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Research Paper

Projected responses of North American grassland songbirds to climate change and habitat availability at their northern range limits in Alberta, Canada

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ABSTRACT. Across North America, grassland songbirds have undergone steep population declines over recent decades, commonly attributed to agricultural intensification. Understanding the potential interactions between the impacts of climate change on the future distributions of these species and the availability of suitable vegetation for nesting can support improved risk assessments and conservation planning for this group of species. We used North American bioclimatic niche models to examine future changes in suitable breeding climate for 15 grassland songbird species at their current northern range limits along the boreal forest-prairie ecotone in Alberta, Canada. Our climate suitability projections, combined with the current distribution of native and tame pasture and cropland in Alberta, suggest that some climate-mediated range expansion of grassland songbirds in Alberta is possible. For six of the eight species projected to experience expansions of suitable climate area in Alberta, this suitable climate partly overlaps the current distribution of suitable land cover. Additionally, for more than half of the species examined, most of the area of currently suitable climate was projected to remain suitable to the end of the century, highlighting the importance of Alberta for the long-term persistence of these species. Some northern prairie-endemic species exhibited substantial projected northward shifts of both the northern and southern edges of the area of suitable climate. Baird's Sparrow (Ammodramus bairdii) and Sprague's Pipit (Anthus spragueii), both at-risk grassland specialists, are predicted to have limited climate stability within their current ranges, and their expansion into new areas of suitable climate may be limited by the availability of suitable land cover. Our results highlight the importance of the preservation and restoration of remaining suitable grassland habitat within areas of projected climate stability and beyond current northern range limits for the long-term persistence of many grassland songbird species in the face of climate change.

Réactions projetées de passereaux de prairie nord-américains aux changements climatiques et à la disponibilité de l'habitat à la limite nord de leur aire en Alberta, Canada

RÉSUMÉ. Partout en Amérique du Nord, les passereaux de prairie ont subi d'importantes baisses de population au cours des dernières décennies, qu'on attribue le plus souvent à l'intensification de l'agriculture. La compréhension des interactions potentielles entre les impacts des changements climatiques sur la future répartition de ces espèces et la disponibilité de végétation favorable à leur nidification peut contribuer à améliorer l'évaluation des risques et la planification des mesures de conservation pour ce groupe d'espèces. Nous avons utilisé des modèles de niches bioclimatiques afin d'examiner les variations futures du climat favorable pour la nidification de 15 passereaux de prairie à la limite nord de leur aire actuelle le long de l'écotone forêt boréale-prairie en Alberta, au Canada. Nos projections du caractère favorable du climat, combinées à la répartition actuelle des pâturages naturels et artificiels et des terres cultivées en Alberta, indiquent qu'une certaine expansion d'aire régie par le climat est possible pour les passereaux de prairie en Alberta. Chez six des huit espèces pour lesquelles nous projetons une expansion de l'étendue de climat favorable en Alberta, ce climat favorable chevauche en partie la répartition actuelle de couverture au sol convenable. De plus, chez plus de la moitié des espèces examinées, nous avons projeté que la majorité de l'étendue de climat favorable actuel resterait favorable jusqu'à la fin du présent siècle, soulignant l'importance de l'Alberta pour la persistance à long terme de ces espèces. Pour certaines espèces de prairie endémiques septentrionales, des déplacements substantiels vers le nord ont été projetés, tant pour la bordure nord que pour la bordure sud de l'étendue de climat favorable. Nous avons prédit que le Bruant de Baird (Ammodramus bairdii) et le Pipit de Sprague (Anthus spragueii), deux spécialistes de prairie en péril, feraient face à une stabilité climatique restreinte dans leurs aires courantes, et leur expansion dans de nouvelles étendues de climat favorable pourrait être limitée par la disponibilité de couverture au sol convenable. Nos résultats mettent en lumière l'importance de préserver et de restaurer les milieux de prairie favorables restants dans les étendues de climat stable projeté et au-delà de la limite nord actuelle des aires de répartition afin d'assurer la persistance à long terme de nombreux passereaux de prairie malgré les changements climatiques.

Key Words: grassland; land cover; MaxEnt; northern Great Plains; songbird; species distribution modeling

INTRODUCTION

Grassland birds have undergone steep population declines across North America in recent decades (Sauer and Link 2011, NABCI 2014), which have been linked to land use changes, especially agricultural intensification resulting in grassland degradation (Askins et al. 2007). Consequently, grassland birds are among the most at-risk avian groups in North America (NABCI 2014). The impacts of historical, current, and future land use changes on grassland birds may be compounded by and will interact with their responses to climate change (Staudt et al. 2013). The tight linkages between grassland bird distributions and climate and yearly weather conditions in North America (Wiens 1974, Rotenberry and Wiens 1991, Niemuth et al. 2008), combined with their high mobility, may enable distributional shifts in response to climate change when new areas of suitable climate and vegetation become available, or existing habitat becomes unsuitable (Skagen and Adams 2012). Across North America. northward shifts in songbird breeding ranges have already occurred in response to climate change (Hitch and Leberg 2007, Zuckerberg et al. 2009, Coristine and Kerr 2015).

Where the potential responses of North American grassland birds to future climate change have been examined, projections indicate expansions of suitable climate area for some species and predicted increases in the abundance of grassland-associated species in the boreal regions (Langham et al. 2015, Stralberg et al. 2015a). Conversely, potentially severe declines in suitable climate area in North America have been projected for other species (Langham et al. 2015). The persistence of grassland songbirds in a changing climate will depend, however, on several factors: the continued suitability of climate within their current ranges, the potential changes in the distribution of suitable climate, and the birds' ability to colonize new areas of suitable climate beyond their current northern range edges. To date, the effect of the availability of suitable land cover on the projected changes in grassland songbird distributions with climate change have not been considered.

Currently, the northern edges of many grassland songbird ranges approach the prairie-boreal forest ecotone, where suitable grassland or agricultural habitat transitions to unsuitable forest habitat. While climate change may cause northward shifts in suitable climate area for grassland songbirds, lags in the transition of forested ecosystems to suitable grassland vegetation may limit the ability of birds to respond in parallel (Stralberg et al. 2015b). In the absence of grassland to cropland conversion, grasslands that currently support songbird populations in their northern range extent are likely to remain important habitat over the next century. Climate-driven changes in those native grassland communities will likely be limited primarily to transitions toward southern Great Plains communities (Rehfeldt et al. 2012), including warm-season grass and shrub-steppe communities (Thorpe 2011). Similarly, non-native agricultural communities and annual cropland are likely to remain as suitable land cover for some species, even as climate changes. Therefore, if projected shifts in suitable climate area for grassland songbirds correspond with currently suitable land cover, the persistence and potential range expansions of these species may be facilitated. If suitable climate area for grassland songbirds shifts outside the current distribution of suitable land cover (i.e., expands into the current boreal region), and lags in native vegetation transition occur, expansion by grassland songbirds into new areas may be limited.

We used bioclimatic niche models to project the distributional responses of 15 grassland songbird species to changes in climate over the next century, and examined differences among baseline (1961–1990) and future time periods (2041–2070 and 2071–2100) to identify potential changes in the amount and location of suitable breeding climate for these species across North America. As a case study, we used the distribution projections in the province of Alberta, Canada (6.6 x 10^5 km²) to examine the stability of the current distributions of grassland songbirds and the potential for range expansions along their northern range limits. This region currently contains the northern range edges for many grassland songbirds and a large proportion of the breeding ranges for several range-restricted species (e.g., Sprague's Pipit [Anthus spragueii]) (Davis et al. 2014). Additionally, dramatic change in the southern boreal forest in Alberta is projected in response to climate change, including expansion of climates suitable for grassland habitats (Rehfeldt et al. 2012). Potential interactions between climate-driven distribution changes and the availability of suitable land cover are likely to be most relevant along northern range edges and in areas with large projected changes in regional ecosystems. Furthermore, northwestern Alberta contains the Peace River parkland, a large, northern region of former native grassland that has been largely converted to agriculture and that is surrounded by boreal vegetation (Natural Regions Committee 2006); this region may provide suitable habitat for northward expansion of some grassland songbirds. To identify how the current distribution of grassland and agricultural land cover may facilitate or limit potential songbird distribution shifts in Alberta, we examined the degree of correspondence between projected climate suitability and land cover types in Alberta. The combined assessment of suitable climate area projections, the climate stability of current ranges, and the potential influence of land cover to either facilitate or limit climate-driven distribution shifts provides a more complete understanding of the potential climate vulnerabilities and opportunities faced by these species, and can be used to incorporate climate change considerations into management and conservation planning.

METHODS

Avian survey data and study area

We compiled data from avian surveys conducted throughout Canada, the continental United States, and Alaska for 15 grassland songbird species routinely observed in the northern Great Plains (Table 1). The compiled data came primarily from two sources: roadside point counts conducted as part of the North American Breeding Bird Survey (BBS) (Sauer et al. 2014) in 1967-2014, and species checklist data from the Western Hemisphere eBird reference data set that span 1947-2012 (Sullivan et al. 2009, Munson et al. 2013). We limited observations from the BBS to those with exact stop locations (22,085 stops from 780 routes in 32 provinces and northern states). Observations from the eBird data set were limited to June observations, and included only stationary, traveling, and area search surveys (we omitted incidental or casual observations). We further limited eBird surveys to those where the area surveyed was less than the spatial resolution of the climate data (4 km x 4 km), so that we could be reasonably certain that the survey occurred within a single grid cell. These data were supplemented with off-road point-count surveys from avian monitoring conducted by the Alberta

Common name	Scientific name	$egin{array}{c} {\sf AOU} \ {\sf code}^\dagger \end{array}$	Habitat [‡]	Specialization§	Occurrence locations	
Baird's Sparrow	Ammodramus bairdii	BAIS	G	Endemic	1741	
Bobolink	Dolichonyx oryzivorus	BOBO	G	Secondary	10472	
Brewer's Sparrow	Spizella breweri	BRSP	G	Secondary	2222	
Chestnut-collared Longspur	Ĉalcarius ornatus	CCLO	G	Endemic	1640	
Clay-colored Sparrow	Spizella pallida	CCSP	G	Secondary	9913	
Grasshopper Sparrow	Ammodramus savannarum	GRSP	G	Secondary	7192	
Horned Lark	Eremophila alpestris	HOLA	G/C	Secondary	14274	
Lark Bunting	Calamospiza melanocorys	LARB	G	Endemic	2020	
Lark Sparrow	Chondestes grammacus	LASP	G	Secondary	3523	
Le Conte's Sparrow	Ammodramus leconteii	LCSP	G	Secondary	2093	
McCown's Longspur	Rhynchophanes mccownii	MCLO	G	Endemic	537	
Savannah Sparrow	Passerculus sandwichnesis	SAVS	G/C	Secondary	21803	
Sprague's Pipit	Anthus spragueii	SPPI	G	Endemic	2094	
Vesper Sparrow	Pooecetes gramineus	VESP	G/C	Secondary	14235	
Western Meadowlark	Sturnella neglecta	WEME	G	Secondary	16336	

Table 1. Habitat use, specialization, and number of occurrences used in climate suitability modeling for 15 grassland songbird species.

[†] AOU: American Ornithological Union

[‡]G: native and tame grassland/hay; C: annual cropland. Refer to Table A1.1 for classification rationale.

[§] Described by Knopf (1994). Endemic species are those thought to have evolved within the Great Plains, typically within specific ecological niches within the grasslands; secondary species are those considered secondarily evolved to grasslands that are typically more widespread, or more closely associated with other ecoregions (e.g., Brewer's Sparrow and the Great Basin shrubsteppe). Le Conte's Sparrow and Bobolink are not classified by Knopf (1994); both species have widespread distributions beyond the Great Plains, so are classified as secondary species here.

Biodiversity Monitoring Institute in 2003–2014 and from research projects conducted in Alberta and Saskatchewan, Canada between 2005 and 2007 (Davis et al. 2013). The resulting data set included observations from 39,063 unique locations. Species observations were summarized across years as the occurrence of each species at each location; the number of occurrence locations ranged from 537 (McCown's Longspur) to 21,803 (Savannah Sparrow) (Table 1).

We limited the modeling extent to that of the surveyed locations, which included analogous future climates for all but the southernmost portion of the study area (Rehfeldt et al. 2012) (Fig. 1A). The southern limit was defined by the Mexico–United States border, and the northern limit by the level II ecoregions of North America (CEC 1997) that delimit the southern Arctic.

Climate data

To construct the bioclimatic niche models and future projections, we used available historical baseline and projected future climate data for North America (data supplement to Stralberg et al. 2015a). These data comprise interpolated climate data at a 4-km resolution for the 1961-1990 baseline period based on the PRISM model (Daly et al. 2008) and downscaled projections for two 30vear future periods (2041-2070 and 2071-2100). The future climate projections were based on global climate model (GCM) projections from the CMIP3 multi-model data set associated with the fourth Intergovernmental Panel on Climate Change assessment report (Meehl et al. 2007), from which projected anomalies were added to the 4-km baseline data using the delta method and bilinear interpolation (Wang et al. 2012). We selected data from four complementary GCMs to represent a range of projected future climates for North America (Stralberg et al. 2015a): the German ECHAM5/MPI-OM, the Canadian CCCMA-CGCM3.1(T47), the American GFDL-CM2.1, and the United Kingdom UKMO- HadGEM1. In addition, we used an

ensemble mean climate projection derived from 19 GCMs. We adopted the SRES A2 emissions scenario (IPCC 2001), which most closely reflects the current trend in global carbon emissions (Friedlingstein et al. 2014).

We relied on a subset of seven bioclimatic variables from the climate data set (Table 2), which was selected to avoid extreme collinearity (Dormann et al. 2012), prioritize seasonal over annual variables, or include variables relevant to vegetation communities. We retained some variables with high correlations because our objective was prediction, rather than interpretation (Dormann et al. 2012), and because machine-learning modeling methods are relatively robust to correlated covariates (Merow et al. 2013). Within the model building data set (surveyed grid cells), the most highly correlated variables were summer climate moisture index and annual climate moisture index (r = 0.88).

Table 2. Ranked predictor variable importance across all 15 species, determined from the ranked bootstrap-averaged single variable $AUCs^{\dagger}$ for each species.

Rank	Variable description
1	Annual climate moisture index (modified Penmnan-Monteith
	method) [‡]
2	Mean summer (May to September) precipitation (mm)
3	Extreme minimum temperature over 30 years (°C)
4	Summer (June to August) climate moisture index (modified
	Penman-Monteith method) [‡]
5	Degree-days above 5°C (growing degree days)
6	Degree-days below 0°C (chilling degree days)
7	Difference between the mean temperature of the coldest month
	and the mean temperature of the warmest month, as a measure
	of continentality (°C)
[†] AUC:	area under the curve

Fig. 1. (A) Model extent and distribution of background points used to model climate suitability for grassland songbirds in North America. (B) Distribution of crop and native/tame grassland and hayland cover in Alberta (Agriculture and Agri-Food Canada 2013).



Bioclimatic niche modeling

We used the maximum entropy method of bioclimatic niche modeling to generate predictions of current climate suitability for the baseline period and projections of climate suitability for both future 30-year time periods (MaxEnt v. 3.3.3) (Phillips et al. 2006, Elith et al. 2011). MaxEnt is a machine-learning algorithm, widely used as a robust approach to bioclimatic niche modeling based on species occurrence records (Elith et al. 2011). We used this presence-only modeling approach because we could not assume absence at the 4 km x 4 km grid-cell level used to build models (based on climate data resolution).

Occurrence records were aggregated across survey locations within each 4 km x 4 km grid cell of the climate data, thereby reducing nonindependence between records. To accommodate potential sampling bias in the species occurrence data (e.g., due to spatial aggregation of survey locations, or associated with roadside sampling) (Wellicome et al. 2014), we restricted our background points to surveyed grid cells (n=15,534) (Phillips et al. 2009) (Fig. 1).

Species models were constructed in MaxEnt from 50 replicates using linear, quadratic, product, and threshold features to accommodate potential nonlinearities in interactions among predictors. Each of these features is a transformation of the covariates used to constrain the model: the covariates themselves, the squares of the covariates, the interactions between two covariates, and step functions of the covariates equivalent to a piecewise constant spline, respectively (Phillips et al. 2006). In each replicate, occupied grid cells were randomly assigned into training (70%) and testing (30%) data sets. All other settings were left at the default values. Replicate models for each species were projected onto the baseline and future climates across North America, and then averaged to predict climate suitability in each set of climate conditions. Relative climate suitability was determined from the MaxEnt cumulative output, which represents the empirical cumulative probability distribution function and ranges from 100, representing perfect suitability, to 0, representing unsuitable conditions (Phillips et al. 2006).

Model performance

Model performance was evaluated using the area under the curve of the receiver operating characteristic plot (ROC AUC) (Fielding and Bell 1997); an AUC > 0.7 indicates good model performance, whereas an AUC = 0.5 indicates a model with predictive capability no better than chance (Manel et al. 2001). AUC is a widely used, but imperfect measure, of model performance for presenceabsence and presence-only models (Lobo et al. 2008, Merow et al. 2013). For MaxEnt models, AUC is a measure of how the model distinguishes between occurrences and background points (Elith et al. 2011). Therefore, models of widespread species that occupy a large proportion of the background points (here, all surveyed locations) will necessarily have lower AUC values than those of species with more localized distributions (Lobo et al. 2008). Our selection of background cells based on locations where at least one grassland bird species was observed reduced AUC values, relative to evaluation against a broader set of background points.

Table 3. Predictive performance of average MaxEnt models for each grassland songbird species. Average models are based on 50
bootstrapped replicates with a 70%-30% training-testing split of the occupied 4 x 4 km grid cells (n) in each replicate. Sensitivity and
specificity were evaluated using the threshold that maximized the sum of sensitivity and specificity for each species. Sensitivity was
evaluated using the threshold identified from the training data set applied to the test data set. Specificity was evaluated using the same
threshold, applied to all unoccupied background cells.

Species	n	Test AUC [†]	SD	Test sensitivity	SD	Specificity	SD	
Baird's Sparrow	706	0.951	0.003	0.951	0.020	0.922	0.009	
Bobolink	4299	0.777	0.005	0.873	0.018	0.767	0.014	
Brewer's Sparrow	783	0.927	0.005	0.910	0.022	0.864	0.011	
Chestnut-collared Longspur	667	0.953	0.004	0.954	0.022	0.918	0.008	
Clay-colored Sparrow	3810	0.832	0.004	0.880	0.014	0.896	0.006	
Grasshopper Sparrow	3154	0.776	0.007	0.764	0.029	0.773	0.025	
Horned Lark	5281	0.699	0.006	0.694	0.031	0.757	0.030	
Lark Bunting	704	0.946	0.005	0.914	0.027	0.910	0.013	
Lark Sparrow	1965	0.839	0.006	0.827	0.028	0.788	0.021	
Le Conte's Sparrow	1211	0.901	0.004	0.925	0.016	0.852	0.007	
McCown's Longspur	272	0.966	0.005	0.927	0.043	0.929	0.018	
Savannah Sparrow	8117	0.654	0.005	0.812	0.037	0.699	0.034	
Sprague's Pipit	790	0.939	0.004	0.930	0.024	0.885	0.011	
Vesper Sparrow	5377	0.704	0.006	0.718	0.026	0.759	0.024	
Western Meadowlark	5662	0.763	0.005	0.883	0.025	0.814	0.024	
[†] AUC: area under the curve								

We also evaluated model sensitivity and specificity as measures of model performance. Species-specific thresholds that maximized the sum of model sensitivity and specificity (Liu et al. 2013), included as part of the MaxEnt modeling results, were used to convert the continuous predictions of climate suitability into binary predictions of suitable/unsuitable climate. We evaluated sensitivity as the proportion of test grid cells correctly predicted as suitable, and specificity as the proportion of background grid cells where the species was not observed ("pseudo-absences") that were correctly predicted as unsuitable. Threshold selection can have a large influence on the interpretation of modeled suitable climate and, therefore, the interpretation of distributional shifts in response to climate change (Nenzén and Araújo 2011), and there is little agreement on the best choice. However, the maximum sum of sensitivity and specificity threshold is well supported as a reasonable choice for presence-only models when evaluated against other methods across a range of prevalence values (Liu et al. 2005, 2013).

Projected changes in breeding climate suitability in North America and Alberta

Using the binary predictions of core suitable climate area from each GCM and the average predictions across GCMs, we calculated the projected changes in the area of suitable breeding climate between the baseline and future time periods in North America and Alberta for each species. Using these binary predictions, we also examined the climate stability of each species' current Alberta range by calculating the proportion of suitable climate area in the baseline period that was projected to remain suitable in each future time period.

Projected breeding climate suitability correspondence with current land cover in Alberta

We used the 2013 Annual Crop Inventory from Agriculture and Agri-Food Canada (AAFC) (AAFC 2013) to classify land cover

in the agricultural region of Alberta (Fig. 1B; reclassification rules are presented in Appendix 2, Table A2.1). The AAFC data are generated at 30-m resolution from satellite inventory, and distinguish between annual crop, native grassland, and tame pasture/hayland covers. We combined these latter two classes over concerns that they were not well differentiated (S. Davis, *personal communication*), so our "native/tame grassland" class contained all native and tame grassland and pasture land cover, including hay, and our "cropland" class was limited to annual row crops.

We defined suitable land cover for each species according to previously reported breeding habitat preferences (Table 1; rationales are presented in Appendix 1, Table A1.1). We examined changes in the degree of overlap between currently suitable land cover and the projected area of suitable climate by calculating the proportional change in area of suitable land cover within projected suitable climate, relative to the baseline prediction.

Current predictions and future projections were based on the average of the bootstrapped MaxEnt models for each species. Means, 95% confidence intervals, and standard errors were based on the core areas projected by each of the four unique GCMs, and thus do not represent the full range of uncertainty represented by variability in replicated models. Projected future distribution maps, presented in Appendix 3, were based on the ensemble climate data. ArcGIS (v.10.1; ESRI) was used to process all species occurrence data and MaxEnt model outputs. Data summaries and figures were prepared in R (v.2.15.2) (R Core Team 2015).

RESULTS

Model performance

Averaged across all species, the climate variables with the highest rank importance were annual climate moisture index and mean summer precipitation (Table 2, Appendix 4). AUC values for the baseline climate models for 13 of 15 species were ≥ 0.7 (Table 3).

The other two species, Savannah Sparrow and Horned Lark, were among the species for which we had the greatest number of occupied cells relative to our background locations (52% and 34%, respectively) (Table 3) (background n = 15,534). The models for these two species and for Vesper Sparrow, another widely distributed species, also had relatively low sensitivity and specificity (Table 3). For all other species, both model sensitivity and specificity exceeded 0.75, and for four species, both sensitivity and specificity exceeded 0.9 (Table 3). The binary maps generated using the maximum sum of specificity and sensitivity threshold for the baseline period (Appendix 3, Fig. A3.1) compared well with published North American range maps for most species (Poole 2005), indicating this threshold was a reasonable choice to reflect baseline suitable climate conditions.

Projected changes in breeding climate suitability in North America

End-of-century increases in suitable climate area in North America were projected for five of the 15 grassland songbird species (95% CI did not include zero) (Appendix 5, Fig. A5.1). Horned Lark had the greatest predicted proportional expansion in suitable climate area (55 \pm 14%; mean \pm 95% CI), followed by Lark Sparrow (50 \pm 16%), Bobolink (42 \pm 10%), Western Meadowlark ($29 \pm 19\%$), and Clay-colored Sparrow ($19 \pm 4\%$). Three species were projected to experience reductions in suitable climate area in North America by the end of the century. McCown's Longspur had the largest projected proportional decline (-83 \pm 7%), followed by Brewer's Sparrow (-57 \pm 12%), and Savannah Sparrow (-21 \pm 5%). The projected changes in suitable climate area in North America for the remaining seven species were more equivocal, with greater variability among GCMs relative to the magnitudes of change projected, and distribution changes rather than expansions or contractions projected in most cases.

In general, suitable climate area in North America for the 15 grassland songbird species was projected to shift northward, but the degree of shift was variable (Appendix 3, Fig. A3.1). For example, suitable climate area for the Chestnut-Collared Longspur and Lark Bunting was projected to shift gradually northward, while projected northward shifts in suitable climate area for Sprague's Pipit and Baird's Sparrow were more dramatic, especially by the end of the century (Appendix 3, Fig. A3.1). For other species, including Lark Sparrow and Horned Lark, suitable climate area was projected to expand to the north, with little change at the southern edge, resulting in an overall projected expansion across North America (Appendix 3, Fig. A3.1). Projected suitable climate area for Brewer's Sparrow and McCown's Longspur declined dramatically, with limited geographical shift (Appendix 3, Fig. A3.1).

Projected changes in breeding climate suitability in Alberta

Eight of 15 species were projected, on average, to experience increases in suitable climate area in Alberta by the end of the century (Fig. 2). The projected expansion for most species resulted from northward expansion of suitable climate area in Alberta, originating in the parkland region in northwest Alberta (e.g., Chestnut-collared Longspur, Lark Bunting, Lark Sparrow, Grasshopper Sparrow), with no or limited change in southern areas of the province (Appendix 3, Fig. A3.2). The greatest increase was projected for Bobolink, with an atypical pattern of suitable climate expansion from east to west across the province (Appendix 3, Fig. A3.2). Lark Sparrow and Grasshopper Sparrow were also both projected to show a many hundred-fold increase in suitable climate area in Alberta by the end of the century.

Five species were projected to experience end-of-century declines in suitable climate area in Alberta (Fig. 2). Three of these species, Savannah Sparrow (-24 ±10%; mean ± 95% CI), Clay-colored Sparrow (-26 \pm 15%), and Le Conte's Sparrow (-48 \pm 29%), were species with widespread suitable climate areas in Alberta in the baseline period that shifted northward and out of Alberta over time. McCown's Longspur (-57 \pm 29%) and Brewer's Sparrow (-57 \pm 40%) were projected to experience a decline in suitable climate area in Alberta that corresponded to a decline rather than a shift in suitable climate area across North America (Appendix 3, Fig. A3.2). Projected changes in suitable climate area in Alberta for Baird's Sparrow and Sprague's Pipit were more equivocal (95%) CI included zero), with greater variability among GCMs relative to the change projected (Fig. 2). However, both species were projected to experience northward shifts of both the northern and southern distribution limits of suitable climate (Appendix 3, Fig. A3.2).

There was considerable variation within species in the magnitude of change in suitable climate area among the projections from the four GCMs. For 11 of 15 species, however, the direction of change at the end of the century was consistent, regardless of GCM (Fig. 2). Individual climate model projections varied for Baird's Sparrow, Brewer's Sparrow, Chestnut-collared Longspur, and Sprague's Pipit. Of the four models, the warmest and driest scenarios represented by the United Kingdom model (UKMO-HadGEM1; hotter and drier) and the American model (GFDL-CM2.1; drier) generated larger increases or decreases in suitable climate area compared to the other three models and the ensemble projection.

Stability of projected suitable breeding climate in Alberta

By the end of the century, most species were projected to experience declines in the area of stable suitable climate, although nine species were, on average, projected to maintain at least 50% of their baseline suitable climate area (Fig. 3). The species projected to maintain the most stable climate area over time were those with limited losses of suitable climate area over time were those with limited losses of suitable climate area in southern Alberta (e.g., Horned Lark, Lark Bunting, Lark Sparrow, and Western Meadowlark), or with limited areas of suitable climate predicted in the baseline period (Bobolink) (Fig. 3). By the end of the century, the three species with the smallest projected areas of stable climate were Baird's Sparrow ($7 \pm 3\%$), Brewer's Sparrow ($8 \pm 3\%$), and Sprague's Pipit ($23 \pm 10\%$).

Projected suitable breeding climate and current land cover in Alberta

In Alberta, six of 15 species were projected to experience increases in suitable land cover within projected suitable climate: Bobolink, Grasshopper Sparrow, Horned Lark, Lark Bunting, Lark Sparrow, and Western Meadowlark (Fig. 4). The projected distributions of these six species occupied increasingly large areas **Fig. 2.** Projected change in the area of suitable climate in Alberta, Canada from the historical baseline (1961–1990) for two future time periods, based on North American models. The mean change (\pm 95% CI [black circles]) was determined from the four unique global climate models (GCMs) (CCCMA CGCM3.1; MPI ECHAM5/MPI-OM; GFDL CM2.1; UKMO-HadGEM1 [open symbols]). Changes in areas projected using the ensemble climate data (yellow squares) correspond to the maps in Figure A3.2. Note the difference in scales between panels.



of potentially suitable land cover in the province (Fig. 1B; Fig. 2; Appendix 3, Fig. A3.2). Although Chestnut-collared Longspur was projected to experience an expansion in suitable climate area in Alberta (Fig. 2), the expansion did not overlap the distribution of suitable land cover, resulting in a relatively stable projection for the correspondence between suitable land cover and suitable climate over time (although variation among models was large) (Fig. 4A).

Several species with localized distributions that occupy native and tame pasture but not cropland, including Sprague's Pipit, Baird's Sparrow, Brewer's Sparrow, and McCown's Longspur, were projected to experience declines in suitable land cover within their





projected suitable climate (up to $-82 \pm 8\%$ for Baird's Sparrow) (Fig. 4A). For McCown's Longspur and Brewer's Sparrow, this suitable land cover area corresponded to $35 \pm 14\%$ and $42 \pm 11\%$ of their projected suitable climate areas in Alberta at the end of the century, respectively, which reflected the relatively spatially stable but shrinking areas of suitable climate in Alberta for these species. In contrast, for Baird's Sparrow and Sprague's Pipit, this suitable land cover area corresponded to only $6 \pm 2\%$ and $7 \pm 3\%$

of their respective projected areas of suitable climate at the end of the century, respectively, which reflected the northward shift in suitable climate for both species into regions of the province that are dominated by unsuitable land cover, including cropland and forest (Appendix 3, Fig. A3.2).

Four generalist grassland songbirds were also projected to experience declines in suitable land cover within their projected suitable climates, regardless of whether they occupied cropland **Fig. 4.** Projected change in area of currently suitable land cover within suitable climate from the historical baseline (1961–1990) for two future time periods in Alberta, Canada. The mean change (\pm 95% CI) was determined from the four unique global climate models. Symbols as in Fig. 2. Species are separated according to use of land cover types for breeding: (A) 12 species that use both native and tame pasture and hayland, and (B) three species that additionally use cropland (Table 1). Note the difference in scales between panels.



(Savannah Sparrow and Vesper Sparrow) (Fig. 4B) or not (Le Conte's Sparrow and Clay-colored Sparrow) (Fig. 4A). For all four species, these declines reflected northward shifts in suitable climate into the forested regions of Alberta where neither cropland nor native or tame pasture land covers currently exist (Fig. 1; Appendix 3, Fig. A3.2), and for all but Vesper Sparrow, reflected the overall projected decline in suitable climate area in the province.

DISCUSSION

Based on climate model projections of substantially warmer conditions over the next century, we projected northward expansions in suitable breeding climate for more than 50% of grassland songbird species that breed in the North American Great Plains region. These projected expansions were due in large part to increased climate suitability within Alberta and other Canadian prairie provinces, which confirms the importance of these areas as climate refugia for grassland birds. For generalist species that can take advantage of existing agricultural landscapes and grassland patches outside their current breeding range, our land cover inventory within Alberta suggested that these expansions may be manifest fairly readily. For species with more specialized habitat requirements, however, our analysis suggested that the projected increase in climate suitability would not be accompanied by suitable vegetation for nesting due to lags in the transition of native grassland vegetation communities. For the one-third of species that were projected to experience decreases in suitable climate area within Alberta, we found that grassland specialists were especially vulnerable to vegetation lags, given the loss of southern habitats.

Land cover constraints on future suitable habitat for grassland songbirds

The potential for grassland songbirds to occupy areas of projected suitable climate depends on a variety of factors. In addition to intrinsic species' characteristics like site fidelity and dispersal ability, and external factors such as prey availability (Wiens et al. 2009, Skagen and Adams 2012), the rate at which boreal and parkland vegetation transitions to grassland along the grassland-boreal ecotone will impact future grassland songbird distributions. Species that are reliant on native grasslands may be especially constrained by this limitation, being less able to capitalize on potential agricultural expansion. However, predicting ecosystem transition rates and vegetation distributions is complicated by disturbance and successional dynamics, grass species' dispersal, and edaphic constraints (e.g., Schneider et al. 2009).

Vegetation models that combine climate projections with future natural disturbance estimates suggest that native grassland ecosystems have the potential to move into much of the parkland region in Alberta by mid-century (Schneider et al. 2009, Stralberg et al. 2016), especially considering that drought-tolerant grasses already exist in small patches and on drier, south-facing slopes in the region (Natural Regions Committee 2006, Schneider 2013). However, land use in this region is largely agricultural (Fig. 1B), with existing vegetation communities increasingly dominated by non-native agronomic species (e.g., timothy [Phleum pretense] and smooth brome [Bromus inermis]) (Government of Alberta 2013). Given the persistence of these non-native species (Christian and Wilson 1999), opportunities for native grassland expansion by natural dispersal may be limited. Over longer time frames (e.g., end of century), similar expansion into the boreal region may be supported by scattered grasslands within that region (Schneider 2013), yet an absence of dry-adapted grasses, competition with sown non-native grasses along roadsides, and other disturbances will likely limit native grassland expansion (Sumners and Archibold 2007, Schneider 2013).

The warming and drying that is predicted to push grasslandassociated climates and vegetation into Alberta's parkland and boreal regions will also likely drive native grassland plant communities from the Great Plains of the United States into Alberta (Thorpe 2011, Schneider 2013). Predicted changes in native grassland composition and structure include a transition from mid to short grasses and potential changes in productivity (Sauchyn and Kulshreshtha 2008, Thorpe 2011), which may alter native grassland suitability for some songbird species. For example, increases in short grasses may reduce suitability for species like Sprague's Pipit that prefer taller and denser vegetation (Fisher and Davis 2011). Conversely, habitat suitability may increase for other species, like the Grasshopper Sparrow, that prefer nesting in short and sparse vegetation (Dechant et al. 2002).

For grassland songbirds that occupy pasture or cropland in addition to native grasslands, the future availability of suitable

land cover will also depend on changes in agricultural land use in response to climate change. This includes potential transitions from crop cultivation to perennial agricultural cover, like hay, and potential northward expansion of agricultural activity into the boreal region, where it is currently limited (Thorpe 2011). For some species, however, with projected northward expansion but for which the value of tame pasture for their conservation is unclear (e.g., Chestnut-collared Longspur and Baird's Sparrow), preservation of native grassland at the northern extent of the current grassland ecoregion may become increasingly important for supporting their populations (Dale et al. 1997, Lloyd and Martin 2005, COSEWIC 2012). Understanding the value of new native grasslands outside the current grassland ecoregions for these species remains an avenue for future research.

Regions of climate stability and climate change resilience

Given the complexity and uncertainty associated with projecting future distributions of vegetation and land use, areas with relatively stable climate suitability will be particularly important for species persistence as climate change progresses. Our model projections suggest that most of the currently suitable climate for most grassland songbirds in Alberta will remain suitable over the next century, which highlights the importance of these regions for the long-term persistence of grassland songbirds. These areas are likely to maintain relatively stable vegetation communities in the absence of land use change (Ashcroft 2010), and will likely retain populations of grassland songbirds that could act as reservoirs to support range expansions if suitable habitat is restored. Species with small areas of projected climate stability in their current ranges will be more heavily dependent on shifting their distributions into areas with suitable land cover.

For two species of conservation concern in Canada and Alberta, Sprague's Pipit and Baird's Sparrow, our models projected large northward shifts in the distribution of suitable climate, with only small core areas of stable climate remaining. Because they are species of concern with small population sizes, they may be among the species least capable of expanding into newly suitable areas, as their current potential climatic niches are less likely to be fully occupied (Wiens et al. 2009). Furthermore, the more specific habitat requirements of these northern prairie-endemic species and the limited projected overlap of future areas of suitable climate with currently suitable land cover also suggests that the future distributions of these species will rely heavily on the successful transition of parkland and boreal vegetation to grassland vegetation. To the extent that the appearance of newly suitable habitat lags behind climatic shifts, the shifts in suitable climate area projected for these species could exacerbate recent population declines (COSEWIC 2010, 2012).

Limitations and uncertainty

We limited our analysis of land cover suitability to two broad categories of land cover within the agricultural region in Alberta. This definition of suitable land cover may have underestimated total suitable land cover in the province for widespread species, like Savannah Sparrow and Le Conte's Sparrow, that occupy grassland patches and other unforested habitats in the boreal region (Lowther 2005, Wheelwright and Rising 2008). Furthermore, grassland songbird habitat selection is certainly more complex than the distinction between pasture and annual cropland: some species differentially occupy pastures in response to grazing intensity and vegetation structure (e.g., Chestnutcollared Longspur) (COSEWIC 2009), or select habitat based on land use (e.g., hay versus pasture; Clay-colored Sparrow) (McMaster and Davis 2001). Provincial- or national-scale land cover data that reliably distinguish between native grasslands, tame pastures, and hay are not currently available; however, our approach represents a first step toward understanding how interactions between land cover and climate suitability may limit or facilitate grassland songbird distribution changes.

Using bioclimatic niche models to describe the potential impacts of climate change on species distributions is subject to a set of assumptions, particularly that (1) climate variables are an important predictor of species' distributions, and (2) species' distributions are at equilibrium with current climate conditions (Araújo and Peterson 2012). While climate has been found to be an important predictor of avian distributions (Araújo et al. 2009, Cumming et al. 2014), the inclusion of land use and land cover variables in species distribution models can refine projections of future suitable ranges, especially for species that show strong associations with certain land cover or land use types (Barbet-Massin et al. 2012, Sohl 2014, Stralberg et al. 2015*a*). However, because future projections of land use change in the Great Plains and Boreal regions are currently unavailable, this remains an area for further research.

The assumption that species distributions and climatic niches are in equilibrium can be particularly problematic for declining species, like many of the grassland songbirds we examined, because their potential climatic niches are less likely to be fully occupied (Araújo and Pearson 2005, Wiens et al. 2009). Despite our use of a broad spatial and temporal data set in model calibration (Araújo and Peterson 2012), our models may have been prone to omission errors that would have underestimated the area of suitable climate in North America (Wiens et al. 2009). Additionally, most species observations in the modeling data set were from after 1980, and were temporally mismatched to the baseline climate data (1961–1990). In using these data sets, we have assumed that any recently observed climate change has been more rapid than the songbirds' response. Consequently, our projections may have also underestimated changes in the distribution of suitable climate for some species.

The interpretation of bioclimatic niche models is also subject to various sources of uncertainty independent of model assumptions, including uncertainty in the data, the choice of modeling algorithm, the selection of climate and other predictor variables, and the set of global climate models used to generate future projections (Wiens et al. 2009). Of these, uncertainty associated with global climate model selection was identified as the greatest contributor to variation in model projections for boreal songbirds (Stralberg et al. 2015*a*). For most of the species we examined, the direction of change in area of suitable climate models.

Comparisons among outcomes from alternative modeling frameworks can help identify areas of consensus and areas for further work. For example, for species identified by Langham et al. (2015) as having ranges with limited projected climate stability and limited potential for range expansion in North America, we similarly identified limited climate stability and declines in suitable climate area at their northern range limits in Alberta, thereby providing support at a regional level for the continental assessment. Similarly, Langham et al. (2015) classified six of our 15 species as stable, and for all but one, we also projected large areas of climate stability (over 70% of the baseline area) in Alberta. For the species we examined that were identified by Langham et al. (2015) as having an anticipated reliance on range expansions for persistence, we projected only one to experience increasing areas of suitable climate overlap with suitable land cover in Alberta, which indicates the importance of considering potential land cover constraints in the evaluation of risk associated with projected range shifts.

CONCLUSION

Our approach represents another step toward understanding the potential consequences of climate change for grassland songbirds, including the potential for range expansion at their northern range edges. While uncertainty remains around the precise magnitudes and rates of change in suitable climate area and land cover, our projections suggest that some climate-mediated range expansion into areas of suitable land cover in Alberta is possible for many species. However, species with specialized habitat requirements and large projected changes in the distribution of suitable climate (Baird's Sparrow and Sprague's Pipit), and species with dramatic projected reductions in suitable climate area at both a continental and regional scale with limited climate stability (Brewer's Sparrow and McCown's Longspur) are likely very vulnerable to climate change. In the context of declining grassland songbird populations across North America, improved understanding of the potential consequences of interactions between climate change and land cover can support long-term conservation planning and management for these species. In particular, preservation and restoration of suitable grassland habitats within areas of projected climate stability along northern range edges could enhance the likelihood of long-term persistence of grassland songbirds within their current ranges. Additionally, planning to support potential range expansions, including restoration or creation of native grassland habitats outside the current grassland ecoregion, will become increasingly important to address climate change-related risks for some species.

Responses to this article can be read online at: http://www.ace-eco.org/issues/responses.php/866

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BIRD STUDIES CANADA

Appendix 1. Breeding habitat classifications.

Table A1.1. Breeding habitat classifications and rationale for the 15 grassland songbirds considered in this study (continued on next two pages).

Common Name	Scientific Name	Habitat†	Rationale
Baird's Sparrow	Ammodramus bairdii	G	This species occupies native mixed-grass and fescue prairie habitat and seeded pasture and hay. ^{1, 2, 3} Its breeding success can be poor in non-native habitats, but it is more tolerant of agriculture than other grassland obligates. ⁴ It is not observed breeding in cropland. ⁵
Bobolink	Dolichonyx oryzivorus	G	This species occupies tall-grass or mixed-grass prairie habitat. ⁶ It is not abundant in row crops and transitions from forage crops to row crops have been identified as a contributing factor to this species' recent decline. ⁷
Brewer's Sparrow	Spizella breweri	G	shrubsteppe habitats dominated by big sagebrush (<i>Artemisia tridentata</i>) that are uncommon in Alberta and is rarely observed in cropland or other agricultural habitat. ⁸ We included it in in our analysis because of occurrence records from the Dry Mixedgrass region of southeastern Alberta ⁹
Chestnut- collared Longspur	Calcarius ornatus	G	This species occupies short-grass and mixed- grass prairie habitat. ^{10, 11} It exhibits some preference for native over seeded pasture, but occurs in both. ^{12, 13} It does not typically nest in cultivated fields. ^{5, 14}
Clay-colored Sparrow	Spizella pallida	G	This species uses both native and tame pastures for nesting. ^{12, 15, 16} Cropland is not used for breeding, and occurrence in cropland is lower than in pasture. ^{2, 16}

†Habitat: Native and tame grassland/pasture and hay (G); Annual cropland (C).

¹Green et al. (2002), ²McMaster and Davis (2001), ³Davis et al. (1999), ⁴COSEWIC (2012), ⁵Martin and Forsyth (2003), ⁶Martin and Gavin (1995), ⁷COSEWIC (2010*a*), ⁸Rotenberry et al. (1999), ⁹ABMI (2014), ¹⁰Hill and Gould (1997), ¹¹COSEWIC (2009), ¹²Davis and Duncan (1999), ¹³Lloyd and Martin (2005), ¹⁴Owens and Myres (1973), ¹⁵Grant and Knapton (2012), ¹⁶Dechant et al. (2002*a*).

Table A1.1 continue	d (completed on next	page).
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-			This species breeds in moderately open
Grasshopper	Ammodramus	G	grassland habitat and both native and tame
Sparrow	savannarum		cropland but at very low density ^{2, 18}
			This species is common and widespread in open
Horned Lark	Eremophila		habitats, especially with some bare ground and
	alpestris	G/C	short grasses, and frequently occupies cropland habitats. ^{2, 14, 19}
			This species occupies grassland and shrub-
Lark Bunting	Calamosniza		steppe habitats, and breeds in native and tame
Lark Dunning	melanocorys	G	pastures and cultivated hayfields. ^{20,21} It
	2		occasionally uses cropland but is much more
			This species occupies structurally open habitats
			including native and tame vegetation, with a
Lark		G	preference for ecotones between grassland and
Sparrow	Chondestes grammacus		shrub or forested habitats. ^{22, 23} Cropland use by
			this species is uncommon because of the
			absence of woody vegetation in cropland habitat. ^{22, 23}
			This species occupies open uplands and
Le Conte's	Ammodramus	C	lowlands, including in prairie and aspen
Sparrow	leconteii	G	parkiand. ²¹ It typically nests in nayland, tame
			detected in cropland ²⁵
			This species occupies native short-grass and
McCown's	Dhum ah amh an ag		mixed-grass prairie and tame pasture. ^{26, 27}
Longspur	<i>Knynchophanes</i> mccownii	G	Cropland use has appeared since the 1990s, but
	meeownii		is associated with low productivity and may be
			an ecological trap. ^{2, 5, 28}
Savannah	Passerculus		This species uses a variety of tame pasture and
Sparrow	sandwichnesis	G/C	in cropland ^{5, 29}
			This species is closely associated with grazed
Sprague's	Anthus	G	native mixed-grass prairie in good condition. ³⁰ It
Pipit	spragueii		occurs and nests in low numbers in tame pasture
			and is rarely recorded in cropland. ^{30,31}

¹⁷Vickery (1996), ¹⁸Dechant et al. (2002*b*), ¹⁹Beason (1995), ²⁰Shane (2000), ²¹Dechant et al. (2002*c*), ²²Dechant et al. (2003*a*), ²³Martin and Parrish (2000), ²⁴Lowther (2005), ²⁵Dechant et al. (2003*b*), ²⁶With (2010), ²⁷Dechant et al. (2002*d*), ²⁸COSEWIC (2006), ²⁹Wheelwright and Rising (2008), ³⁰Davis et al. (2014), ³¹COSEWIC (2010*b*).

Table A1.1 completed.

Vesper Sparrow	Popacatas		This species occupies a broad range of grassland
	Tobeceles	G/C	habitat types, including native and tame pasture
	gramineus		and cultivated cropland. ^{2,12, 32}
Western Meadowlark	C 11		This species is most common in native
	Sturnella	G	grasslands and perennial grassland cover and is
	neglecta		uncommon in cropland. ^{2,14, 33}

³²Jones and Cornely (2002), ³³Davis and Lanyon (2008).

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Appendix 2. Classification of the Agriculture and Agri-Food Canada Annual Crop Inventory layer.

Table A2.1. Reclassification table for converting Agriculture and Agri-Food Canada (AAFC) Annual Crop Inventory¹ land cover classifications into two land cover types differentially used by grassland songbirds: cropland, and native and tame grassland/hay.

AAFC Annual Crop Inventory Raster Attribute Labels	AAFC Annual Crop Inventory Raster Codes	Reclassified Raster Attributes
Agriculture (generalized), Fallow, Cereals, Barley, Other Cereals, Millet, Oats, Rye, Spelt, Triticale, Wheat, Switchgrass, Winter Wheat, Spring Wheat, Corn, Tobacco, Ginseng, Oilseeds, Borage, Camelina, Canola/Rapeseed, Flaxseed, Mustard, Safflower, Sunflowers, Soybeans, Pulses, Peas, Beans, Lentils, Vegetables, Potatoes, Sugarbeets, Other Vegetables, Sod, Herbs, Buckwheat, Canaryseeds, Hemp, Vetch, Other Crops	120, 121, 130, 131, 132, 133, 134, 135, 136, 137, 138, 139, 140, 141, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 160, 162, 167, 174, 175, 177, 178, 179, 192, 193, 194, 195, 196, 197, 198, 199	Cropland (row crops, low crops, not including orchards, vine crops)
Pasture/Forages	110, 122	Native and Tame Grassland/Hay
Cloud, Water, Exposed LandBaren, Urban/Developed, Greenhouses, Shrubland, Wetland, Fruits, Berries, Orchards, Other Fruits, Vineyards, Hops, Nursery, Forest, Coniferous, Broadleaf, Mixedwood	10, 20, 30, 34, 36, 50, 80, 180, 181, 188, 189, 190, 191, 194, 200, 210, 220, 230	No Data

¹AAFC (2013)

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AAFC (Agriculture and Agri-Food Canada). 2013. AAFC Annual Crop Inventory. Government of Canada, Ottawa, ON. [online] URL: <u>http://www.data.gc.ca</u>. Accessed 23 October 2014.

Appendix 3. Mapped baseline predictions (1961-1990) and future projections of climate suitability in North America and Alberta, Canada for the 15 grassland songbirds considered in this study.

















Figure A3.1. Baseline predictions (1961-1990) and future projections (2041-2070 and 2071-2100) of North American climate suitability for 15 grassland songbirds. The black line delineates core suitable climate area for each species as determined by species specific thresholds. Future projections are based on ensemble climate data from 19 global climate models and the A2 SRES emissions scenario.

















Figure A3.2. Baseline predictions (1961-1990) and future projections (2041-2070 and 2071-2100) of climate suitability for 15 grassland songbirds in Alberta, Canada, based on North American models. The black line delineates core suitable climate area for each species as determined by species specific thresholds. Future projections are based on ensemble climate data from 19 global climate models and the A2 SRES emissions scenario.

Appendix 4. Ranked predictor variable importance for each species.

Table A4.1 Ranked predictor variable importance for each species based on the average single variable AUC across bootstrap runs. Four letter species codes are presented in Table 1. Predictor variable definitions are presented in Table 2.

	BAIS	BOBO	BRSP	CCLO	CCSP	GRSP	HOLA	LARB	LASP	LCSP	MCLO	SAVS	SPPI	VESP	WEME
Annual climate moisture index	1	2	3	1	4	2	1	1	1	3	2	3	2	1	1
Mean summer precipitation	2	4	1	3	5	4	5	3	7	5	1	7	1	6	3
Extreme minimum	3	5	7	4	2	3	4	4	5	2	6	4	3	2	4
temperature															
Summer climate moisture	4	6	2	2	7	6	2	2	2	7	3	5	5	5	2
index															
Growing degree days	6	1	5	7	3	1	3	7	3	4	4	2	6	4	5
Chilling degree days	5	3	6	5	1	5	7	6	4	1	5	1	4	3	7
Continentality	7	7	4	6	6	7	6	5	6	6	7	6	7	7	6



Appendix 5. Projected changes in suitable climate in North America.

Figure A5.1. Projected changes in core suitable climate area in North America from the historical baseline (1961-1990) for the 2050s (2041-2070) and the 2080s (2071-2100). The mean change (± 95% CI; black circles) is determined from the four unique GCMs (CCCMA CGCM3.1; MPI ECHAM5/MPI-OM; GFDL CM2.1; UKMO-HadGEM1; open symbols). Changes in areas projected using ensemble climate data (yellow squares) correspond to the maps in Figure A3.1.