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Habitat suitability and the constraints of migration in New World warblers

David P. L. Toews

D. P. L. Toews (toews@cornell.edu), Cornell Lab of Ornithology, Cornell Univ., 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

Identifying the factors that influence geographic range limits can illustrate the various ecological, physiological, and evolutionary constraints imposed on a species. The range limits of migratory birds are particularly challenging to study as they occur in disjunct regions at different times of the year, which can impose different constraints. Travel between breeding and wintering regions poses a significant energetic and navigational challenge to birds, although it is not clear how these movements influence breeding dispersal and range expansion. Here I ask whether the possible costs of migration limit the breeding ranges of wood warblers, a group of birds with an extensive history of ecological and evolutionary studies. I used occurrence records for multiple wood warbler species, breeding primarily in the boreal forest of North America, to generate environmental niche models. I tested for over-prediction of habitat suitability into the western boreal forest, where most these species do not have occurrence records but where there is presumably suitable habitat. I found that some of these vagile taxa, primarily found east of the Rocky Mountains, also have predicted habitat suitability that extends into the north and west, where they have little to no occurrence records. I discuss several possible explanations for this discordance. In particular, the patterns are consistent with the costs of a long-distance migration limiting the benefits of range expansion, as migration may become too onerous as the distance between breeding and wintering areas increases. These results speak to the process of niche filling more generally and call attention to an under-appreciated explanation for why migratory species may not fully occupy their fundamental niche.

Studies of species' range limits have demonstrated various types of dispersal barriers that restrict range expansions. In the simplest scenario, a taxon with a narrow physiological tolerance may be limited from moving into a new habitat with a challenging environmental regime (Hutchison 1965, Jankowski et al. 2013). Alternatively, a species may not occur in a region that may contain suitable habitat because it simply has not had the ability or time to disperse (i.e. a consequence of historical contingency). For example, mountain ranges and river barriers may present sufficient challenges to impede movements into suitable habitats. Biotic interactions can also be important, such as the presence of predators, pathogens, or another species that competes for similar resources (Price and Kirkpatrick 2009, Sexton et al. 2009). These latter two scenarios (historical contingency and competition) can generate discordance between a species' fundamental and realized niche, whereby suitable habitat may not be utilized (Hutchison 1965). These ideas have been discussed conceptually by several authors (Sóberon and Peterson 2005, Sóberon 2007, Elith and Leathwuck 2009), particularly in the context of how they can be indirectly informed by environmental niche models. While there have been many studies of the determinants of species' ranges, there are still several outstanding questions regarding the relative importance of factors that may restrict a species from expanding into presumably suitable habitat.

Migratory animals have particularly complex range determinants because – by definition – they occur in disjunct regions at different times, sometimes separated by thousands of kilometres. In many species, the process of migrating between these distant areas is a navigationally complex and energetically demanding task (Alerstam 1990). Much research in avian systems has suggested that migration is the result of a tradeoff between the costs of moving long distances and the benefits of several factors, including higher seasonal abundance of resources in different areas (Alerstam 1990) and/or release from high levels of predation (McKinnon et al. 2010). Presumably, the benefits of migration are reduced when the challenges of the journey become too onerous. For example, it is very likely that the energy required for long migrations might prohibit breeding range expansion, particularly if a species is strongly tied to a distant wintering area. While this is an intuitive postulate, only a small number of studies have rigorously tested it. For instance, two studies have addressed this question at a continental scale: Böhning-Gaese et al. (1998) and Bensch (1999). These studies used distributional information to show that many migratory species – as compared to year-round residents – exhibit biogeographic patterns consistent with dispersal reduction both within and between continents. Bensch (1999) found that Palearctic migratory species are significantly less likely to have ranges that include both

Scandinavia and western Eurasia than resident species. These results imply that migratory species – presumed to have the ability to disperse long distances – do not do so in many cases (although see Thorup 2006).

In these comparative studies, there were there were no explicit tests about the possible suitability of uninhabited regions. In other words, did these species not disperse to these regions because they were not able to, or the habitats were not appropriate? Engler et al. (2014) addressed this by comparing known occurrence locations with the results of species distribution modelling. They studied the citril finch *Carduelis citrinella*, investigating the conspicuous absence of this species in presumably suitable habitat. Engler et al. (2014) found evidence that accessible regions north of the species' extent of occurrence were in fact suitable, at least based on environmental niche models. They suggest this could be due to factors that were not included in the niche modelling framework, but also raise the possibility that the constraints of migration could limit the expansion of citril finches into these areas (Engler et al. 2014).

Here I employ a similar conceptual approach to Engler et al. (2014), but in a comparative framework across many species. I ask whether the presumed constraints of migration might limit the northern and western breeding range expansion of a group of New World warblers in North America. This group of birds, in the Parulidae family, are small, colourful passerines that are primarily insectivorous and many are Neotropical migrants (Winger et al. 2011, Gómez et al. 2016). They are a particularly tractable system for studying range limits given the extensive knowledge of their ecological, evolutionary and biogeographic histories (Price et al. 2000). In addition, most of the species in North America are migratory: they breed in the US and Canada between the end of May and August and winter in the southern US, the Caribbean, and Central and South America between September and April. Wood warblers are also visually and aurally conspicuous and therefore have reasonably high detectability in citizen science surveys (Rosenberg and Blancher 2005), which is a large and growing source of distributional data (Sullivan et al. 2009).

For this study I tested the idea that, in some cases, these warblers are restricted from occurring in certain regions of suitable breeding habitat because of the constraints imposed by long migrations to and from their wintering grounds. I focused on the subset of warblers that breed in the boreal forest. Many of the dominant tree species that make up the boreal forest – and are utilized by these warbler species for nesting and foraging – extend throughout Canada and into Alaska (e.g. black spruce *Picea mariana*, white spruce *P. glauca,* trembling aspen *Populus tremuloides,* balsam poplar *Populus balsamifera* and white birch *Betula papyrifera*; Brandt 2009). In contrast, many of the warbler species that rely on these trees for nesting and breeding have ranges that occur only as far west as northern Alberta and British Columbia. Therefore, at a superficial level, there is a notable discordance between presumably suitable habitat and the occupied ranges of these vagile warblers.

To test whether there is evidence of unused suitable habitat, I employed environmental niche models (ENMs) and quantified whether predictions of habitat suitability matched the known warbler distributions. I predicted that if there are strong constraints imposed by migration, then these constraints would express themselves as a restricted occurrence into the northwest of North America, even the presence of suitable habitat. In other words, the ENMs would over-predict habitat suitability, where there are few breeding occurrence records for many of these warblers (Fig. 1).

Methods

Species selection

The first criteria I used to decide whether to include a taxon in the analysis was whether any portion of its range occurred within the boreal forest. My intent was to address the discordance between occurrence and habitat suitability across the boreal eco-region, therefore my analysis necessarily focused on only those warblers that have most of the ranges within this boundary. I used the map generated by Brandt (2009) that outlined the geographic extent of the boreal zone and hemiboreal zones. I combined both regions – boreal and hemiboreal – for the analysis and refer to them jointly as the 'boreal forest'. I used the range maps generated by BirdLife International and NatureServe (2015) to identify the breeding extent of the warblers. I only included those species that had most their range within the boreal forest (e.g. Fig. 2A–B). There are several warblers that are more cosmopolitan throughout North America (i.e. the yellow warbler *Setophaga petechia* and the common yellowthroat *Geothlypis trichas*) that I excluded because of their wide distribution and poorly resolved subspecific boundaries. I included only those species that have expanded throughout the western portion of the boreal forest, with ranges extending at least 110°W. I excluded two species – the American redstart *Setophaga ruticilla* and Tennessee warbler *Leiothlypis peregrine* – that have much of their ranges within the boreal forest, but also extend outside of this area, across the Rocky Mountains and into the interior of British Columbia (Sibley 2014).

In some cases, there are evolutionarily distinct eastern-boreal warblers that have not been identified as species-level taxa by nomenclature committees. For example, strong east–west differences have been noted within yellow-rumped warblers (i.e. myrtle and Audubon's warblers *Setophaga [coronata] coronata* and *S. [c.] auduboni,* respectively; Brelsford et al. 2011, Toews et al. 2016), eastern and western Wilson's warblers *Cardellina pusilla* (Irwin et al. 2011, Ruegg et al. 2014), and eastern and western orange-crowned warblers *Oreothlypis celata* (Bull et al. 2010). For these species groups, I used information from the most recent genetic studies to inform the range boundaries between eastern and western taxa.

Applying these criteria resulted in 17 taxa that were included in the analysis. I classified these taxa into four broad biogeographic classes (Fig. 2). The majority of species (n = 10) had a strictly eastern-boreal distribution: their ranges occur throughout most of the boreal forest, but do not extend far into the north or west (Fig. 2A). In some cases, eastern-boreal species also have a sister taxon that occurs in the west (e.g. the black-throated green *Setophaga virens,* in the east and Townsend's warblers *S. townsendi,* in the west), where the western species occurs throughout British

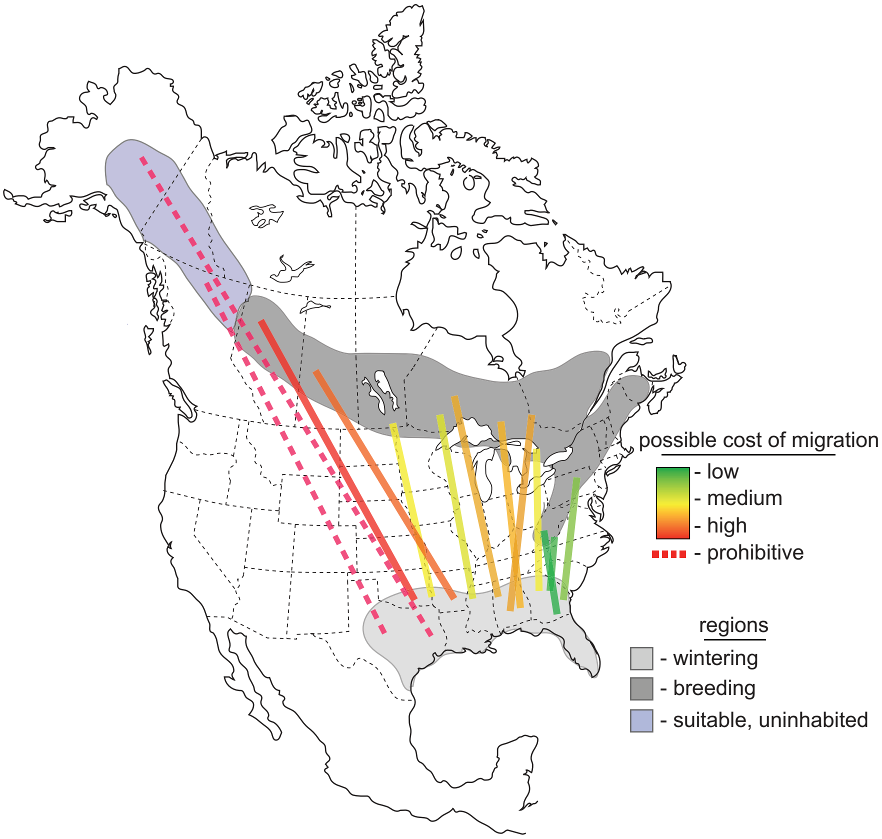

Figure 1. Conceptual schematic for how the possible costs of migration for eastern New World warblers might translate into the observation of uninhabited, but suitable regions in northwestern North America.

Columbia and into Alaska (n = 3; Fig. 2D). I included these species in the analysis and focused the analysis only on the eastern group. In the case of the Wilson's warbler, where the east–west split is not currently recognized as a species-level designation and where the current subspecies boundary is not well delineated, I only included those records east of the British Columbia – Alberta border, excluding records from southwestern Alberta (within the range of the interior-western subspecies, *C. p. pileolata;* Irwin et al. 2011).

I also included four warblers that have ranges that extend throughout the entire boreal forest, including far into the northwest. This is the case for the blackpoll warbler *Setophaga striata* and the northern waterthrush *Parkesia noveboracensis* (Fig. 2B) as well as myrtle/Audubon's warblers and eastern/western orange-crowned warblers. These latter two species have a closely related western group; I only included records for the eastern group (Fig. 2C).

Environmental niche modelling

To estimate habitat suitability I combined citizen science occurrence records with distribution modelling as implemented in MAXENT 3.3.3k (Phillips et al. 2006). I used geo-referenced occurrence records downloaded from the eBird digital repository, including records through to 2014 (Sullivan et al. 2009). To include only breeding occurrences, I retained only those records between June and July. While several species begin breeding in May and others continue breeding through August, these months also include many instances where birds were on migration. To keep this as consistent across species as possible I focused on the months – June and July – that would confidently exclude birds on migration. From the raw data I removed any identically duplicated records from the same locality. Using QGIS, I then filtered all the records to retain only those points that occur within the defined boundaries of the boreal forest (Brandt 2009). I did this to later generate an objective and robust set of background points to evaluate the model predictions. In some cases, however, this excludes occurrence records south of the boreal forest, particularly in southern Ontario and the northeastern US. Therefore, the resulting environmental niche models should only be considered as reflective of suitability within the boreal zone and not outside.

Citizen science data – most of which is collected opportunistically – is a robust resource of locality data, although there are a number of important caveats. In particular, several sampling biases can be problematic for the kinds of modelling approaches I use here. For example, areas primarily accessible by roads and near 'birding hotspots' will have inflated occurrence records (Sullivan et al. 2009). Dealing with this kind of 'accessibility bias' is challenging, although I partially controlled for any resulting observer clusters by using the spThin package in R (Aiello-Lammens et al. 2015). This program uses an algorithm to estimate nearest neighbour distances and thins data to retain points only within a given distance. I explored several distances and found that retaining points

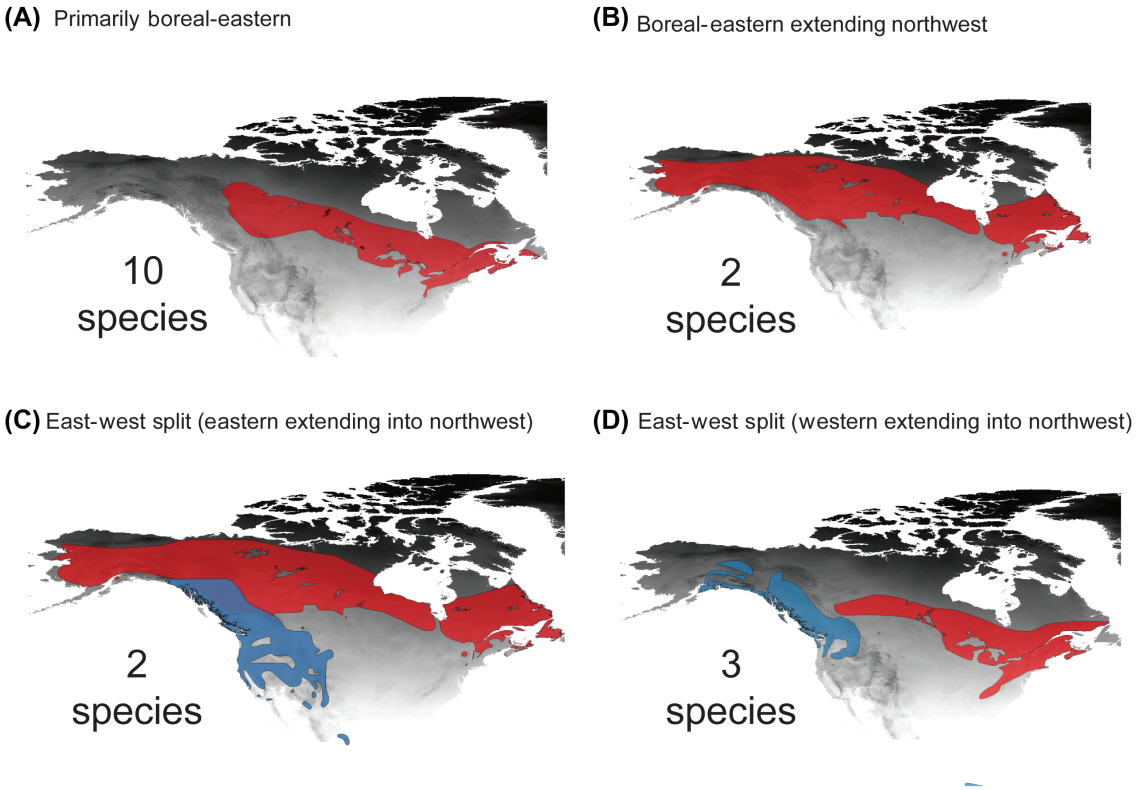

Figure 2. The broad scale biogeographic patterns for taxa included in the study. (A) species that inhabit most of the boreal forest, but only east of the Rocky Mountains – they do not breed in the northwest (e.g. cape-may warbler). (B) species that also inhabit the boreal, but also extend far into the northwest (e.g. blackpoll warbler and northern waterthrush). (C) eastern species (red; e.g. myrtle warblers) that have a similar distribution as (B), but also have a western counterpart (blue; e.g. Audubon's warblers). (D) eastern species (red; e.g. black-throated green warblers) that have a similar limited distribution into the northwest as (A), but also have a western counterpart (blue; e.g. Townsend's warblers).

within 20 km was suitable. Importantly, this distance is also larger than the resolution of the environmental predictor variables that I used to generated the ENMs.

Another source of sampling bias occurs across a broader latitudinal gradient, with high latitude regions in Canada and Alaska having fewer occurrence records, in part due to a smaller number of observers. This is a challenging to sampling bias to control for, particularly given that these northern regions are towards the edge of many species' ranges and could be the result of an observer bias or true reduced occurrence of a species. However, this bias is unlikely to strongly influence the conclusions of the current study because it operates in the opposite direction of the alternative hypothesis tested: fewer points at high latitude regions will reduce the importance of high latitude predictor variables, making the models less likely to over-predict into the northern regions.

To generate ENMs, I used the 'dismo' package in R, which implements MAXENT, and relied on the default tuning settings. I included four WorldClim environmental data products, in addition to elevation, each with a resolution of 2.5 arc-minutes, as predictor variables in the model (temperature min, max and mean, as well as precipitation average; Hijmans et al. 2005). For the temperature and precipitation data, I included the mean values for the periods during the breeding season (June and July). Restricting the environmental data to only the breeding months is an approach used in other recent studies of migratory birds (Engler et al. 2014, Gómez et al. 2016). I also included the 'tree cover' and 'deciduous' continuous field data sets from the Global Land Cover Facility (De Fries et al. 1998). To evaluate the models, I generated background points in QGIS (i.e. 'pseudoabsences') using points distributed randomly throughout the boreal zone (n = 2184) and each model was compared to this same background set of points. I chose only those background points within the boreal forest in North America as this region is presumably reachable by all the species. In the context of this study – testing for suitable habitat in the boreal zone – it is also the most biologically relevant, and objectively delineated, ecological region. In line with conventions for testing these kinds of ENMs I retained 20% of the original occurrence records for each species to test the predictive power of the models.

I estimated the quality of the models by quantifying the area under the curve (AUC). While it is a widely-used threshold-independent statistic, the strength of AUC for quantifying prediction accuracy has been criticized (Lobo et al. 2008, Li and Guo 2013) and, therefore, these results should be treated with some caution. I calculated the average AUC across 10 iterations of the modelling procedure. I conducted this analysis for all the occurrence records for taxa that are primarily boreal-eastern breeders (i.e. distributions

A and D in Fig. 2). I also computed multivariate environmental similarity surfaces (MESS; Elith et al. 2010). MESS analysis compares the multivariate similarity between a given point on the map with the given predictor variables. This can be used to identify geographic regions of where environments are highly similar/dissimilar as compared to the set of reference points.

For the four species that have occurrence records in the northwest (i.e. those with distributions B and C in Fig. 2) I used their occurrence data to test the efficacy of the modelling approach described above. For these tests I analysed only an 'eastern' subset of the data and used the resulting ENMs to test whether there was predicted suitable habitat in the northwest. I then compared the predicated suitability with actual occurrence records – withheld from the original model – in the northwest. To generate the ENMs, I used a similar approach as described above (i.e. I removed duplicate records, clipped records to the extent of the boreal forest, and thinned the data points), but I used only those points east of 120°W (the approximate longitude of the northern portion of the British Columbia – Alberta border). I then used the ENM prediction to estimate the suitability values of actual occurrence records west of 120°W. For each group, I compared the median suitability of the actual points to a set of random points within the boreal zone (n = 1142), west of 120°W. To illustrate the resulting ENMs I used two methods. First, I calculated the average raw MAXENT suitability score using the 'raster calculator' in QGIS. As a second approach, I used the 'equal training sensitivity and specificity' thresholds for each species to generate binary predicted presence/absence maps, which I then summed across all the species. (Schidelko et al. 2013).

Data deposition

MAXENT output files for all 17 species are available in ASCII format through Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.15423> (Toews 2017).

Results

ENMs across all of the 17 species showed strong predictive accuracy when evaluated with a testing dataset. In each case, AUC values were equal to or higher than 0.81 and the mean AUC across all the species was 0.88 (Table 1). Across the 10 iterations of the modelling procedure the standard deviations in AUC were extremely low (< 0.02). The mean temperature across the breeding season was identified as the top environmental predictor in 9 of the 13 boreal eastern breeding warblers.

Using the four species that occur throughout the boreal zone, but that also extend into the northwest (i.e. the biogeographic patterns illustrated in Fig. 2B–C), I tested the efficacy of estimating possible over-prediction of suitable habitat into the northwest (Fig. 3). Across all four of these species, habitat suitability – as estimated from only the breeding records east of the Rocky Mountains – was on average higher for actual occurrence records in the northwest than compared to a random distribution of points, although this difference was small. This suggests that this approach to test whether there are suitable, uninhabited regions in the northwest is valid, at least based on this assessment.

I found that many of the warblers that occur primarily in the boreal forest – but breed only east of the Rocky Mountains – showed evidence of non-zero habitat suitability into west and northwest (Fig. 4, 5). Some species, like the magnolia, palm, cape-may and Wilson's warblers, showed high levels of suitable habitat in Alaska and the Yukon (Fig. 5). In contrast, other species, like the Connecticut warbler and the blackburnian warbler, showed less over-prediction into the northwest (Fig. 5). Consistent across most of the species, however, were three areas of moderate suitability in the west where there are few occurrence records. The first region is in the interior of Alaska, around the intermountain plateau surrounding the city of Fairbanks (identified as region A in Fig. 4). The second region of high suitability – also in Alaska – is in the Matanuska-Susitna valley, near the city of Anchorage

Table 1. Species information, biogeographic classifications and output of niche modelling analysis.

Common name	Scientific name	Biogeographic pattern (Fig. 2)	No. of occurrence points after thinning*	AUC of model	Equal training sensitivity and specificity
Connecticut warbler	*Geothlypis agilis*	A	348	0.92	0.43
Black-and-white warbler	*Mniotilta varia*	A	1183	0.89	0.47
Ovenbird	*Seiurus aurocapilla*	A	1318	0.89	0.48
Bay-breasted warbler	*Setophaga castanea*	A	599	0.89	0.45
Blackburnian warbler	*Setophaga fusca*	A	772	0.93	0.43
Magnolia warbler	*Setophaga magnolia*	A	1276	0.86	0.48
Palm warbler	*Setophaga palmarum*	A	586	0.84	0.45
Chestnut-sided warbler	*Setophaga pensylvanica*	A	907	0.93	0.45
Cape-may warbler	*Setophaga tigrina*	A	537	0.87	0.45
Canada warbler	*Cardellina canadensis*	A	577	0.91	0.42
Northern waterthrush	*Parkesia noveboracensis*	B	east, 1040; west, 316	0.83	0.48
Blackpoll warbler	*Setophaga striata*	B	east, 493; west, 233	0.81	0.41
Orange-crown warbler	*Oreothlypis celata*	C	east, 415; west, 310	0.83	0.45
Myrtle warbler	*Setophaga coronata*	C	east, 1669; west, 477	0.83	0.50
Wilson's warbler	*Cardellina pusilla*	D	581	0.85	0.46
Mourning warbler	*Geothlypis philadelphia*	D	822	0.91	0.45
Black-throated green warbler	*Setophaga virens*	D	780	0.92	0.44

*East and west refer to those species that were used to validate the modelling approach. The points east of 120°W were used to generate the ENM. The suitability estimates of actual occurrence records west of 120°W were compared to a distribution of random points (Fig. 3).

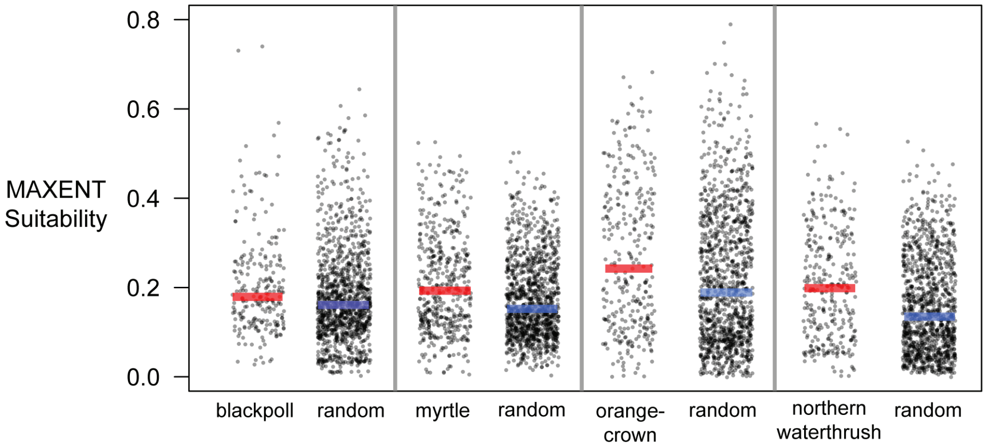

Figure 3. Habitat suitability estimates for species that occur into the northwest (Fig. 2B–C) based on breeding occurrence records east of the British Columbia – Alberta border (120°W). These are compared to random points distributed west in this area. The red bars show the median for actual occurrence records; black bars show the median values for random points. In each case the median of the actual occurrence records are higher than the random points, although this difference is not large in some cases.

(identified as region B in Fig. 4). Finally, there is a region of high suitability in north–central British Columbia, through the Peace River Valley near the city of Price George (identified as region C in Fig. 4). The average predicted suitability was 0.09 (max 0.26), 0.10 (max 0.33), and 0.10 (max 0.41) for regions A, B and C, respectively. There was very little over-predicted suitability in the west based on binary analysis, which illustrated only those regions above the MAXENT equal training sensitivity and specificity threshold (Supplementary material Appendix 1 Fig. A18). Finally, the MESS analysis (Supplementary material Appendix 1 Fig. A19) showed much of the high latitude regions in North America have similar environmental variables as compared to the reference points (i.e. high MESS values). However, towards the south – along the Gulf of Mexico and the Pacific Coast of Mexico – much lower MESS values imply non-analogous environmental conditions.

Discussion

This application of niche modeling, combined with the analysis of many occurrence records, allowed me to identify apparently suitable but unoccupied habitat for multiple species of migratory passerines that occur across the boreal forest in North America. I suggest five possible explanations for the observation of over-prediction into the west for some of these eastern, boreal wood warblers: a result of poor model predictions, historical contingency, dispersal barriers, the presence of a competitor, and the constraints of migration. I consider each possibility in turn.

Poor performance of the modelling approach used here is an important consideration. For example, the regions of high suitability in Alaska and British Columbia may be an artefact of using such broad scale climate and remote sensing data to understand the habitats that these birds interact with on a much finer scale. Indeed, these warblers may not find these habitats suitable at all. This is difficult to address without additional experimental data (Hargreaves et al. 2014), although this kind of data is logistically challenging to gather in migratory warblers. However, the ecology of these species – particularly in terms of the tree composition of their breeding territories – superficially implies that these areas are likely to be suitable. For example, the distribution of several tree species, which many of these warblers use for nesting and foraging (e.g. black spruce *Picea mariana* and trembling aspen *Populus tremuloides*), are abundant in all the higher suitability regions identified in Fig. 4 (Brandt 2009, Sibley 2014). Combining the broad scale approach used here with smaller scale vegetation surveys of breeding territories would

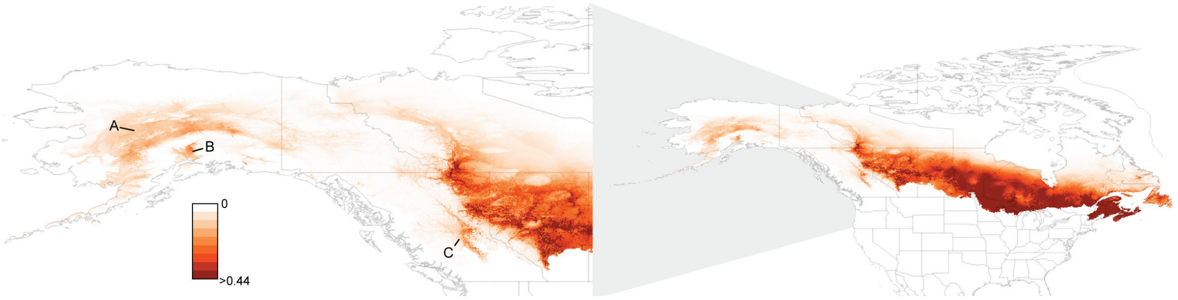

Figure 4. The average MAXENT suitability output across the eastern species that do not have breeding records into the northwest. The three regions of over-predicted high suitability in the detailed inset are: (A) the interior of Alaska, around the intermountain plateau surrounding the city of Fairbanks; (B) in the Matanuska-Susitna valley, near the city of Anchorage and (C) in north–central British Columbia, through the Peace River Valley near the city of Price George.

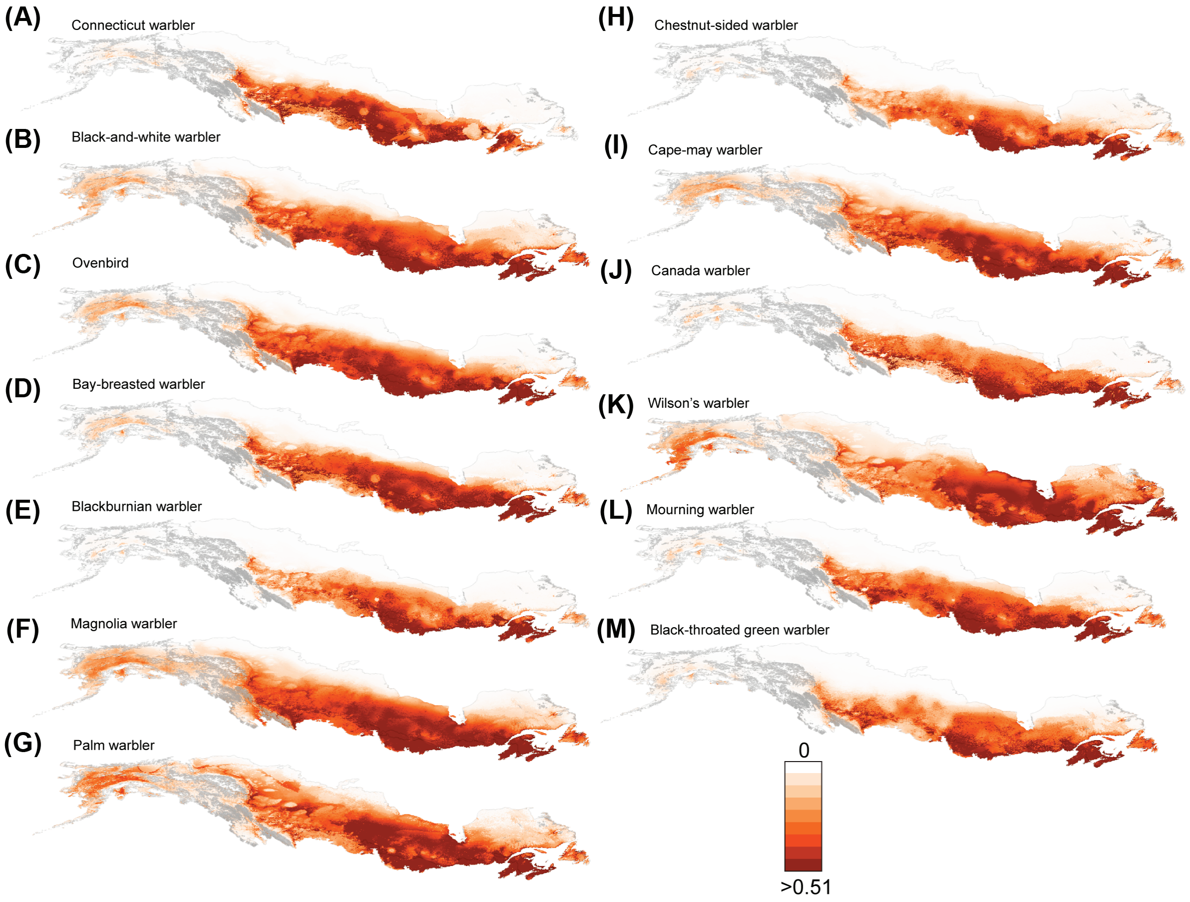

Figure 5. Individual MAXENT suitability output across the eastern species that do not have breeding records into the northwest, clipped to the extent of the boreal forest.

be better able to address the limitations associated with using this kind of indirect data.

Another explanation invokes non-equilibrium distributions and historical contingency. A scenario of historical contingency posits that these warblers have simply not had enough time to disperse into the west and may well in the future, if given enough time. Considering the relatively recent retreat of the glaciers – in a geological context – it is indeed plausible that there has not been enough time for these species to disperse further into the north. However, in many cases these taxa are known for being quite vagile, and vagrant eastern warblers regularly show up in southern Alaska (Gibson et al. 2015). For example, mourning *Geothlypis philadelphia*, cape-may *S. tigrina*, magnolia *S. magnolia*, chestnut-sided *S. pensylvanica* and palm warblers *S. palmarum* are all identified as casual visitors in southern Alaska; black-throated green *S. virens* and Canada warblers *C. canadensis* are both identified as accidental vagrants, with one or two records (Gibson et al. 2015). Clearly, for a breeding population to be established, both males and females need to occur contemporaneously at a given site. However, given the regularity over which these species are observed as vagrants, it seems plausible that breeding populations would have established over the past several thousand years.

The most notable dispersal barrier to expansion into this region of North America are alpine expanses of the Rocky Mountains. The fact that many avian species and subspecies have range limits that track the contours of this large mountain range implies that this is an important barrier for many species (Swenson and Howard 2005). Indeed, across all of the ENMs, regions of low predicted suitability align closely with the alpine habitat of the Rockies. However, at least in northern BC and the southern Yukon, the height of the Rockies is lower than further to the south, and there is non-alpine habitat connecting interior Alaska, northern BC and Alberta. Moreover, within-species studies of avian populations on either side of the Rockies suggest it is not always a strong barrier to gene flow. For example, in genetic studies of boreal chickadees *Poecile hudsonicus* (Lait and Burg 2013) and black-capped chickadees *Poecile atricapillus* (Adams and Burg 2015), both of which occur on either side of the mountain range, there was only mixed evidence of a barrier to gene flow across the Rockies. Boreal chickadees, in particular, showed very little evidence of genetic structure across this putative dispersal barrier (Lait and Burg 2013). Therefore, while the Rockies are a conspicuous suture zone coincident with the range limits for several avian species, this may be more a product of historical expansion from common refugia, as opposed to a current barrier to dispersal.

The presence of a competitor is particularly relevant for those species that have related western taxa that occur into the west: black-throated green, mourning, and eastern Wilson's warblers may compete and be excluded by their western counterparts: Townsend's, MacGillivray's, and western Wilson's warblers, respectively. Indeed, the two former pairs are known to hybridize extensively where they co-occur (Irwin et al. 2011, Toews et al. 2011), thus it is plausible that they compete for resources. However, the number of species that have a related western counterpart is only a small minority of those included in the current study. Therefore, competitive exclusion from a congener does not seem to be a general explanation for restricted occurrence for most species.

The final explanation for this pattern of uninhabited, but presumed suitable habitat, is the possible constraints imposed by a long-distance migration. Under this scenario, species may be strongly tied to their overwintering locations and, by expanding further into the north, this makes their migration too onerous. If this is indeed true – that breeding range dispersal is strongly tied to overwinter ranges – this has important implications for our understanding how range limits may evolve in this diverse group of wood warblers. This pattern of limited expansion into the west and northwest in these boreal breeding warblers is particularly interesting when contrasted with other, non-migratory boreal Passerines. For example, the ranges of the boreal chickadee, pine grosbeak, red crossbill, red-breasted nuthatch and gray jay, all track the range of the boreal zone throughout much of eastern and central Canada (Sibley 2014). However, they also occur far north into interior and western Alaska, unlike most of the migratory warblers studied here. Indeed, as far as I am aware, there are no non-migratory Passerines that have conspicuous range limits in northern Alberta or northeastern British Columbia similar to what these migratory warblers exhibit.

It is important to note, however, that there are some eastern warblers that do occur far into the northwest (i.e. Fig. 2B–C), suggesting these kinds of northern expansions are possible. I suggest two possible scenarios that may have facilitated their expansion into the northwest. First, during western expansion, a species may concurrently incorporate novel overwintering habitats and/or migration routes. This is most likely the case for myrtle warblers, as evidence suggests that myrtle warblers that breed in interior Alaska migrate down the Pacific coast and winter along the coast of California and Oregon (Hunt and Flashpohler 1998). This Pacific overwintering site is disjunct from the main overwintering site of myrtle warblers, which is concentrated in the southeastern US and the Caribbean (Hunt and Flashpohler 1998, Toews et al. 2014). Therefore, in this case, the evolution of a novel overwintering site and/or plasticity in their overwintering locations has possibly allowed for a shorter migration and may have facilitated the expansion of breeding territories into the northwest.

The evolution of novel migration and overwintering sites may also be one of the factors that has promoted divergence between several eastern and western groups, as divergent migration and overwintering behaviours may translate into reproductive isolation between breeding populations. Migratory pathways are often conserved within groups (Ruegg and Smith 2002) and upon secondary contact – after sustained periods of geographic isolation – divergent migratory behaviours can promote reproductive isolation. This is most likely the case between coastal and interior Swainson's thrush *Catharus ustulatus* (Delmore and Irwin 2014). These two taxa have evolved very distinct migratory patterns and there is some suggestion that hybrids between them inherit an intermediate – and possibly inferior – migratory behaviour, promoting reproductive isolation between the subspecies (Delmore and Irwin 2014).

A second possibility for an expansion into the northwest is simply to be a 'superior' migrator. This is most likely the case for blackpoll warblers and northern waterthrush. Blackpoll warblers, in particular, are celebrated as having an extraordinary migratory capacity. These 12 gram birds breed in the high latitudes of Alaska and then migrate to and winter as far south as Venezuela (DeLuca et al. 2013). A recent geolocator study of blackpoll warblers recorded a three-day non-stop flight over open water during their journey south, which is an impressive feat for such a small bird (DeLuca et al. 2015). Clearly there are significant costs associated with this kind of long migration and there are likely important morphological and physiological adaptations that have facilitated this behaviour. However, the fact that this kind of long migration is observed implies that expansion into the northwest is possible while still maintaining a distant southern overwintering site.

In conclusion, I found evidence that several regions of western North America appear to contain suitable habitat for warblers that occur throughout the boreal forest, but only breed east of the Rocky Mountains. While there are a number of likely explanations for this over-prediction of suitable habitat, I suggest that the constraints of migration may be the most plausible and worthy of future investigations. The fact that a handful of species do breed in this region of the northwest – and travel great distances to get there – suggests that it is possible to express both behaviours (i.e. northwest breeding and far southeast wintering). However, the observation that most of the eastern boreal species do not is consistent with the constraints of migration playing an important part in structuring the discordance between these species' fundamental and realized niches.

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Supplementary material (Appendix jav-01157 at <www.avianbiology.org/appendix/jav-01157>). Appendix 1.