



Climate change and the origin of migratory pathways in the Swainson's thrush, *Catharus ustulatus*

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ABSTRACT

Aim To provide a spatially explicit model of how geographic distributions at the last glacial maximum (LGM) and post-glacial colonization routes shaped current migratory pathways in the Swainson's thrush, *Catharus ustulatus*, a long-distance migratory bird.

Location The Swainson's thrush breeds in boreal forest regions of the United States and Canada as well as in riparian woodlands along the Pacific coast of North America.

Methods Palaeodistribution modelling is combined with mtDNA phylogeography to predict the breeding range of the Swainson's thrush at the LGM. Quantitative environmental analysis and bioclimatic modelling are used to reconstruct the most likely post-glacial colonization pathways. A maximum likelihood method for estimating growth rates is used to approximate the relative change in population size since the LGM.

Main conclusions The palaeodistribution models are concordant with the Swainson's thrush mtDNA phylogeography, suggesting that the inland and coastal groups were geographically isolated in eastern (inland) and western (coastal) regions at the LGM. Estimates of change in population size based on genetic data are remarkably consistent with estimates of change in range size, suggesting that the coastal group has undergone a 2- to 3-fold demographic and range expansion, while the inland group has undergone a 6- to 12-fold demographic and range expansion since the LGM. Bioclimatic analyses strongly support the hypothesis that populations expanding out of the east into previously glaciated areas in the west were undergoing a natural extension of their range by tracking the changes in climatic conditions. The combination of bioclimatic and molecular analyses is consistent with the idea that coastal and inland groups expanded from separate eastern and western regions after the LGM and that the current migratory pathway of the inland group retraces its post-glacial colonization route.

Keywords

Bioclimatic modelling, *Catharus ustulatus*, migration, migratory pathway, mtDNA, North America, phylogeography, Pleistocene, population expansion, Swainson's thrush.

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INTRODUCTION

Migration has evolved independently in a wide range of organisms as an adaptation to seasonal and geographic variation in resource abundance (Baker, 1978; Dingle, 1996). Avian migration in particular has long fascinated evolutionary biologists, in part because of the extraordinary distances of the

annual migratory journeys of some birds. While the origin of avian migration remains controversial (Zink, 2002; Rappole, 2003), it is generally accepted that migratory behaviour is a labile trait (Berthold *et al.*, 1992; Berthold, 2001; Helbig, 2003; Perez-Tris *et al.*, 2004), and that the original capacity for migration evolved deep in the avian lineage (Dingle, 1996; Helbig, 2003). Perhaps a more tractable question than the

origin of migration is the modification of migratory pathways (Zink, 2002) and the importance of new pathways to future diversification within species (Irwin & Irwin, 2004). The evolution of new migratory pathways can facilitate ecological, morphological, physiological and life-history evolution (Gwinner, 1996; Telleria & Carbonell, 1999; Perez-Tris & Telleria Jose, 2002; Wiltshcko & Wiltshcko, 2003), and therefore may be important to speciation.

It is widely accepted that glacial cycling during the Pleistocene significantly modified migratory pathways (Rappole, 1995; Berthold, 2001) and was responsible for intraspecific and sister-species-level divergence in many songbird species (Avisé & Walker, 1998; Johnson & Cicero, 2004; Weir & Schluter, 2004; Lovette, 2005). It is generally accepted that Pleistocene climate cycles contributed directly to divergence between most of the closely related North American species pairs as well as to intraspecific divergence between subspecies (Lovette, 2005). The effects of glacial cycling on songbird divergence are most pronounced in northern populations that were more susceptible to fragmentation from advancing ice sheets (Weir & Schluter, 2004). The vicariant events responsible for genetic divergence are also thought to have resulted in divergence in migratory pathways (Rappole, 1995; Berthold, 2001; Ruegg & Smith, 2002). Evidence in support of this hypothesis comes from the fact that in many species current migratory pathways retrace hypothesized post-glacial colonization routes (Rappole, 1995; Berthold, 2001; Ruegg & Smith, 2002). While molecular data provide support for the idea that geographic isolation during the late Pleistocene may account for intraspecific and sister-species-level divergence in some North American songbirds (Avisé & Walker, 1998; Johnson & Cicero, 2004; Weir & Schluter, 2004; Lovette, 2005), our understanding of how species distributions were influenced by climate change is based largely on habitat shifts extrapolated from palaeobotanical records (Mengel, 1964; Weir & Schluter, 2004).

One explanation for the lack of empirical research on changes in species distributions through time is that spatially explicit reconstructions of historical ranges are difficult without adequate fossil evidence. This problem is particularly acute in birds because their hollow bones do not easily fossilize. To overcome this problem, bioclimatic modelling approaches have been used either alone (Hilbert *et al.*, 2004; Peterson *et al.*, 2004) or in conjunction with phylogenetic methods (Hugall *et al.*, 2002) to identify previously isolated populations and approximate the location of historical refugia. Bioclimatic modelling uses climatic variables associated with point localities where a species has been observed to infer the current climatic envelope of the species. Spatially continuous layers of palaeoclimatic conditions can be obtained from climate models (often referred to as global circulation models, GCMs). The palaeodistribution is modelled by projecting the current climatic envelope onto layers of palaeoclimatic conditions, assuming that the distribution in climatic space remains stable across time (Davis *et al.*, 1998; Hugall *et al.*, 2002; Peterson *et al.*, 2004).

Consilience across additional lines of inference can strengthen the insights obtained from palaeodistribution modelling. Phylogenetic methods designed to test for population subdivision and changes in population size through time provide independent and complementary support to inferences drawn from palaeodistribution modelling. An important recent advancement in population genetics is the use of coalescent or genealogical methods that model the ancestral history of a random sample of genes from a population (Hudson, 1990). Coalescent methods for estimating growth rates make use of more of the information in the data (Hudson, 1990; Kuhner *et al.*, 1998) than do older methods (Slatkin & Hudson, 1991; Rogers & Harpending, 1992; Rogers, 1995). Therefore, coalescent methods are expected to estimate changes in population size more accurately than do methods based upon pairwise sequence differences (Slatkin & Hudson, 1991; Rogers & Harpending, 1992; Rogers, 1995). Together, phylogenetic methods and palaeodistribution modelling provide a spatially explicit framework in which to assess where and when divergence occurred (Hugall *et al.*, 2002).

The Swainson's thrush, *Catharus ustulatus* (Nuttall), provides an ideal system in which to test how past geographic distributions and post-glacial colonization routes shaped current migratory pathways. The Swainson's thrush is a long-distance migratory passerine that breeds in the boreal forest regions of the United States and Canada as well as in riparian woodlands along the Pacific coast of North America, and winters from southern Mexico to the northern tip of Argentina (Fig. 1). Results from a survey of mtDNA variation across the breeding grounds indicate a net sequence divergence of 0.69% between coastal and inland groups (Ruegg & Smith, 2002). The degree of divergence between coastal and inland groups is lower than for many other sister taxon comparisons that have been attributed to mid- to late-Pleistocene divergence (Avisé & Walker, 1998; Johnson & Cicero, 2004; Weir & Schluter, 2004; Lovette, 2005), suggesting that the two groups diverged recently and have since come into secondary contact (Ruegg & Smith, 2002; Fig. 1). In addition, genetic and banding-recapture data show that coastal and inland groups follow distinct migratory pathways – western inland birds migrate to eastern North America before turning south towards their wintering grounds in South America, and coastal birds migrate along the west coast of North America to their wintering grounds in Mexico and Central America (Ruegg & Smith, 2002; Fig. 1). Ruegg & Smith (2002) hypothesized that patterns of migration in the Swainson's thrush reflect shifts in the breeding range subsequent to the last glacial maximum (LGM).

We provide a spatially explicit model of how geographic distributions at the LGM and post-glacial colonization routes shaped current migratory pathways in the Swainson's thrush. Our hypothesis is that geographic isolation in eastern and western regions at the LGM resulted in divergence between coastal and inland groups, and that populations expanding out of the east into previously glaciated areas in the west were undergoing a natural extension of their range by tracking the

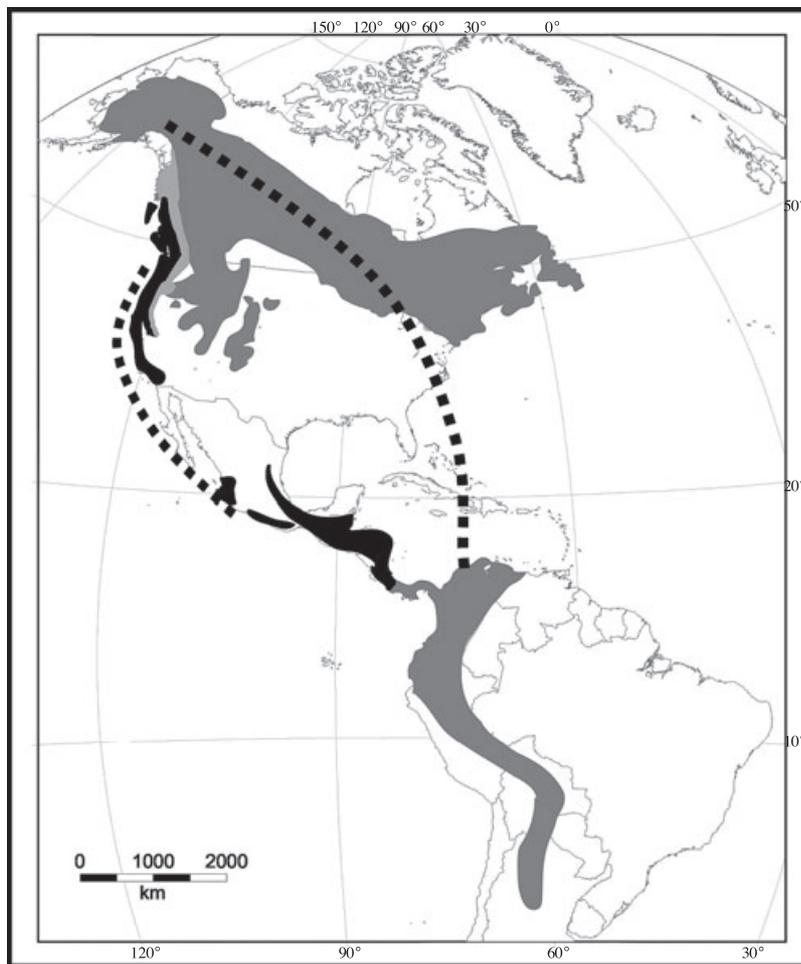


Figure 1 Predicted breeding and wintering ranges of coastal (black) and inland (dark grey) groups of the Swainson's thrush (based on a range map from the Cornell Laboratory of Ornithology with range data by Nature-Serve). The map projection is Lambert azimuthal equal-area. Potential areas of overlap based upon the mtDNA phylogeography for the Swainson's thrush are shown in light grey. Dotted lines represent generalized migratory pathways of coastal and inland groups based on banding data reconstructions from Ruegg & Smith (2002). Actual migratory routes of specific populations are not shown.

change in climatic conditions. We generate a series of predictions testable using bioclimatic modelling and an analysis of genetic data. We begin by defining the current climatic envelope for coastal and inland groups using bioclimatic modelling. We then project the current climatic envelope onto simulated climatic conditions at the LGM to assess support for the hypothesis of divergence in allopatry. Next we use bioclimatic analyses to reconstruct the most likely post-glacial colonization pathway. We predict that if inland populations isolated in the east at the LGM were undergoing a natural extension of their climatic envelope by shifting their breeding distribution north and west as the glaciers receded, then the climatic envelope of all inland regions should be more similar to one another than the climatic envelope of any inland region is to the climatic envelope of the Pacific coastal region (Fig. 2). Finally, to provide independent and complementary support to our bioclimatic analyses, we re-analyse previously reported mtDNA data for the Swainson's thrush using a coalescent method for estimating growth rates (Kuhner *et al.*, 1998). We predict that, if our palaeodistribution models are accurate, our approximations of change in range size should be concordant with the relative change in population size estimated from the genetic data (Hugall *et al.*, 2002). In light of the palaeodistribution models and genetic analyses presen-

ted here, we develop a framework for assessing how past geographic distributions and post-glacial colonization routes may shape current migratory pathways in other species.

METHODS

Point locality data collection

Point locality data were collected from a variety of sources including the Global Biodiversity Facility (<http://www.gbif.org/> visited 02/06), the USGS Patuxent Wildlife Research Center (<http://www.pwrc.usgs.gov/bbl/homepage/default.htm>, visited 02/06), the Museum of Vertebrate Zoology, the Royal British Columbia Museum, and field surveys. Specimen localities without coordinates were georeferenced to the nearest 0.01° using internet-based gazetteers (<http://geonames.usgs.gov/>, http://geonames.nrcan.gc.ca/search/search_e.php, visited 02/06). The georeferenced records were checked for errors by mapping them by country, state, province and month of observation, and aberrant records were corrected where possible or removed from the analysis. When breeding information (enlarged gonads or signs of nesting) was available, we restricted our selection to breeding birds. In cases where no breeding information was available, we used

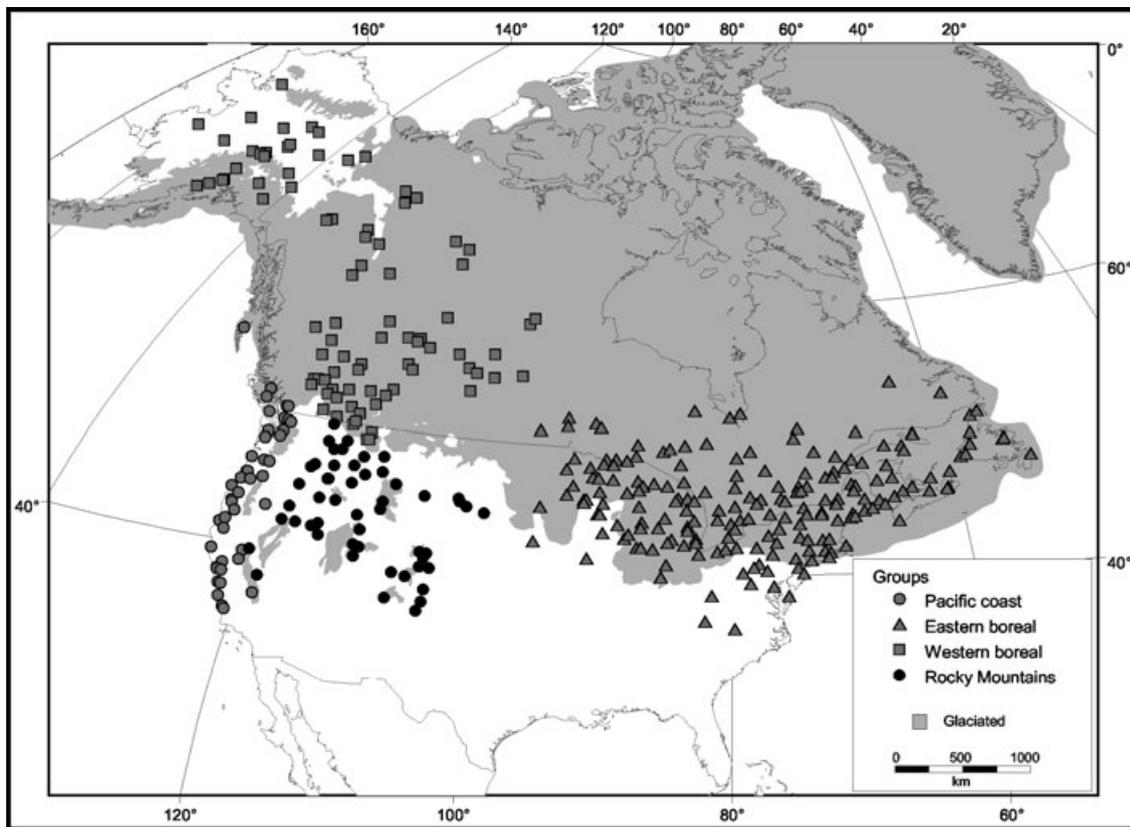


Figure 2 The current breeding distribution of the Swainson's thrush separated into four categories: eastern boreal, Pacific coast, western boreal, and Rocky Mountains. The points represent sampling localities. The map projection is Lambert azimuthal equal-area.

point localities for the month of July, the month when individuals are most likely to be breeding and least likely to be migrating or dispersing (Mack, 2000). Occurrence records are often biased towards areas that are easily accessible or near cities or other areas of high population density (Hijmans *et al.*, 2000), and such geographic bias can influence the result of bioclimatic modelling. Our occurrence records appeared to show more intense sampling in the densely populated north-east USA and much less sampling in more isolated areas in Canada. To remove some of this putative bias we created a grid of 100×100 km cells and randomly selected a single point from each cell with one or more sampling points. This procedure reduced the number of records from 177 coastal and 659 inland sites to 43 coastal and 327 inland sites, but they were more evenly distributed across the known range. Subspecies range distributions (Mack, 2000) in combination with mtDNA haplotype distributions from Ruegg & Smith (2002) and Ruegg (unpublished) were used to group point locality data into coastal and inland subspecies groups (herein referred to as coastal and inland groups).

Climate data

We used two sets of monthly climate data for precipitation and temperature. For current conditions (means for 1950–2000) we used WorldClim, a global climate data base with a spatial

resolution of *c.* 1 km (Hijmans *et al.*, 2005). To describe the climatic envelope occupied by coastal and inland groups on the breeding grounds we used 10 environmental variables: annual mean temperature, temperature seasonality (coefficient of variation across months), mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, annual precipitation, precipitation seasonality, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter. For palaeoclimate data at the LGM we used data generated with the ECHAM3 model (Deutsches Klimarechenzentrum Modellbetreuungsgruppe, 1992) downloaded from the PMIP website (<http://www-lsce.cea.fr/pmip/>, visited 02/06). We calculated the differences between the model runs for current and past conditions and downscaled them using bilinear interpolation. Past climate was then calculated as the sum of the current (WorldClim) climate and the downscaled model difference. We projected the data onto a Lambert equal-area projection and aggregated the data to cells of 10 km spatial resolution.

Analysis of climatic space on the breeding grounds

To investigate differences in climatic space occupied by coastal and inland groups during the breeding season, we performed a principal component analysis (PCA) using SPSS version 11.0.2

(SPSS Inc.). To determine whether separation in climatic space was statistically different we performed a multivariate analysis of variance (MANOVA) in which groups constituted the fixed factor and PCA axis scores were dependent variables (SPSS version 11.0.2, SPSS Inc).

Bioclimatic modelling of current and last glacial maximum distributions

Bioclimatic model comparisons suggest that variation between methods for predicting current species distributions is generally small (Segurado & Araújo, 2004), but there is a larger variation between methods for predicting distributions across time (Thuiller, 2004). We chose the BIOCLIM model (Nix, 1986; Busby, 1991) as implemented in DIVA-GIS (Hijmans *et al.*, 2004) because its straightforward methodology produces a model with sufficient generality to allow for prediction across time (Hugall *et al.*, 2002). BIOCLIM treats the environmental data values at the locations of species occurrence as multiple one-tailed percentile distributions; that is, it creates a percentile distribution for each variable, with the 5 percentile treated the same as the 95 percentile. For each grid cell and each environmental variable, BIOCLIM assesses whether the data values are within the observed distribution (i.e. between the 0 and 100 percentile), and, if they are, the position in this distribution is calculated. The lowest score across environmental values is then mapped. We ran the model creating the percentile distributions from the current climate and projected these onto the layers of current and LGM climate conditions. The palaeodistribution models were limited to potential breeding distributions south of the glacier's edge based upon glacier reconstruction maps (Dyke *et al.*, 2003). To test for model performance in the current environment, we calculated the area under the ROC (receiver operating characteristic) curve (AUC); an AUC score above 0.7 is considered good model performance (Fielding and Bell, 1997). To calculate the ROC curve we used *k*-fold cross-validation, in which the data were divided into five sets – the model was run five times and in each run a different set of points was used as test points and the other four sets were used as training points. To determine the optimal threshold for determining presence and absence we used the maximum Kappa criterion, a test statistic used to determine the point where the agreement between test and training data sets is highest. To assess the similarity between the modelled breeding niches, we calculated the degree of climate model overlap from one group into the range of the other. To quantify the amount of range change since the LGM, we determined the range size under current and LGM conditions and calculated an area ratio (current range)/(range at LGM).

Range expansion

To test whether post-glacial range expansion into the western boreal forest zone was more likely out of the eastern boreal forest, the Rocky Mountains, or the Pacific coast, we tested for ecological similarity using bioclimatic models for each region

separately. The current distribution was separated into four categories, namely eastern boreal, Pacific coast, western boreal, and Rocky Mountains (Fig. 2). The southern edge of the glacier at the LGM was used as the cut-off between western boreal to the north and the Rocky Mountain region to the south. A bioclimatic model was created for each region and the degree of overlap with the western boreal forest region was calculated.

Re-analysis of mtDNA data

To compare estimates of population expansion in coastal and inland groups, we re-analysed 45 previously reported control-region sequences (domains II and III) from 10 populations across the geographic range of the Swainson's thrush (Ruegg & Smith, 2002) using a maximum likelihood approach for estimating growth rates based on a genealogical model (Kuhner *et al.*, 1998). Sequences from within coastal and inland clades were grouped together for a total of 22 coastal individuals and 23 inland individuals. Maximum likelihood estimates of the parameters θ ($=2N\mu$ where μ is the mutation rate and N is the effective population size) and g (the exponential growth parameter in units of μ^{-1}) were made using Fluctuate (Kuhner *et al.*, 1998). Simulation studies have shown that adding additional sequences after approximately 10 sequences per group is ineffectual in improving the estimations (Kuhner *et al.*, 1998). We employed 10 short Monte Carlo chains of 4000 steps and five long chains of 20,000, with sampling increments of 20. To ensure stability of parameter estimates, each analysis was repeated five times and averaged to obtain the final calculations. The maximum likelihood estimates of θ and g were used to calculate the relative change in population size from the LGM to the present following the equation

$$N_t = \theta e^{-(g\mu)t},$$

where N_t is the population size at time t , μ is equal to the number of substitutions per site per generation mutation rate (Kuhner *et al.*, 1998), and the generation time is 2 years (Mack, 2000). No calibrations of the mutation rate are available for taxa closely allied to Swainson's thrush, and estimates of the rate of sequence divergence for the control region vary widely. Therefore, we used upper and lower bounds of 0.01 and 0.1 substitutions per site per million years, based on comparative studies of the rate of evolution of domain II (the most highly conserved region) and III (the second most highly conserved region) sequences in other taxa (Baker & Marshall, 1997; Ruokonen & Kvist, 2002).

RESULTS

Analysis of climatic space on the breeding grounds

The PCA on climatic variables indicates that coastal and inland groups occupy clearly distinct climatic regions on the breeding grounds, providing the potential for ecological differentiation (Fig. 3a,b). Coastal populations occupy regions with a higher annual mean temperature, less precipitation during the

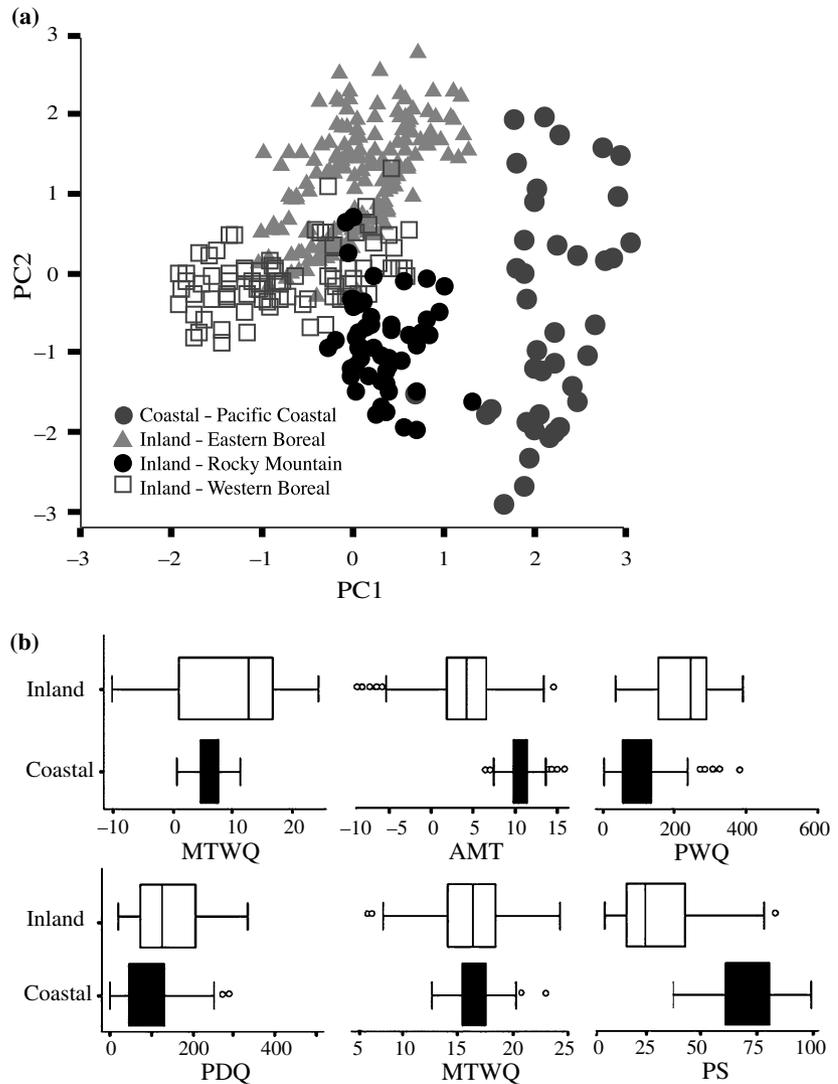


Figure 3 Analysis of climatic space occupied by coastal and inland groups during the breeding season. (a) Scatter plot of PC-1 and PC-2 scores for the Pacific coastal group and the three inland groups – western boreal, Rocky Mountains, and eastern boreal. (b) Box plots of the six environmental variables with the highest loading scores separating coastal and inland groups along PC-1 (MTWQ – mean temperature of the warmest quarter, AMT – annual mean temperature, PWQ – precipitation of the warmest quarter, PDQ – precipitation of the driest quarter, MTWQ – mean temperature of the warmest quarter, and PS – precipitation seasonality). The box represents the interquartile range that contains 50% of the values. The lines extend from the box to the highest and lowest values, excluding outliers, and the line across the box indicates the median.

warmest quarter, less precipitation during the driest quarter, and higher precipitation seasonally than inland populations (Fig. 3b). PC-1 accounted for 40% of the total variation and was dominated by differences in temperature and precipitation (loading scores: mean temperature of the driest quarter = 0.904, annual mean temperature = 0.631, temperature seasonality = -0.932, and precipitation of the coldest quarter = 0.831), while PC-2 accounted for 27% of the variance and was dominated by precipitation variables (loading scores: precipitation of the driest quarter = 0.901, and annual precipitation = -0.574). The separation of the coastal and inland populations along both PC-1 and PC-2 was highly significant (overall: $F_{2,759} = 367.8$, $P < 0.001$; PC-1: $F_{2,759} = 708.8$, $P < 0.001$; PC-2: $F_{2,759} = 8.6$; $P < 0.001$).

Bioclimatic modelling of current and last glacial maximum distributions

A test of model performance revealed high mean AUC scores of 0.723 and 0.934 for inland and coastal models, respectively,

suggesting that the BIOCLIM method accurately modelled the actual distribution. The optimal threshold according to the maximum Kappa criterion was 2.2 for the inland group and 0.6 for the coastal group; thus, these values were used as the thresholds for presence and absence in our predicted ranges. The modelled current range of the inland group was 6,590,900 km², spreading from north-eastern Alaska to the east coast of the United States and Canada (Fig. 4a), with large areas of predicted suitability in north-western Canada and the Canadian provinces of Ontario and Quebec (Fig. 4a). The size of the modelled current range of the coastal group was approximately 5% of the size of the inland group, spanning only 336,000 km² along the west coast of North America (Fig. 4a). The regions that were predicted most suitable for the coastal group were in coastal Oregon and Washington (Fig. 4a). An analysis of model similarity revealed that there was no overlap between the predicted ranges of the two groups.

The predicted range of the inland group during the LGM was 1,033,000 km², with one continuous area in the eastern USA and several smaller isolated patches in the Rocky

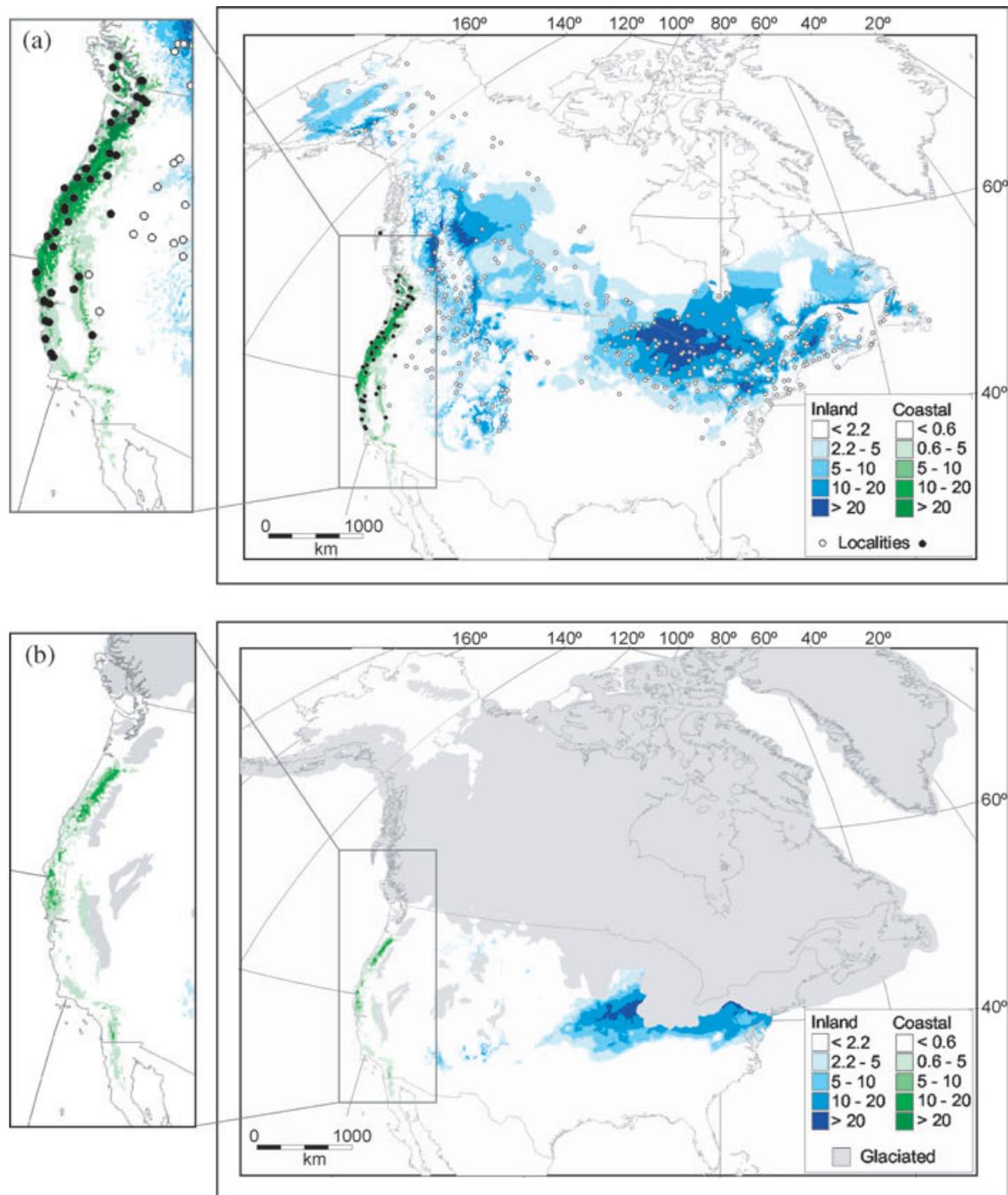


Figure 4 Ranges predicted with a bioclimatic model of coastal and inland groups of the Swainson's thrush. (a) Current breeding distribution of the Swainson's thrush and associated occurrence records, demonstrating good model fit of the model to the data and no overlap between the two models. (b) Palaeodistribution of coastal and inland groups at 21,000 yr BP, supporting the hypothesis of geographic isolation at the LGM. The map projection is Lambert azimuthal equal-area.

Mountains and the south-western USA (Fig. 4b). The predicted range of the coastal group during the LGM was 118,300 km², with three major disjunct areas in the west – one in the Sierra Nevada, one in Mexico (mostly in the state of Baja California), and one long continuous area along the coast of the USA in the states of California, Oregon and Washington (Fig. 4b). The current range of the inland group was

approximately 6.4-fold larger than the range at the LGM with an overlap of 316,500 km², suggesting that the range has significantly expanded as well as shifted northwards (Table 1; Fig. 4b). The current predicted range of the coastal group was approximately 2.8-fold larger than the range size predicted for the LGM with an overlap of approximately 109,500 km², suggesting that, while the range has expanded, it still

Table 1 Maximum likelihood estimates of θ ($= 2Ne$) and g (the exponential growth parameter) and $\Delta\ln L$ support for $g > 0$

Population	Area ratio*	g (SD)	θ (SD)	$\Delta\ln L$
Coastal	2.80	2567.34 (570.10)	0.01076 (0.00418)	7.0
Inland	6.40	6300.39 (603.48)	0.04242 (0.01006)	57.0

*Area ratio is predicted current range size of coastal and inland populations divided the predicted range size at the LGM.

occupies most of the area that it occupied at the LGM (Table 1; Fig. 4b).

Range expansion

When the current distribution was separated into the five categories of western boreal, western coastal, eastern boreal, Rocky Mountains and eastern boreal plus Rocky Mountains, and tested for ecological similarity between each region, we found no overlap between western boreal and western coastal, 11,167 km² of overlap between western boreal and the Rocky Mountains, 10,948 km² of overlap between western boreal and the east, and 29,140 km² of overlap between western boreal and the east plus Rocky Mountain region. The data indicate that the places where the Swainson's thrush occurs in the western boreal region are more ecologically similar to eastern boreal and Rocky Mountain regions than to the western coastal region.

Estimates of population growth

The estimated growth parameter (g) was strongly positive in both groups, but g for the inland group was three times larger than g for the coastal group, suggesting that inland populations have undergone a larger demographic expansion (Table 1; Fig. 5). While our estimates vary widely depending upon the mutation rate, both suggest that significant population expansion has occurred over the last 21,000 years. Under a conservative mutation rate of 0.01 substitutions per site per million years, the coastal group was at 35% [$100(N_t/N_0)$, where N_0 is the current effective population size] and the inland group was at 8% of its current effective population size at the LGM (Fig. 5). Under a high mutation rate (0.1 substitutions per site per million years), the estimated population sizes of both coastal and inland group were $< 1\%$ of their current size at the LGM.

DISCUSSION

Geographic isolation at the last glacial maximum

The palaeodistribution models are concordant with the molecular analysis, suggesting that coastal and inland groups probably diverged while isolated in eastern and western regions at the LGM and have since undergone significant range expansions. Estimates of change in relative population size

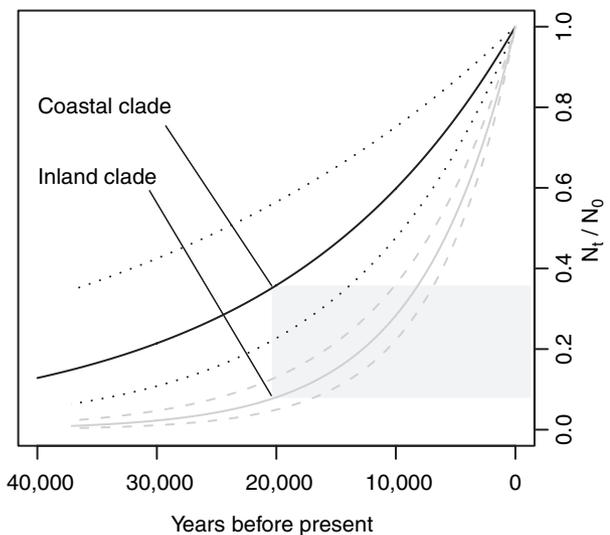


Figure 5 Change in relative population sizes (N_t/N_0), where N_t is the effective population size at time t and N_0 is the current effective population size) through time for the inland and coastal groups of the Swainson's thrush. Estimates based on a maximum likelihood method for jointly determining the parameters θ ($= 2N\mu$, where μ is the mutation rate and N is the effective population size) and g (the exponential growth parameter in units of μ^{-1} ; Kuhner *et al.*, 1998) and assuming a mutation rate of 0.01 substitutions per site per million years. Dotted and dashed lines represent the growth curves for inland and coastal clades, respectively, given a value of $g \pm 2$ SD listed in Table 1.

based on genetic data provide independent and complimentary support to our estimates of change in range size, suggesting that the inland group has undergone a significantly larger demographic and range expansion since the LGM. Remarkably, both forms of inference suggest that the coastal group has undergone a 2- to 3-fold demographic and range expansion, while the inland group has undergone a 6- to 12-fold demographic and range expansion since the LGM. Reconstructing historical distributions without fossil data is extremely difficult. Both genetic estimates of population-size change through time and estimates of change in range size through time based on climatic models are prone to a high degree of error. However, the strength of the current study lies in the fact that the two independently derived estimates of population change reach the same conclusion, namely, that coastal and inland populations expanded from separate eastern and western regions after the LGM.

Estimates of changes in species distributions at the LGM based upon habitat shifts extrapolated from palaeobotanical records are consistent with our palaeodistribution models for the Swainson's thrush (Mengel, 1964; Pielou, 1991; Weir & Schluter, 2004). Weir & Schluter's (2004) reconstruction of the ranges of boreal forest birds at the LGM based on approximate distributions of three species of spruce (Lindbladh *et al.*, 2003) indicates the presence of three disjunct populations: one in the east, south of the glacier's edge, one in the Rocky Mountains, and one along the Pacific coast. Our model for the distribution

of the Swainson's thrush at the LGM provides strong support for a Pacific coastal and an eastern population, but very weak support for a Rocky Mountains population. An advantage of palaeodistribution models over habitat reconstructions is that palaeodistribution models are based on the environmental association of a particular species and therefore account for species-specific responses to climate change (Iverson & Prasad, 1998; Hodkinson, 1999). The disadvantages of palaeodistribution models include the potential for variation in the predicted range depending upon model choice (Thuiller, 2004) and reliance on the assumption that the distribution in climatic space remains stable across time (Davis *et al.*, 1998). Individually, each method of inference is fraught with potential pitfalls, but we consider consilience across phylogenetic, palaeodistribution models and habitat reconstructions a more robust approximation of the biogeographic history of the Swainson's thrush.

Range expansion

Our data support the hypothesis that climate change following the LGM allowed the inland group to expand its range, while the coastal group remained restricted to the Pacific coast. An analysis of ecological similarity between four subdivided regions of the current range revealed that populations in all three inland regions are climatically more similar to one another than any one inland region is to the Pacific coast region where the coastal haplotype is found. Based on our bioclimatic models alone, we cannot reject the possibility of a Rocky Mountains to western boreal forest colonization pathway. However, the absence of genetic differentiation between Rocky Mountains populations and eastern boreal populations, combined with the lack of suitable habitat in the Rocky Mountains at the LGM predicted from the palaeodistribution models, suggests that an eastern boreal to western boreal forest colonization pathway is the most likely alternative. These data suggest that populations expanding out of the east into previously glaciated areas in the west were undergoing a natural extension of their range by tracking the change in climatic conditions. The fact that molecular analyses and spatial modelling result in the same inferences about range dynamics is consistent with the idea that the observed climatic envelopes reflect the ecological boundaries of coastal and inland groups (Hugall *et al.*, 2002). Ecological differences between coastal and inland forms may help to explain why the coastal populations remained restricted to the Pacific coast while inland populations underwent a cross-continental range expansion.

Potential for climatic niche divergence

Highly significant differences in environmental variables combined with no overlap between predicted ranges show that coastal and inland populations occupy distinct climatic regions on their breeding grounds. Previous studies have used bioclimatic modelling to distinguish between niche divergence

and conservatism (Peterson *et al.*, 1999), equating a species climatic envelope with its ecological niche. When sister species are modelled separately and there is significant overlap between the areas of predicted occurrence, niche conservatism is inferred (Peterson *et al.*, 1999); on the other hand, no overlap between predicted areas of occurrence suggests niche divergence (Peterson *et al.*, 1999; Graham *et al.*, 2004). Given this interpretation, our data support the idea that climatic niches can evolve over relatively short evolutionary time-scales (Schluter, 2000; Rice *et al.*, 2003) and contrast with the idea that climatic niches are highly conserved between sister taxa (Peterson *et al.*, 1999; Wiens, 2004). The potential for niche divergence in the Swainson's thrush may be further accelerated by divergence in migratory pathways and over-wintering locations. Divergent selection on the migratory program (timing of arrival, length of the migratory journey and orientation direction) as well as selection on the wintering grounds may further differentiate coastal and inland groups (Bensch *et al.*, 1999; Irwin & Irwin, 2004). Future research in this system will focus on how differences in the climatic niche and migratory strategies may limit gene flow between closely related taxa (Endler, 1973; Cicero, 2004).

CONCLUSIONS

The combination of palaeodistribution modelling and molecular analyses presented here provides a spatially explicit example of how geographic distributions at the LGM and post-glacial colonization routes shaped current migratory pathways in the Swainson's thrush. The potential for climatic niche differentiation coupled with the evolution of distinct migratory pathways may be important to divergence between coastal and inland groups of the Swainson's thrush and other species with intraspecific divergence in migratory strategies. Divergent selection on the migratory programme (timing of arrival, length of the migratory journey and orientation direction) as well as selection on the wintering grounds may further differentiate distinct migratory forms (Bensch *et al.*, 1999; Irwin & Irwin, 2004). Secondary contact between populations with divergent migratory strategies (migratory divides) have been documented in many migratory species (Ticehurst, 1938; Hedenstrom, 1987; Helbig, 1991; Bensch *et al.*, 1999). Future research may reveal the importance of divergence in migratory pathways to reproductive isolation between distinct migratory forms.

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