



# Landscape-scale habitat availability, and not local geography, predicts migratory landbird stopover across the Gulf of Maine

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While it is clear that many migratory behaviors are shared across taxa, generalizable models that predict the distribution and abundance of migrating taxa at the landscape scale are rare. In migratory landbirds, ephemeral concentrations of refueling birds indicate that individual behaviors sometimes produce large epiphenomena in particular geographic locations. Identifying landscape factors that predict the distribution and abundance of birds during migratory stopover will both improve our understanding of the migratory process and assist in broad, regionally relevant conservation. In this study we used autumnal passerine stopover data from a five-year period and eleven stopover sites across coastal Maine, USA, to test four broad hypotheses of migrant distribution and abundance that have been supported in other regions: a) the community characteristics of the pool of potential migrants, b) a site's local geography, c) landscape composition and configuration measured at different spatial scales, and d) interactions between these factors. Our final model revealed that birds concentrate at 'habitat islands', sites that possess a disproportionate percentage of the vegetated habitat in the 4-km surrounding landscape. The strength of this pattern, however, was inversely proportional to a species' remaining migratory distance. Our results corroborate several studies that emphasize the importance of land cover composition at finer spatial scales (< 80 km<sup>2</sup>) for predicting the stopover distribution and abundances of migratory birds. This suggests that different migrants likely assess stopover sites with similar mechanisms along their migratory route, and these commonalities may be broadly applied to identify stopover locations of conservation importance across the continent.

Stopover sites are extraordinarily important for birds making the costly journey from breeding grounds to nonbreeding grounds. The majority of total migration time for passerines is spent on stopover (Hedenstrom and Alerstam 1997, Dänhardt and Lindström 2001), although stopover habitat selection has only recently been explicitly modeled (Cohen et al. 2014). To predict the effects of future landscape alteration on migratory birds, we need to understand how individual choices made during migratory stopover produce population and community-level patterns of abundance. Here we present a community-scale comparison of stopover habitat use over five years across eleven monitoring stations spanning a 15 000 km<sup>2</sup> region of coastal Maine, USA. We use this broad-scale dataset to test the efficacy of a number of hypothesized drivers of stopover abundance that have been identified by previous studies along the major North American migratory flyways. These factors include a) the characteristics of the taxa that are available to use a site for stopover (hereafter the 'migratory community'), b) local site position relative to major landforms (i.e. local geography), c) the landscape characteristics at multiple spatial scales, and d) interactions among these various factors (Table 1). Together, these taxa-, landscape-, and site-related factors likely combine to determine stopover site use each migratory season. Using a suite of previously unstudied stopover locations, we

tested whether a set of these factors could predict the integrated seasonal use of a site by the entire landbird migratory community over the autumnal migratory season. Integrated seasonal use is an estimate of the total number of migrants that stop at a given site throughout an entire migratory season, and it is thus a proxy for a site's importance to a migratory bird taxon or regional community.

One potential determinant of the distribution of migrants during stopover at a locale is the variety of migratory strategies employed by the migratory community. Landbirds differ in their energetic constraints and consequently in their need for migratory stopover (Moore et al. 1995) as a function of the distance to their non-breeding locale (Table 1: Migratory strategy hypothesis 1, M1), foraging guild (Table 1: M2), and other unique characteristics of their phylogeny (taxonomic family) (Table 1: M3). Ultimately, however, these strategies affect whether an individual will use a specific stopover site, and the integrated use of a site by all migrants should be partially determined by the composite strategies of the entire migratory community. For example, species traveling over 5000 km may have considerably different stopover habitat requirements than species spending the non-breeding season within 1500 km of their breeding grounds (M1). Similarly, site use is influenced by energetic constraints, and migrants that are plastic in their dietary behavior (Parrish 2000) may

Table 1. Citations that found support for each general hypothesis of migrant distribution tested in this study (non-exhaustive). The right column indicates whether or not our study supported the referenced hypothesis.

Hypothesis	Explanatory variables	Citation	Supported
Migratory community characteristics (M)	M1: migration strategy	Carlisle et al. 2004	Yes
	M2: foraging guild	Parrish 2000 Rodewald and Brittingham 2004 Wilson et al. 1982	No
	M3: taxonomic group	Suthers et al. 2000	Yes
Local geography (G)	G1: distance from the coastline	Bonter et al. 2009 Buler and Moore 2011 Ralph 1981 (Stewart et al. 1974) Alerstam and Pettersson 1977	No
	G2: NE to SW position within the Gulf of Maine	Drury and Keith 1962 McCann et al. 1993	No
	G3: mainland vs island site	McCann et al. 1993	No
	G4: island size	Suomala et al. 2010 Martin 1980	No
Landscape characteristics (L)	<b>Landscape composition</b>		
	L1: total percentage of vegetated habitat	This study	No
	L2: total percentage of four land cover types	Bonter et al. 2009	No
	L3: proportional vegetated habitat availability	Buler and Moore 2011 Buler et al. 2007 Moore et al. 1990 Cohen et al. 2014 This study	Yes
	L4: proportional availability of four land cover types	This study	No
	<b>Landscape configuration</b>		
L5: vegetation patch dynamics (patch density and patch area)	Martin and Karr 1986 Rodewald and Brittingham 2004 Vitz and Rodewald 2007 Matthews and Rodewald 2010 Wilson et al. 1982 Cohen et al. 2014	No	
Combinations and interactions of above hypotheses (I)	I1: combination of variables	Bonter et al. 2009 Vitz and Rodewald 2007 Wilson et al. 1982 Buler and Moore 2011	Yes

exhibit different stopover choices than birds that are dietary specialists (M2). In New Jersey, broad stopover habitat use was similar by taxonomic family, with most families preferring similar successional stages and different families choosing different habitat types (M3) (Suthers et al. 2000).

Migrant use of a locale during stopover may also be determined by local geography, including a site's distance from a major coastline (Table 1: Geographical hypothesis 1, G1), its position along a coastline (Table 1: G2), and whether or not the site is found on an island (Table 1: G3) of a given size (Table 1: G4). Coastlines, for one, are known to concentrate migrant landbirds unwilling to cross open water without suitable weather conditions (Gauthreaux 1971). Even in favorable weather conditions, however, migrants use coastal habitats in large numbers (Kuenzi et al. 1991), especially during the fall in eastern North America, when the prevailing winds drive migrants toward the coast (Williams et al. 1977, Moore et al. 1995). This effect may be augmented in the fall because the migratory community is dominated by young of the year, which use the coast to visually orient during their first passage south (Ralph 1981). We might expect then, that distance from the coast would correlate inversely with stopover site use (G1). Further, the northeast–

southwest orientation of Maine's coastline has the potential to concentrate large numbers of birds. As birds traveling from the northwestern US reach the coast at various points, but all continue southwest along the coastline (Drury and Keith 1962, Richardson 1978), we may detect more birds at sites within the southwestern extent of the region than within the more northeastern extent (G2). Islands may produce different patterns of stopover relative to continuous coastal shorelines as well (G3), as has been reported along two different stretches of North American shoreline (McCann et al. 1993). Similarly, island size may be correlated with bird abundance in migration (Martin 1980, Suomala et al. 2010) (G4), as it is in the breeding season (Freemark and Merriam 1986, Blake and Karr 1987, Suomala et al. 2010).

Landscape characteristics are a third broad category of factors that have been found to predict patterns of migrant stopover. Landscape characteristics can be broken into two, more specific groups; landscape composition and landscape configuration. Landscape composition includes variables describing the relative amount of various land cover types such as the total percentage of vegetated lands (Table 1: Landscape characteristic hypothesis, L1), the total percentage of various broad land cover types found within the landscape

(Table 1: L2), and the proportional habitat availability (the proportion of any type of land cover versus all other cover types: L3 and L4). To our knowledge, habitat availability has not been tested directly as a driver of migrant stopover behavior, but it is a keystone of habitat selection theory more broadly (Johnson 1980, McDonald et al. 2005). There is considerably more research on the importance of the landscape configuration for migrants. In landscapes where resources are patchy, migrant foraging and habitat use can vary by patch size or patch density (Table 1: L5). Several studies in the midwestern US have found differential use of habitat patches and their edges during migration (Wilson et al. 1982, Vitz and Rodewald 2007).

Landscape composition and configuration are widely used predictors of habitat use more broadly, but success in their use is tightly dependent on scale. At large spatial scales (> 450 km<sup>2</sup>), the proportion of vegetated lands versus un-vegetated lands may be a significant driver of stopover site use (L3). Many authors have recognized the importance of finer scale habitat availability in predicting migrant habitat use (Hutto 1985, Moore et al. 1995). Buler et al. (2007) reasoned that hardwood forest cover in the northern Gulf of Mexico region might be a proximate cue for birds selecting a stopover site. Mathematical formulations have confirmed these predictions (Farmer and Wiens 1998, Simons et al. 2000), although empirical support is lacking (Buler et al. 2007). If birds use vegetation composition as a cue for habitat use at finer scales, migrant stopover distribution may vary by the local availability of certain land cover types relative to the availability in the larger region (L4).

Patterns of migratory stopover may also be influenced by the interactions among factors (Table 1: Interaction hypothesis 1, I1). In a review of migratory habitat selection studies, Petit (2000) reported an interaction between stopover habitat use and foraging guild in three of five studies. During fall migration in the Rocky Mountains, Carlisle et al. (2004) found differential habitat use between neotropical and temperate migrants, suggesting an interaction between migration distance and habitat type.

In this study we test the ability of these four broad, previously identified factors (migrant community, geography, landscape characteristics, and their interactions) to predict the distribution and abundance of 50 common migratory landbird species among 11 previously unstudied stopover locations across five autumn migration seasons.

## Methods

### Study region and sites

We used fall migrating-landbird data from eleven monitoring stations in the Downeast and Midcoast regions of Maine, USA from August–October 2007–2012 (excluding 2008) that used regionally standardized, passive mist-netting (Table 2). The stations are located along 180 km of coastline (Fig. 1). These sites span both sides of the mouth of the Penobscot River (the longest river system within Maine and the second longest river system that enters the Gulf of Maine). Birds often utilize rivers as migratory corridors (Bagg 1923, Skagen et al. 1998, Martell et al. 2001, Lehnen

and Kremetz 2005), and with its north-south orientation the Penobscot River may serve as an important landmark for birds migrating along the Atlantic flyway. Wherever possible, nets were erected in five main habitat types (forest, shrub, mowed or grazed field, and transitional edges in field-shrub and shrub-forest) within each site to prevent confounding the habitat of capture with the stopover site of capture. One of our eleven sites did not possess a field component (Cross Island) and two sites did not possess forest components (Seal and Petit Manan islands).

Five of the eleven monitoring sites were located on the mainland or on islands separated from the mainland by less than 1/20 of their width (Fig. 1). The site furthest from the coast, McFarland Hill, is located 3 km west of Frenchman Bay (9 km from the Gulf of Maine) in the interior of Mount Desert Island (MDI). Mount Desert Island has an area of 280 km<sup>2</sup>, is the largest island off the coast of Maine, and is located only 800 m from the mainland at its closest. Our second mainland site, Seawall, is located on the headlands of the southernmost tip of MDI, 16 km southwest of McFarland Hill. Three additional mainland sites, Petit Manan Point, Schoodic Point, and Schoodic Head, are located on peninsulas to the northeast of MDI.

We monitored migrants on six, off-shore islands (Fig. 1). Great Duck Island is a 0.75-km<sup>2</sup> island located 11 km further out into the Gulf of Maine from the Seawall site. Petit Manan Island and Cross Island are both located north-east of MDI (Fig. 1). All other island sites (Isle Au Haut, Seal Island, and Metinic Island) are located to the southwest of MDI at varying distances from the mainland.

### Bird captures

Each fall mist-nets were opened 30 min before sunrise and closed six hours after opening, when the conditions permitted. The number of nets opened on any given day varied by weather conditions (e.g. wind and rain), and we therefore used normalized daily capture rates with each site's daily total net-hours (the time each net was open summed daily across all nets at a site) instead of raw number of birds captured. We banded all birds with uniquely numbered aluminum bands during their initial capture.

We described patterns of bird abundance across our sampling region using 'integrated seasonal use', which we define as the mean detection rate of each species ( $n = 50$ ) at each site during each year a site was operated. We only included a species' seasonal use when it was not present in our region year round and we captured > 10 individuals across all sites within a given year. Not all commonly captured species were captured at each site during each year. Specifically, the individual sampling unit ( $n = 667$ ) was measured as the detection rate (captures divided by net-hours) of each species detected within each site per year ( $n = 20$  site-years: Table 2).

Because habitat selection and the integrated use of the community is partially a function of the number of individuals available for stopover, we calculated the integrated seasonal use using only detections during the 'peak' of migration for each species and year. To standardize our estimate of peak-migration time, we pooled daily capture rates for each species from all sites operated in a specific

Table 2. Operating organization, years of operation, and percentage of broad land cover types within the site (100 m buffer surrounding all mist-nets) and the value of proportional habitat availability (vegetated versus non-vegetated spaces) at the 4 km scale. Organizational abbreviations: Univ. of Maine (UMaine), Acadia National Park (ANP), Maine Coastal Island National Wildlife Refuge (MCINWR), Biodiversity Research Inst. (BRI).

Site	Operating organization(s)	Year(s) operated	% conifer forest	% mixed forest	% human development	% shrub-land	% grass-land	% non-habitat	Proportional hab. avail. (4 km)
Cross Island	UMaine MCINWR	2013	65	0	0	3	0	32	9.65
Great Duck Island	UMaine ANP	2010–2011	8	29	0	0	22	41	34.64
Isle Au Haut	BRI	2009	85	6	0	0	0	9	3.08
McFarland Hill (MDI)	UMaine ANP	2010–2011	1	74	3	8	10	4	1.11
Metinic Island	UMaine MCINWR	2009–2011	41	0	0	0	59	<1	36.84
Petit Manan Island	MCINWR	2009	0	0	0	0	29	71	106.31
Petit Manan Point	MCINWR	2010–2012	0	90	0	0	10	0	4.76
Seal Island	MCINWR	2007 and 2009	0	0	0	14	1	85	61.28
Seawall (MDI)	UMaine ANP	2010–2012	18	59	12	1	0	10	2.32
Schoodic Peninsula 1	UMaine	2009	63	0	24	0	0	13	3.88
Schoodic Peninsula 2	UMaine ANP	2012	46	49	0	0	0	5	3.76

year, obtained the quartile passage dates (the date at which 25 and 75% of the individuals of a particular species had been captured), and calculated site-specific annual mean capture rates using only the two middle observation quartiles. Because the assigned inner-quartile passage window ('peak') varied for each species with each year, this

method not only centers our analyses of habitat use during the periods when more of the preferred habitats will be filled, it also controls for variation in migratory phenology among both years and species. Table 3 describes variation in the number of days for the 'peak' migration of each year across all species.

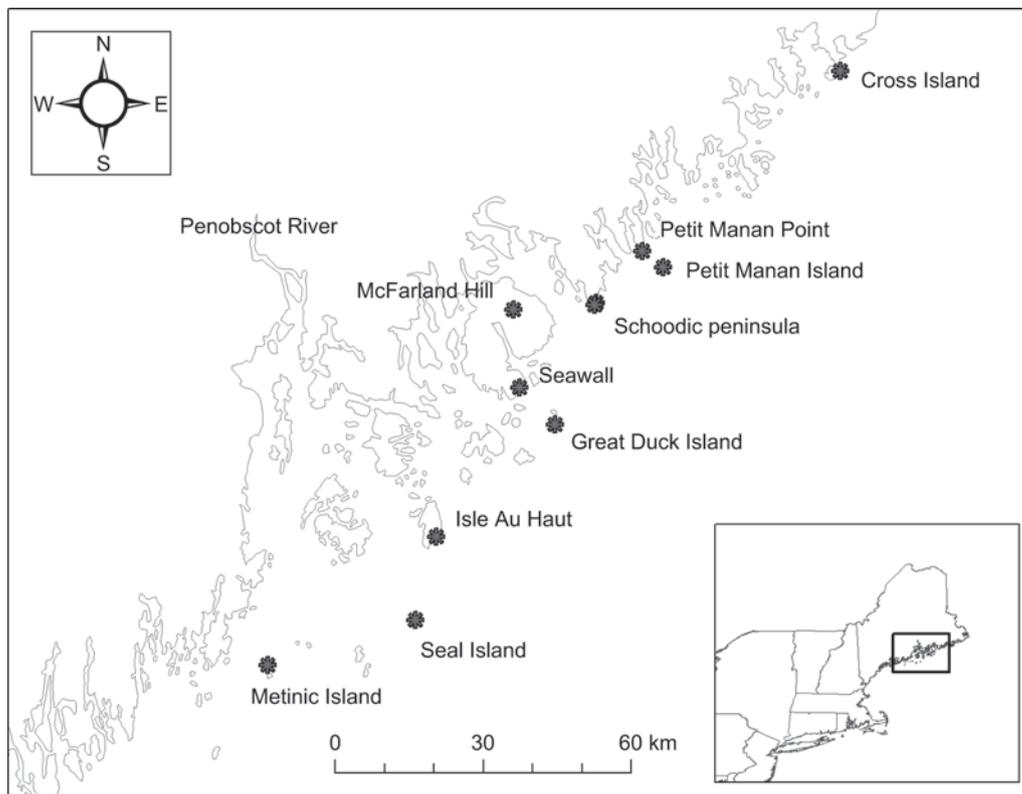


Figure 1. Diagram of our coastal transect of migration monitoring stations in the Downeast and Midcoast regions of Maine, USA. Note there are two migration monitoring stations located on Schoodic Peninsula.

Table 3. The range of capture days and the species corresponding to the range for 'peak' migration for each year and the yearly median of capture days.

Year	Minimum no. of days (species)	Maximum no. of days (species)	Median no. of days
2007	1 (Traill's flycatcher)	28 (hermit thrush)	11
2009	4 (black-throated green warbler)	24 (yellow-shafted flicker)	13
2010	6 (chestnut-sided warbler)	38 (song sparrow)	18
2011	7 (palm warbler)	49 (song sparrow)	20
2012	6 (myrtle warbler)	44 (hermit thrush)	22

### Migratory community characteristics

We tested for the ability of three metrics of the migratory community to predict habitat use: migratory strategy (Table 1: M1), foraging guild (M2), and taxonomic group (M3). As an additive effect, each of these three variables tests whether the average relative use across our entire region differs by taxa. We used migration distance as an index for migratory strategy (M1) by calculating the difference between the latitude at the center of our region (MDI) and the latitudinal midpoint of the nonbreeding range (as defined by Erickson et al. 2011). This method estimates the median distance remaining in migration for each species and provides a continuous variable for migratory distance as birds pass through our region. Species were further grouped based on their diet during fall migration (M2) as insectivores, granivores, frugivores, and generalists using previous categorizations created from three sources (Parrish 1997, Suomala et al. 2010, Erickson et al. 2011). Finally, we included taxonomic family (M3) as a covariate to control for phylogenetic differences in stopover behavior independent of the other species characteristics.

### Local geographic characteristics

We tested for the ability of four geographic variables to predict stopover distribution and abundance: distance from the coastline (Table 1: G1), the northeast-southwest position of each site along the coast of the Gulf of Maine (G2), mainland versus island (G3), and island size for island sites (G4). These four variables each attempt to explain variation in bird use among sites within our sampled region. Each site's distance from the coast and distance from a reference point along a northeast-southwest axis was calculated using the linear referencing toolbox within ArcGIS 10 (ESRI 2011). Island sizes (m<sup>2</sup>) were obtained from Maine Coastal Island National Wildlife Refuge and Acadia National Park. We nested island size within the binomial, dummy variable for island so that island size was only included in the model when the dummy variable equaled one (island).

### Landscape characteristics

We also attempted to explain variation in bird use among sites using landscape composition and landscape configuration metrics. Our eighteen landscape-characteristic variables included the total percentage of vegetated lands (Table 1: L1), total percentage of each of four land cover types (coniferous forest, mixed coniferous-hardwood forest,

shrubland, and human development: L2), the proportional availability of all vegetated habitats (L3) and of each of the four more specific land cover types (L4) within the sampled site versus the surrounding landscape, and indices for patch size and patch density for each of the four cover types (L5).

We assessed each of these eighteen metrics at multiple spatial scales, given that birds may respond to landscape features while landing (Ktitorov et al. 2008) from a variety of altitudes. To do so, we first defined each stopover site as the area within a 100 m buffer of all mist-nets. Because of uncertainty in the appropriate spatial extent to consider as available habitat for migrants moving through an area, we then calculated land cover percentage and proportional habitat availability for each of the eighteen landscape-characteristic variables at four scales. The largest scale was established using a buffer of the maximum visibility (16 km) gathered from a weather station centrally located within the study region and along the coast (Hancock County – Bar Harbor Airport), and we defined three finer scales at 75% (12 km), 50% (8 km), and 25% (4 km) of this distance.

We delineated land cover types using the Maine Land Cover Dataset (MeLCD). The MeLCD dataset is the most current layer with the highest resolution encompassing the entire study region. The MeLCD layer was derived from Landsat Thematic Mapper 5 and 7 imagery (1999–2001) and refined to the State of Maine requirements using SPOT 5 panchromatic imagery from 2004 with a spatial resolution of 5 × 5 m to create a land cover classification with 23 land cover types. We aggregated land cover from the 22 MeLCD classes by similarity in vegetation height (i.e. how they would presumably appear to a bird from the air) and the vegetation descriptions provided in the layer's metadata (< [www.maine.gov/megis/catalog/metadata/melcd.html](http://www.maine.gov/megis/catalog/metadata/melcd.html) >). This resulted in six broad land cover types (coniferous forest, mixed coniferous-hardwood forest, shrubland, human development, grassland, and non-habitat). We did not calculate either raw percentages or proportional availabilities for both the grassland (which included agricultural lands) and non-habitat cover types (e.g. open water, bare land, roadway/runway), because they comprise such a small percentage of the landscape relative to other habitats (4.5 and 3.2% respectively). Further, grasslands do not provide similar quality and abundance of food resources for autumnal landbird migrants relative to the other habitat types (Hutto 1998, Yong et al. 1998).

Total percentage of land cover for each coverage type was calculated by dividing the area of each type by the total area of all land within each of the four spatial scales. Proportional habitat availability was calculated by dividing the percent of each land cover type within a site (the 100 m buffer around nets) by the percent of each land cover type found within each of the four spatial scales (including the area within the site). We calculated patch size and density using FRAGSTATS (McGarigal et al. 2012). Specifically we determined the degree of fragmentation (patch density) and patch size (patch area weighted mean) for each of our four habitat types within each stopover site and spatial scale described previously.

### Interactions

Regional patterns of migratory stopover are most likely driven by an assortment of factors interacting together. For

example, different foraging guilds may be captured differently among sites. For this reason we considered all possible two-way interactions between migratory community characteristics and both the local geography variables and the landscape characteristics (Table 1: I1).

### Statistical analysis

To test the ability of parameters identified by past migration studies to explain migratory habitat use within an untested region (the Gulf of Maine), we initially calculated 79 explanatory variables within our hypotheses as described above. To reduce this initial candidate set of fixed effects for model selection, we performed a random forest analysis (Liaw and Wiener 2002, Team 2012).

While also used for regression and machine learning, random forests can rank candidate variable importance by quantifying each variable's ability to classify a dependent variable ( $\log_{10}$ -transformed mean annual species capture rate, in this case) using iterative subsets of a data set (Cutler et al. 2007). Random forests show high predictive accuracy and are applicable even in high-dimensional problems with correlated variables. Because random forests are constructed with regression trees, they inherently account for interactions by allowing variables to occur multiple times within a tree at different nodal levels. We selected variables to include in our final model selection by identifying a cut-off in the scree plot of variable importance values produced by a random forest. We tested all variables that produced a decrease in nodal purity greater than 4.0 (Fig. 2).

We then constructed a series of linear mixed-effects models ( $n = 6$ ) using maximum likelihood (package 'nlme' in R; Pinheiro et al. 2012). We used all single variables and all possible combinations of the interactions between the highly ranked migratory community characteristics (migratory distance and foraging guild) and landscape variables (proportional vegetated habitat availability at 4 km). Capture rates and proportional habitat availability at 4 km were  $\log_{10}$  transformed to meet model assumptions. All models, including the null, included taxonomic family as a fixed effect to account for family-specific capture probabilities. Since we

are trying to predict site use, site was our primary sampling unit. Since site is pseudoreplicated across years we included year as a fixed effect (along with family) in all models and site as the highest-level random effect to control for the pseudoreplication. Further we sampled species within each site as indicators of the use of that site by the entire migratory community. Species nested within site was included as a random variable in all models as we considered each species a random sample of all the species that were likely to use that site in a given year. We then selected the top model using AIC model selection (Burnham and Anderson 2004).

To validate this model ranking (and account for ranking stability), we used a bootstrap method on each model with  $AIC < 5.0$  ( $n = 3$ ). Each of the three top models were bootstrapped twenty times, using a different bootstrapped dataset (with replacement). The AIC scores for each, twenty-model iteration were then averaged before we compared mean AIC scores to determine our final model ranking. Because our initial variable reduction technique (the random forest) removed all of our candidate variables representing local geography, we added each geographic variable into the final model separately and examined the resulting model performance using AIC scores as a test of our geographic hypotheses.

### Results

On average, 36 species with sufficient detections were observed each fall season (range of species = 18–47; range of the number of detections per species per year = 10–4072). Of the species detected, approximately 70% were neotropical migrants. We operated mist-nets for a total of 58 304 h over 20 site-years.

The random forest technique identified four single variables: migratory distance, taxonomic family, foraging guild, and proportional vegetated habitat availability (at the finest spatial scale – 4 km) for use in our candidate model set (Fig. 2). Our bootstrapped model selection process identified one top model (Table 4) that included five fixed effects (in addition to the random effect of species nested within site). This top-ranked model included four single variables

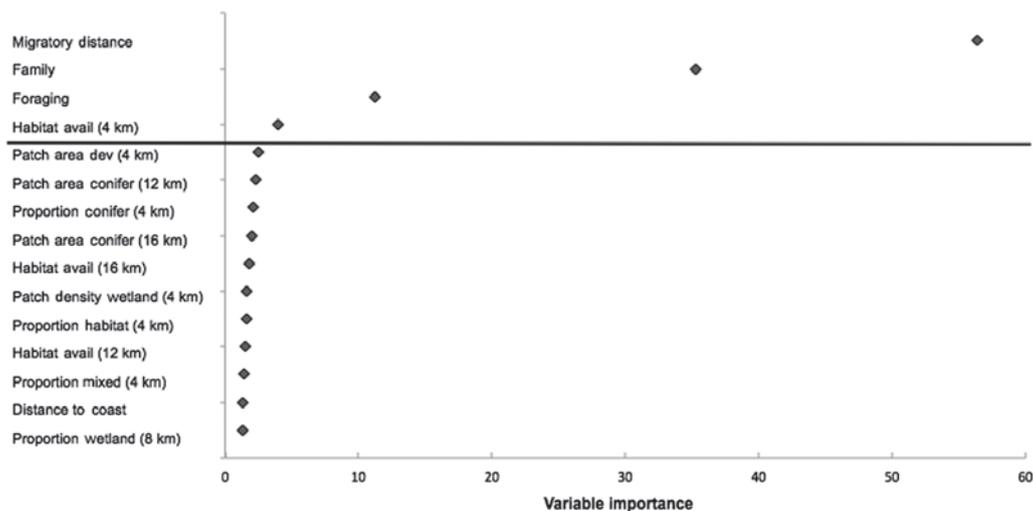


Figure 2. Random forest scree plot indicating variable importance of the top 15 predictors of yearly detection rates of each species at each site (of 79 variables explored) produced by a random forest of 500 regression trees.

Table 4. AIC model selection results for all bootstrapped models and the null model predicting migrant stopover site selection within the coastal region of Maine, United States (2007, 2009–2012), the difference in AIC relative to the top model, and number of model parameters (*k*). Distances within parentheses following the variables below indicate the scale at which they were calculated.

Model	AIC	ΔAIC	<i>k</i>
Taxonomic family + Year + Migratory distance + Habitat availability (4 km) + Migratory distance × Habitat availability (4 km)	857.5	0	5
Taxonomic family + Year + Migratory distance + Habitat availability (4 km)	859.7	2.2	4
Taxonomic family + Year + Migratory distance + Habitat availability (4 km) + Foraging guild + Migratory distance × Habitat availability (4 km) × Foraging guild × Habitat availability (4 km)	872.1	14.6	7
Null: Taxonomic family + Year	883.2	25.7	2

(taxonomic family, year, migratory distance, and proportional vegetated habitat availability at the 4-km scale) and one interaction term (migration strategy by habitat availability). No single geographic variable (i.e. distance from mainland, island versus mainland, or island size) improved the fit of the final model; in fact, all geographic variables increased the AIC value of the final model ( $\Delta\text{AIC} = 0.8\text{--}1.9$ ). Our top model contained five variables predicting  $\log_{10}$ -transformed detection rates of migrant bird species (Table 4). Of the five variables, all had significant effects: taxonomic family, year, migratory distance, vegetated habitat availability at the 4 km scale, and the interaction between migratory distance and vegetated habitat availability (Table 5).

Proportional vegetated habitat availability at the 4-km scale was significant as a single predictor (Table 5 and Fig. 3). As proportional habitat availability increased, so did captures of the total migratory community, regardless of migratory distance, such that use was highest at sites that possessed high amounts of habitat in a landscape relatively devoid of habitat (i.e. habitat islands). We also found a significant interaction between migratory distance and vegetated habitat availability. Stopover habitat use for the shortest distance migrants was most strongly associated with proportional vegetated habitat availability. As the median migratory distance of a species increased, however, the funneling effect of vegetated habitat availability decreased (Table 5 and Fig. 4).

Migratory distance and year were also significant single predictors of site use. We captured, on average more short distance than long distance migrants and more birds per unit effort in 2007 and 2009 than in later years (Table 5).

The mean detection rates of taxonomic families were remarkably similar, despite wide variation in the total number of individuals captured for each species. Among all of the species considered, only capture rates of the Turdidae were different than those of the reference family (Cardinalidae: Table 5). We suggest that this pattern occurred because of two major reasons. First, variation among species within each category dampened the variation among species overall. Second, our calculations for detection rate using only 'peak' migration periods (the middle two quartiles of passage

Table 5. Comparison of parameter estimates and 95% confidence intervals of the final selected model. Parameter estimates are based on the  $\log_{10}$ -transformed detection rates. Parameter estimates of categorical variables are calculated in reference to the baseline listed. The number of species within each categorical variable is shown in the parentheses. Significant parameters are indicated by\*.

Variable	Final model	
	Parameter estimate	95% Confidence interval
Migration distance	$7.75 \times 10^{-08}$	$2.09 \times 10^{-09}$ , $1.53 \times 10^{-07*}$
Proportional habitat avail. 4-km	0.42	0.21, 0.64*
Year		
2007	Reference	
2009	-0.20	-0.42, 0.03
2010	-0.40	-0.63, -0.17*
2011	-0.46	-0.69, -0.23*
2012	-0.43	-0.67, -0.19*
Family		
Cardinalidae (n = 2)	Reference	
Cuculidae (n = 1)	-1.89	-1.18, 0.20
Emberizidae (n = 8)	-0.14	-0.58, 0.31
Fringillidae (n = 1)	-0.30	-0.93, 0.33
Icteridae (n = 1)	-0.39	-1.00, 0.21
Mimidae (n = 1)	-0.52	-1.07, 0.03
Parulidae (n = 20)	-0.32	-0.73, 0.10
Picidae (n = 2)	-0.38	-0.88, 0.12
Regulidae (n = 1)	0.18	-0.36, 0.71
Tryglodytidae (n = 1)	-0.85	-1.76, 0.05
Turdidae (n = 5)	-0.45	-0.89, -0.02*
Tyrannidae (n = 4)	-0.32	-0.76, 0.12
Vireonidae (n = 3)	-0.20	-0.67, -0.19
Migration strategy × habitat 4-km	$-8.05 \times 10^{-8}$	$-1.40 \times 10^{-7}$ , $-2.16 \times 10^{-8*}$

time for each year) was successful in creating directly comparable detection rates at the family scale. In general, longer distance migrants are assumed to migrate faster than short distance migrants (Ellegren 1993). In support of this, species with lower total capture abundances tended to pass through the study region in a shorter time period, such that capture rates during their brief peak were similar to more abundant species during their wider migratory peak (Table 3).

## Discussion

Our analysis of migrant landbird stopover patterns in coastal Maine revealed that landscape composition at fine spatial scales (< 4 km, i.e. close to landing) in combination with a species' relative remaining migratory distance explained stopover site use across space and among years. Our predictive abilities were not improved by considering larger scale landscape variables or a site's local geographical position. Specifically, more isolated habitat patches (i.e. habitat islands) concentrated migrants, and this pattern was strongest among shorter distance migrants. This pattern was not driven by an oceanic island effect, as islands of habitat showed similar patterns of bird use regardless of the specific make-up of the non-vegetated matrix (e.g. open water, bare ground, and roads). Further, models with an indicator

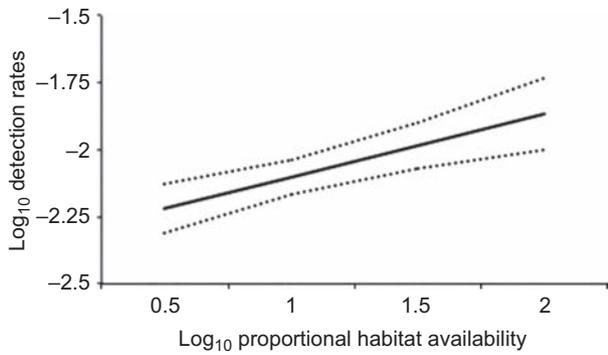


Figure 3. The predicted  $\log_{10}$ -transformed detection rates ( $\pm 95\%$  CI) of migratory songbirds as a function of the proportional availability of habitat (versus non-vegetated spaces) across eleven migration monitoring stations.

variable for oceanic island did not perform better than those with the habitat availability metric. Studies in urban parks such as Central Park in New York City (Seewagen and Slayton 2008) and desert oases in North Africa (Bairlein 1988) have revealed that habitat islands in any non-vegetated matrix are important stopover sites, which suggests that proportional habitat availability may be widely applicable for predicting stopover distributions globally.

The importance of habitat at the 4-km scale supports the broader hypothesis that migratory animal decision-making is hierarchical (Hutto 1985, Moore et al. 1995). At large regional scales, this migratory paradigm suggests that the primary drivers of stopover habitat are factors extrinsic to habitat, such as weather and individual energetic status

(Moore et al. 1995). Our results agree; we found no relationship between larger landscape characteristics and stopover site use within our region. At finer spatial scales, like the one we have identified here, factors intrinsic to the habitat itself, such as food availability (Olsen et al. 2015), structure (Sherry and Holmes 1985, Winker et al. 1992, Moore and Aborn 2000), and predator risk likely become increasingly important in decisions of habitat use (Hutto 1985). It is reasonable to assume that the important landscape characteristics in our model are very coarse cues for these intrinsic habitat factors, as seen in studies conducted along the Gulf of Mexico (Buler et al. 2007, Buler and Moore 2011). Buler et al.'s (2007) work found that hardwood forest cover at a finer (5 km radius) spatial scale predicted migrant use best. While our study corroborates the fine spatial scale at which migrants are making decisions, we found that proportional habitat availability and not forest cover is most important for migrants in the Gulf of Maine. This leaves open the possibility that even finer scale selection occurs within stopover sites (although we did not measure that explicitly in this study). We hypothesize that gross, vegetated habitat availability within a few kilometers influences site selection upon landing, and this selection is further refined among habitat patches at finer spatial scales during stopover (Hutto 1985, Martin and Karr 1986).

In a similar way to spatial scale, habitat use is also controlled by additional factors at shorter time scales than the seasonal use metrics investigated here. Nightly weather conditions such as the magnitude and direction of wind, precipitation, and cloud cover have all been shown to affect the numbers of birds stopping over at a particular site (Moore et al. 1995, Dänhardt and Lindström 2001, Adams

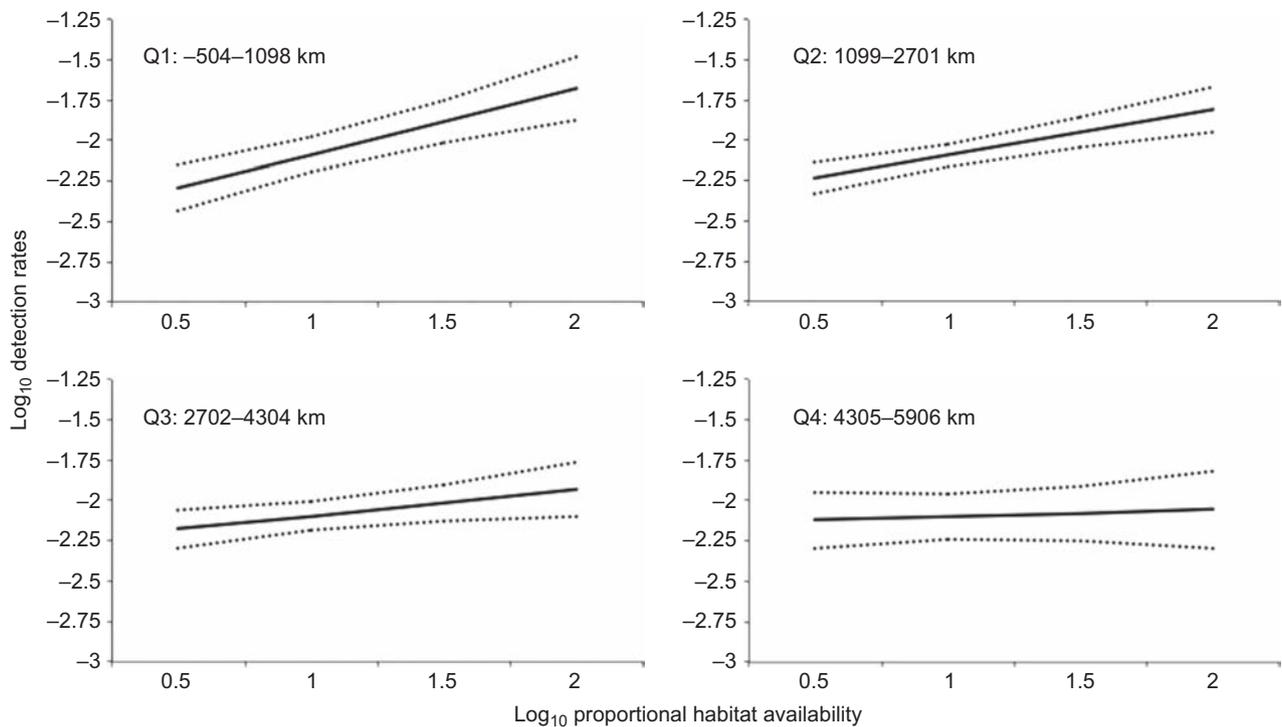


Figure 4. The predicted  $\log_{10}$ -transformed detection rates ( $\pm 95\%$  CI) of migratory songbirds as a function of the proportional availability of habitat (versus non-vegetated spaces) across eleven migration monitoring stations for species in each of the four quartiles of migratory distance (the distance from the region of capture to the midpoint of the nonbreeding range).

2014), especially off-shore islands where its thought many birds using them were blown there (Richardson 1978). Unless weather conditions are consistently different among sites, which is unlikely given the spatial scale of our study, daily variation in these weather conditions and their associated effects on migrant behavior should cancel out over the length of a migration season. Previous study within the Gulf of Maine, however, has hypothesized that site-specific variation in weather produces consistent differences in stopover behavior. Specifically, off-shore islands should concentrate birds more than other sites as birds are blown off course into the Gulf (Richardson 1978). Our study found no evidence for meteorological forcing in this way over a migratory season, as an indicator variable for island and the distance of islands to the coast did not improve our predictions of site use over our top models. While it remains possible that particular storm systems could produce this pattern in the short term, our results suggest that these events do not drive site use by landbird migrants at the scale of a full migratory season. From a land prioritization and conservation standpoint, local habitat availability should do a better job at maximizing benefit for migratory populations.

Our results are also consistent with the hypothesis that landbird migration occurs as a broad front over both land and water at sub-continental scales (Nisbet 1970, Richardson 1976, 1978, Alerstam and Pettersson 1977). The ability of relatively rare habitats to concentrate birds is expected when spatially homogeneous migrating flocks are attracted to the nearest visible landscape features prior to stopover. If birds were distributed more heterogeneously during migratory flights (i.e. not in a 'broad front'), this concentrating effect could still occur, but local geography would also be needed to explain site use due to the initial heterogeneity in birds available for stopover. We found no support for such a two-step explanation across our coastal transect.

We recognize that bird use of a stopover site occurs not only directly after a nocturnal migratory flight but also after relocation flights during stopover within the broader landscape as individuals search for more suitable habitat (Chernetsov et al. 2007, Mills et al. 2011, Taylor et al. 2011, Woodworth et al. 2014). Our study confounds these various types of use. Both categories of movement, however, are important contributors to overall site use and should be considered in discussions of stopover habitat use at any scale.

Many predictors of stopover habitat use from previous studies were not important for the Gulf of Maine. These factors are thus not universal predictors, but they could still be important regionally (Table 1). For instance, we did not find a difference between migrant abundance on islands versus the mainland as McCann et al. (1993) did. The proportional habitat availability effect we show here, however, predicts higher use for any relatively rare habitat on the landscape, which would include islands of habitat in water as well as islands in any other non-vegetated landscapes. We might have found a similar island effect as McCann et al. (1993) had we not controlled for landscape characteristics (which they did not). The overall inability of other local geographic variables to predict site use may be a function of the scale of our region. For instance, we may have detected an effect of

distance to the coast on site use if we had monitored areas further inland.

## Landscape characteristics and migratory distance

The ability of stopover oases to concentrate shorter distance migrants more readily than longer distance migrants, as we show here, remains untested elsewhere. Our reported concentration in site use was attributable to all vegetated habitat types and not to any specific vegetation component (unlike Buler et al. 2007). Our results suggest that the conservation consequences of habitat fragmentation, at least in our region, are likely different for shorter versus longer distance migrants as a result of their habitat selection behaviors during migration.

Because our sites are relatively close to the breeding grounds for many species captured within the Gulf of Maine, the longest distance migrants may be less energetically strained early in their migration, and thus not driven to stop in landscapes where suitable habitat is rare. Short to medium distance migrants, however, stop more frequently along their routes (Newton 2008) and thus may be more likely to search for habitat even in areas where it is less available. This behavioral difference (likely produced by different physiological constraints) would cause areas with less available habitat to concentrate shorter distance migrants more. As longer distance migrants travel further south and become increasingly energetically compromised, we would predict that the relationship between proportional habitat availability and stopover site use would approximate the pattern we show here for shorter distance migrants. Indeed, the concentrated use of North African oases by longer distance migrants after crossing a water barrier (Bairlein 1988) appears to support this prediction.

## Conservation implications

Moore et al. (2005) emphasized that the conservation of migratory habitat should be scale dependent. Our study found migratory landbirds were strongly associated with habitat characteristics at scales where governmental and other agencies are able to focus their conservation efforts. The greatest gains for stopover use by all bird guilds are thus to be made by maximizing vegetated habitats (vs non-habitat). This also means that in areas where there is little vegetated habitat (urban landscapes and offshore islands), the remaining small patches may be disproportionately important for the local migratory community relative to similarly sized patches in areas of more contiguous habitat. When increasing habitat widely across the landscape is not possible, the conservation of these small patches should be a priority for migratory stopover habitat use.

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