Non-random distribution of individual genetic diversity along an environmental gradient

Mélody Porlier*, Marc Bélisle and Dany Garant

Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada

Improving our knowledge of the links between ecology and evolution is especially critical in the actual context of global rapid environmental changes. A critical step in that direction is to quantify how variation in ecological factors linked to habitat modifications might shape observed levels of genetic variability in wild populations. Still, little is known on the factors affecting levels and distribution of genetic diversity at the individual level, despite its vital underlying role in evolutionary processes. In this study, we assessed the effects of habitat quality on population structure and individual genetic diversity of tree swallows (*Tachycineta bicolor*) breeding along a gradient of agricultural intensification in southern Québec, Canada. Using a landscape genetics approach, we found that individual genetic diversity was greater in poorer quality habitats. This counter-intuitive result was partly explained by the settlement patterns of tree swallows across the landscape. Individuals of higher genetic diversity arrived earlier on their breeding grounds and settled in the first available habitats, which correspond to intensive cultures. Our results highlight the importance of investigating the effects of environmental variability on individual genetic diversity, and of integrating information on landscape structure when conducting such studies.

Keywords: agricultural intensification; environmental change; individual genetic diversity; landscape genetics; population structure; tree swallow

1. INTRODUCTION

Maintenance of genetic diversity is essential for a natural population's potential to evolve and adapt (Fisher 1930; Lenormand 2002). Accordingly, populations or species with low genetic diversity, and thus low adaptive potential, will generally have little chance of persisting in the face of rapid modifications of their environment (Burger & Lynch 1995; Etterson 2004). This is especially important in the actual context of rapid global environmental changes linked to the increasing human population and the expansion of its activities (Hannah *et al.* 1995; IPCC 2007). For example, the perturbation of natural habitats through fragmentation or habitat loss is currently one of the major causes of the decline of wild populations and the extinction of species worldwide (Wilcove *et al.* 1998; Baille *et al.* 2004). Such habitat modifications will in most cases lead to a reduction in genetic diversity, increased levels of inbreeding and a reduction in fitness, which will ultimately increase extinction risks (Frankham 1995). In this context, it becomes particularly important to quantify how variation in ecological factors linked to habitat quality might affect and shape observed levels of genetic variability in wild populations.

The recent emergence of the field of landscape genetics, which integrates population genetics, landscape ecology and spatial analyses, provides an effective integrated approach to understand how landscape and

ecological processes influence genetic variability in wild populations (Manel *et al.* 2003; Storfer *et al.* 2007). As a result, an increasing number of population genetic studies have quantified the effects of different landscape and ecological parameters on gene flow and resulting population differentiation at various scales and for different taxa (Keyghobadi *et al.* 2005; Spear *et al.* 2005; Vandergast *et al.* 2007; Dionne *et al.* 2008). Further studies have investigated how the interaction between habitat features and individual behaviour can shape population genetic structure and differentiation (Clark *et al.* 2008; Zheng *et al.* 2009). Much less emphasis has, however, been put on the assessment of the ecological factors that can potentially affect the amount and distribution of genetic diversity at the individual level. This is of great concern given that individual genetic diversity plays a vital underlying role in population genetics and evolutionary processes, for instance through sexual and natural selection (Kretzmann *et al.* 2006; Kempenaers 2007).

Yet, several studies have underlined the importance of individual genetic diversity at various levels. For instance, extra-pair mating often results in higher offspring individual heterozygosity in various species of birds (Foerster *et al.* 2003; Suter *et al.* 2007), mammals (Cohas *et al.* 2006; Bishop *et al.* 2007) and fishes (Garant *et al.* 2005a; but see Dibattista *et al.* 2008). Also, studies have found evidence for female mate choice based on the level of individual heterozygosity of potential mates (reviewed in Kempenaers 2007). Positive associations have also been found between individual genetic diversity and sexually selected traits in male birds, such as crown colour (Foerster *et al.* 2003) and song complexity

* Author for correspondence (melody.porlier@usherbrooke.ca).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rstb.2009.0010> or via <http://rstb.royalsocietypublishing.org>.

One contribution of 14 to a Theme Issue 'Eco-evolutionary dynamics'.

(Marshall *et al.* 2003). Importantly, several associations have been reported between increased individual genetic diversity and greater fitness-related traits, such as reproductive success (Tomiuk *et al.* 2007; Zedrosser *et al.* 2007), recruitment (Hansson *et al.* 2001) and survival (Kretzmann *et al.* 2006), across different taxa. However, none of these studies considered the potential interplay between individual genetic diversity and environmental variability, a critical step towards providing an accurate evaluation of a species' evolutionary potential in changing environments as well as an assessment of the links between ecological and evolutionary dynamics in the wild (see Pelletier *et al.* 2009).

The main objective of this study was to assess how ecological and landscape parameters affect the levels and distribution of individual genetic diversity in a wild bird population sampled throughout a gradient of agricultural intensification in southern Québec, Canada. The expansion and intensification of agricultural practices are major causes of current habitat loss and degradation (Soulé *et al.* 1990; Venter *et al.* 2006). Agricultural practices throughout Europe and North America have drastically changed since the beginning of the twentieth century, mainly due to an increased mechanization of agricultural work, a greater use of pesticides, herbicides and chemical fertilizers, as well as the development and use of new and hybrid plant varieties (Tscharntke *et al.* 2005). In southern Québec and elsewhere, these modifications have transformed the agricultural landscapes, originally composed of hayfields and pastures, associated with a significant residual forest cover and the presence of marginal habitats, such as hedgerows and wetlands, into large, intensively managed crops of cereal, soya bean and maize (Bélanger & Grenier 2002; Benton *et al.* 2003; Tscharntke *et al.* 2005). This transformation and homogenization of agricultural landscapes have been linked to the decline in diversity and abundance of many bird species associated with farmland (Benton *et al.* 2003; Donald *et al.* 2006). The tree swallow (*Tachycineta bicolor*), a small migratory passerine, is one such species susceptible to be affected by the habitat modifications caused by agricultural intensification. Similar to many species of aerial insectivorous birds, tree swallow populations in Canada have declined during the past 20 years, one of the most important reductions in population sizes being observed in the province of Quebec, with an average annual decline of 4.6 per cent between 1997 and 2007 (Downes & Collins 2008). The breeding activities of tree swallows occur mostly in open habitats, including agricultural fields, where they are dependent upon marginal habitats, such as drainage ditches and wetlands for foraging, and upon standing dead trees comprising nesting cavities since they are obligate second-cavity nesters (Robertson *et al.* 1992). Given these food and breeding site requirements, habitat modifications resulting from agricultural intensification are possible causes of the tree swallows' recent decline. Indeed, it has been recently shown that tree swallows have a smaller clutch size as well as a lower fledging success in landscapes mostly composed of intensively managed agricultural fields (Ghilain & Bélisle 2008).

The specific objectives of our study were twofold. First, we assessed the population genetic structure of tree swallows in southern Québec using a landscape genetics approach based on microsatellite markers and geographic information system (GIS)-based information. Second, we quantified the effects of landscape features and ecological parameters on the levels and distribution of individual genetic diversity in tree swallows along a gradient of agricultural intensification. Since the reproductive success of tree swallows is lower in intensively managed agricultural areas, we assessed whether the tree swallows' individual genetic diversity was negatively related to agricultural intensification.

2. MATERIAL AND METHODS

(a) Study system and data collection

We monitored the breeding activities of tree swallows in a network of 400 nest-boxes distributed among 40 farms (10 nest-boxes per farm) over an area of approximately 10 200 km² in southern Québec, Canada (figure 1; see Ghilain & Bélisle (2008) for a more detailed description of the study system). This area is characterized by a longitudinal gradient of agricultural intensification ranging from a forested landscape with interspersed small-scale hayfields and pastures (henceforth referred to as extensive cultures) to the east, to a dominance of large-scale, intensively managed monocultures of maize, cereal and soya bean crops (referred to as intensive cultures) to the west (figure 1). This transition from extensive to intensive cultures is associated with forest cover reduction and fragmentation, landscape homogenization caused by the loss of marginal habitats such as hedgerows and wetlands, and an increase in field size.

Each nest-box was visited every 2 days throughout the breeding season (from April to mid-August) in 2006 and 2007. Geographical coordinates of each nest-box were obtained using a handheld Trimble GEOEXPLORER GPS (Trimble, Sunnyvale, CA, USA). Nest building was monitored at each visit before females laid their first egg, and main breeding parameters were then recorded for each breeding attempt: laying date (date of first egg laid); clutch size (number of eggs); number of nestlings (number of hatched young); and number of fledglings (number of nestlings aged 12 days). We also defined a settlement date for each nest-box, which corresponded to the earliest observation of nest material for the first breeding attempt in a given nest-box. Adult tree swallows were caught in their nest-boxes either during nest building, while incubating, or when feeding nestlings aged from 4 to 12 days. Each bird was weighed and banded at first capture with a US Fish and Wildlife Service aluminium band. Blood samples were taken from the brachial vein and transferred on a qualitative P8 grade filter paper (Fisher Scientific), air-dried and individually stored in hermetically sealed plastic bags at room temperature until DNA extraction. Adult tree swallows that were found dead inside nest-boxes in 2007 ($n=12$) were collected and stored at -80°C until DNA extraction. Sex was determined based either on the presence of a brood patch (females) or cloacal protuberance (males) or using molecular tools (see below).

(b) Landscape variables

Local-scale landscape composition was assessed for both study years by estimating the relative cover of culture types within 500 m from each nest-box. We determined the type of culture covering each parcel of land that

Figure 1. Distribution of the 40 farms used to study tree swallows (*T. bicolor*) along a gradient of agricultural intensification in southern Québec, Canada. Land cover types are based on a mosaic of classified Landsat-TM satellite images (Canadian Wildlife Service 2004) and include forest cover (medium grey), extensive cultures (e.g. hayfields and pastures; light grey) and intensive cultures (e.g. maize, cereals, soya beans; white). The St Lawrence River is shown in dark grey at the western limit of our study area. Circles indicate farm locations.

surrounded nest-boxes either using the Generalized Crop Database (Financière Agricole du Québec 2007) or by visual assessment of culture type associated with each parcel of land. Landscape composition was then reported on orthophotographs (scale: 1/40 000; Ministère des Ressources naturelles et de la Faune du Québec 2000), and cover percentages were calculated using ARCVIEW GIS SPATIAL ANALYST v. 2.0a (ESRI 2005).

Large-scale landscape composition for each nest-box was also calculated by estimating the cover percentage of extensive and intensive cultures within 1 and 5 km radii based on Landsat-7 satellite images taken from August 1999 to May 2003 (Canadian Wildlife Service 2004). We chose a maximum radius of 5 km because it corresponds to the maximum distance travelled by tree swallows when collecting food for their young, and since landscape-composition effects on their brood parameters have been shown to be maximal at this spatial scale (Ghilain & Bélisle 2008). We also included analyses using cover percentages measured within 1 km radius around each nest-box as it represents an intermediate distance between our local- (500 m) and large (5 km)-scale analyses. For each nest-box, we also calculated the nearest distance to the St Lawrence River, since this measure is suggested to be linked with the arrival dates of tree swallows in our study system (based on the recordings of first spring observations of tree swallows in southern Québec—eBirds 2006). All measurements were obtained with ARCVIEW GIS SPATIAL ANALYST v. 2.0a (ESRI 2005). Correlations between and within culture types at different spatial scales as well as between culture types and distance from the St Lawrence River were calculated using the R statistical environment v. 2.7.1 (R Development Core Team 2008).

(c) Genetic analyses

(i) Microsatellite genotyping

DNA extractions were carried out from a 25 mm² piece of filter paper impregnated with blood. We used a proteinase K overnight digestion followed by NaCl extraction as detailed in Aljanabi & Martinez (1997). Microsatellite polymorphism was then analysed at the following 10 loci: TBI 81, TBI 104, TBI 106 (Stenzler 2001), IBI Ms5-29 and IBI Ms3-31 (Crossman 1996), developed for tree swallows, and HrU5, HrU7 (Primmer *et al.* 1995) as well as Hir 17, Hir 19 and Hir 22 (Tsyusko *et al.* 2007), developed for barn swallows (*Hirundo rustica*). Briefly, PCRs were performed in a 10 µl volume (8 mM Tris-HCl (pH 9.0); 40 mM KCl; 0.08% Triton X-100; 3.0–3.5 mM MgCl₂; 0.004 mg BSA; 80 µM dNTPs; 500 mM unlabelled primer; 250 mM labelled primer; 1U AmpliTaq Gold (Applied Biosystems) and 10–20 ng DNA template) using a GeneAmp 9700 thermal-cycler (Applied Biosystems). The thermal profile consisted of an initial denaturation step of 6 min at 94°C, followed by 36 cycles at 94°C for 30 s, 54°C (HrU5)/55°C (Hir 17, Hir 22)/56°C (TBI 106, IBI Ms3-31)/58°C (IBI Ms5-29, HrU7, TBI 81, TBI 104)/60°C (Hir 19) for 45 s and 72°C for 45 s, with a final elongation step of 10 min at 72°C. PCR products were visualized on an AB-3130 automated DNA sequencer and alleles were scored using GENEMAPPER (Applied Biosystems).

(ii) Molecular sexing

Individuals for which sex could not be determined on a phenotypic basis were sexed by amplification of the chromohelicase-DNA binding (CHD) genes, using the P2 and P8 primers (Griffiths *et al.* 1998). The final PCR conditions were as follows: 8 mM Tris-HCl (pH 9.0); 40 mM KCl, 3.0 mM

Table 1. Pearson's correlation coefficients between ecological and landscape variables. (Values above diagonal refer to year 2006, below diagonal to 2007. All values are significant at $p < 0.001$.)

	extensive cultures (500 m)	extensive cultures (1 km)	extensive cultures (5 km)	intensive cultures (500 m)	intensive cultures (1 km)	intensive cultures (5 km)	distance from St Lawrence River (km)
extensive cultures (500 m)	—	0.757	0.398	−0.797	−0.668	−0.631	0.655
extensive cultures (1 km)	0.656	—	0.630	−0.560	−0.601	−0.578	0.548
extensive cultures (5 km)	0.376	0.630	—	−0.391	−0.459	−0.576	0.514
intensive cultures (500 m)	−0.798	−0.496	−0.379	—	0.875	0.798	−0.767
intensive cultures (1 km)	−0.664	−0.601	−0.459	0.876	—	0.893	−0.758
intensive cultures (5 km)	−0.659	−0.578	−0.576	0.821	0.893	—	−0.856
distance from St Lawrence River	0.656	0.548	0.514	−0.772	−0.758	−0.856	—

MgCl₂; 0.008 mg BSA, 80 µM dNTPs, 500 mM of each primer, 2U AmpliTaq Gold (Applied Biosystems) and 20–40 ng DNA template. PCRs were also carried out on a GeneAmp 9700 thermocycler, with a thermal profile starting with an initial denaturing step at 95°C for 6 min, followed by 35 cycles of 95°C for 1 min, 52°C for 45 s and 72°C for 45 s, with a final run of 52°C for 1 min and 72°C for 10 min. Amplified bands from CHD-W and CHD-Z were distinguished on 3 per cent agarose gels.

(d) Data analysis

The occurrence of genotyping errors was investigated using MICROCHECKER v. 2.2.3 (Van Oosterhout *et al.* 2004). The presence of null alleles was assessed using CERVUS v. 3.0.3 (Marshall *et al.* 1998), and tests of linkage disequilibrium (LD), Hardy–Weinberg equilibrium (HWE) and heterozygote deficiency were performed using GENEPOP v. 4 (Raymond & Rousset 1995). Sequential Bonferroni correction for multiple tests was applied to null alleles, HWE and LD analyses (Rice 1989).

(i) Population genetic structure

We first assessed the extent of genetic differentiation among farms in our study system by computing pairwise F_{ST} estimates between farms for each year, as well as overall mean F_{ST} value for each year, using ARLEQUIN v. 3.0 (Excoffier *et al.* 2005). Significance of F_{ST} values was assessed using 10 000 permutations. We further analysed the extent of spatio-temporal variability of the genetic structure by conducting a hierarchical analysis of gene diversity using the analysis of molecular variance (AMOVA) implemented in ARLEQUIN. In the AMOVA, we assessed the component of genetic diversity attributable to the variance (i) between years (temporal component), (ii) among farms within years (spatial component), and (iii) among individuals within farms.

To assess potential patterns of isolation by distance (IBD), we performed a Mantel test (Mantel 1967), which measures the association between matrices of pairwise genetic and geographical distance, using SPAGEDI v. 1.2 (Hardy & Vekemans 2002). However, since all pairwise F_{ST} values among farms were non-significant (see §3), we instead performed an analysis at the individual level. We thus used Lynch & Ritland's (1999) measure of relatedness (r_{xy}) to infer a genetic distance between all pairs of individuals and then related these measures to Euclidian pairwise geographical distances, which were calculated from the geographical coordinates of the nest-boxes in which tree swallows were captured. Five thousand matrix

randomizations were performed to assess the statistical significance of tests in each year.

We further used a Bayesian clustering approach, without any *a priori* assumption of population structuring, in order to detect the occurrence of a potential population genetic structure. We first estimated the most likely number of genetic clusters in our dataset using STRUCTURE v. 2.2 (Pritchard *et al.* 2000). We performed the analyses using the admixture model with correlated allele frequency and the following parameters values: $\lambda = 1.0$, a burn-in period of 50 000 iterations and 250 000 replicates of the Markov chain. Five independent runs were conducted for each value of K (number of populations), with K ranging from 1 to 40 (the maximum value of K being set to the number of farms in our study system), and the $\log \Pr(X|K)$ averaged for each K . Analyses were conducted separately for each year. Since the maximum value of log likelihood was reached at $K = 1$ for both years, indicating a single genetic cluster, no further analyses were performed to assess the extent of differentiation among groups.

(ii) Individual genetic diversity

Individual genetic diversity was assessed using internal relatedness (IR; Amos *et al.* 2001). IR is a multilocus estimate derived from Queller & Goodnight's (1989) measure of relatedness, which estimates the resemblance between parental half-genotypes within an individual and weights the importance of each allele according to its frequency in the population (Amos *et al.* 2001). IR values were calculated using an Excel macro (IRmacroN4) available at: <http://www.zoo.cam.ac.uk/zoostaff/amos/#ComputerPrograms>. We also estimated individual genetic diversity using the homozygosity by loci (HL) index (see Aparicio *et al.* 2006) but present only the results pertaining to IR, since IR and HL were highly correlated ($r = 0.98$, $p < 0.001$).

(e) Statistical analyses

Since landscape composition variables showed strong, positive correlations across scales (table 1), and as a result led to identical qualitative effects of culture types on genetic diversity across spatial scales, we present only the results obtained with cultures measured within 500 m of nest-boxes. We tested for the effects of extensive and intensive cultures at 500 m on IR using general linear regression models. We accounted for possible differences between males and females, as well as between years, by including sex and year as factors in our analyses. In order to determine which landscape or ecological parameters were the most important determinants of the distribution of individual genetic diversity, we built a series of models containing all possible

combinations of explanatory variables (distance from the St Lawrence River, proportion of extensive and intensive cultures at 500 m, year and sex) and compared them using Akaike's information criterion (AIC; defining the model with the lowest AIC value as the best model). We also computed the weight of evidence of each model (w_i), which corresponds to the likelihood that a model is the best one in the model set given the data (Burnham & Anderson 2002). However, given the strong negative correlation between extensive and intensive cultures (table 1), we tested only for the effect of one of these variables at a time in our final analyses. As the effects of extensive and intensive cultures always pointed to the same conclusions (through opposite effects), we decided to report only the results for extensive cultures as they showed the best fit to our data. The presence of second-order quadratic relationships among variables was also tested, but none were significant.

We further investigated whether the settlement behaviour of individuals could play a role in the spatial distribution of individual genetic diversity by testing the effects of IR on the settlement dates of individuals, using generalized linear models (GLM) with a Poisson error structure and a log link function, which also included distance from the St Lawrence River, individual body mass and year as explanatory variables. Settlement dates and measures of body mass were defined for 726 individuals. Since the first date of settlement differed between 2006 and 2007, we standardized our data by defining the first settlement date in each year as being day 1. We again built a series of models containing all possible combinations of explanatory variables for this analysis, and compared them using AIC and their weight of evidence. No evidence for over-dispersion was found in any of the models tested. All statistical tests were performed using the R statistical environment v. 2.7.1. (R Development Core Team 2008).

3. RESULTS

(a) Microsatellite polymorphism

Three out of the 10 amplified loci (HrU5, TBI 106 and Hir 17) showed significant departures from HWE and high probabilities of null alleles and so were discarded from the analyses. A total of 815 individuals (144 of which were captured during both study years) were genotyped at up to seven loci (mean number $\pm$ s.d. of adults analysed per farm: 2006: 12.7 ± 0.8 ; 2007: 11.1 ± 0.9). Individuals for which sex could not be determined and/or those that were genotyped at less than three loci ($n=6$) were removed from the analyses. Number of alleles per locus varied from 6 to 20 (mean: 12.1), with a mean expected heterozygosity of 0.78 (range: 0.63–0.88; table 1 in the electronic supplementary material). We found no significant percentage of null alleles and no evidence of LD for any pairwise comparison of loci after sequential Bonferroni correction (results not shown). Three out of the seven loci (IBI Ms3-31, HrU7 and Hir 22) showed significant deviation from HWE when both years were analysed together (see table 1 in the electronic supplementary material). These three loci were nevertheless included in the remaining analyses as none of them showed consistent deviation across years. Mean IR for individuals caught dead in nest-boxes did not differ significantly from the rest of the population (mean IR $\pm$ s.d. of dead individuals:

Figure 2. Effect of the proportion of extensive cultures within 500 m of each nest-box on the number of fledglings. For illustration purposes, each circle represents mean values ($\pm$ s.e.) for eight classes of proportion of extensive cultures. The effect of the proportion of extensive cultures at 500 m on the number of fledglings was significant ($b=1.288 \pm 0.587$, $p=0.035$) when analysed using a linear mixed model with farm identity included as a random term ($n=515$).

-0.03 ± 0.18 , mean IR $\pm$ s.d. for the remaining individuals: 0.04 ± 0.20 , $t=1.30$, $p=0.22$).

(b) Population genetic structure

Overall F_{ST} values across farms were small and non-significant (2006: $F_{ST}=-0.001$, $p=0.73$; 2007: $F_{ST}=-0.002$, $p=0.83$), with pairwise F_{ST} values ranging from -0.110 to 0.150 for 2006 and from -0.081 to 0.082 for 2007. All pairwise comparisons were non-significant after sequential Bonferroni correction, indicating no genetic differentiation among farms within our study area. AMOVA analyses also revealed no significant variance partitioning of genetic diversity between study years (-0.04% , $p=0.86$) or among farms within years (-0.12% , $p=0.91$). Bayesian clustering analyses performed with STRUCTURE revealed that maximum log-likelihood values of the data were obtained at $K=1$ for both study years, indicating the presence of a single genetic cluster over the study area. Yet, analyses of IBD revealed a significant positive relationship between the pairwise relatedness of individuals and geographical distance in 2007 ($b=5.04 \times 10^{-8}$, $p=0.001$, $r=6.73 \times 10^{-5}$), indicating that more genetically similar individuals distributed themselves further apart than expected by chance. This relationship was also observed in 2006 but did not reach significance ($b=2.66 \times 10^{-8}$, $p=0.09$, $r=1.65 \times 10^{-5}$).

(c) Environment and individual genetic diversity

We first confirmed that the proportion of extensive cultures at 500 m was positively related to fledging success over the study period (see figure 2; see also Ghilain & Bélisle 2008), thus suggesting that habitat quality increases with the amount of extensive cultures. IR increased with the proportion of extensive cultures within 500 m of nest-boxes (table 2; figure 3). Thus, contrary to our expectations, a higher proportion of extensive cultures in the landscape is related to higher values of IR (i.e. lower genetic diversity). The best five models following comparisons based on AIC all

Table 2. Effects of culture types on adult tree swallows' individual genetic diversity as measured by IR. ((a) Full extensive culture (500 m) general linear model, with significance of each term included in the model. (b) Final extensive culture (500 m) model, with a significant term only. Number of observations = 952.)

(a) full extensive model				(b) final extensive model		
variable	<i>t</i> -statistic	d.f.	<i>p</i> -value		estimate	s.e.
extensive cultures (500 m)	2.71	1	0.007	extensive cultures (500 m)	0.083	0.031
year (2006 versus 2007)	−0.71	1	0.477			
sex	0.11	1	0.914

Figure 3. Relationship between extensive cultures within 500 m around each nest-box and IR. Each circle represents mean values ($\pm$ s.e.) for each farm in the study system ($n=952$).

contained the proportion of extensive cultures at 500 m as an explanatory variable (see table 2 in the electronic supplementary material). Results were also consistent across loci, with six out of seven loci showing a positive association between extensive cultures at 500 m and IR. No significant effects of sex or year were found for any of the analyses (see table 2; see also the electronic supplementary material, table 2). Interactions between extensive cultures and sex as well as between extensive cultures and year were also tested and were not significant (results not shown).

Settlement date was positively correlated with the distance from the St Lawrence River ($r=0.15$, $p<0.001$). These results effectively suggest that tree swallows consistently enter our study area from the St Lawrence River during spring migration. We further found a significant positive relationship between the IR and settlement date of individuals (table 3; figure 4a), suggesting that individuals of higher genetic diversity settle earlier on their breeding sites. IR was included in the best two models in the AIC analyses (see table 3 in the electronic supplementary material), providing further support for the importance of individual genetic diversity in explaining the settlement pattern of individuals. Again, results were consistent across loci, with six out of seven loci showing a positive association between IR and settlement date. A more detailed inspection of this relationship revealed that it seems mainly driven by females ($b=0.295$, $p=0.024$, $n=456$) rather than males ($b=0.006$, $p=0.97$, $n=270$). Interestingly, we also found that individuals

with larger body mass arrived earlier in our study area (table 3, figure 4b). This relationship was found for both females ($b=-0.107$, $p<0.001$) and males ($b=-0.105$, $p=0.001$). The effects of IR and body mass seem largely independent as the correlation between them is very low and non-significant ($r=-0.01$, $p=0.78$).

We also assessed whether early settlement on the breeding sites translated into a higher reproductive success for tree swallows. We found no direct relationships between individual genetic diversity or settlement date and clutch size, brood size or number of fledglings (results not shown). However, settlement date ($r=0.52$, $p<0.001$), but not individual genetic diversity ($r=0.05$, $p=0.32$), was significantly correlated with laying date, which itself influences clutch size and the number of fledglings in our study system (Ghilain & Bélisle 2008).

4. DISCUSSION

Here we assessed the population genetic structure and the distribution of individual genetic diversity of a wild bird species along a gradient of agricultural intensification. We found no evidence of population genetic structuring over time or space for tree swallows, using either traditional population genetics methods or a landscape genetics approach. However, we found a non-random distribution of individual genetic variability that depended on landscape features. Specifically, individuals of greater genetic diversity were found in less extensive agricultural landscapes, which are composed of poorer quality habitat. This pattern seems to be partly generated by the earlier arrival and settlement of the most genetically diversified individuals into breeding sites closer to the St Lawrence River, which also correspond to less extensive agricultural habitats.

(a) Population genetic structure

Tree swallows in our study area belong to a single genetic population, with no apparent barrier to gene flow resulting from landscape heterogeneity. Birds, in general, are expected to show relatively lower levels of population differentiation than other taxa due to their high dispersal potential (Crochet 2000). Yet, some studies have found evidence for fine-scale genetic structure between social units in cooperatively breeding species (Double *et al.* 2005; Temple *et al.* 2006; Woxvold *et al.* 2006), and a few others have shown landscape-based population genetic structure

Table 3. GLM (Poisson error structure and log-link function) of effects of IR, distance from the St Lawrence River, year and body mass on tree swallows' settlement dates. (Number of observations = 726.)

variable	<i>z</i> -statistic	d.f.	<i>p</i> -value	estimate	s.e.
internal relatedness	2.06	1	0.040	0.221	0.107
distance from St Lawrence River	6.60	1	<0.001	0.006	0.001
year (2006 versus 2007)	1.86	1	0.064	0.079	0.043
body mass	−6.12	1	<0.001	−0.080	0.013

Figure 4. Effects of (a) IR and (b) body mass on the settlement date of tree swallows. Settlement dates correspond to adjusted values from a GLM (Poisson error structure and log link function) including IR, body mass, distance from the St Lawrence River and year ($n=726$).

(Barr *et al.* 2008; Hull *et al.* 2008). However, the vast majority of studies reporting a relationship between habitat fragmentation and genetic structure involved non-migratory birds (Bates 2002; Caizergues *et al.* 2003; Segelbacher *et al.* 2008). The effects of habitat fragmentation on migratory passerines are, on the other hand, equivocal, as several studies have found no effect of fragmentation on genetic structure (Galbusera *et al.*

2004; Veit *et al.* 2005), while others have shown that agricultural land cover can reduce dispersal and gene flow between populations (Lindsay *et al.* 2008).

Several species-specific processes could help explain the lack of genetic substructure in our study system. First, natal dispersal over large distances (our study: mean $\pm$ s.d. = 10 ± 15 km; $n=8$; see also Winkler *et al.* (2005) for similar natal dispersal distance) probably plays an important role in the homogenization of the population structure. The return rate of nestlings born in our study area is quite low (approx. 1% of the nestlings banded in 2006 returned as breeders in 2007, in comparison with values ranging from 3.0 to 4.9% found in other tree swallow populations; Shutler & Clark 2003; Winkler *et al.* 2005), but is still arguably sufficient to limit the potential genetic substructuring in our system. Also, we found that more related individuals tended to be more geographically distant than expected by chance alone. While this trend was fairly weak, it still suggests another possible constraint acting against genetic population substructuring in our system. Finally, extra-pair fertilization is an additional mechanism potentially contributing to the homogenization of the genetic structure of tree swallows. Although data specific to our population are lacking, the tree swallow is one of the species with the highest levels of extra-pair paternities among birds, with above 75 per cent of nests containing at least one extra-pair young (reviewed by Griffith *et al.* 2002). Furthermore, female tree swallows seek extra-pair copulations with more geographically distant males (Dunn *et al.* 1994; Kempenaers *et al.* 2001; Stapleton *et al.* 2007) as well as with more genetically dissimilar males (Stapleton *et al.* 2007), thereby increasing the possible homogenizing effect of this behaviour on the genetic population structure of this species.

(b) Non-random distribution of individual genetic diversity

Intraspecific competition for nest sites in tree swallows leads to two predictions relative to the distribution of individuals within the landscape. First, theoretical work suggests that individuals of higher phenotypic and genetic quality should occupy the best habitats (Stamps 2006). In birds, for example, individuals in better condition may be favoured during competition for better quality habitats, or be able to prospect a greater number of potential breeding sites than individuals in lower condition (Stamps 2006). Empirical studies have indeed found support for this prediction (Seddon *et al.* 2004; Garant *et al.* 2005b). For example, Seddon *et al.* (2004) found that, in a population of subdesert mesite (*Monias benshii*), territory size, which is

positively related to habitat quality, increases with male heterozygosity. Here we not only failed to find the expected relationship between individual genetic quality (measured as genetic diversity) and habitat quality, but also even found support for the inverse relationship. A first possible explanation for this counter-intuitive result is that the resulting distribution of individual genetic diversity might be due to stronger selection acting against breeding individuals with lower genetic quality in a poorer habitat. If selection consistently removes individuals of lower genetic diversity (higher IR) in less extensive habitats, then we expect to see a reduction in variance of IR in such habitats. A closer inspection of our dataset indeed suggests a general increase in the variance in IR values with a more extensive habitat (comparisons of variance in IR among subsets of individuals distributed among eight subsets of extensive cultures, $r = 0.74$, $p = 0.035$).

Another possible explanation for the observed inverse association between habitat and individual quality is related to the differential settlement pattern in our study system. In general, individuals of higher quality should also be the first to arrive and settle on their breeding grounds, since migratory birds that arrive earlier generally gain access to better quality habitats (Smith & Moore 2005; Sergio *et al.* 2007), have higher chances of acquiring a mate (Lozano *et al.* 1996; Currie *et al.* 2000) and are more likely to be in good condition and sustain the costs of an early arrival (Møller 1994). Accordingly, we found that individuals with larger body mass and females with greater genetic diversity settled earlier on their breeding sites. Only, in our system, the migration routes followed by swallows seem to affect the habitats that are encountered first. Indeed, tree swallows in southern Québec follow the St Lawrence River before entering their breeding grounds, and therefore initially fly above intensively managed habitats that are of lower quality for this species (figure 1; Ghilain & Bélisle 2008).

The association we found between higher levels of genetic diversity and earlier settlement is, to our knowledge, the first documented evidence of a relationship between genetic diversity and breeding settlement in birds. Such a pattern has, however, been documented for mammals, as Hoffman *et al.* (2004) found that male Antarctic fur seals (*Arctocephalus gazella*) with lower IR values arrived first on their breeding grounds and were more likely to hold territories in poor breeding seasons, possibly due to their greater competitive ability. Since we have no direct measures of inter-individual competition other than settlement order, the underlying processes involved in the final distribution of individuals in our system remain to be investigated.

(c) *A possible mismatch between habitat quality and preference?*

Breeding sites occupied earlier by birds often correspond to high-quality, preferred habitats (Battin 2004). Our results suggest a possible mismatch between habitat quality and preference of tree swallows. It has been shown that birds can assess habitat quality based on vegetation structure (Orians & Wittenberger 1991) or by using social information from the previous

breeding season, such as fledging number and quality (Doligez *et al.* 2002; Parejo *et al.* 2007). Although the cues used by tree swallows to assess habitat quality when searching for a potential breeding site remain unclear, two factors suggest that more extensive agricultural fields should correspond to their preferred habitats. First, agricultural intensification is commonly linked to a homogenization of the vegetation structure, itself associated with a diminution of the abundance and diversity of insects and arthropods (Schweiger *et al.* 2005). We can thus reasonably expect that, based on either vegetation or food availability cues, tree swallows' preferred habitats should correspond to the more extensive farms. Second, since reproductive success of tree swallows in our study area is higher in more extensive habitats (Ghilain & Bélisle 2008), social information obtained during prospecting at the end of a breeding season should also lead to a preference for sites located on more extensive agricultural land. Thus, our findings that the levels of individual genetic diversity are higher in poorer quality habitats could suggest the presence of other cues used by tree swallows to assess habitat quality, or the role of other mechanisms involved in breeding site selection in this species.

Our results emphasize the importance of integrating spatial information on habitats as well as spatial patterns of migration to better predict individual habitat selection. Theoretical and empirical studies relating habitat preference and quality often focus on resident species and thus assume that individuals have a complete knowledge of the quality of available habitats (Battin 2004). However, migratory birds have to select a breeding site in a short time-frame upon their arrival from migration, often within a few days or even hours (Battin 2004). Early arriving individuals may thus choose to settle rapidly in a suboptimal habitat instead of further exploring the landscape for better quality territories, especially if nest site availability is a limiting factor in this habitat. For example, Aebischer *et al.* (1996) have shown in Savi's warbler (*Lucostella luscinioides*) that individuals arriving first on breeding grounds chose territories based on the presence of available nesting sites, rather than food availability. Tree swallows, which are obligate secondary-cavity nesters, are dependent on either natural cavities or nest-boxes for breeding. Nest site availability may thus constrain nest site selection rather than food availability, since tree swallows are also able to travel through distances above 10 km for foraging (Dunn & Whittingham 2005), which could partly explain why early arriving individuals would choose to settle in the first available breeding sites despite their lower habitat quality. Individuals settling earlier in our study area may still gain some benefits through earlier egg laying (see also Aebischer *et al.* 1996; Smith & Moore 2005). However, negative effects of agricultural intensification on reproductive success seem to outweigh the indirect benefits of early settlement in our study system. Indeed, clutch size, the number of fledglings and fledging probability are higher in more extensive habitats, despite the later laying dates in those habitats (Ghilain & Bélisle 2008). Our results thus raise the possibility that

less extensive habitats closer to the St Lawrence River, where reproductive success is lower, may act as an ecological trap. Ecological traps are defined as low-quality habitats that are preferred by individuals, causing a mismatch between habitat preference and fitness (Gates & Gysel 1978). Rapid ecological changes are usually suggested to be important factors modulating the formation of ecological traps, as individuals may not have enough time to adjust to such changes, through behavioural plasticity or adaptation, and thus end up using cues formerly predictive of good quality habitats (Schlaepfer et al. 2002; Battin 2004). Habitat modifications due to human activities may have led to the formation of an ecological trap in our tree swallow population, since agricultural intensification in southern Québec has rapidly transformed the landscape in less than 40 years (Bélanger & Grenier 2002) and thus nest site availability may have previously served as a good indicator of habitat quality for tree swallows in the former more extensive landscape.

In conclusion, we have shown that ecological and landscape characteristics influence the distribution of individual genetic diversity in a wild bird population. Our results confirm the usefulness of combining molecular tools, spatial analyses and data on population ecology and underline the importance of incorporating the effects of habitat quality and behavioural patterns when assessing factors shaping genetic diversity in the wild. Our results also highlight the value of collecting data over large scales to reveal the ecological effects of habitat modifications and their interactions with evolutionary processes.

We are grateful to the research assistants who helped collect data in the field and to the 40 farm owners who allowed us to use their land for our research. We especially acknowledge Mélissa Lieutenant-Gosselin for her help with laboratory work. We also want to thank two anonymous referees for their constructive comments on the manuscript. This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants (D.G. and M.B.), by a New Researcher start-up programme grant from the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) (D.G.), by the Canadian Foundation for Innovation (CFI; D.G. and M.B.) and by the Canada Research Chair in Spatial and Landscape Ecology (M.B.). All procedures were in accordance with the Animal Care and Use Committee of Université de Sherbrooke, Canada (protocol DG-01).

REFERENCES

- Aebischer, A., Perrin, N., Krieg, M., Studer, J. & Meyer, D. R. 1996 The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. *J. Avian Biol.* **27**, 143–152. (doi:10.2307/3677143)
- Aljanabi, S. M. & Martinez, I. 1997 Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Res.* **25**, 4692–4693. (doi:10.1093/nar/25.22.4692)
- Amos, W., Wilmer, J. W., Fullard, K., Burg, T. M., Croxall, J. P., Bloch, D. & Coulson, T. 2001 The influence of parental relatedness on reproductive success. *Proc. R. Soc. B* **268**, 2021–2027. (doi:10.1098/rspb.2001.1751)
- Aparicio, J. M., Ortego, J. & Cordero, P. J. 2006 What should we weigh to estimate heterozygosity, alleles or loci? *Mol. Ecol.* **15**, 4659–4665. (doi:10.1111/j.1365-294X.2006.03111.x)
- Baille, J. E. M., Hilton-Taylor, C. & Stuart, S. N. (eds) 2004 *2004 IUCN red list of threatened species: a global species assessment*. Cambridge, UK: IUCN.
- Barr, K. R., Lindsay, D. L., Athrey, G., Lance, R. F., Hayden, T. J., Tweddle, S. A. & Leberg, P. L. 2008 Population structure in an endangered songbird: maintenance of genetic differentiation despite high vagility and significant population recovery. *Mol. Ecol.* **17**, 3628–3639. (doi:10.1111/j.1365-294X.2008.03868.x)
- Bates, J. M. 2002 The genetic effects of forest fragmentation on five species of Amazonian birds. *J. Avian Biol.* **33**, 276–294. (doi:10.1034/j.1600-048X.2002.330310.x)
- Battin, J. 2004 When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* **18**, 1482–1491. (doi:10.1111/j.1523-1739.2004.00417.x)
- Bélanger, L. & Grenier, M. 2002 Agriculture intensification and forest fragmentation in the St Lawrence valley, Quebec, Canada. *Landsc. Ecol.* **17**, 495–507. (doi:10.1023/A:1021443929548)
- Benton, T. G., Vickery, J. A. & Wilson, J. D. 2003 Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**, 182–188. (doi:10.1016/S0169-5347(03)00011-9)
- Bishop, J. M., O'Ryan, C. & Jarvis, J. U. M. 2007 Social common mole-rats enhance outbreeding via extra-pair mating. *Biol. Lett.* **3**, 176–179. (doi:10.1098/rsbl.2006.0607)
- Burger, R. & Lynch, M. 1995 Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution* **49**, 151–163. (doi:10.2307/2410301)
- Burnham, K. P. & Anderson, D. R. 2002 *Model selection and inference: a practical information-theoretic approach*. New York, NY: Springer.
- Caizergues, A., Ratti, O., Helle, P., Rotelli, L., Ellison, L. & Rasplus, J. Y. 2003 Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. *Mol. Ecol.* **12**, 2297–2305. (doi:10.1046/j.1365-294X.2003.01903.x)
- Canadian Wildlife Service 2004 *Occupation du sol à partir des images classifiées Landsat-7, Sud du Québec, 1999–2003*. Québec, Canada: Environnement Canada, région du Québec.
- Clark, R. W., Brown, W. S., Stechert, R. & Zamudio, K. R. 2008 Integrating individual behaviour and landscape genetics: the population structure of timber rattlesnake hibernacula. *Mol. Ecol.* **17**, 719–730. (doi:10.1111/j.1365-294X.2007.03594.x)
- Cohas, A., Yoccoz, N. G., Da Silva, A., Goossens, B. & Allaine, D. 2006 Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. *Behav. Ecol. Sociobiol.* **59**, 597–605. (doi:10.1007/s00265-005-0086-8)
- Crochet, P. A. 2000 Genetic structure of avian populations—allozymes revisited. *Mol. Ecol.* **9**, 1463–1469. (doi:10.1046/j.1365-294X.2000.01026.x)
- Crossman, C. C. 1996 *Single locus DNA profiling in the tree swallow Tachycineta bicolor: a comparison of methods*. Kingston, Canada: Queen's University.
- Currie, D., Thompson, D. B. A. & Burke, T. 2000 Patterns of territory settlement and consequences for breeding success in the northern wheatear *Oenanthe oenanthe*. *Ibis* **142**, 389–398. (doi:10.1111/j.1474-919X.2000.tb04435.x)

- Dibattista, J. D., Feldheim, K. A., Gruber, S. H. & Hendry, A. P. 2008 Are indirect genetic benefits associated with polyandry? Testing predictions in a natural population of lemon sharks. *Mol. Ecol.* **17**, 783–795. (doi:10.1111/j.1365-294X.2008.03833.x)
- Dionne, M., Caron, F., Dodson, J. J. & Bernatchez, L. 2008 Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. *Mol. Ecol.* **17**, 2382–2396. (doi:10.1111/j.1365-294X.2008.03771.x)
- Doligez, B., Danchin, E. & Clobert, J. 2002 Public information and breeding habitat selection in a wild bird population. *Science* **297**, 1168–1170. (doi:10.1126/science.1072838)
- Donald, P. F., Sanderson, F. J., Burfield, I. J. & van Bommel, F. P. J. 2006 Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agric. Ecosyst. Environ.* **116**, 189–196. (doi:10.1016/j.agee.2006.02.007)
- Double, M. C., Peakall, R., Beck, N. R. & Cockburn, A. 2005 Dispersal, philopatry, and infidelity: dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). *Evolution* **59**, 625–635. (doi:10.1554/04-166)
- Downes, C. M. & Collins, B. T. 2008 *Canadian bird trends web site version 2.2*. Ottawa, Canada: Canadian Wildlife Service, Environment Canada.
- Dunn, P. O. & Whittingham, L. A. 2005 Radio-tracking of female tree swallows prior to egg-laying. *J. Field Ornithol.* **76**, 259–263.
- Dunn, P. O., Robertson, R. J., Michaud-Freeman, D. & Boag, P. T. 1994 Extra-pair paternity in tree swallows: why do females mate with more than one male? *Behav. Ecol. Sociobiol.* **35**, 273–281. (doi:10.1007/BF00170708)
- ESRI 2005 *Patch analyst 2.0a patch for French language*. Redlands, CA: ESRI.
- Ettersson, J. R. 2004 Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. II. Genetic architecture of three populations reciprocally planted along an environmental gradient in the great plains. *Evolution* **58**, 1459–1471. (doi:10.1554/03-375)
- Excoffier, L., Laval, G. & Schneider, S. 2005 ARLEQUIN, version 3.0: an integrated software package for population genetic data analysis. *Evol. Bioinform. Online* **1**, 47–50.
- Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford, UK: Oxford University Press.
- Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J. T. & Kempenaers, B. 2003 Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* **425**, 714–717. (doi:10.1038/nature01969)
- Frankham, R. 1995 Conservation genetics. *Annu. Rev. Genet.* **29**, 305–327. (doi:10.1146/annurev.ge.29.120195.001513)
- Galbusera, P., Githiru, M., Lens, L. & Matthysen, E. 2004 Genetic equilibrium despite habitat fragmentation in an Afrotropical bird. *Mol. Ecol.* **13**, 1409–1421. (doi:10.1111/j.1365-294X.2004.02175.x)
- Garant, D., Dodson, J. D. & Bernatchez, L. 2005a Offspring genetic diversity increases fitness of female Atlantic salmon (*Salmo salar*). *Behav. Ecol. Sociobiol.* **57**, 240–244. (doi:10.1007/s00265-004-0854-x)
- Garant, D., Kruuk, L. E. B., Wilkin, T. A., McCleery, R. H. & Sheldon, B. C. 2005b Evolution driven by differential dispersal within a wild bird population. *Nature* **433**, 60–65. (doi:10.1038/nature03051)
- Gates, J. E. & Gysel, L. W. 1978 Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**, 871–883. (doi:10.2307/1938540)
- Ghilain, A. & Bélisle, M. 2008 Breeding success of tree swallows along a gradient of agricultural intensification. *Ecol. Appl.* **18**, 1140–1154. (doi:10.1890/07-1107.1)
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002 Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**, 2195–2212. (doi:10.1046/j.1365-294X.2002.01613.x)
- Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998 A DNA test to sex most birds. *Mol. Ecol.* **7**, 1071–1075. (doi:10.1046/j.1365-294x.1998.00389.x)
- Hannah, L., Carr, J. L. & Landerani, A. 1995 Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodivers. Conserv.* **4**, 128–155. (doi:10.1007/BF00137781)
- Hansson, B., Bensch, S., Hasselquist, D. & Akesson, M. 2001 Microsatellite diversity predicts recruitment of sibling great reed warblers. *Proc. R. Soc. B* **268**, 1287–1291. (doi:10.1098/rspb.2001.1640)
- Hardy, O. J. & Vekemans, X. 2002 SPAGeDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol. Ecol. Notes* **2**, 618–620. (doi:10.1046/j.1471-8286.2002.00305.x)
- Hoffman, J. I., Boyd, I. L. & Amos, W. 2004 Exploring the relationship between parental relatedness and male reproductive success in the Antarctic fur seal *Arctocephalus gazella*. *Evolution* **58**, 2087–2099. (doi:10.1554/04-099)
- Hull, J. M., Hull, A. C., Sacks, B. N., Smith, J. P. & Ernest, H. B. 2008 Landscape characteristics influence morphological and genetic differentiation in a widespread raptor (*Buteo jamaicensis*). *Mol. Ecol.* **17**, 810–824.
- IPCC 2007 *Climate change 2007: impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change* (eds M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden & C. E. Hanson). Cambridge, UK: Cambridge University Press.
- Kempenaers, B. 2007 Mate choice and genetic quality: a review of the heterozygosity theory. *Adv. Stud. Behav.* **37**, 189–278. (doi:10.1016/S0065-3454(07)37005-8)
- Kempenaers, B., Everding, S., Bishop, C., Boag, P. & Robertson, R. J. 2001 Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*). *Behav. Ecol. Sociobiol.* **49**, 251–259. (doi:10.1007/s002650000305)
- Keyghobadi, N., Roland, J. & Strobeck, C. 2005 Genetic differentiation and gene flow among populations of the alpine butterfly, *Parnassius smintheus*, vary with landscape connectivity. *Mol. Ecol.* **14**, 1897–1909. (doi:10.1111/j.1365-294X.2005.02563.x)
- Kretzmann, M., Mentzer, L., DiGiovanni, R., Leslie, M. S. & Amato, G. 2006 Microsatellite diversity and fitness in stranded juvenile harp seals (*Phoca groenlandica*). *J. Hered.* **97**, 555–560. (doi:10.1093/hered/esl043)
- Lenormand, T. 2002 Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17**, 183–189. (doi:10.1016/S0169-5347(02)02497-7)
- Lindsay, D. L., Barr, K. R., Lance, R. F., Tweddle, S. A., Hayden, T. J. & Leberg, P. L. 2008 Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). *Mol. Ecol.* **17**, 2122–2133. (doi:10.1111/j.1365-294X.2008.03673.x)
- Lozano, G. A., Perreault, S. & Lemon, R. E. 1996 Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *J. Avian Biol.* **27**, 164–170. (doi:10.2307/3677146)
- Lynch, M. & Ritland, K. 1999 Estimation of pairwise relatedness with molecular markers. *Genetics* **152**, 1753–1766.
- Manel, S., Schwartz, M. K., Luikart, G. & Taberlet, P. 2003 Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* **18**, 189–197. (doi:10.1016/S0169-5347(03)00008-9)

- Mantel, N. 1967 The detection of disease clustering and a generalized regression approach. *Cancer Res.* **27**, 209–220.
- Marshall, R. C., Buchanan, K. L. & Catchpole, C. K. 2003 Sexual selection and individual genetic diversity in a songbird. *Proc. R. Soc. B* **270**, S248–S250. (doi:10.1098/rsbl.2003.0081)
- Marshall, T. C., Slate, J., Kruuk, L. E. B. & Pemberton, J. M. 1998 Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**, 639–655. (doi:10.1046/j.1365-294x.1998.00374.x)
- Møller, A. P. 1994 Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav. Ecol. Sociobiol.* **35**, 115–122. (doi:10.1007/BF00171501)
- Orians, G. H. & Wittenberger, J. F. 1991 Spatial and temporal scales in habitat selection. *Am. Nat.* **137**, S29–S49. (doi:10.1086/285138)
- Parejo, D., White, J., Clobert, J., Dreiss, A. & Danchin, E. 2007 Blue tits use fledgling quantity and quality as public information in breeding site choice. *Ecology* **88**, 2373–2382. (doi:10.1890/06-2000.1)
- Pelletier, F., Garant, D. & Hendry, A. P. 2009 Eco-evolutionary dynamics. *Phil. Trans. R. Soc. B* **364**, 1483–1489. (doi:10.1098/rstb.2009.0027)
- Primmer, C. R., Møller, A. P. & Ellegren, H. 1995 Resolving genetic relationships with microsatellite markers: a parentage testing system for the swallow *Hirundo rustica*. *Mol. Ecol.* **4**, 493–498. (doi:10.1111/j.1365-294X.1995.tb00243.x)
- Pritchard, J. K., Stephens, M. & Donnelly, P. 2000 Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.
- Queller, D. C. & Goodnight, K. F. 1989 Estimating relatedness using genetic markers. *Evolution* **43**, 258–275. (doi:10.2307/2409206)
- R Development Core Team 2008 *R: a language and environment for statistical computing*. Vienna, Austria: R Development Core Team.
- Raymond, M. & Rousset, F. 1995 GENETPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J. Hered.* **86**, 248–249.
- Rice, W. R. 1989 Analyzing tables of statistical tests. *Evolution* **43**, 223–225. (doi:10.2307/2409177)
- Robertson, R. J., Stutchbury, B. J. & Cohen, R. R. 1992 Tree swallow (*Tachycineta bicolor*). In *The birds of North America* (eds A. Poole, P. Stettenheim & F. Gill), pp. 1–28. Washington, DC: Academy of Natural Sciences.
- Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. 2002 Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480. (doi:10.1016/S0169-5347(02)02580-6)
- Schweiger, O. et al. 2005 Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *J. Appl. Ecol.* **42**, 1129–1139. (doi:10.1111/j.1365-2664.2005.01085.x)
- Seddon, N., Amos, W., Mulder, R. A. & Tobias, J. A. 2004 Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird. *Proc. R. Soc. B* **271**, 1823–1829. (doi:10.1098/rspb.2004.2805)
- Segelbacher, G., Manel, S. & Tomiuk, J. 2008 Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). *Mol. Ecol.* **17**, 2356–2367. (doi:10.1111/j.1365-294X.2008.03767.x)
- Sergio, F., Blas, J., Forero, M. G., Donazar, J. A. & Hiraldo, F. 2007 Sequential settlement and site dependence in a migratory raptor. *Behav. Ecol.* **18**, 811–821. (doi:10.1093/beheco/arm052)
- Shutler, D. & Clark, R. G. 2003 Causes and consequences of tree swallow (*Tachycineta bicolor*) dispersal in Saskatchewan. *Auk* **120**, 619–631. (doi:10.1642/0004-8038(2003)120[0619:CACOTS]2.0.CO;2)
- Smith, R. J. & Moore, F. R. 2005 Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behav. Ecol. Sociobiol.* **57**, 231–239. (doi:10.1007/s00265-004-0855-9)
- Soulé, J., Carré, D. & Jackson, W. 1990 Ecological impact of modern agriculture. In *Agroecology* (eds C. R. Carroll, J. H. Vandermeer & P. Rosser), pp. 165–188. New York, NY: McGraw-Hill.
- Spear, S. F., Peterson, C. R., Matocq, M. D. & Storfer, A. 2005 Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). *Mol. Ecol.* **14**, 2553–2564. (doi:10.1111/j.1365-294X.2005.02573.x)
- Stamps, J. A. 2006 The silver spoon effect and habitat selection by natal dispersers. *Ecol. Lett.* **9**, 1179–1185. (doi:10.1111/j.1461-0248.2006.00972.x)
- Stapleton, M. K., Kleven, O., Lifjeld, J. T. & Robertson, R. J. 2007 Female tree swallows (*Tachycineta bicolor*) increase offspring heterozygosity through extrapair mating. *Behav. Ecol. Sociobiol.* **61**, 1725–1733. (doi:10.1007/s00265-007-0404-4)
- Stenzler, L. M. 2001 *Genetic population structure in two bird species with contrasting dispersal behavior: the tree swallow and the Florida scrub jay*. Ithaca, NY: Cornell University Press.
- Storfer, A. et al. 2007 Putting the ‘landscape’ in landscape genetics. *Heredity* **98**, 128–142. (doi:10.1038/sj.hdy.6800917)
- Suter, S. M., Keiser, M., Feignoux, R. & Meyer, D. R. 2007 Reed bunting females increase fitness through extra-pair mating with genetically dissimilar males. *Proc. R. Soc. B* **274**, 2865–2871. (doi:10.1098/rspb.2007.0799)
- Temple, H. J., Hoffman, J. I. & Amos, W. 2006 Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the white-breasted thrasher, *Ramphocinclus brachyurus*. *Mol. Ecol.* **15**, 3449–3458. (doi:10.1111/j.1365-294X.2006.03006.x)
- Tomiuk, J., Stauss, M., Segelbacher, G., Fietz, J., Kompf, J. & Bachmann, L. 2007 Female genetic heterogeneity affects the reproduction of great tits (*Parus major* L., 1758) in low-quality woodlands. *J. Zool. Syst. Evol. Res.* **45**, 144–150. (doi:10.1111/j.1439-0469.2006.00382.x)
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. 2005 Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* **8**, 857–874. (doi:10.1111/j.1461-0248.2005.00782.x)
- Tsyusko, O. V., Peters, M. B., Hagen, C., Tuberville, T. D., Mousseau, T. A., Møller, A. P. & Glenn, T. C. 2007 Microsatellite markers isolated from barn swallows (*Hirundo rustica*). *Mol. Ecol. Notes* **7**, 833–835. (doi:10.1111/j.1471-8286.2007.01719.x)
- Vandergast, A. G., Bohonak, A. J., Weissman, D. B. & Fisher, R. N. 2007 Understanding the genetic effects of recent habitat fragmentation in the context of evolutionary history: phylogeography and landscape genetics of a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmidae: Stenopelmatus). *Mol. Ecol.* **16**, 977–992. (doi:10.1111/j.1365-294X.2006.03216.x)
- Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M. & Shipley, P. 2004 MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Notes* **4**, 535–538. (doi:10.1111/j.1471-8286.2004.00684.x)

- Veit, M. L., Robertson, R. J., Hamel, P. B. & Friesen, V. L. 2005 Population genetic structure and dispersal across a fragmented landscape in cerulean warblers (*Dendroica cerulea*). *Conserv. Genet.* **6**, 159–174. (doi:10.1007/s10592-004-7831-9)
- Venter, O., Brodeur, N. N., Nemiroff, L., Belland, B., Dolinsek, I. J. & Grant, J. W. A. 2006 Threats to endangered species in Canada. *Bioscience* **56**, 903–910. (doi:10.1641/0006-3568(2006)56[903:TTESIC]2.0.CO;2)
- Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. 1998 Quantifying threats to imperiled species in the United States. *Bioscience* **48**, 607–615. (doi:10.2307/1313420)
- Winkler, D. W., Wrege, P. H., Allen, P. E., Kast, T. L., Senesac, P., Wasson, M. F. & Sullivan, P. J. 2005 The natal dispersal of tree swallows in a continuous mainland environment. *J. Anim. Ecol.* **74**, 1080–1090. (doi:10.1111/j.1365-2656.2005.01007.x)
- Woxvold, I. A., Adcock, G. J. & Mulder, R. A. 2006 Fine-scale genetic structure and dispersal in cooperatively breeding apostlebirds. *Mol. Ecol.* **15**, 3139–3146. (doi:10.1111/j.1365-294X.2006.03009.x)
- Zedrosser, A., Bellemain, E., Taberlet, P. & Swenson, J. E. 2007 Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. *J. Anim. Ecol.* **76**, 368–375. (doi:10.1111/j.1365-2656.2006.01203.x)
- Zheng, C., Ovaskainen, O. & Hanski, I. 2009 Modelling single nucleotide effects in *phosphoglucose isomerase* on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Phil. Trans. R. Soc. B* **364**, 1519–1532. (doi:10.1098/rstb.2009.0005)