

STRUCTURE DE POPULATION ET DIVERSITÉ GÉNÉTIQUE DE L'HIRONDELLE
BICOLORE (*Tachycineta bicolor*) LE LONG D'UN GRADIENT DE QUALITÉ
D'HABITAT

par

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de l'obtention du grade de maître ès science (M.Sc.)

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La diversité génétique est un élément essentiel au maintien et à l'adaptation des populations en milieu naturel. Or, l'expansion actuelle de la population humaine et de ses activités entraîne de nombreux changements globaux susceptibles d'affecter les populations naturelles. Les perturbations de l'habitat peuvent notamment être responsables d'une réduction de la diversité génétique au sein des populations et des individus, diminuant le potentiel adaptatif et augmentant les risques d'extinction des populations. Dans ce contexte, il est crucial de comprendre l'influence des variables écologiques sur la variabilité génétique des populations en milieu naturel.

L'objectif de ma maîtrise est de déterminer, à l'aide d'une approche de génétique du paysage, la structure de population et l'effet de la qualité de l'habitat sur la diversité génétique de l'Hirondelle bicolore (*Tachycineta bicolor*), le long d'un gradient d'intensification agricole au sud du Québec. J'ai déterminé la présence d'une seule population au sein de l'aire d'étude ainsi qu'une légère association positive entre l'apparement des individus et la distance géographique, suggérant un mécanisme d'évitement de la consanguinité. Ensuite, j'ai montré que, dans notre système d'étude, la diversité génétique individuelle de l'Hirondelle bicolore est négativement reliée à la qualité de l'habitat. Ce résultat contre-intuitif s'explique probablement par la configuration du paysage dans cette région : suite à la migration, l'Hirondelle bicolore entre dans notre système d'étude *via* le fleuve Saint-Laurent, près duquel se trouvent les habitats de qualité inférieure; les premiers habitats disponibles rencontrés sont donc de moins bonne qualité. Or, les individus génétiquement plus diversifiés arrivent plus tôt dans le système d'étude et s'établissent dans les premiers habitats disponibles, générant cette relation négative entre qualité génétique individuelle et qualité de l'habitat.

Cette étude souligne l'importance des paramètres liés à la qualité de l'habitat et au comportement sur la diversité génétique en milieu naturel, en plus de constituer l'une des premières quantifications de l'effet de facteurs écologiques sur les niveaux et la distribution de la diversité génétique mesurée au niveau individuel.

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INTRODUCTION

La diversité génétique est un élément essentiel pour le maintien et l'adaptation des populations en milieu naturel (Fisher, 1930 ; Saccheri *et al.*, 1998 ; Spielman *et al.*, 2004). En effet, une réduction de la diversité génétique au sein des populations limite leur capacité à s'adapter à de nouvelles conditions de leur environnement (Burger et Lynch, 1995 ; Etterson, 2004). De plus, au niveau individuel, la diversité génétique est positivement associée à plusieurs traits liés au fitness, tels la résistance aux maladies (Acevedo-Whitehouse *et al.*, 2003), la survie (Coltman *et al.*, 1998 ; Kretzmann *et al.*, 2006), la probabilité de recrutement (Jensen *et al.*, 2007) et le succès reproducteur (Tomiuk *et al.*, 2007 ; Zedrosser *et al.*, 2007). Les niveaux de variabilité génétique observés en milieu naturel sont cependant susceptibles d'être affectés par des modifications de l'environnement, tels la perte des habitats naturels, la diminution de leur qualité ou leur fragmentation. En effet, ces modifications de l'environnement, en entraînant une diminution potentielle de la taille effective des populations ainsi qu'une réduction de la connectivité entre populations, peuvent affecter les forces évolutives (migration, sélection, dérive génique) influençant du même coup la structure et la diversité génétique des populations (Slatkin, 1985 ; Whitlock et Barton, 1997). Par exemple, plusieurs études montrent que la fragmentation de l'habitat augmente le niveau de différenciation génétique entre populations, dû à une réduction du flux génique (Keyghobadi, 2007 ; Whitlock, 1992). De plus, les populations fragmentées ou en déclin peuvent subir une diminution de leur diversité génétique au niveau populationnel (Frankham, 1996 ; Keyghobadi, 2007). L'isolement et la réduction de la taille effective de population peuvent aussi être liés à une hausse des niveaux de consanguinité et une diminution de la diversité génétique individuelle (Andersen *et al.*, 2004 ; Ortego *et al.*, 2008a).

Les changements environnementaux sont donc susceptibles d'affecter autant la structure des populations que les niveaux de diversité génétique au sein des populations et des individus. L'explication des mécanismes sous-jacents à la diversité génétique observée est alors essentielle autant pour la compréhension de l'évolution que pour l'établissement du potentiel de conservation des espèces. Or, l'une des conséquences majeures de l'expansion

de la population humaine et de ses activités est la grande vitesse des changements environnementaux actuels, notamment la destruction rapide des habitats naturels (Hannah *et al.*, 1995 ; IPCC, 2007). Nous observons présentement une réduction de la biodiversité à l'échelle mondiale (Dirzo et Raven, 2003), la perturbation des habitats naturels étant de loin la principale cause actuelle de l'extinction d'espèces et de populations (Baille *et al.*, 2004 ; Wilcove *et al.*, 1998). Cependant, malgré l'importance des changements environnementaux actuels et en dépit de l'intérêt majeur de ce genre de précision pour la biologie évolutive, peu d'études ont tenté de quantifier l'influence de variables écologiques liées à la qualité de l'habitat sur la variabilité génétique observée en milieu naturel, particulièrement au niveau de la diversité génétique individuelle.

Structure de population et variabilité génétique

Marqueurs moléculaires

La capacité à détecter la variation génétique dépend tout d'abord du pouvoir de résolution des marqueurs moléculaires utilisés (Parker *et al.*, 1998 ; Sunnucks, 2000). L'avènement de nouvelles techniques d'analyses moléculaires vers la fin des années 1980, comme l'amplification par réaction de polymérase en chaîne, a permis l'utilisation de plusieurs marqueurs moléculaires hautement polymorphiques, tels les microsatellites (Jarne et Lagoda, 1996). Ces derniers consistent en des régions neutres de l'ADN nucléaire contenant des séquences de 2 à 6 paires de bases répétées en tandem, dont le nombre de répétitions est très variable, dû à des mutations fréquentes lors de la réplication de l'ADN (Queller *et al.*, 1993). Ce fort taux de polymorphisme confère à ces marqueurs un plus grand pouvoir de détection de la variabilité génétique entre individus et populations comparativement à d'autres types de marqueurs traditionnellement utilisés en génétique des populations, tel les allozymes et l'ADN mitochondrial (Parker *et al.*, 1998 ; Ryman *et al.*, 2006). Les microsatellites sont maintenant couramment utilisés en génétique des populations, permettant entre autres la détection d'événements récents de migration (Bergl et Vigilant, 2007 ; Kuehn *et al.*, 2007), de structure génétique à fine échelle géographique (Nussey *et al.*, 2005 ; Shorey *et al.*, 2000), de déclin de taille de population (Garza et Williamson, 2001 ; Lee *et al.*, 2001) et d'effets de perturbations récentes de l'habitat sur la

variabilité génétique (Gerlach et Musolf, 2000 ; Martinez-Cruz *et al.*, 2007 ; Williams *et al.*, 2003).

Génétique du paysage

L'intégration de données génétiques provenant de tels marqueurs polymorphiques à de nouvelles méthodes d'analyses statistiques et d'outils informatiques puissants a permis l'émergence d'un nouveau domaine de recherche, la génétique du paysage (Manel *et al.*, 2003). Cette approche, qui combine génétique des populations, écologie du paysage et analyses spatiales, permet notamment de définir une structure de population sans avoir à déterminer *a priori* le nombre et l'emplacement des populations, ainsi que de mettre en relation des patrons de variabilité génétique observés avec des caractéristiques liées au paysage ou à l'environnement (Manel *et al.*, 2003 ; Storfer *et al.*, 2007).

L'approche traditionnelle en génétique des populations est basée sur l'échantillonnage de populations discrètes préalablement identifiées. Bien que, dans certains cas, il soit relativement facile de déterminer les frontières des populations, par exemple dans le cas d'organismes aquatiques dans différents lacs (Adams et Hutchings, 2003) ou différentes rivières (Tessier *et al.*, 1997), il arrive plus souvent que les individus soient distribués de façon plus continue dans l'espace, par exemple dans le cas d'organismes ayant une grande capacité de dispersion, comme les oiseaux. Cette distribution continue rend donc la délimitation des populations plus difficile et arbitraire. Or, de nouvelles méthodes d'analyse, tels les tests d'inférence bayésienne, permettent d'utiliser l'information obtenue à partir de génotypes individuels afin de détecter le nombre le plus probable de populations au sein d'une aire de distribution donnée et d'assigner chaque individu à une population (Dawson et Belkhir, 2001 ; Manel *et al.*, 2005 ; Pritchard *et al.*, 2000). Ce type d'analyse est maintenant couramment utilisé afin de définir la structure de population en milieu naturel (Coulon *et al.*, 2008 ; Croteau *et al.*, 2007 ; Dionne *et al.*, 2008), permettant la détection de populations différenciées même chez des espèces possédant une forte capacité de dispersion et en présence de flux génique entre populations (Martinez-Cruz *et al.*, 2004 ; Senar *et al.*, 2006). De plus, l'intégration de l'information sur la localisation géographique des individus aux analyses bayésiennes permet de détecter l'emplacement géographique de

discontinuités entre populations, et donc d'identifier des barrières au flux génique (Coulon *et al.*, 2006 ; Fedy *et al.*, 2008 ; Guillot *et al.*, 2005 ; McCairns et Bernatchez, 2008).

Dans d'autres cas, la structure de population suit un modèle d'isolement par la distance, où les individus géographiquement plus éloignés sont également plus différenciés (Wright, 1943). Le test de Mantel (Mantel, 1967) permet de mettre en évidence la présence d'isolement par la distance en testant la corrélation entre une matrice de distances génétiques (entre populations ou individus) et une matrice de distances géographiques (Crispo et Chapman, 2008 ; Francisco *et al.*, 2007 ; Hull *et al.*, 2008 ; Sumner *et al.*, 2001). Une association entre la variabilité génétique et la distance géographique peut également être mise en évidence par des analyses d'autocorrélation spatiale, qui permettent de tester si le génotype d'un individu à un endroit donné est dépendant du génotype des individus situés dans son voisinage (Smouse et Peakall, 1999 ; Sokal et Neal, 1978). Cette méthode offre la possibilité de détecter une structure de population à une échelle très fine, en plus de permettre de déterminer l'échelle spatiale à laquelle une structure génétique est observée (Double *et al.*, 2005 ; Elmer *et al.*, 2007 ; Temple *et al.*, 2006).

D'autres approches permettent d'intégrer de façon explicite l'effet de variables environnementales à l'étude de la génétique des populations, permettant une meilleure compréhension des processus écologiques sous-jacents à la variabilité génétique observée. Par exemple, les tests de Mantel partiels (Smouse *et al.*, 1986) peuvent être utilisés afin de déterminer si des paramètres écologiques permettent de mieux expliquer la structure génétique observée que la distance géographique seule. Plusieurs études ont ainsi montré l'effet de la composition du paysage sur la connectivité et la différenciation génétique entre populations, permettant de déterminer quelles caractéristiques du paysage facilitent ou contraignent le flux génique entre populations (Keyghobadi *et al.*, 1999 ; Spear *et al.*, 2005 ; Stevens *et al.*, 2006). Par exemple, Lindsay *et al.* (2008) ont ainsi trouvé que la différenciation génétique entre populations de paruline à dos noir (*Dendroica chrysoparia*) est positivement corrélée à la distance géographique et au pourcentage de terres agricoles entre populations, et négativement reliée au pourcentage de couvert forestier.

La génétique du paysage est donc un domaine de recherche prometteur permettant de mieux comprendre l'effet de modifications de l'habitat sur la variabilité génétique des populations. Cependant, plusieurs avenues de recherche sont encore à explorer dans ce domaine. Tout d'abord, un grand nombre d'études montrant les effets de modifications de l'environnement sur la variabilité génétique des populations sont effectuées en comparant les niveaux de différenciation entre populations et en estimant la diversité génétique au sein des populations situées en milieu perturbé et en milieu « contrôle » (Caizergues *et al.*, 2003 ; Dhuyvetter *et al.*, 2005 ; Johansson *et al.*, 2005 ; Keyghobadi *et al.*, 2005 ; Lesbarreres *et al.*, 2006 ; Segelbacher *et al.*, 2003 ; Stow *et al.*, 2001 ; Sumner, 2005 ; Williams *et al.*, 2003 ; Yamamoto *et al.*, 2004). Or, de telles approches descriptives ne permettent pas de quantifier l'effet des variables écologiques liées à la perturbation des habitats sur la variabilité génétique observée. Bien que certaines méthodes d'analyse, tels les tests de Mantel partiels, permettent d'expliquer les niveaux de différenciation génétique entre populations par des variables liées au paysage, celles-ci ne peuvent pas être appliquées à l'étude de la diversité génétique au sein des populations et des individus, et ne permettent pas de tester et de quantifier l'effet de plusieurs variables écologiques et de leurs interactions sur la variabilité génétique observée. L'utilisation de méthodes statistiques telles les régressions multiples et l'analyse canonique par correspondance serait plus appropriée afin de tester de telles relations. En effet, plusieurs associations ont ainsi été trouvées entre les niveaux de différenciation génétique entre populations et la salinité de l'eau (McCairns et Bernatchez, 2008), les interactions interspécifiques (Manier et Arnold, 2006), la structure des communautés forestières (Gram et Sork, 2001), et les patrons de drainage, l'altitude et les niveaux de pêche sportive et d'ensemencements (Angers *et al.*, 1999). Cependant, peu d'études ont utilisé ce type d'approche afin d'évaluer l'impact de modifications environnementales récentes (voir cependant Raeymakers *et al.*, 2008). Ce type d'analyse peut également être appliqué à l'étude des niveaux et de la distribution de la diversité génétique au niveau individuel (Manel *et al.*, 2003). Or, à notre connaissance, aucune étude effectuée à ce jour n'a quantifié les effets de variables écologiques liées à la perturbation des habitats naturels sur la diversité génétique individuelle, malgré l'importance de cette dernière en biologie évolutive et en conservation.

Intensification de l'agriculture et conséquences sur les oiseaux champêtres

L'une des principales causes de la perturbation des habitats naturels liée aux activités humaines est l'expansion et l'intensification des pratiques agricoles (Soulé *et al.*, 1990). En Amérique du Nord, les pratiques agricoles ont subi d'importants changements depuis le début du 20^e siècle avec l'avènement de la mécanisation du travail agricole, l'utilisation de pesticides et de fertilisants chimiques et le développement de nouvelles variétés et de plants hybrides (Bélanger et Grenier, 2002 ; Jobin *et al.*, 2003). Cette transition des méthodes traditionnelles vers l'agriculture intensive a entraîné un changement profond du paysage, notamment dans les régions du sud du Québec. Dans la vallée du Saint-Laurent, par exemple, l'agriculture, l'urbanisme et les industries occupent une part prépondérante du paysage, laissant moins de 25% du couvert forestier intact (Bélanger et Grenier, 2002). Conséquemment, les paysages agricoles sont maintenant caractérisés par une mosaïque d'îlots d'habitats naturels séparés les uns des autres par des terres agricoles, des routes, des villes et des villages.

De nombreuses études documentent les effets de ces perturbations de l'habitat sur diverses espèces, notamment chez les oiseaux des zones tempérées (Hole *et al.*, 2002) et plus particulièrement en Amérique du Nord (Venter *et al.*, 2006 ; Wilcove *et al.*, 1998). Par exemple, par rapport à l'agriculture traditionnelle ou aux fermes organiques, les cultures intensives abritent une moins grande biodiversité et abondance d'oiseaux (Beecher *et al.*, 2002 ; Freemark et Kirk, 2001). De plus, Chamberlain *et al.* (2000) ainsi que Benton *et al.* (2002) ont mis en évidence une association entre le déclin de différentes populations d'oiseaux en Angleterre et un gradient temporel d'intensification agricole. Plusieurs études suggèrent que ce déclin serait dû à une diminution dans l'abondance des arthropodes, source de nourriture pour bon nombre d'espèces aviaires, en raison de l'utilisation de pesticides et de l'homogénéisation des cultures associées à l'agriculture intensive (Benton *et al.*, 2002 ; Britschgi *et al.*, 2006 ; Vickery *et al.*, 2001 ; Wilson *et al.*, 1999). Les pesticides ont également un effet direct sur le succès reproducteur des oiseaux, notamment chez l'Hirondelle bicolore (*Tachycineta bicolor*) (Bishop *et al.*, 1999). De plus, la diminution de l'hétérogénéité de l'habitat, due à la moins grande diversité des cultures et à la disparition de milieux humides et d'habitats marginaux tels que les boisés, les haies et

les arbres morts, peut être responsable de la diminution de l'abondance et de la richesse de plusieurs espèces d'oiseaux (Freemark et Kirk, 2001) ; les plans d'eau et les habitats marginaux constituant un habitat important et une source majeure de nourriture pour les oiseaux en milieu agricole (Gunnarsson *et al.*, 2006). L'expansion de l'agriculture, en causant une fragmentation ainsi qu'un déclin des populations chez un grand nombre d'espèces d'oiseaux, serait donc également susceptible d'entraîner plusieurs changements au niveau de leur variabilité génétique. La plupart des études portant sur les effets de la fragmentation de l'habitat sur la variabilité génétique des oiseaux sont toutefois effectuées sur des espèces résidentes (Bates, 2002 ; Caizergues *et al.*, 2003 ; Segelbacher *et al.*, 2008). Les effets des modifications de l'habitat sur des espèces de passereaux migrateurs sont moins connus; certaines études montrant une absence d'effets de la fragmentation du paysage sur la variabilité génétique (Croteau *et al.*, 2007 ; Galbusera *et al.*, 2004 ; Veit *et al.*, 2005), alors que d'autres démontrent que certains paramètres liés au paysage, par exemple la présence de terres agricoles, peut augmenter la différenciation génétique entre populations (Lindsay *et al.*, 2008).

Objectifs de recherche

L'objectif général des travaux présentés dans ce mémoire est de déterminer quelle est la relation entre la qualité de l'environnement et la variabilité génétique de l'Hirondelle bicolor (*Tachycineta bicolor*), le long d'un gradient d'intensification agricole.

Pour ce faire, j'utilise un système d'étude composé d'un réseau de 400 nichoirs, distribués sur 40 fermes (10 nichoirs par ferme) situées au sud du Québec, et couvrant un territoire d'environ 10 200 km² (voir Figure 1, Chapitre I). Cette région est caractérisée par un gradient d'intensification agricole, allant de petites fermes laitières, fourrages et pâturages (cultures extensives) à l'est, à de grandes monocultures de maïs, de soya et autres céréales (cultures intensives) à l'ouest. Cette transition de cultures extensives vers des cultures intensives est associée à une réduction du couvert forestier et une fragmentation accrue de l'habitat, ainsi qu'une homogénéisation du paysage due à la perte d'habitats marginaux, tels des boisés, haies, milieux humides et marécages, couplée à une augmentation de la superficie des terres agricoles. Une des espèces d'oiseaux particulièrement susceptible

d'être affectée par cette intensification des pratiques agricoles est l'Hirondelle bicolore. Comme dans le cas de plusieurs espèces d'oiseaux insectivores, les populations d'Hirondelle bicolore au Québec ont subi un important déclin durant les 20 dernières années, avec un taux moyen annuel de diminution de taille de population de 4,6% entre 1997 et 2007 (Downes et Collins, 2008). L'Hirondelle bicolore est un petit passereau migrateur se reproduisant dans l'ensemble de l'Amérique du Nord (Robertson *et al.*, 1992). Durant la saison de reproduction, cette espèce se retrouve principalement en milieux ouverts, et est dépendante de la présence d'habitats marginaux, tels que plans d'eaux et milieux humides, qui consistent en une source importante de nourriture, ainsi que d'arbres morts comprenant des cavités leur permettant de nicher (Robertson *et al.*, 1992). Ces caractéristiques font en sorte que les modifications de l'habitat dues à l'intensification agricole sont probablement l'une des principales causes expliquant le déclin de cette espèce au cours des dernières décennies. De plus, il a effectivement été montré que le succès reproducteur de l'Hirondelle bicolore sur notre système d'étude est plus faible (taille de portée et nombre d'oisillons à l'envol plus faibles) en milieux agricole intensif (Ghilain et Bélisle, 2008). Finalement, l'Hirondelle bicolore se reproduit aisément en nichoir et se laisse manipuler facilement, sans conséquences sur sa reproduction, ce qui facilite grandement le suivi de populations et la prise de données sur cette espèce (Jones, 2003).

Plus spécifiquement, les travaux présentés dans ce mémoire visent à combiner information génétique obtenue à l'aide de marqueurs microsatellites et variables écologiques et spatiales afin de : 1) établir la structure génétique populationnelle de l'Hirondelle bicolore dans mon système d'étude, à l'aide d'une approche de génétique du paysage ; 2) quantifier l'effet de variables écologiques et du paysage sur le niveau de différenciation entre les populations, s'il y a lieu, ainsi que sur la diversité génétique mesurée au niveau individuel. Étant donné que le succès reproducteur de l'Hirondelle bicolore dans notre système d'étude est plus faible en milieux agricoles intensifs, nous avons testé l'hypothèse que la diversité génétique sera plus faible dans ce type d'habitat.

CHAPITRE 1
NONRANDOM DISTRIBUTION OF INDIVIDUAL GENETIC DIVERSITY
ALONG AN ENVIRONMENTAL GRADIENT

par

MÉLODY PORLIER, MARC BÉLISLE & DANY GARANT

Philosophical Transactions of the Royal Society B, accepté pour publication

Dans le contexte actuel de changements rapides et globaux, il est particulièrement important de comprendre comment les modifications de l'habitat affectent le potentiel d'adaptation des populations. Un aspect critique de cette problématique consiste à mettre en évidence les mécanismes sous-jacents à la diversité génétique observée en milieu naturel. Peu d'études se sont cependant attardées aux effets de la variabilité de l'environnement sur la quantité et la distribution de la diversité génétique mesurée au niveau individuel, malgré l'importance de cette dernière pour l'évolution et la conservation des espèces. Cet article vise à comprendre et quantifier l'influence du paysage et des facteurs écologiques et comportementaux sur la diversité génétique individuelle de l'Hirondelle bicolore (*Tachycineta bicolor*), en milieu naturel. J'ai effectué la majorité de la collecte de données et d'analyses de laboratoire et statistiques menant aux résultats présentés dans l'article, en plus d'avoir rédigé la première version du manuscrit. Marc Bélisle a contribué au travail par son soutien logistique, sa collaboration aux analyses statistiques et sa révision finale du manuscrit, et Dany Garant a supervisé chacune des étapes de ce projet et contribué à la rédaction de la version finale du manuscrit. Cet article a été accepté pour publication dans la revue *Philosophical Transactions of the Royal Society of London B*, dans le cadre d'un numéro spécial portant sur l'émergence d'un nouveau créneau de recherche nommé «Eco-evolutionary Dynamics», qui vise à quantifier l'importance des interactions entre processus écologiques et évolutifs. L'originalité de cette recherche réside dans l'intégration de paramètres spatiaux, écologiques et comportementaux pour expliquer la variabilité génétique observée en milieu naturel. De plus, il s'agit d'un des premiers travaux quantifiant l'effet de variables écologiques sur la diversité génétique mesurée au niveau individuel.

Abstract

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 Quebec, Canada. Using a landscape genetics approach, we found that individual genetic diversity was greater in poorer quality habitats. This counterintuitive 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

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 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. this issue). 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; Kempnaers et al. 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. 2005; 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 Kempnaers 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 (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 toward 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. this issue).

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 Quebec, 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 20th century, mainly due to an increased mechanisation of agricultural work, a greater use of pesticides, herbicides and chemical fertilisers as well as the development and use of new and hybrid plant varieties (Tscharntke et al. 2005). In Southern Quebec 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, soybean and maize (Bélanger & Grenier 2002; Benton et al. 2003; Tschardt et al. 2005). This transformation and homogenisation 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. Like 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 Québec, with an average annual decline of 4.6% 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 recent tree swallow's 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 Quebec using a landscape genetics approach based on microsatellite markers and 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 if tree swallows' individual genetic diversity was negatively related to agricultural intensification.

MATERIALS AND METHODS

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 Quebec, Canada (Fig. 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 soybean crops (referred to as intensive cultures) to the west (Fig. 1). This transition from extensive to intensive cultures is associated with forest cover reduction and fragmentation, landscape homogenisation caused by the loss of marginal habitats such as hedgerows and wetlands, and an increase in field size.

Each nest-box was visited every two 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, Californie, 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 – 12 days. Each bird was weighed and banded at first capture with a U.S. Fish and Wildlife Service aluminum 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).



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

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 surrounded nest-boxes using either 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: 1/40000; Ministère des Ressources naturelles et de la Faune du Québec 2000), and cover percentages were calculated using ArcView GIS Spatial Analyst 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 km 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 has 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 recordings of first spring observations of tree swallows in Southern Quebec - eBirds 2006). All measurements were obtained with ArcView GIS Spatial Analyst 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).

Genetic analyses

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 ten 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, PCR reactions were performed in a 10- μ L 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 μ M dNTPs; 500 mM unlabelled primer; 250 mM labelled primer; 1U AmpliTaq Gold (Applied Biosystems) and 10–20 ng DNA template] using a GeneAmp 9700 thermalcycler (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 sec, 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 sec and 72°C for 45 sec, 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).

Molecular sexing

Individuals for which sex could not be determined on a phenotypic basis were sexed by amplification of the CHD genes, using the P2 and P8 primers (Griffiths et al. 1998). The final PCR reaction conditions were as follows: 8 mM Tris-HCl pH 9.0; 40 mM KCl, 3.0 mM MgCl₂; 0.008 mg BSA, 80 μ M dNTPs, 500 mM of each primer, 2U AmpliTaq Gold (Applied Biosystems) and 20–40 ng DNA template. PCR reactions were also carried out on a GeneAmp 9700 thermalcycler, 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 sec and 72°C for 45 sec, 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% agarose gels.

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).

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 were 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 (i) variance between years (temporal component); (ii) variance among farms within years (spatial component), and (iii) variance 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 geographic distance, using SPAGeDi v.1.2 (Hardy & Vekemans 2002). However, since all pairwise F_{ST} values among farms were non-significant (see Results section), we instead performed an analysis at the individual level. We thus used Lynch and 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 geographic 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.

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 index (HL; see Aparicio et al. 2006) but only present the results pertaining to IR, since IR and HL were highly correlated ($r = 0.98$, $p < 0.001$).

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 only present 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 internal relatedness 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 (see Table 1), we only tested for the effect of one of these variable 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 results for extensive cultures as it showed the best fit to our data. The presence of second-order quadratic relationships among variables were also tested but none were significant.

Table 1. Pearson's correlation coefficients between ecological and landscape variables.

	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	---

Values above diagonal refer to year 2006, below diagonal to 2007

All values significant at $p < 0.001$

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 internal relatedness 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 combination 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).

RESULTS

Microsatellite polymorphism

Three 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 7 loci (mean number \pm SD 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 that were genotyped at less than 3 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 to 0.88) (Supplementary table 1). We found no significant percentage of null alleles and no evidences of linkage disequilibrium for any pairwise comparison of loci after sequential Bonferroni correction (results not shown). Three out of the 7 loci (IBI Ms3-31, HrU7 and Hir 22) showed significant deviation from HWE when both years were analyzed together (see Supplementary table 1). These three loci were nevertheless included in the remaining analyses as none of them showed consistent deviation across years. Mean

internal relatedness for individuals caught dead in nest-boxes did not differ significantly from the rest of the population (mean IR \pm SD of dead individuals: -0.03 ± 0.18 , mean IR \pm SD for the remaining individuals: 0.04 ± 0.20 , $t = 1.30$, $p = 0.22$).

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% , $p = 0.91$), respectively. 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 isolation by distance revealed a significant positive relationship between the pairwise relatedness of individuals and geographic 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 ($b = 2.66 \times 10^{-8}$, $p = 0.09$, $r = 1.65 \times 10^{-5}$).

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 Fig. 2; see also Ghilain & Bélisle 2008), thus suggesting that habitat quality increases with the amount of extensive cultures. Internal relatedness increased with the proportion of extensive cultures within 500 m of nest-boxes (Table 2, Fig 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 contained the proportion of extensive cultures at 500 m as an explanatory variable (see Supplementary table 2). Results were also consistent across loci with 6 out of 7 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 Supplementary 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).

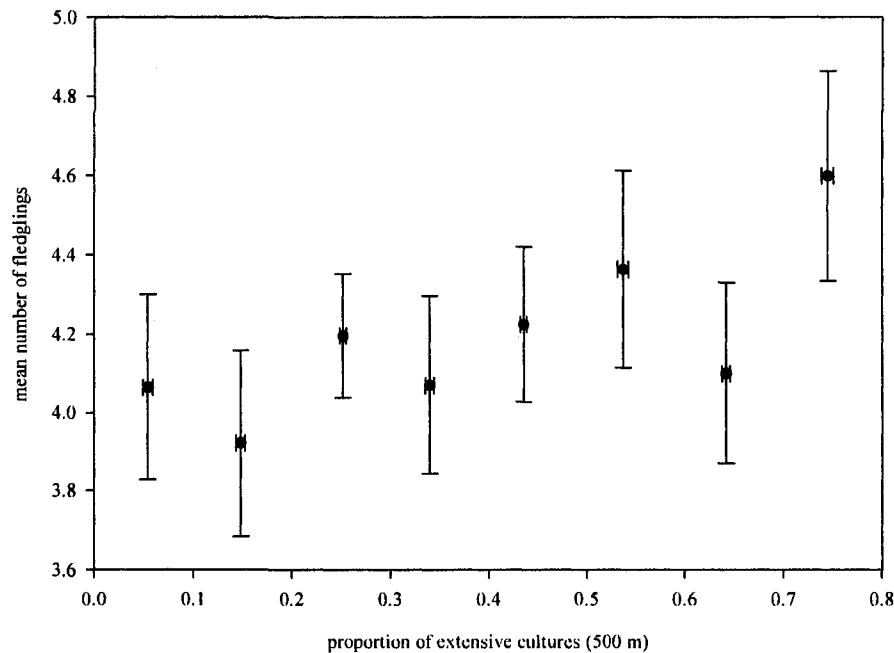


Figure 2. Effect of the proportion of extensive cultures within 500 m of each nest-box on the number of fledglings. For illustration purposes, each circle represents mean values (\pm SE) for 8 classes of proportion of extensive cultures. The effect of the proportion of extensive cultures at 500 m on 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 ($N = 515$).

Table 2. Effects of culture types on adult tree swallows' individual genetic diversity as measured by internal relatedness. (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 significant term only. Number of observations = 952.

(a) Full extensive model				(b) Final extensive model		
Variable	t statistic	df	p-value		Estimate	SE
Extensive cultures (500 m)	2.71	1	0.007	Extensive cultures (500 m)	0.083	0.031
Year (2006 vs 2007)	-0.71	1	0.477			
Sex	0.11	1	0.914			

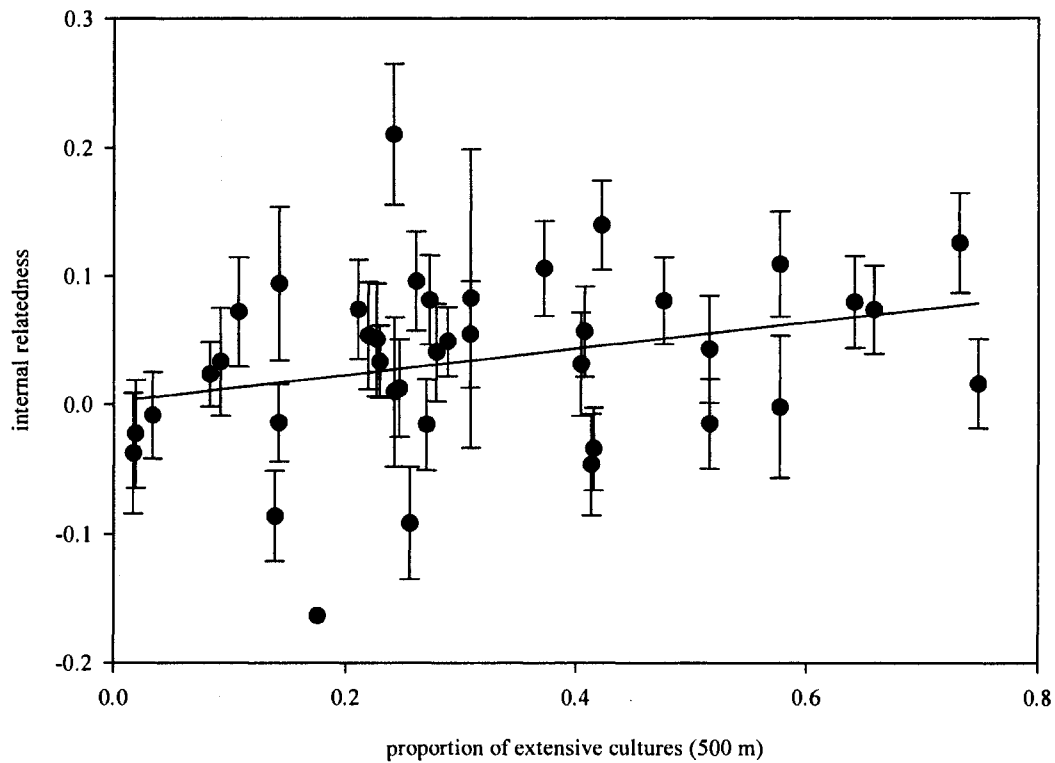


Figure 3. Relationship between extensive cultures within 500 m of around each nest-box and internal relatedness. Each circle represents mean values (\pm SE) for each farm in the study system (N = 952).

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 internal relatedness and settlement date of individuals (Table 3, Fig. 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 Supplementary table 3), providing further support for the importance of individual genetic diversity in explaining the settlement pattern of individuals. Again, results were consistent across loci, with 6 out of 7 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, Fig. 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 ($r = -0.01$, $p = 0.78$).

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

Variable	z statistic	df	p-value	estimate	SE
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 vs 2007)	1.86	1	0.064	0.079	0.043
Body mass	-6.12	1	< 0.001	-0.080	0.013

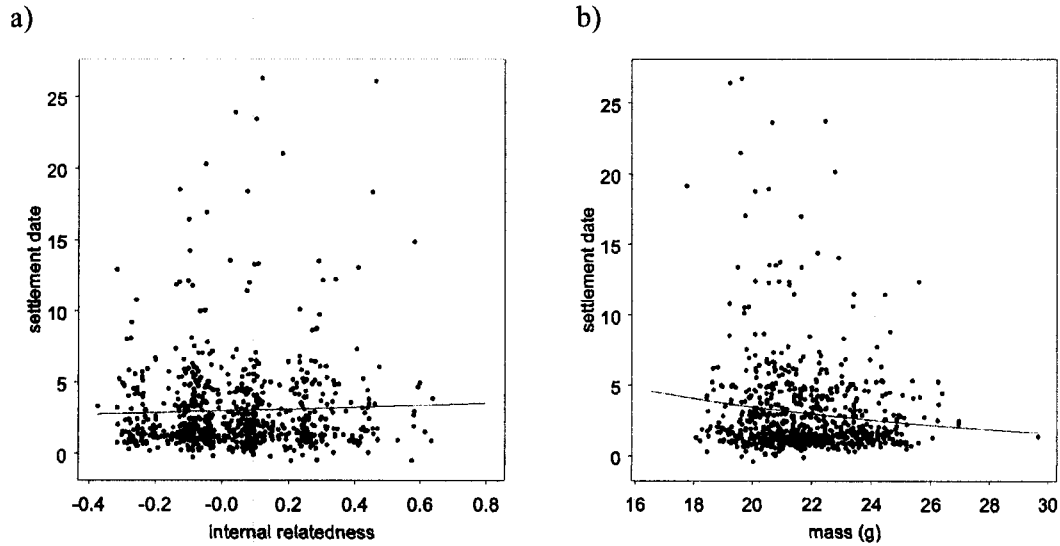


Figure 4. Effect of internal relatedness (a) and body mass (b) on the settlement date of tree swallows. Settlement dates correspond to adjusted values from a generalised linear model (Poisson error structure and log-link function) of including internal relatedness, body mass, distance from the St. Lawrence River and year (N = 726).

We also assessed if 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 number of fledglings in our study system (Ghilain & Bélisle 2008).

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 nonrandom 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.

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 evidences 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 (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 SD = 10 km \pm 15 km; N = 8; see also Winkler et al. (2005) for similar natal dispersal distance) probably plays an important role in the homogenisation of the population structure. The return rate of nestlings born in our study area is quite low [ca. 1% of the nestlings banded in 2006 returned as breeders in 2007; in comparison to values ranging from 3.0% - 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 homogenisation 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% 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 homogenising effect of this behaviour on the genetic population structure of this species.

Nonrandom 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, we even found support for the inverse relationship. A first possible explanation for this counterintuitive 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 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 internal relatedness values with more extensive habitat (comparisons of variance in IR among subsets of individuals distributed among 8 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 which habitats are encountered first. Indeed, tree swallows in Southern Quebec follow the St. Lawrence River before entering their breeding grounds, and therefore initially fly above intensively managed habitats which are of lower quality for this species (Fig 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 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 interindividual competition other than settlement order, the underlying processes involved in the final distribution of individuals in our system remain to be investigated.

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 homogenisation 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. Furthermore, 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 luscinoides*) 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 > 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, 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 Quebec 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 behavioral 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.

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CONCLUSION

L'objectif de ma maîtrise était de déterminer, en utilisant une approche de génétique du paysage, la structure de population et l'influence de la qualité environnementale sur la diversité génétique de l'Hirondelle bicolore, le long d'un gradient d'intensification agricole au sud du Québec.

Dans un premier temps, nous avons trouvé la présence d'une seule population d'Hirondelle bicolore au sein de notre aire d'étude, malgré une potentielle fragmentation de l'habitat due à l'intensification de l'agriculture dans cette région. Cette homogénéisation de la structure génétique pourrait être due à la grande capacité de dispersion natale chez cette espèce, correspondant en général à des distances d'environ 10 km (Chapitre I, Winkler *et al.*, 2005). De plus, l'Hirondelle bicolore est une espèce d'oiseaux chez laquelle le taux de fertilisations hors couple est des plus élevés (Griffith *et al.*, 2002), et chez laquelle il a été montré que les femelles recherchent des partenaires hors couple géographiquement éloignés (Dunn *et al.*, 1994 ; Kempnaers *et al.*, 2001) et génétiquement dissimilaires (Stapleton *et al.*, 2007), ce qui pourrait également contribuer à homogénéiser la structure génétique. Nous avons également mis en évidence une légère corrélation négative entre distance géographique et similarité génétique entre paires d'individus, signifiant que les individus spatialement rapprochés sont moins génétiquement semblables que prévu selon une distribution aléatoire. Bien que les processus expliquant la présence d'un tel patron dans notre système d'étude restent à être élucidés, ce résultat pourrait découler d'un mécanisme d'évitement de la consanguinité. Par exemple, la dispersion natale, particulièrement lorsque biaisée par le sexe, a été montrée chez plusieurs espèces d'oiseaux comme mécanisme d'évitement de consanguinité (Eikenaar *et al.*, 2008 ; Ortego *et al.*, 2008b ; Szulkin et Sheldon, 2008 ; Wheelwright et Mauck, 1998).

Ensuite, nous avons testé la relation entre la diversité génétique individuelle de l'Hirondelle bicolore et le niveau d'intensification agricole. Contrairement à notre hypothèse de départ, nous avons trouvé que les individus ayant un niveau de diversité génétique plus élevé se trouvent dans les milieux agricoles plus intensifs, soit dans des

habitats de moins bonne qualité. Or, les démonstrations théoriques prédisent que les individus de meilleure qualité, en étant plus compétitifs ou en ayant une plus grande capacité de prospection d'habitats, devraient s'approprier les territoires de qualité supérieure (Stamps, 2006), ce qui a été confirmé par plusieurs études empiriques effectuées sur des espèces d'oiseaux (Garant *et al.*, 2005b ; Seddon *et al.*, 2004). Nous avons donc testé par la suite si d'autres facteurs liés au paysage et à l'établissement des individus dans notre système d'étude avaient une influence sur la distribution de la diversité génétique individuelle de l'Hirondelle bicolore dans notre système d'étude. Nos résultats montrent que, suite à la migration printannière, l'Hirondelle bicolore entre dans notre système d'étude via le fleuve Saint-Laurent ; les individus arrivant plus tôt dans la région s'établissent dans des sites de nidification situés plus près du fleuve. Or, chez de nombreuses espèces d'oiseaux, la date d'arrivée sur le site de reproduction est corrélée à la qualité individuelle (Aebischer *et al.*, 1996 ; Bensch et Hasselquist, 1991 ; Sergio *et al.*, 2007 ; Smith et Moore, 2005). Nous avons donc testé si les individus s'établissant en premier dans notre site d'étude, et par conséquent plus près du fleuve Saint-Laurent, avaient une diversité génétique plus élevée. Une telle relation expliquerait le patron observé de distribution de la diversité génétique, puisque le gradient d'intensification agricole dans cette région est relié à la distance par rapport au fleuve Saint-Laurent, les habitats de moins bonne qualité se retrouvant plus près du fleuve. Nos résultats appuient effectivement cette hypothèse : les individus arrivant en premier dans notre système d'étude suite à la migration sont les individus possédant une plus grande diversité génétique ainsi qu'une masse corporelle plus élevée; ceux-ci s'établiraient dans les premiers sites de nidification disponibles rencontrés, soit plus près du fleuve Saint-Laurent et par conséquent dans des habitats de moins bonne qualité.

Implications et perspectives futures

Les travaux présentés dans ce mémoire montrent l'importance de l'intégration de données spatiales, de variables écologiques et des caractéristiques biologiques d'une espèce sur l'étude de la génétique des populations. Il s'agit, à notre connaissance, de la première quantification des effets de variables écologiques sur la diversité génétique individuelle en milieu naturel. De plus, aucune étude n'a précédemment documenté une association entre

la diversité génétique et la date d'établissement des individus chez une espèce d'oiseau, bien qu'une telle relation ait été montrée chez des mammifères (Hoffman *et al.*, 2004). Finalement, la plupart des études portant sur la sélection de l'habitat sont effectuées sur des espèces résidentes, et se basent sur des théories de répartition des individus dans le paysage qui assument que les individus ont une connaissance de chacun des milieux disponibles au moment de la sélection de l'habitat (Battin, 2004). Or, nos résultats suggèrent que de tels modèles ne seraient pas appropriés dans le cas d'espèces suivant un corridor de migration précis, et montrent l'importance de prendre en considération les patrons spatiaux de migration lors d'études portant sur la distribution des individus dans le paysage.

La distribution non-aléatoire de la diversité génétique individuelle que nous avons mis en évidence pourrait avoir des implications importantes quant à l'étude des effets de l'intensification agricole sur le succès reproducteur de l'Hirondelle bicolore dans notre système d'étude. Il serait d'abord intéressant de quantifier l'effet de la diversité génétique individuelle et la qualité de l'environnement ainsi que de leur interaction sur le succès reproducteur des individus. Nos résultats montrent en effet que les individus ayant une diversité génétique plus élevée se retrouvent en milieux de moindre qualité (milieux intensifs), où le succès reproducteur (notamment en terme du nombre d'oisillons à l'envol) est plus faible (Ghilain et Bélisle, 2008). Cependant, ces individus, en s'établissant plus tôt sur leur site de reproduction, ont également une date de ponte plus hâtive. Or, il a été montré qu'une phénologie de reproduction plus hâtive peut avoir un effet positif sur le succès reproducteur chez plusieurs espèces d'oiseaux (Aebischer *et al.*, 1996 ; Garant *et al.*, 2007 ; Sheldon *et al.*, 2003 ; Smith et Moore, 2005 ; Tomiuk *et al.*, 2007), incluant l'Hirondelle bicolore dans notre système d'étude (Ghilain et Bélisle, 2008). Cela suggère que la diversité génétique individuelle pourrait avoir un effet positif sur le succès reproducteur chez cette population d'Hirondelle bicolore, possiblement entre autres *via* une date de ponte plus hâtive, mais également entraîner indirectement une diminution du succès reproducteur étant donné la corrélation négative entre diversité génétique et qualité de l'habitat. Un tel résultat pourrait également impliquer une sous-estimation de l'effet négatif de l'intensification agricole sur le succès reproducteur des individus, puisque ce dernier serait partiellement compensé par la présence des individus de meilleure qualité en milieu agricole intensif.

ANNEXE 1

Supplementary table 1. Number of alleles, range size (bp), expected heterozygosity (HE), and observed heterozygosity (HO) (for 2006 and 2007 separately and for both study years analysed together), for each of the 7 microsatellite loci used in the final analyses. Values were calculated using genotypes from 815 adult individuals captured in 2006 and 2007.

locus	no. of alleles	range (bp)	HE	HO (2006)	HO (2007)	HO (2006-2007)
IBI Ms5-29	8	134 - 160	0.650	0.637	0.630	0.633
IBI Ms3-31	13	114 - 131	0.860	0.796	0.826	0.812
HrU7	6	143 - 158	0.691	0.627	0.646	0.632
TBI 81	14	250 - 278	0.889	0.879	0.888	0.883
TBI 104	12	230 - 252	0.718	0.715	0.725	0.720
Hir 19	12	143 - 188	0.806	0.793	0.786	0.787
Hir 22	20	232 - 308	0.856	0.781	0.770	0.774

ANNEXE 2

Supplementary table 2. Five best general linear models assessing the influence of landscape and ecological parameters on the internal relatedness of tree swallows as determined by Akaike's Information Criterion and their weight of evidence (w_i). The statistical significance of the parameters included in the models are shown. Number of observations = 952.

Supplementary table 2. Five best general linear models assessing the influence of landscape and ecological parameters on the internal relatedness of tree swallows as determined by Akaike's Information Criterion and their weight of evidence (w_i). The statistical significance of the parameters included in the models are shown. Number of observations = 952.

AIC	Δ AIC	d.f.	w_i	year	distance from St. Lawrence River	extensive cultures (500m)	intensive cultures (500m)	sex
-3093.93	-	2	0.208	-	-	0.008	-	-
-3092.43	1.50	3	0.098	-	0.478	0.013	-	-
-3092.42	1.50	3	0.098	0.481	-	0.007	-	-
-3091.94	1.99	3	0.077	-	-	0.070	0.916	-
-3091.93	2.00	3	0.077	-	-	0.008	-	0.968

ANNEXE 3

Supplementary table 3. Four best generalized linear models (Poisson error structure and log-link function) assessing the influence of landscape and ecological parameters on the settlement date of tree swallows as determined by Akaike's Information Criterion and their weight of evidence (w_i). The statistical significance of the parameters included in the models are shown. Number of observations = 726.

AIC	Δ AIC	d.f.	w_i	IR	year	distance from St. Lawrence River	body mass
3625.62		5	0.504	0.040	0.064	< 0.001	< 0.001
3627.07	1.45	4	0.244	0.043	-	< 0.001	< 0.001
3627.84	2.22	4	0.166	-	0.069	< 0.001	< 0.001
3629.16	3.54	3	0.086	-	-	< 0.001	< 0.001

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