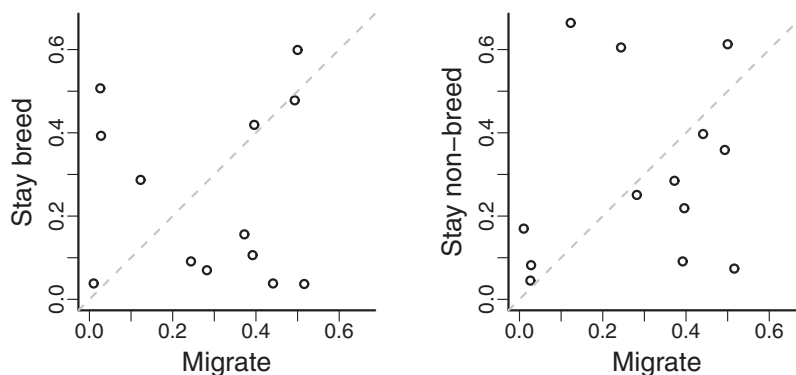


Figure 4 Climatic niche overlap for different potential migration strategies in migrant *Sylvia* warblers. Migration does not lead to consistently higher climatic niche overlap than resident strategies. 'Migrate', niche overlap between breeding and non-breeding grounds actually experienced by the species; 'stay breed', hypothetical niche overlap resulting from staying on the breeding grounds all year; 'stay non-breed', hypothetical niche overlap resulting from staying on the non-breeding grounds all year; dashed grey line, identity line; $n = 13$.

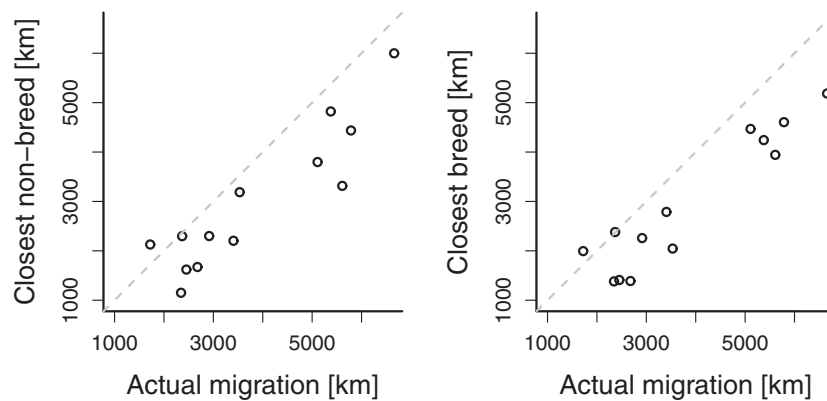


Figure 5 Migration distance and distance to the closest suitable non-breeding and breeding areas in migrant *Sylvia* warblers. At points below the identity line, the actual migration distance is longer than the distance to the closest suitable areas. 'Actual migration', average distance between known breeding and non-breeding ranges; 'closest non-breed', average distance between known breeding range and closest suitable non-breeding area; 'closest breed', average distance between known non-breeding range and closest suitable breeding area; dashed grey line, identity line; $n = 13$.

nen *et al.*, 2006). Environmental niches should be regarded as dynamic entities over the seasonal and total life cycle of species and closer examination of how niches vary over time may be beneficial for future studies that aim to model niches and distributions (Jackson *et al.*, 2009).

The second reason for the absence of the predicted trade-off may relate to our assumptions about costs. Assessing the potential costs of adaptations for spatial mobility versus environmental tolerance in an evolutionary context may reveal that these costs are too small for the predicted trade-off to occur under current spatio-temporal environmental dynamics. For example, residents might incur low costs for tolerating seasonality in environmental conditions if this seasonality has only a minor effect on resources such as food. Although we were unable to directly consider resources, this would be a worthwhile direction for future studies of niche dynamics.

The final reason no trade-off was observed may be that quantifying the niche at the species level ignores the fact that subpopulations and individuals may select specific environments from the total available niche space, e.g. short-distance versus trans-Saharan migrant subpopulations in *S. atricapilla* (Shirihai *et al.*, 2001), and hence might experience different niche overlaps.

Niche tracking

By examining which part of the total environmental niche space is available to the *Sylvia* warblers when and where, we can compare the niche overlap that results from alternative hypothetical migration strategies and so evaluate whether an observed migration pattern maximizes niche overlap and can thus be considered evidence for 'tracking' (Reside *et al.*, 2010). Migration in *Sylvia* warblers does not appear to be a function of climatic niche tracking because the climatic niche overlap associated with migration is no greater than under a hypothetical resident strategy. The low niche overlap between winter climate on the breeding and on the non-breeding

grounds suggests, however, that overwintering on the breeding grounds would require tolerance of deviations from the breeding conditions in a different direction of environmental niche space than under migration. A resident strategy may thus expose migratory *Sylvia* warblers to cold, unproductive winters, which the species may be less able to tolerate than the winter conditions likely to be found further south. Evidence for climatic niche tracking between breeding and non-breeding ranges in birds has been ambiguous so far, with sizeable overlaps between breeding and non-breeding climate in some species (Joseph & Stockwell, 2000; Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Marini *et al.*, 2010) but not in others (Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004).

Geographical proximity

During the spring and autumn migrations, *Sylvia* warblers fly approximately 20% further than the journey to the nearest predicted area with suitable climate and land cover. Although these results imply that *Sylvia* warblers travel significantly greater distances than optimal, given the broad scale of our environmental data, they do not necessarily reject the possibility that *Sylvia* warblers optimize their migration distance according to niche availability at the continental scale. Migration distance is also likely to be influenced by factors such as biotic interactions, potential genetic constraints on the migration routes of bird populations, and the influence of geographical barriers and the availability of stop-over sites (Alerstam *et al.*, 2003; McKinnon *et al.*, 2010; Tøttrup *et al.*, 2012), which we do not explicitly address. These factors might counteract a perfect optimization of linear geographical migration distance, e.g. if the shortest route has unsuitable stopover sites, requires crossing geographical barriers or results in encounters with predators or competitors. Our results indicate that future research on migration should consider niche availability in geographical space along with these other potential drivers.

Implications

Our hypothesis-driven approach (Fig. 1) is part of an emerging trend to investigate macroecological patterns through analyses of temporal dynamics (Fisher *et al.*, 2010). We show that niche tracking cannot be assumed without considering the availability of environmental niche conditions in space and time and without evaluating the niche dynamics of alternative movement strategies. Similar hypotheses could be explored for other ecological phenomena and taxa, such as diel migration in zooplankton, plant dormancy or the effect of environmental availability over geological time-scales on the evolution of niches and ranges.

Although we believe valuable insights can be gained from using large-scale biogeographical data in analyses of niche availability, an important caveat when interpreting results derived from large-scale species distribution modelling is that only certain broad-scale aspects of an organism's niche are captured. It is also worth noting that our results are consistent with climate not being the major determinant of broad-scale distribution in *Sylvia* warblers, and range limits being influenced by processes related to biotic interactions and dispersal ability (Laube *et al.*, 2013).

Niche availability is relevant for predicting how species' ranges will respond to climate change. Our results for the *Sylvia* warblers suggest that they might not track predicted shifts in their preferred climatic conditions (Barbet-Massin *et al.*, 2009; Doswald *et al.*, 2009). We have shown that *Sylvia* warblers are likely to seek out specific environments in different seasons. If species depend on a succession of different niches in different seasons or developmental stages, a new suite of models is required to reflect these temporal shifts in niche requirements, instead of modelling one comprehensive annual environmental niche (Heikkinen *et al.*, 2006). Moreover, if climate change alters niche availability, existing migration strategies may no longer be viable. Exploring how species deal with spatio-temporal desynchronization in different niche dimensions will be crucial for predicting how species will respond to the emergence of novel climates (Williams *et al.*, 2007), yet this phenomenon is not reflected in most correlative species distribution models that are fitted with time-averaged data and assume a constant correlation structure between environmental variables (Jiménez-Valverde *et al.*, 2009). Our results highlight that niche-tracking behaviour is complex and that assuming simple climate tracking when predicting future range shifts may be too simplistic.

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SUPPORTING INFORMATION

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

Appendix S1 Results of all analyses using a 50% gridding threshold for the *Sylvia* ranges.

Appendix S2 Peak breeding and wintering times of *Sylvia* warblers.

BIOSKETCHES

Irina Laube is interested in understanding the interplay of species' ecology and evolution and how this influences range dynamics in space and time against the backdrop of past environmental change.

Catherine Graham is a macroecologist/landscape ecologist whose work investigates the effects of spatial and temporal arrangements of habitats on ecological and evolutionary processes and uses this information to inform conservation policy.

Katrin Böhning-Gaese works on the evolution, ecology and conservation of ecological communities. She focuses on the impact of global change on biodiversity and ecosystem functions.

Author contributions: I.L., C.H.G. and K.B.-G. conceived the ideas; I.L. collected and analysed the data; I.L. led the writing with contributions from C.H.G. and K.B.-G.

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