1   **Running Head**: Modeling Distribution Dynamics

2   **Title**: **Fire, humans and climate: modeling distribution dynamics of boreal forest**

3   **waterbirds.**

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1 **Abstract**

2 Understanding the effects of landscape change and environmental variability on ecological

3 processes is important for evaluating resource management policies, such as the emulation of

4 natural forest disturbances. We analyzed time-series of detection/nondetection data using

5 hierarchical models in a Bayesian multi-model inference framework to decompose the dynamics

6 of species distributions into responses to environmental variability, spatial variation in habitat

7 conditions, and population dynamics and interspecific interactions, while correcting for

8 observation errors and variation in sampling regimes. We modeled distribution dynamics of 14

9 waterbird species (broadly defined, including wetland and riparian species) using data from two

10 different breeding bird surveys collected in the Boreal Shield ecozone within Ontario, Canada.

11 Temporal variation in species occupancy (2000 – 2006) was primarily driven by climatic

12 variability. Only two species showed evidence of consistent temporal trends in distribution: ring-

13 necked duck (*Aythya collaris*) decreased and red-winged blackbird (*Agelaius phoeniceus*)

14 increased. The models had good predictive ability on independent data over time (1997 – 1999).

15 Spatial variation in species occupancy was strongly related to the distribution of specific land

16 cover types and habitat disturbance: fire and forest harvesting influenced occupancy more than

17 did roads, settlements or mines. Bioclimatic and habitat heterogeneity indices and geographic

18 coordinates exerted negligible influence on most species distributions. Estimated habitat

19 suitability indices had good predictive ability on spatially independent data (Hudson Bay

20 Lowlands ecozone). Additionally, we detected effects of interspecific interactions. Species

21 responses to fire and forest harvesting were similar for 13 of 14 species; thus, forest harvesting

22 practices in Ontario generally appeared to emulate the effects of fire for waterbirds over time

23 scales of 10-20 years. Extrapolating to all 84 waterbird species breeding on the Ontario shield,

1 however, suggested that up to 30 species may instead have altered (short-term) distribution

2 dynamics due to forestry practices. Hence, natural disturbances are critical components of the

3 ecology of the boreal forest and forest practices which aim to approximate them may succeed in

4 allowing the maintenance of the associated species, but improved monitoring and modeling of

5 large-scale boreal forest bird distribution dynamics is necessary to resolve existing uncertainties,

6 especially on less-common species.

7

8 Key-words: boreal forest; Canada; disturbance; forest management; habitat suitability; habitat

9 use; natural disturbance emulation; occupancy; Ontario; species distribution models; species

10 interactions; waterbirds.

1 **Introduction**

2 Despite a large body of ecological research on landscape management and conservation, the

3 existence and applicability of general guidelines for the ecological management of landscapes is

4 often debated. A recent review (Lindenmayer et al. 2008) identified several directions for

5 research, among which was a need for better understanding of the effects of large-scale

6 disturbances on ecological processes (see also Turner 2010). Such knowledge is critical for

7 implementing policies intended to manage natural resources sustainably (Crow and Perera 2004,

8 Long 2009). Similarly, predicting species responses to climate change is increasingly important

9 (Stenseth and Mysterud 2002, Van der Putten et al. 2010) yet challenging, given that future

10 climate is projected not only to be warmer, but increasingly variable (Easterling et al. 2000) in a

11 spatially complex way (Portmann et al. 2009). Thus, applications of ecological approaches to

12 management require an explicit consideration of timescales (Hastings 2010). Furthermore,

13 management questions typically require quick responses based on the simplest combination of

14 data and models (Hilborn and Mangel 1997, Bunnefeld et al. 2007, Adkison 2009), thus

15 challenging ecologists to derive the most efficient use of existing data (Rushton et al. 2004), to

16 better test hypotheses about the effects of natural and anthropogenic change (Wintle et al. 2010),

17 particularly at large scales of space and time.

18 The successful emulation of natural disturbance regimes paradigm for forest management

19 (ENDR, see Perera et al. 2004, Long 2009) depends on understanding the effects of large-scale

20 disturbances on ecological processes. The use of ENDR is increasingly popular among

21 managers, especially in areas where forest fires are common, and constitutes the basis of forest

22 management policies in various jurisdictions across the Canadian boreal forest (e.g. Ontario

23 Ministry of Natural Resources (OMNR) 2001, Alberta Sustainable Resource Development

1   (ASRD) 2006). Thus, understanding natural disturbance dynamics and developing methods to

2   assess management outcomes at relevant spatial and temporal scales is increasingly important.

3   To fully assess the efficacy of forest harvesting practices with respect to ENDR requires an

4   assessment of responses by plant and animal communities to different disturbance regimes;

5   research has focused on the distribution and community composition of forest birds (Kardynal et

6   al. 2009, Kardynal et al. 2011), as well as arthropods (Buddle et al. 2006) and mammals (Nielsen

7   et al. 2008, Zwolak 2009) in managed and naturally disturbed forests. Nonetheless, it remains

8   unclear to what extent ENDR fosters conservation of birds (Van Wilgenburg and Hobson 2008).

9   Large-scale studies, necessary to better evaluate the extent to which timber harvest and wildfire

10   produce similar responses in animal communities, especially for broad-ranging mobile species

11   (Fisher and Wilkinson 2005), are relatively rare, and few take into account multiple types of

12   disturbances (Van Wilgenburg and Hobson 2008). Such large-scale studies are complicated

13   because the effects of human disturbances on species' distributions or community composition

14   (Brawn et al. 2001) may be comparatively small next to effects of large-scale environmental

15   gradients or other community attributes (Bunn et al. 2010, Gotelli et al. 2010).

16   Previous studies used various species distribution models (SDMs, reviewed in Guisan

17   and Thuiller 2005, Franklin 2010, Drew et al. 2011), or climate envelope models (reviewed in

18   Heikkinen et al. 2006) to predict species responses to environmental variation. These models

19   may however be insufficient to understand and predict species responses to environmental

20   change (e.g. Pearson and Dawson 2004, Beale et al. 2008, Sinclair et al. 2010). In particular,

21   short-term climate variability (weather) might be more influential than long-term climate

22   averages (Reside et al. 2010) and species distributions may also be strongly influenced by the

23   distribution of resources (e.g. landcover, Heikkinen et al. 2006). Furthermore, disturbances are a

1   fundamental ecological process causing large landscape modifications and maintaining spatio-

2   temporal variation in environmental conditions (Brawn et al. 2001, Bradstock et al. 2005). Hence

3   SDMs need to explicitly include disturbances as potential predictors when predicting species

4   distributions under future conditions (Vallecillo et al. 2009). Similarly, population dynamics

5   (Guisan and Thuiller 2005, Gaston 2009) and biotic interactions (Guisan and Thuiller 2005,

6   Brooker et al. 2007, Gotelli et al. 2010) may play a fundamental role in species distributions.

7   Thus, SDMs need to be better rooted in ecological theory to identify ecologically relevant

8   variables and to better model the dynamics of species distributions over multiple spatio-temporal

9   scales (see also Rushton et al. 2004). Furthermore, robust analyses should use standardized

10   modeling frameworks incorporating the effects of uncertainty and error (Guisan and Thuiller

11   2005, Royle and Dorazio 2008).

12   We developed an integrated approach to model dynamics of species' distributions in

13   response to environmental variability. We partitioned the effects of multiple disturbances

14   (natural and human-made) over large spatial scales, while accounting for environmental

15   gradients and population processes, and correcting for observation errors. We applied the

16   approach to the boreal forest of Ontario, where fire and forest harvesting have been mapped at a

17   fine resolution over very large areas comprised of industrially logged forests, as well as large

18   tracts exposed mostly to natural disturbances, principally wildfire. Despite it being an important

19   breeding ground in North America, there is a general lack of information about how waterbirds

20   respond to environmental variation there (Blancher and Wells 2005). Thus we combined

21   information from multiple types of surveys of breeding waterbird distributions (*sensu lato*,

22   including waterfowl, wetland, and riparian species) and addressed three related questions: (i)

23   Which spatial and temporal processes have the largest influence on boreal forest waterbird

1   distributions and at what spatio-temporal scales do they act? (ii) Is the distribution of boreal

2   waterbirds similar between landscapes subjected to human or natural disturbance regimes, as

3   predicted under the hypothesis that, at large spatial scales, human disturbance emulates natural

4   disturbance? (iii) Are there general patterns in habitat suitability among groups of waterbird

5   species, and is there evidence for interspecific interactions?

6   **The Conceptual Model**

7   *Building the conceptual model* - Building a conceptual model of the processes involved is

8   the first step in developing species distribution models (Guisan and Thuiller 2005, see also

9   Cushman and Huettmann 2010 chapter 1 for the importance to form strong links between theory,

10   data, and inferential approaches). Species distribution dynamics at a given site and time are the

11   outcome of many processes acting over several spatial and temporal scales (Figure 1; note that

12   observed patterns may also be affected by the confounding effects of observer or sampling bias).

13   A first distinction can be made between spatial and temporal components (in addition to

14   interspecific interactions). One group of processes generating spatial variation in the suitability

15   of sites for a species are stable habitat relationships with average climatic conditions

16   (bioclimate), specific landcover types (e.g. forest cover) and topography (Guisan and

17   Zimmermann 2000, Holt and Barfield 2008, Holt 2009, Wiens et al. 2010). Spatial disturbance

18   processes directly affect these stable habitat relationships (e.g. Vallecillo et al. 2009), modifying

19   the suitability of an area by changing landcover types (e.g. burned forest) or by influencing or

20   altering surrounding habitats (e.g. roads). Climate variability instead is a temporal process as it

21   may alter local climatic conditions in a given year or season (Reside et al. 2010); over large

22   landscapes this process may also vary spatially. Finally, population dynamics introduce

23   consistent variation over time in species distribution patterns, e.g. increase in probability of

1   occupancy with an increase in abundance (Royle and Dorazio 2008); similarly, the presence or

2   absence of a species may alter the probability of occupancy by another species (Heikkinen et al.

3   2007).

4   This conceptual scheme (Figure 1) aids in clarifying the different ways a given process

5   may act (e.g. climate), in identifying different types of environmental predictors for a given

6   process (e.g. climate indices vs. local climate variability measures for modeling climate

7   variability), and in setting out *a priori* multiple competing hypotheses (e.g. climate envelope *vs*.

8   habitat disturbance models) whose support from the data can be evaluated using multi-model

9   selection techniques (Burnham and Anderson 2002, Link and Barker 2006). Specifically, for the

10   aims of the current paper, we set out six competing models for boreal forest waterbird

11   distribution dynamics (Table 1).

12   *Implementing the conceptual model* – To model species distribution dynamics, we used

13   time series data of species distributions (yearly time scale). We modeled the dynamics of

14   waterbird (broadly defined, including wetland and riparian species) occupancy patterns (note

15   also that boreal birds are not dispersal limited). Modeling occupancy (the proportion of occupied

16   sampling units) provides similar information to models of abundance with the benefit of reduced

17   data collection costs (MacKenzie et al. 2006, Royle and Dorazio 2008), and thus may be a more

18   attractive state variable for conservation management purposes (Guillera-Arroita et al. 2010).

19   To compare the effects of timber harvest and fire on bird distributions, we used the boreal

20   Shield ecozone of Ontario as it comprises industrially logged forests as well as large tracts

21   exposed mostly to natural disturbances. Furthermore, multiple, large scale, annual bird surveys

22   are available for this area (Figure 2). We used hierarchical models (McMahon and Diez 2007,

23   Royle and Dorazio 2008) to decompose the observed variance in distribution dynamics into

1 different levels of variation and to obtain robust estimates of the effects of the predictor

2 covariates, accounting for observation or sampling bias (as well as spatial autocorrelation).

3 **Methods**

4 Study area

5 The study area coincided with the boreal Shield ecozone within the province of Ontario (about

6 600000 km^2; Figure 2). This ecozone is part of the Precambrian Shield and comprises two forest

7 types, the Great Lakes St. Lawrence forest type in the south and Boreal Forest proper in the

8 north. The area is mostly forested (64% forest cover older than 20 years), dominated by conifers

9 in the north (black spruce *Picea mariana*, balsam fir *Abies balsamea*, jack pine *Pinus banksiana*,

10 tamarack larch *Larix lariciana*), whereas deciduous species are more frequent in the south (white

11 birch *Betula papyrifera*, trembling aspen *Populus tremuloides*, balsam poplar *Populus*

12 *balsamifera*, sugar maple *Acer saccharum*, beech *Fagus grandifolia*), with an abundance of

13 wetlands, rivers and lakes (13% open water; 11% wetland cover; see www.nrcan.gc.ca). A

14 fundamental characteristic of the boreal forest is the dynamic disturbance regime caused

15 predominantly by frequent forest fires. Human population density is low and industrial timber

16 harvest and mining constitute the primary anthropogenic disturbances (overall, 10% of the

17 landcover is regenerating forest after fire or forest harvesting; 1% grasslands or crops; 1% mines

18 or settlements). Timber harvest is restricted to the southern region north of which the forest is not

19 commercially harvested (Figure 2). The limit of commercial forest harvesting also marks the

20 limit of the road network in Ontario.

21 Bird Data sets

22 Two large scale bird survey datasets cover the entire Ontario Shield ecozone: the Waterfowl

23 Breeding Population and Habitat fixed-wing Survey (FWS) and the Ontario Breeding Bird Atlas

1 (OBBA2, the second to be conducted). To test the predictive ability over time of models

2 developed using data from the latter survey, we also used point count data collected by the North

3 American Breeding Bird Survey (BBS, see Sauer et al. 2008).

4 *Ontario Breeding Bird Atlas data (OBBA2)* – We obtained point count data conducted by

5 the Ontario Breeding Birds Atlas initiative (http://www.birdsontario.org/) and GIS layers of the

6 sampled grids through Nature Counts, a node of the Avian Knowledge Network, Bird Studies

7 Canada (http://www.naturecounts.ca/). The OBBA2 was designed by dividing the Province of

8 Ontario into 47 regions (roughly coincident with municipal boundaries, varying from ~2000 to

9 >100000 km^2), each assigned to a regional coordinator who coordinated the data collection and

10 assembled teams to ensure sufficient coverage by point counts within the region (Ontario

11 Breeding Bird Atlas 2001). Point counts, recording all bird species seen or heard, lasted 5

12 minutes and comprised both roadside and off-road locations (out of >30000 point count locations

13 20% were located at >200m from any road), located within 10 x 10 km squares (a target was set

14 at 25 point counts per square; see below for more information). Roadside locations were selected

15 randomly *a priori*, off-road locations (>200m from roads) were selected proportional to the

16 habitat composition of each square (e.g. 75% in forest interior, if 75% of the square was covered

17 by forest, paying attention to consider all habitat types, including wetlands and the border of

18 waterbodies) and at least 300m apart from each other. Point counts were collected by voluntary

19 birders over 5 years in Ontario from 2001 throughout 2005 during the peak breeding season,

20 between May 24 and July 10 for southern Ontario and June 1 and July 10 for northern Ontario,

21 starting from sunrise to maximum five hours after. Due to logistical constraints in conducting

22 point counts in the north (e.g. absence of roads), considerably more squares were covered in the

23 southern section of the province, mostly by volunteer participants, whereas many squares in the

1   north were sampled by teams of professional biologists or very experienced observers arranged

2   in teams to cover specific areas.

3   *Waterfowl Breeding Population and Habitat Survey data (FWS)* - The Waterfowl

4   Breeding Population and Habitat Survey is conducted every May over selected routes in North

5   America using fixed wing aircraft by the U.S. Fish and Wildlife Service and the Canadian

6   Wildlife Service (Smith 1995). In eastern Canada the survey has been conducted since 1990. The

7   survey provides counts of breeding adult waterfowl (determined at the species or genus level),

8   observed from a fixed-wing aircraft flying at a speed of 145–167 km/h and a height of 30–50 m

9   above ground level. Waterfowl are counted by a crew of two, a pilot biologist and an observer.

10   Transects lines are 400 m wide and are composed of a series of 28.8 km sections (referred to as

11   'segments'; each segment covers therefore an area of 11.5 km^2); the length of transects varies

12   from around 250 km to 850 km (hence transects cover an area of around $100 - 340$ km^2).

13   Transects are grouped into strata (covering a total area of around 50000 to 250000 km^2). Each

14   crew decides the exact starting date for each stratum, based on the climate and phenology

15   specific to each year and region; for our study area, all surveys were conducted between the end

16   of May and early June. Given that it is important to account for detectability, including observer

17   effects, but observer IDs were only available from the year 2000 onwards, we used data from

18   2000 – 2006 for model training (i.e., parameter estimation and inference).

19   Geographic Information Systems data

20   *Climate data*. – We used four "climate envelope" variables (see Table A2) to quantify the

21   spatial variation in climate across the study area (BIOCLIMATE) – annual mean temperature

22   (accurate to 0.1 degrees Celsius), temperature seasonality (standard deviation x 100), maximum

23   temperature of the warmest month (accurate to 0.1 degrees Celsius), and precipitation seasonality

1 (coefficient of variation). We derived climatic variables from publically available global gridded

2 maps at 10 km resolution (Hengl 2009) downloaded from http://spatial-analyst.net/worldmaps/.

3 Furthermore, we measured local climatic variability for each sampling unit (e.g., each segment

4 of the FWS surveys) as deviation from the 30-year mean monthly value ("climate normals") of

5 temperature (˚Celsius), precipitation (mm), snowfall (cm), or hours of bright sunshine,

6 respectively. These local values were derived by interpolating monthly climate normals data for

7 May, June and July (corresponding to the bird survey months) downloaded from the National

8 Climate Data and Information Archive (www.climate.weatheroffice.ec.gc.ca) for each year

9 (1997-2006) and for each weather station with high quality data in Ontario, Quebec and

10 Manitoba (weather stations from neighboring provinces were included to avoid boundary issues).

11 To interpolate local values, we used thin plate regression spline GAM models where each

12 climatic variable was modeled as a bivariate smooth function of the geographic coordinates,

13 stratified by year (for details see Wood 2006 chapter 5). Overall, these GAM models fitted the

14 weather data very well, accounting for 75% - 98% of the variability. Using the interpolated

15 yearly maps, we obtained the predicted climate variability at each sample unit. We used May

16 climate variability for all datasets, corresponding to the arrival of most migrants. For the OBBA2

17 data, which were collected primarily in June (but also May and July), during the model screening

18 step (see below), we compared models with May climate variability measures to models with

19 measures of the climate variability during the month of data collection for each sampling unit.

20 *Landcover data*. – We used detailed road maps for Ontario (National Road Network data;

21 public roads, not forest roads) from the GeoBase portal (http://www.geobase.ca/geobase/en/) to

22 derive road densities (km/km^2) for each survey unit using ArcView 3.2 (year 2000; ESRI,

23 Redlands, California). Landcover data were derived from the Ontario Provincial Landcover Data

1   Base (www.nrcan.gc.ca). The Ontario Land Cover Data Base was derived by the Ontario

2   Ministry of Natural Resources (OMNR) from digital, multispectral LANDSAT Thematic

3   Mapper data recorded circa 1990 (range 1986 - 1997). Forest cutover and burn cover classes

4   were updated using 1996 coverage data for the Great Lakes St. Lawrence forest region and most

5   of the Boreal forest region. Thus, each area cut or burned can be classified as Recent Cut (areas

6   cut by forest harvesting within ten years prior to 1996), Recent Burn (areas burned within ten

7   years prior to 1996), and an indistinguishable, post-early succession class, Old Cut or Burn

8   (areas subjected to fire or forest disturbance between 1976-1986; areas disturbed before 1976 are

9   classified again as forest). Given these time frames for forest disturbance/succession we modeled

10   bird distribution dynamics until 2006 (i.e., until 10 years after 1996).

11   Resolution of the landcover data was 25m. Data were classified into 28 landcover classes,

12   which we grouped into 11 classes: open water, bogs & fens, marsh & swamps; coniferous forest;

13   deciduous forest; grasslands & crops; recent burns; recent cuts; old cuts & burns; mines &

14   settlements; bare areas and unclassified raster cells (the latter accounted for <1% of the area). For

15   each bird sampling unit we calculated the proportion of the area covered by each of the 11

16   landcover variables. Using the habitat proportion values we also calculated a habitat

17   heterogeneity index, as in Gotelli et al. (2010), for each survey unit. The index ranges between

18   zero (only one single habitat type present) and close to one (all habitat types equally present).

19   Statistical Modeling

20   All statistical modeling was done using the R environment for statistical computing (R

21   Development Core Team 2010) version 2.11.1. An efficient approach to fit hierarchical models

22   is to use mixed effects model techniques (Pinheiro and Bates 2000, Bolker et al. 2009) – for a

23   recent example applied to large-scale bird distribution modeling see Rittenhouse et al. (2012).

1   Specifically, hierarchical logistic-regression models were developed using generalized mixed

2   effects logistic regression models (GLMMs) with the lme4 library (Bates and Sarkar 2007). We

3   used version 0.999375-35, with the associated Matrix package version 0.999375-43 (Bates and

4   Maechler 2010). The lme4 library includes methods for fitting crossed random effects structures

5   to large datasets using generalized mixed effects models (see also Austin 2010), which we

6   ranked using multimodel inference (Burnham and Anderson 2002). Multimodel inference is a

7   powerful tool that allows inference conditional on a model set and not only on a single selected

8   model, thereby accounting for uncertainties associated with model choice (Link and Barker

9   2006, Link and Barker 2009). Multimodel inference is comprised of two parts: model selection

10   and model averaging (both preceded by the model building phase).

11   *Model building* – For all models we included a common random effects structure with

12   which to account for survey design and observer effects (Table 1). For the FWS data, the

13   response was segment-year detection/non-detection data collected between 2000 and 2006 for

14   the training data (N = 1752 for each species). We included four grouping factors as random

15   intercepts, to allow the mean probability of occupancy to be different for each group from the

16   overall population mean. Three of these random effects accounted for the sampling design:

17   segment (252 unique IDs), transect (15 unique IDs), and the stratum-by-year interaction to

18   account for differences in survey start dates mentioned above (26 unique IDs). The fourth

19   random effect accounted for observer effects, with a unique ID associated with each observer-

20   pair combination (8 unique IDs for the data from year 2000 to 2006). To correct for consistent

21   temporal trends (see Figure 1), we included year as fixed effect numerical covariate in all

22   models. For each species, we evaluated the most appropriate polynomial parameterization for the

23   year covariate – linear, quadratic or cubic – using the BIC criterion (Schwarz 1978), selecting

1   the model with the minimum BIC value (see below for a justification for the use of the BIC

2   criterion). This combination of random and fixed effects terms constituted the baseline model as

3   well as the common model structure for all competing models (Table 1).

4   For the OBBA2 point count data, the response was detection/non-detection data within

5   each survey square-year combination collected between 2001 and 2005 for the training data (N =

6   1966 for each species). A baseline structure similar to the FWS model was developed for the

7   OBBA2 point count data: route (the 10 x 10 km squares; 1361 unique IDs), block (100 x 100 km

8   blocks containing 10 squares; 99 unique IDs) and region (22 unique IDs) accounted for the

9   spatial sampling design, whereas the observer ID (432 unique IDs) accounted for observer

10   effects (many observers recorded point counts in multiple squares, which allowed separation of

11   the random effects). Year was entered as numerical fixed effect, as a linear or polynomial term.

12   Note that there was not sufficient information (i.e. only five different years) to enter year as

13   random effect (variances are not reliably estimated with a limited number of levels). The number

14   of point counts per square and year varied, as the aim was to spread the point counts over

15   different days and years for each square (Ontario Breeding Bird Atlas 2001). To correct for

16   unequal sampling effort among squares (median = 15 point counts per year, range 1 – 84) and

17   estimate species-specific optimal sampling effort, we included the number of point counts as a

18   numeric covariate fixed effect. For each species, we evaluated three different polynomial model

19   structures for sampling effort – linear, quadratic or cubic – selecting the most appropriate based

20   on the BIC criterion (in all cases a quadratic or cubic term had the lowest BIC value, indicating

21   that detectability was leveling off with sampling effort). Finally, we included a 2-level dummy

22   factor as a fixed effect to account for consistent differences between the southern and northern

23   sections caused by the different sampling regimes.

1   To aid model convergence and the interpretation of effect sizes and parameter estimates,

2 we mean-centered and standardized all numeric covariates (see Table A2 for the mean and SD

3 values used); specifically, to facilitate comparison between numeric covariates and factors, we

4 standardized the numeric covariates by dividing by two standard deviations (Gelman 2008,

5 Schielzeth 2010). Landcover covariates were centered on the value of overall habitat availability

6 for each cover type within the Ontario Boreal Shield ecozone (see Table A1); otherwise

7 covariates were mean-centered before standardization. Standardizing covariates also alleviates

8 the problem of multicollinearity between predictor variables (Zuur et al. 2010), but to further

9 reduce this confounding effect, we excluded covariate combinations that were correlated at $r > 0.6$

10 (Spearman's rank correlation). Instead of excluding one of the correlated variables, however, we

11 selected the most appropriate one for each species using model comparison techniques in the

12 model screening step (see below). Thus, to build the climate envelope model (Table 2), we

13 evaluated five different parameterizations, each with only one of the five different climate

14 envelope covariates included. Further, climate envelope covariates were also strongly correlated

15 with latitude ($r > 0.9$ in our system); the latter is often also correlated with the distribution of

16 specific landcover types (e.g., deciduous cover). Hence, contrary to the common practice of

17 including these covariates into the same model, we treated these as competing models (e.g., a

18 climate envelope model vs. a geographic gradient model, see Table 1) and, using model

19 averaging techniques, we could obtain a final model containing parameter estimates for

20 correlated predictor variables (Anderson 2008).

21   We avoided overfitting by limiting interactions to 2-way interactions for the segment-

22 level or square-level covariates (252 and 1361 distinct spatial units for the FWS and OBBA2

23 data, respectively), whereas for the climate variability covariates, which varied between years

1   (1752 and 1966 presence/absence records in total for each species for FWS and OBBA2 data,

2   respectively), 3-way interactions were included in the model-screening step (see below). We

3   checked for residual spatial autocorrelation using variograms in the geoR library version 1.6-29

4   (Ribeiro Jr and Diggle 2001); in all cases no residual autocorrelation was detected as random

5   effects appeared to control spatial correlation (Betts et al. 2009, Zuur et al. 2009).

6   *Choice of model selection criteria* – Different criteria can be used for model selection,

7   but the choice must be carefully evaluated as results may differ and the issue is not resolved by

8   statistical theory (see also Murtaugh 2009). Raffalovich et al. (2008) provided strong evidence

9   that, for large sample sizes as in our case, BIC has the greatest ability to identify most of the

10   generating processes, while AIC and other criteria (except stepwise selection) should be avoided

11   (see also Link and Barker 2006, Arnold 2010). We tested this using the FWS data. We ran

12   occupancy models with and without an uninformative randomly distributed variable (generated

13   using random number algorithms or by permutation of one of the predictor covariates) and

14   compared them using BIC (for a similar approach see Whittingham et al. 2005). We repeated this

15   procedure 1000 times, for different distributions of random covariates and for different species.

16   In all cases, the BIC correctly excluded the random covariates, whereas AIC favored their

17   inclusion (ΔAIC <2). Thus, for our datasets we used BIC, excluding all covariates causing an

18   increase in BIC of more than two units (note, ΔBIC <= 2 indicates similar support for keeping

19   covariates in a model).

20   *Model screening step* – To find the most appropriate parameterization of each of the six

21   competing models (Table 1) for each species, we used a 2-step screening procedure of candidate

22   models for each of the final six competing models. First, we found the most appropriate set of

23   alternative covariates to include (e.g., choosing among correlated predictor covariates, see

1   above) and second, we found the most appropriate model complexity (note, all models included,

2   in addition, the three covariates modeling forest harvesting and fire disturbance: Recent Cut,

3   Recent Burn, Old Cut or Burn, see Table A2). For example, for the Disturbance model (Table 1),

4   we first selected the most appropriate parameterization to model the effect of urban areas or

5   mines. We compared two alternative parameterizations, a 2-level dummy factor to distinguish

6   sampling units with or without urban areas or mines, or a numeric covariate (proportion of

7   sampling unit covered by urban areas or mines). For the Climate Variability model, we chose

8   between using deviations from the normal temperature and deviations from the normal snowfall

9   (the two measures were correlated); hence, together with the previous two comparisons, this lead

10   to four different parameterizations to evaluate for the Climate Variability model. Four additional

11   different parameterizations were evaluated for the Climate Envelope models, to identify the most

12   appropriate climate envelope covariate to include for each species. Last, for the Landcover

13   model we considered four additional groups of covariates – open water, wetland, forest, and

14   grasslands/crops – but, to avoid the unit-sum constraint of proportion data, we selected the most

15   appropriate among the alternative combinations of three of the landcover covariates. To model

16   the effects of wetland and forest cover, we also evaluated for each species whether it was more

17   appropriate to allow for a difference in the response to marshlands vs. bogs and fens (similarly,

18   for coniferous vs. deciduous cover). Thus, for the Landcover model, we selected the most

19   appropriate among a total of 21 different covariate combinations. Candidate sets always included

20   interaction terms and, if there were multiple models with $\Delta BIC <= 2$, we selected the more

21   complex model to retain biologically relevant covariates. Note that the screening procedure was

22   repeated for each of the six competing model groups, in order to keep them independent.

1   Having selected the most appropriate covariates to include for each model, we used a

2   backwards elimination procedure – an efficient alternative to all-subset comparisons (Sauerbrei

3   et al. 2008) – to find the most parsimonious model structure for the fixed effects, with two

4   constraints. First, each of the six models had to include at least one of the defining covariates

5   (e.g. a landcover variable for the Landcover model). Second, the three covariates modeling forest

6   harvesting and fire disturbance (Recent Cut, Recent Burn, Old Cut or Burn) were always left in,

7   to allow a test of the natural disturbance emulation hypothesis.

8   *Testing the natural disturbance emulation hypothesis* – We used BIC-based multi-model

9   selection and model averaging procedures to evaluate the support for the predictions of the

10   natural disturbance emulation paradigm (ENDR) of forest management. Observed bird species

11   distributions might differ between areas subjected to forest disturbance and non-disturbed areas,

12   and might vary over time with forest succession, but the patterns should not differ between areas

13   disturbed by fire and areas disturbed by forest harvesting. Hence, we established four *a priori*

14   models to evaluate these predictions: a model including separate parameter estimates for the

15   response to recent burns and cuts; two models each including only one of the two covariates (this

16   amounts to setting the parameter estimate to zero for the excluded covariate, see Burnham and

17   Anderson 2002); a model with both covariates excluded (i.e. no response to either disturbance); a

18   model including a covariate measuring the total area covered by both disturbances (Recent Cut

19   and Burn). The last two models would be in agreement with the natural disturbance emulation

20   hypothesis, whereas the others would falsify it. To estimate variation over time in the response to

21   forest disturbance we also compared each of the four ENDR models to a model with the

22   covariate Old Cut and Burn (i.e. areas cut or burned within 10 years) excluded, and we evaluated

23   the support for a single covariate measuring the total extent of forest in re-growth (Regen; i.e.,

1   forest disturbed after 1976). All six ENDR models were compared based on BIC values, as

2   described previously. This model comparison was repeated for each of the five model groups

3   which included disturbance covariates (i.e. except the baseline model, see Table 1), using the

4   final model structure selected with the model screening step described previously. Support for

5   the natural disturbance emulation hypothesis was then evaluated using model averaging as

6   described below.

7   *Evaluating temporal variation* – In the final step before model averaging, we evaluated

8   the support for different covariates to model temporal variation. After the model screening step

9   and the ENDR test, all six competing models (Table 1) retained 'Year' covariate (of linear or

10   polynomial form, depending on the species). For each model, we then evaluated the support for

11   the hypothesis that the population was stable (i.e. by excluding the year covariate) as well as for

12   the hypothesis that temporal variation is driven by large-scale climate variability caused by the

13   El Nino Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO). Specifically, for

14   the latter, we did this by excluding the year covariate and including the ENSO and/or NAO

15   covariate(s) (Table A2). To also evaluate the relative influences of large- versus local-scale

16   climatic variability, we included the ENSO and NAO covariates in models with and without the

17   covariates for local climate variability (the 'deviation-from-climate-normals' covariates; Table

18   A2). Note that, given how we set up our competing models (Table 1) and the model screening

19   procedure, all models up to this step always included at least one local climate variability

20   covariate (except for the baseline model).

21   *Model averaging* – Having selected the most adequate parameterization for each of the

22   six competing models, after the model screening and the ENDR and temporal variation tests, we

23   used Bayesian multimodel inference combined with the BIC criterion as a computationally

1   simple asymptotic approximation of the Bayes factor (for details see Link and Barker 2006, Link

2   and Barker 2009) for inferential purposes. Using the BIC combined with uniform prior weights

3   for the set of competing models, we obtained BIC weights, using the same formula as for AIC

4   weights (Burnham and Anderson 2002). BIC weights are approximate posterior probabilities

5   indicating the relative degree of support from the data for each model in the set. An appealing

6   feature of model averaging procedures is that they generally provide more robust point estimates

7   and more adequate standard errors for all parameters, as estimates are not any longer conditional

8   on a single model but include the uncertainty associated with model selection. Furthermore, a

9   measure of the relative importance of each covariate can be obtained by summing, for each

10   covariate, the weights of all models where the covariate was included (Burnham and Anderson

11   2002).

12   *Assessing the predictive ability* – We assessed the predictive ability on temporally and

13   spatially independent data by selecting data collected from 1997 – 2000 (1997 – 1999 for the

14   FWS data) for the Ontario Shield ecozone (i.e., same area but different time) and data collected

15   in 2000 – 2006 (2001 – 2005 for OBBA2 data) in the Hudson Bay Lowlands ecozone (i.e. same

16   time but different area; see Figure 2); for the importance of using independent data for model

17   validation see Wenger & Olden (2012). Given our interest in assessing the ecological relevance

18   of the estimated environmental predictors of waterbird occupancy dynamics, and not in

19   predictive ability per se, we assessed the predictive power of the model averaged fixed effects

20   predictors (the Habitat Suitability Index, HSI), without including the additional variance

21   accounted for by the random effects (where the latter account for sampling and observer effects).

22   Measuring predictive ability is not trivial for binomial data, as the accuracy of estimation

23   depends on overall prevalence, sample size and true degree of agreement (Liu et al. 2011), and

1   the traditionally used AUC and Kappa-statistics are potentially misleading (Lobo et al. 2008).

2   Therefore, following recommendations provided by Liu et al. (2011), we provide sensitivity

3   (sens) and specificity (spec) measures, which are conditional probabilities (conditional on the

4   observations) that a known presence (or absence) site is correctly predicted. Second, we used the

5   true-skill statistics (TSS, see Allouche et al. 2006), considered to be one of the best available

6   measures (Liu et al. 2011). It is calculated from the sensitivity and specificity measures (TSS =

7   sens + spec - 1); negative or zero values indicate that the predictive ability is not better than

8   random, positive values (max = 1) indicate better-than-random predictions. TSS is a threshold–

9   dependent measure, but, as for all threshold-dependent measures, by systematically changing the

10   threshold value it can be converted into a threshold-independent value (Liu et al. 2011). As

11   optimization criterion we maximized TSS, which then corresponds to the value of the maximum

12   vertical distance between the ROC curve and the diagonal (MVDr, see Liu et al. 2011). We then

13   used formula σ_1 from Liu et al. (2011) to calculate confidence intervals for TSS. While

14   sensitivity and specificity are probabilities conditional on the observations, there exist two

15   counterparts, positive predictive value (PPV) and negative predictive value (NPV), which are

16   conditional on the predictions (e.g., PPV gives the probability that a predicted presence site is

17   also a true presence); hence, following Liu et al. (2011) we also provide these measures. Finally,

18   we also calculated AUC values, using the somers2 function from the Hmisc package (Harrell Jr.

19   2010) version 3.8-2, and the overall accuracy (total proportion of correct predictions). Liu et al.

20   (2011) also recommended using simulations or randomizations to provide statistical tests, thus

21   for all major accuracy measures used, we evaluated if the estimated value was outside the

22   confidence interval of values obtained by random predictions (N = 10000 repetitions; $\alpha = 0.05$).

23   Specifically, for binomial data there is a direct relationship between overall accuracy of random

1   predictions and prevalence (Fielding 2002). Hence, for each species validation dataset, we

2   generated random presence/absence data with the same prevalence as the test data and calculated

3   the resulting accuracy measures, to obtain a confidence interval for each accuracy measure.

4   *Evaluating interspecific niche overlap and effects of heterospecific presence* – The model

5   averaged predictors (i.e. the habitat suitability indices) were the best estimates of the distribution

6   of single species in relation to environmental variation, after correcting for sampling bias and

7   observer differences. Hence, we used Spearman ranked correlations between predicted habitat

8   suitability indices (i.e., probabilities of occupancy) to measure congruence (or difference) of

9   responses by different species to environmental variation (hence, the term "niche overlap"). To

10   evaluate whether the presence of conspecifics explained further variance in species distributions,

11   in addition to the effects of the other spatio-temporal predictors, we took the residuals from the

12   best fitting model for each species and included those as predictors in the best fitting model of

13   the other species and compared the models using BIC.

14   Finally, many of the cavity nesting waterfowl should have indirect interactions with

15   cavity excavating woodpeckers (assuming that they are at least in some part nest site limited).

16   Thus, we used the OBBA2 Atlas data (specifically, the 5-year breeding evidence data, not the

17   yearly point counts, as the former are more reliable for species that generally breed earlier in the

18   season such as woodpeckers) to generate an index of cavity excavator presence (i.e., at least one

19   woodpecker species recorded as breeding in the area; we repeated this analysis both using all

20   woodpecker species as well as by including only species that excavate cavities large enough for

21   waterfowl – Pileated Woodpecker *Dryocopus pileatus* and Northern Flicker *Colaptes auratus*)

22   and included it as an additional covariate for all FWS segments that crossed at least one sampled

23   OBBA2 square. To test for indirect interactions acting through the effects on forest cover, we

1 allowed also for interactions with the covariates for forest cover, recent burn, recent cut, old

2 cut/burn.

3 **Results**

4 *Which spatial and temporal processes have the largest influence on boreal forest waterbird*

5 *distributions and at what spatio-temporal scales do they act?*

6 For the Ontario Breeding Bird Atlas point count data (OBBA2), most of the variance in breeding

7 season waterbird occupancy patterns was associated with differences among observers (Figure

8 3), even after correcting for differences in the number of point counts (Figure A1) and

9 differences between the northern and southern sampling unit sections (see Figure 3). Importantly,

10 responses were species-specific (Figure A1), i.e. some observers were better able to spot a

11 certain species, but not so other species. After controlling for observer bias, most of the variance

12 was associated with the smallest sampling unit (100 km^2 squares, see Figure 3). Specifically,

13 only for the Common Yellowthroat (*Geothlypis trichas*), the largest variance was not attributed

14 to observer effects but was associated with the 10x10km squares; for the Northern Waterthrush

15 (*Parkesia noveboracensis*) differences between the northern and southern sampling regions were

16 even more influential, whereas for the remaining species (Alder Flycatcher *Empidonax alnorum*,

17 Swamp Sparrow *Melospiza georgiana*, Red-winged Blackbird *Agelaius phoeniceus*, Common

18 Loon *Gavia immer*) the largest variance was attributed to observer effects. In contrast, observer

19 effects accounted for a smaller part of the variance than variation between sampling units for the

20 FWS data. For the FWS data, the largest proportion of the variance was associated with the

21 smallest spatial scale (the segment level, corresponding to scales of 11.5 km^2; see Figure 3),

22 except for American Black Duck (*Anas rubripes*) and Canada Goose (*Branta canadensis*),

23 species for which more variation was associated with the transect level. However, a non-

1 negligible amount of variation was due to observer effects (Figure 3) for all species, except

2 Canada Goose. Specifically, differences between pairs of observers accounted for a large part of

3 the variance for Green-winged teal (*Anas crecca*) and Common Goldeneye (*Bucephala*

4 *clangula*), less, but still influential for Mallard (*Anas platyrhynchos*), even less for Bufflehead

5 (*Bucephala albeola*) and American Black Duck, and only a small amount of variation for Ring-

6 necked Duck (*Aythya collaris*) and Mergansers (*Mergus* sp. and *Lophodytes cucullatus*).

7 Interestingly, the conditional modes (or BLUPs – Best Linear Unbiased Predictors) associated

8 with the eight different pairs of observers showed large differences in probabilities of detecting

9 individuals between observers (e.g., over 30% differences in prevalence for Goldeneye), but

10 interestingly differences between observers were not consistent for different species.

11 To evaluate the variance explained by the fixed effects covariates, we compared the

12 estimated variance associated with the random effects in models with and without including the

13 fixed effects (Pinheiro and Bates 2000). This showed that a large part of the variance associated

14 with the random effects (over 90%, except the variance due to observer effects) could be

15 explained by the fixed effects covariates. Specifically, most of the variance in occupancy was

16 explained by habitat selection, with a similar influence of habitat disturbance and habitat

17 distribution (Figure 4A). The latter was mostly determined by differences in local habitat

18 availability of specific landcover types (Figure 4B). Climatic niche, habitat heterogeneity and/or

19 consistent geographic gradients were markedly less influential for most species (Figure 4B).

20 Most of the temporal variance was determined by year-to-year climate variability (i.e., weather;

21 Fig, 4A); a consistent temporal trend was detected for only two species, Ring-necked Ducks and

22 Red-winged Blackbirds (Figure 4): the model-averaged predicted probability of occupancy

1 decreased from about 65% in 2000 to 55% in 2006 for Ring-necked Duck, whereas for Red-

2 winged Blackbird it increased from ca. 30% in 2001 to 60% in 2005 (Figure A2).

3 *Is the distribution of boreal waterbirds similar between landscapes subjected to anthropogenic*

4 *and natural disturbances, as predicted by the natural disturbance emulation hypothesis?*

5 Fire and timber harvest affected the probability of occupancy of ten of the fourteen waterbird

6 species (Figure 5). Notably, the response varied over time with forest succession and among

7 species: six species responded only to forest disturbances less than 10 years prior to 1996, and

8 not to forest disturbances older than 10; three species responded only to the availability of areas

9 in re-growth greater than 10 years old (Figure 5). Specifically, only the Common Loon

10 responded similarly (positive response) to recent and older forest disturbances as well as to older

11 forest cover; occupancy instead differed depending on availability of open water, as areas with

12 open water and regenerating forest were twice as likely to be occupied compared to areas with

13 open water and mature forest (Table A13). Two other diving species, Goldeneye and Ring-

14 necked Duck, showed evidence for responding similarly to older disturbances and mature forest

15 (but not to recently disturbed forests). Mallard and American Black Duck, instead, avoided

16 recently disturbed as well as mature forest areas, but not successional forests 10 – 20 years post

17 disturbance; the negative response of Mallards was stronger if combined with urban or mining

18 areas (Table A9). Canada Goose and Swamp Sparrow avoided recently burned or logged areas,

19 Red-winged Blackbirds avoided forests older than 20 years. Alder Flycatcher and Common

20 Yellowthroat strongly preferred early successional forests, with Alder Flycatcher also avoiding

21 mature forest. Responses to fire and timber harvest differed for only one species, the Canada

22 Goose, with a larger negative response to recently harvested sites which, however, disappeared

23 after 10 years (Figure 5).

1   Road density affected the distribution of six waterbird species, whereas only two

2   responded to the presence of urban areas or mines (Figure 5). Synanthropic species such as

3   Mallard and Canada Goose occurred more frequently in urban or mining areas or areas with

4   higher road densities (but, for Mallard, not in combination with regenerating forest, Table A9),

5   whereas Common Loon strongly avoided areas with higher road density (Table A13; note that

6   the presence or absence of mines or urbanized areas had no additional or interacting effect).

7   Interestingly, Swamp Sparrows preferred landcover associated with mines or urban areas but

8   avoided areas with higher road density, suggesting that the preference is mainly for microhabitats

9   created in association with mining activities, such as ponds and borrow pits. There were no clear

10   patterns associated with climate variability covariates: large-scale climate indices (mainly El

11   Nino) and local measures of climate variability had similar effect sizes, affecting the same

12   number of species, and for some species (Mergansers, Mallard and Goldeneye) both large-scale

13   climate and local climate variability affected probability of occupancy (Figure 5).

14   The availability of specific landcover types (e.g. open water cover) had the highest effect

15   sizes and affected most species (Figure 5). Generally, diving and cavity nesting species strongly

16   favored forest and open water cover (and/or avoided wetlands), whereas availability of

17   grasslands or agricultural areas affected only Canada Goose (a positive response, consistent with

18   the fact that this is the only grazing species among the set of modeled species). Most species did

19   not respond differently to forest dominated by coniferous versus deciduous trees, except

20   American Black Duck which showed strong avoidance of coniferous forest (Table A4), and

21   Green-winged Teal and Ring-necked Duck which both showed some evidence of a preference

22   for deciduous cover (Tables A5, A11). Two aerial and shrub-associated species, Common

23   Yellowthroat and Alder Flycatcher, strongly avoided forests and open water bodies. Most species

1   did not respond differently to availability of bogs and fens, nor marshes and swamps, except

2   Bufflehead and Merganser (both avoided bogs and fens, but not areas with marshes; Tables S6,

3   S10), whereas Northern Waterthrush was more likely to be found in areas with open water, bogs

4   and fens, or marshes and swamps, but less so in areas with marshes and abundant water cover

5   (Table A15). Bioclimatic covariates or habitat heterogeneity had little or no effects on waterbird

6   distributions, except for Red-winged Blackbirds which had a higher probability of occurrence in

7   areas with higher habitat heterogeneity and, especially, with higher average annual mean

8   temperature (see Figure 5).

9   The model averaged fixed-effects covariates (i.e. the habitat suitability estimates, Tables

10 A4 – A17) not only accounted well for the observed distribution patterns but had also good

11 predictive ability on independent data over time (years 1997-2000) and space (Hudson Bay

12 Lowlands ecozone; see Table A18). Thus reasonable and ecologically relevant habitat suitability

13 models were obtained for boreal forest waterbird species.

14 *Are there general patterns in habitat suitability between groups of waterbird species and, after*

15 *controlling for habitat effects, is there evidence for interspecific interactions?*

16 There were strong similarities between habitat preferences of waterfowl as well as among the

17 other waterbirds (Figure 6 A+B); interestingly, only Canada Goose showed strong evidence for

18 different preferences of habitat suitability from all other waterfowl species (i.e., always negative

19 correlations; Table A19A), in accordance with the observed differences in habitat parameter

20 estimates (Figure 5). Green-winged Teal showed some evidence (albeit less consistently than

21 Canada Goose) for a general difference in habitat suitability (although most covariates poorly

22 explained Green-winged Teal occupancy patterns, see Table A21). Notably, no strong or

23 consistent correlations between species could be detected using the raw detection/nondetection

1 data (not shown), because patterns were strongly masked by sampling and detectability biases.

2 After controlling for habitat suitability, strong evidence was found that waterbird occupancy

3 dynamics might also be affected by the presence of other species (Figure 6 C+D). Importantly,

4 all habitat suitability parameter estimates were essentially unaffected when including the

5 presence of other species as predictors in the model (not shown). Finally, following the

6 suggestion from a reviewer, we tested the hypothesis that cavity nesting waterfowl might

7 (in)directly be affected by cavity excavating woodpeckers (assuming that the former are at least

8 in some parts nest site limited). In total 289 FWS segments crossed at least one sampled OBBA2

9 square, 115 without and 174 with one or more recorded breeding excavating species (for a total

10 of 1213 segment-year records). We refitted the selected best models for cavity nesting waterfowl

11 (Bufflehead, Goldeneye, and Merganser) with and without the excavator-species index (we

12 allowed also for interactions with the proportion of forest cover or of recent/old cut/burned areas,

13 to test for indirect effects) and compared the BIC statistics. The data showed no support for an

14 additional effect of an interaction with excavator species ($\Delta BIC >= 4$). The same results was

15 obtained considering only large woodpecker species (Pileated Woodpecker and Northern

16 Flicker).

17 **Discussion**

18 Species distributions are dynamic patterns continuously re-shaped by ecological processes acting

19 across various levels of organization (Holt 2003, Struve et al. 2010) and an explicit consideration

20 of time scales is essential for understanding the underlying mechanisms (Hastings 2010). We

21 showed that species distributions are as affected by climate variability (weather) and habitat

22 disturbance as they are by stable species-habitat relationships. Modeling time series of species

23 occurrences allows a more nuanced understanding of species responses to forest management as

1   well as of species interactions, but reliable results also required accounting for the sampling

2   effort and observer bias.

3   *Temporal variation*

4   Temporal variability was mainly due to year-to-year variation in probability of occupancy. Only

5   two species showed evidence for consistent trends, and were similarly influenced by habitat

6   distribution and by disturbance (Figure 4; note that the trend for Red-winged Blackbirds is

7   consistent with BBS trend data for Ontario). Model selection results (Figure 5), supported also

8   by evidence of predictive ability over time (Table A18A), suggest that the underlying process

9   may be a response to yearly variation in springtime weather (especially related to variation in

10 local precipitation, temperature, or snow fall, or to large-scale variations such as the El Nino

11 Southern Oscillation). Accordingly, the FWS pilots reported empirical observations on the

12 effects of weather on the availability of water bodies and wetlands (i.e. wet or dry years), as well

13 as on plant phenology, and hence on the distribution of waterbirds (U.S. Fish and Wildlife

14 Service 2010). Indeed, Heikkinen et al. (2006) suggested that using only spatial variation in

15 long-term climatic conditions, as modeled by long-term climate covariates (e.g. annual mean

16 temperature), may be insufficient to understand the role of climate in species distribution

17 dynamics and Reside et al. (2010) provided evidence that shifts in vagile desert bird species

18 distributions may be better explained as a response to weather than to average climatic

19 conditions. Here we showed that this may apply also to boreal forest waterbirds and we propose

20 that our approach of using deviations from climate normals as measure of climate

21 variability/weather allows better separation of responses to average climate conditions versus

22 weather than the approach used by Reside et al (2010).

1   Current climate change scenarios (Easterling et al. 2000, Portmann et al. 2009) predict

2   increased climatic variability, thus including this process in species distribution models may

3   provide important insights. For some species, this may be achieved by using readily available

4   large-scale climate indices, especially the El Nino index (Figure 5). Local weather conditions,

5   however, may vary greatly, a pattern not captured by large-scale climate indices (but see Hallett

6   et al. 2004), and indeed several species responded also (or only) to local-scale climate variability

7   (e.g. Bufflehead, Ring-necked Duck and Goldeneye; Figure 5). The results suggest also that

8   species distribution models based on data collected over a single time period may provide a

9   rather incomplete representation of the determinants of species distributions and may be

10   therefore inadequate to predict future responses to environmental change.

11   *Spatial variation — habitat associations*

12   Spatial variation in species distributions was predominantly affected by local-scale spatial

13   processes, mainly variation in habitat conditions related to habitat disturbance and the

14   distribution of specific land cover types; variation in habitat heterogeneity or in bioclimatic

15   conditions were markedly less influential on species occupancy (Figures 3 & 4). These results

16   strongly suggest that species distribution models excluding more specific land cover information

17   (e.g. Gotelli et al. 2010) may be missing some of the most important environmental drivers of

18   species distributions and raises concerns on resulting claims of evidence of species interactions

19   (see below). We obtained robust habitat suitability estimates, as demonstrated by good predictive

20   ability on independent data from the Hudson Bay Lowlands ecozone (Figure 2) and the modeled

21   species-habitat relationships (Figure 5; Tables A4-A17) are in agreement with current knowledge

22   on the better-studied boreal forest waterbird species; it also constitutes some of the first large-

23   scale information for the less-studied ones (Poole 2005). This result is especially important from

1   a management perspective, as we used satellite land cover maps and broad habitat

2   categorizations (Figure 5), facilitating analyses at scales relevant to forest management.

3   Satellite maps suffer from known inaccuracies (Maxie et al. 2010), but our results are in

4   agreement with Thompson et al. (2007) who demonstrated that even marked inaccuracies in

5   habitat maps may not substantially affect the quality of derived habitat suitability estimates. For

6   example, we showed that Swamp Sparrows preferred wetlands associated with mines or urban

7   areas, but avoided areas with higher road density, in accordance with the observation that this

8   species has in the last decades started to colonize small water bodies or wetland areas associated

9   with mines (Poole 2005). Similarly, Canada Goose are correctly identified as a species with a

10 distinct ecology from the other waterfowl species, whereas dabbling or diving species show

11 strong similarities in habitat associations (Figures 5 & 6).

12 *Spatial variation — habitat disturbances*

13 As expected for species living in the boreal forest, disturbance caused by fire or forest harvesting

14 had a large effect on species distribution patterns (Figure 4). The effects were species-specific

15 and changed over time with forest succession (Figure 5), in accordance with the suggestion that

16 it is important to closely consider the underlying generating processes (Vallecillo et al. 2009) to

17 predict bird distributions in response to land cover change. For example, Alder Flycatcher are

18 known to nest in dense shrubs whereas Canada Goose avoid areas without clear visibility around

19 the nest (Poole 2005) and, accordingly, the two species preferred or avoided, respectively,

20 recently disturbed sites, but not areas disturbed more than ten years previously (Figure 5).

21 Waterbirds also responded to roads and mines/settlements, albeit less frequently and with smaller

22 effect sizes, although it must be considered that the study area was generally characterized by

23 very low densities of roads or mines/settlements. In general, modeled responses were as

1   expected, with a positive response by synanthropic species (Mallard, Canada Goose) and

2   avoidance of roads by less-tolerant species such as the Common Loon, in accordance with a

3   recent long-term study in New Hampshire – USA (Kuhn et al. 2011).

4   Understanding species distribution responses to habitat disturbance is also crucially

5   needed for implementing and monitoring the efficacy of natural resource management policies

6   (Crow and Perera 2004, Nitschke 2005, Fenton et al. 2009, Long 2009) but large landscape-scale

7   studies, especially studies comparing multiple disturbance types, are lacking (Van Wilgenburg

8   and Hobson 2008). We undertook one of the first of such large scale investigations and our

9   results (Figure 5) provide strong evidence that the premises of the natural disturbance emulation

10   paradigm, as the basis of Ontario's forest management policy, are supported, at least for

11   waterbirds, as most waterbird species responded similarly to fire and forest harvesting

12   disturbance. However, we modeled the 14 most common species, out of at least 84 waterbird

13   species breeding in the boreal forest of Ontario (based on data from 2001 to 2005 from the

14   Ontario Breeding Bird Atlas). Extrapolating the result that one species (Canada Goose) out of

15   fourteen responded differently to landscapes disturbed by forest harvesting or fire could suggest

16   that the objective of current forest management policies may not be met for up to 30 waterbird

17   species (mean = 6 species; 95% CI 1 – 30 species; 1-sample proportions test with continuity

18   correction), in accordance with some research on forest birds (Van Wilgenburg and Hobson

19   2008) and especially on riparian birds in boreal shoreline forest and riparian areas (Kardynal et

20   al. 2009), but in disagreement with other studies on forest birds (Wyshynski and Nudds 2009).

21   Interestingly, Lemelin et al. (2007) detected a short-term (~ 4 years) and small-scale (2 km)

22   positive response to forest harvesting by Canada Goose and Green-winged Teal in Quebec,

23   contrary to our findings at larger/longer scales in Ontario, and no response by other waterfowl

1 species and hence claimed that boreal forest waterfowl exhibit some resilience to disturbance. A

2 crucial shortcoming of that study, however, was not to correct for the confounding effects of

3 population increases caused by other factors. In fact, Canada Goose increased markedly during

4 the study period analyzed by the authors (see Fig. 2 in Lemelin et al. 2007) strongly suggesting

5 that the apparent positive response to forest harvesting might be a spurious relationship. This

6 highlights the importance of our approach, which allows correction for the effects of

7 confounding variables.

8   Disagreements between research findings regarding responses to timber harvest have

9 been found for other groups such as mammals (Fisher and Wilkinson 2005, Nielsen et al. 2008,

10 Zwolak 2009) and arthropods (Buddle et al. 2006, Work et al. 2010). Differences in the response

11 may be especially marked for resident bird species or become evident after multiple forest

12 harvesting events (Imbeau et al. 2001) and will be strongly affected by specific forest harvesting

13 procedures (Drever et al. 2006, Van Wilgenburg and Hobson 2008, Work et al. 2010), such as

14 the maintenance of non-harvested buffer zones around water bodies and in-block residual tree

15 retention. This debate suggests that experimental tests of model predictions would be desirable,

16 as recently initiated by Kardynal et al. (2009, 2011). Our model predictions (Tables A4-A17) are

17 ideally suited for this objective, providing quantitative and time-varying predictions for different

18 areas over large spatial scales, hence allowing the selection of a convenient set of experimental

19 sites. Similarly, it will be important to continue recording species responses to forest

20 management to allow a refinement of modeling results as well as forest management policies in

21 an adaptive management context. However, the detailed land cover data mapping of forest

22 harvesting and fire disturbances across the Boreal forest of Ontario that allowed us to obtain

23 relevant results are no longer available – the last update being in 2000. In this latter update, the

1 distinction between less-than-ten-year-old disturbances and those between 10 and 20 years has

2 also been dropped (Spectranalysis Inc. 2000), yet our results demonstrate the relevance of this

3 temporal distinction in understanding differences in species responses (Figure 5).

4 *Interspecific interactions*

5 Obtaining robust habitat suitability estimates for each species allowed us to highlight strong

6 commonalities between waterbird species, to identify species with different ecological

7 requirements like the Canada Goose (Figure 6), and to highlight interspecific interactions

8 affecting species distribution patterns (Figure 6). The absence of expected interactions (e.g.,

9 between Mallard and Black Duck) and the observed correlations, however, could also result if

10 there are unmeasured habitat relationships not included in the models confounding estimation of

11 interspecific interactions; or, alternatively, if species interactions occur at finer spatial scales

12 such as the wetland or local wetland complex scales. Consequently, our results highlight the need

13 to exert caution when examining evidence for apparent interspecific interactions from survey

14 data, as the results may be biased by unmeasured habitat relationships (Guisan and Thuiller

15 2005) and scale effects. Our approach is a straightforward and easy way to investigate this issue,

16 and it might be extended to include less-common species using Bayesian multivariate logistic

17 regression models (Sebastián-González et al. 2010, Ovaskainen and Soininen 2011).

18 Furthermore, we investigated if the data provided evidence for the expectation that cavity nesting

19 waterfowl should respond to the presence of cavity excavating woodpeckers. Contrary to this

20 expectation, but in accordance with Lemelin et al. (2007), the data did not provide any support

21 for an effect of cavity excavating species. A cautionary note, however, is that the waterfowl and

22 woodpecker data had been collected by two different surveys (FWS and OBBA2, respectively)

1   using different spatial sampling scales. Our results should therefore be further evaluated using

2   specifically designed surveys.

3   *Observer effects and monitoring design*

4   Management questions often require the most efficient use of existing data (e.g. survey data)

5   even if originally collected for different purposes (Rushton et al. 2004), to avoid time-consuming

6   and costly new data collection. We demonstrated that the FWS fixed-wing survey and OBBA2

7   point count data can be used to obtain robust and management-relevant inferences on waterbird

8   distribution dynamics and ecology in the boreal forest, although both surveys were developed for

9   different purposes and for analyses at larger resolution (e.g. see Smith 1995). For the point count

10   data, waterbirds are generally excluded from the analyses, due to the lower detectability

11   compared to landbirds. We provided a robust model-based approach to solve these issues, using

12   hierarchical models efficiently fitted using GLMM modeling methods. For example, our results

13   indicate that future OBBA2 point counts should collect at least 40 point counts (Figure A1),

14   spread over a set of years to allow modeling of temporal variation. Similarly, observer IDs

15   should always be provided together with the FWS data (contrary to current practice).

16   *Management implications*

17   We showed that by including the effects of climate variability and natural and anthropogenic

18   disturbances into species distribution models, as well as population dynamics, considerably more

19   management relevant information can be obtained from existing large-scale monitoring data.

20   Focusing on boreal forest waterbirds, we found that species responses to fire and forest

21   harvesting were similar for 13 of the 14 most common species; thus, forest harvesting practices

22   in Ontario generally appeared to emulate the effects of fire for waterbirds over time scales of 10-

23   20 years. Extrapolating to all 84 waterbird species breeding on the Ontario shield, however,

1   suggested that up to 30 species may instead have altered (short-term) distribution dynamics due

2   to forestry practices. Hence, natural disturbances are critical components of the ecology of the

3   boreal forest and forest practices which aim to approximate them may succeed in allowing the

4   maintenance of the associated species, but improved monitoring and modeling of large-scale

5   boreal forest bird distribution dynamics will be necessary to resolve existing uncertainties,

6   especially for less-common species. Also, the impact of specific forestry practices, such as mean

7   cutblock size and residual retention, as well as of biotic interactions, will need to be evaluated,

8   using more fine scale and detailed data. Model predictions should be tested with independent

9   data. In addition, the marked responses to climate variability indicates a need to consider the

10   likely effects of climate-change on waterbird distribution dynamics. Finally, while we applied

11   our modeling approach to the Boreal Forest, it should prove of general utility for many other

12   study systems addressing similar questions.

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1 **Ecological Archives material**

2 SUPPLEMENTAL MATERIAL

3 **Appendix 1**

4 Supplemental tables and figures with landcover composition of the study area, a description of the

5 environmental covariates used, information on the modeled waterbird species, tables with parameter

6 estimates and model performance measures, and supplemental figures of estimated model predictions

7 and bird distribution maps.

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1 Table 1. Six competing models of Boreal forest waterbird occupancy in relation to forestry and fire

2 disturbance in Ontario (Canada).

Model	Covariates (fixed effects only)			
Baseline model	YEAR TRENDS + SAMPLING*			
Disturbance model	YEAR TRENDS + SAMPLING*	+ HABITAT DISTURBANCE		
Climate Variability model	YEAR TRENDS + SAMPLING*	+ HABITAT DISTURBANCE	+ CLIMATE VARIABILITY	
Geographic model	YEAR TRENDS + SAMPLING*	+ HABITAT DISTURBANCE	+ CLIMATE VARIABILITY	+ HABITAT HETEROGENEITY	+ GEOGRAPHIC GRADIENT
Bioclimate	YEAR	+ HABITAT	+ CLIMATE	+ HABITAT	+

model	TRENDS + SAMPLING*	DISTURBANCE	VARIABILITY	HETEROGENEITY	BIOCLIMATE
Landcover model	YEAR TRENDS + SAMPLING*	+ HABITAT DISTURBANCE	+ CLIMATE VARIABILITY	+ HABITAT HETEROGENEITY	+ LOCAL HABITAT

1 *Notes*: All models shared the same random effects structure, which modeled the data collection

2 sampling design (e.g. segments, transects and strata for the USFWS fixed winged data) and corrected

3 for Observer and Year effects (the latter modeled as linear or polynomial term, but allowed to simplify

4 to a constant intercept in case the data did not support a consistent year trend). See Table A2 for the

5 covariates used and methods for further details. * Bird Atlas point count data (OBBA2) only; sampling

6 intensity is modeled as a polynomial function of the number of point counts per sampling square and

7 year.

1   Table 2: Waterbird taxa, functional groups and characteristics of survey data used for modeling.

Family	Taxon			Life history		Survey Data	
	Species	Common name	Acronym	Foraging	Nesting	Type[2]	Prevalence[3]
PARULIDAE	*Parkesia noveboracensis*	Northern Waterthrush	NOWA	Ground	Ground	Point counts	0.31
	Geothlypis trichas	Common Yellowthroat	COYE	Glean	Shrub	Point counts	0.59
TYRANNIDAE	*Empidonax alnorum*	Alder Flycatcher	ALFL	Aerial/Glean	Shrub	Point counts	0.51
EMBERIZIDAE	*Melospiza georgiana*	Swamp Sparrow	SWSP	Ground	Ground/Shrub	Point counts	0.42
ICTERIDAE	*Agelaius phoeniceus*	Red-winged Blackbird	RWBL	Ground	Shrub	Point counts	0.28
ANATIDAE	*Branta canadensis*	Canada Goose	CAGO	Dabbling/Ground	Ground	Aerial	0.15

Anas platyrhynchos	Mallard	MALL	Dabbling	Ground	Aerial	0.42
Anas crecca	Green-winged Teal	AGWT	Dabbling	Ground	Aerial	0.13
Anas rubripes	American Black Duck	ABDU	Dabbling	Ground	Aerial	0.21
Aythya collaris	Ring-necked Duck	RNDU	Diving	Ground	Aerial	0.59
Mergus sp. or	Merganser[1]	MERG	Diving	Ground	Aerial	0.57
Lophodytes cucullatus	(all species)			Cavity		
Bucephala clangula	Common Goldeneye	GOLD	Diving	Cavity	Aerial	0.36
Bucephala albeola	Bufflehead	BUFF	Diving	Cavity	Aerial	0.21
GAVIIDAE						
Gavia immer	Common	COLO	Diving	Ground	Point	0.42

Loon

counts

1   *Notes:* Information obtained from the Birds of North America Online (Poole, 2005; retrieved on August 2010 at

2   http://bna.birds.cornell.edu/BNA/). All waterfowl are of the order Anseriformes, all other waterbirds are of the order Passeriformes,

3   except the Comon Loon (order Gaviiformes). [1] Merganser species cannot be reliably distinguished during the FWS fixed wing aerial

4   surveys and are therefore lumped into a generic taxon. [2] Data were collected by the US FWS May Waterfowl Breeding surveys or the

5   Ontario Breeding Bird Atlas point counts (see Methods). [3]Prevalence is the proportion of detections.

1   **Figure legends**

2   Figure 1: Conceptual modeling approach. Bird distribution patterns at a given site and time are

3   the outcome of processes acting over multiple spatial and temporal scales, including bias

4   introduced by the observation process (however, here we focus on the biological part). Whilst

5   often interconnected we suggest to separate these processes first into (predominantly) temporal

6   or spatial components. Temporal variation in observed bird distributions is determined by long-

7   scale processes acting on the population dynamics of a species over its entire annual cycle,

8   whereas variation around these trends is affected by the response of individuals to climate

9   variability (note that population dynamics may also be linked to spatial variation via dispersal

10   dynamics). Spatial variation is governed by the distribution of the physical conditions and

11   biological resources allowing an individual to occupy a given area ("Habitat distribution"); these

12   stable associations may be perturbed by natural or human-induced disturbances ("Habitat

13   disturbance"; note that interspecific interactions are not considered here). This conceptual

14   subdivision clarifies the different ways a given process may act (e.g., note the distinction

15   between spatial - "Bioclimate" - and temporal components - "Climate variability" - of the effects

16   of climate), which in turn aids in selecting the most appropriate covariates ("Covariates") to use

17   for modeling (see text for further details).

18

19   Figure. 2: Study area extent and distribution of bird survey data in Ontario (Canada): the study

20   area (shaded in grey) coincides with the Ontario Shield ecozone; the northern limit of

21   commercial forest harvesting (dotted black line) marks also the limit of the road network in

22   Ontario. The two insets on the right show the distribution in the study area of the May Breeding

23   Waterfowl fixed-wing Surveys (FWS), of the Ontario Breeding Bird Atlas (OBBA) point counts

1 (bottom map), and of the Black Duck Joint Venture helicopter plots and the BBS roadside point

2 count data (top map). The inset on top left shows the distribution of recent cut areas (light grey),

3 recent fires (black) and the FWS transects (grey lines) and OBBA2 point counts (open circles).

4 Survey data from the Hudson Bay Lowlands ecozone (FWS & OBBA2) were used for model

5 validation (see Text).

6

7 Figure 3: Scales of variation of breeding-season probability of occupancy of 14 boreal forest

8 waterbird species in the Ontario Shield ecozone – eight waterfowl taxa monitored by fixed-wing

9 surveys (FWS) between 2000 - 2006; six other waterbird species monitored by Ontario Breeding

10 Atlas point counts (OBBA2) between 2001 – 2005. Variance estimates were obtained from

11 generalized mixed effects logistic models and standardized for each species (to facilitate

12 comparisons) by dividing by the maximum variance value for each species. In all cases, the

13 baseline model (see Table 1) was used to decompose the observed variance into contributions

14 from different scales: the $10 – 100$ km^2 scale, corresponding to the smallest sampling unit

15 ("Level1" - segment or square for the FWS or OBBA2 data, respectively); the 10000 km^2 or 250

16 $– 850$ km^2 scale at the second level (Blocks or Transects for OBBA2 or FWS data, respectively)

17 and the 50000–250000 km scale at the third level (Strata for FWS). In addition, in all cases

18 observer effects were modeled using additional random effects terms ("Observer" and

19 "RegionID", the latter only for OBBA2, accounting for differences between regions supervised

20 by different regional coordinators). Note the strong impact of observer effects as well as the

21 similarities in the patterns of scale dependency between the two sets of waterbird species. See

22 Methods and Results for further explanations.

23

1   Figure 4: Relative importance of spatio-temporal processes acting on the breeding-season

2   probability of occupancy of 14 boreal forest waterbird species in the Ontario Shield ecozone

3   (variable-importance estimates were obtained using multimodel inference). A) Spatial processes

4   (Habitat distribution and habitat disturbance) strongly affected most species; the occupancy of

5   many species was also strongly affected by climate variability, whereas only Red-winged

6   Blackbirds (RWBL) and Ring-necked Ducks (RNDU) showed evidence for consistent multi-year

7   trends of occupancy. B) Habitat distribution was modeled in four different ways and the local

8   distribution of specific landcover types ("Local habitat") predominantly affected the occupancy

9   of waterbirds, whereas habitat heterogeneity was important only for three species (Red-winged

10 Blackbird, Mallard (MALL) and Ring-necked Duck); similarly, larger-scale spatial processes

11 correlated with bioclimate or geographic coordinates had a minor or negligible relative influence

12 for most species, except bioclimate for red-winged blackbird and a consistent geographic trend,

13 not well explained by the other spatial covariates, for the Northern Waterthrush (NOWA).

14

15 Figure 5: Effects of environmental disturbances and resource distribution on the breeding season

16 probability of occurrence of 14 Boreal forest waterbird taxa in the Ontario Shield ecozone

17 (Canada). Model-averaged effect size and confidence intervals were obtained using GLMMs

18 (covariates were centred and standardized by 2 sd). Forest disturbance was modeled as the

19 proportion of the survey area cut (RecCut) or burned (RecBurn) within the last 10 years, or

20 cut/burned between 10 – 20 years ago (OldCutBurn), or as density of roads (RoadDens) or

21 proportion of area occupied by settlements or minings (Mining/ Settlements). Climate variability

22 was modeled using large scale indices (ENSO, NAO) as well as yearly local deviations from 30-

23 year climate normals of average monthly temperature (Tdev), snowfall (Sdev), precipitation

1   (Pdev). Bird survey data were obtained from yearly (2000-2006) fixed-wing waterfowl surveys

2   for American Black Duck (abdu), Green-winged teal (agwt), Bufflehead (buff), Canada goose

3   (cago), Goldeneye (gold), Mallard (mall), mergansers (merg) and Ring-necked duck (rndu), and

4   from point counts (2001-2005) from the Ontario Breeding Bird Atlas for Alder flycatcher (alfl),

5   Common loon (colo), Common yellowthroat (coye), Northern waterthrush (nowa), Red-winged

6   blackbird (rwbl) and Swamp sparrow (swsp). All taxa are ordered according to foraging life-

7   history (Table 1). See Methods for further detail.

8

9   Figure 6: Niche similarity and interspecific co-occurrence effects on waterbird occupancy

10   patterns in the boreal forest in the Ontario Shield ecozone (Canada). Niche similarity is defined

11   as the Spearman-rank correlation between species-specific occupancy estimates obtained from

12   model-averaged habitat suitability indices (controlling for the sampling design, observer effects

13   and sampling effort using a logistic regression generalized mixed effects framework; only values

14   of $\rho > abs(0.30)$ are shown; for full results see Tables S1-S3); effects of heterospecific presences

15   were evaluated after controlling for shared responses to environmental conditions and observer

16   effects or sampling bias. A) Similarity between occupancy estimates of waterfowl, based on

17   FWS fixed-wing survey data (years 2000 – 2007); note that only for Canada goose the

18   correlation was always negative. B) Similarity between occupancy estimates of waterbirds based

19   on Ontario Breeding Atlas point count data (years 2001-2005); contrary to waterfowl, the

20   correlations were always positive between these six species. C) Heterospecific presence effects

21   on waterfowl occupancy; note that only for Canada goose the probability of occupancy was not

22   affected by any of the other seven species analyzed. D) Heterospecific presence effects for the

1   other six waterbird species; note that, contrary to waterfowl, also negative effects were detected.

2   See text for additional explanations and species acronyms.

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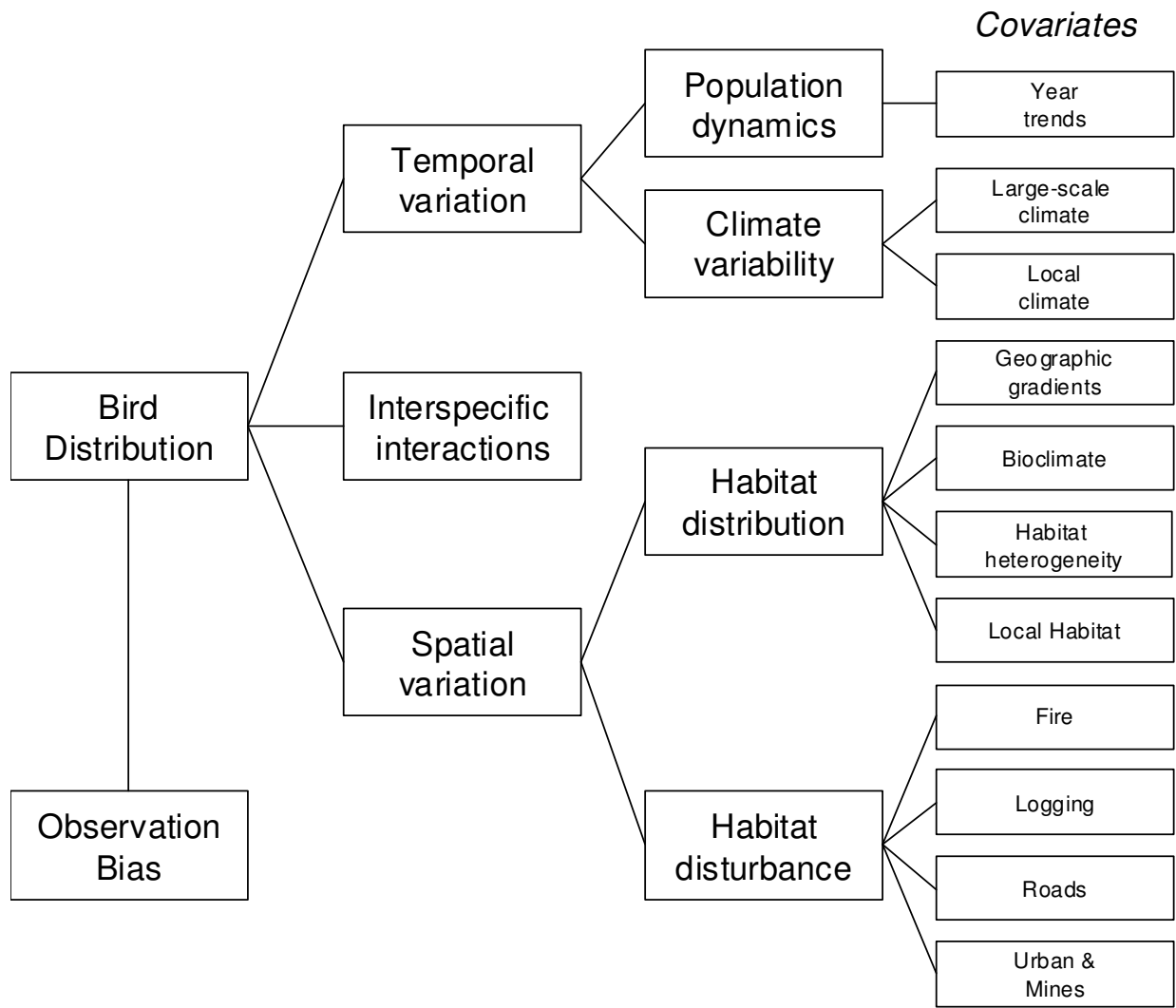
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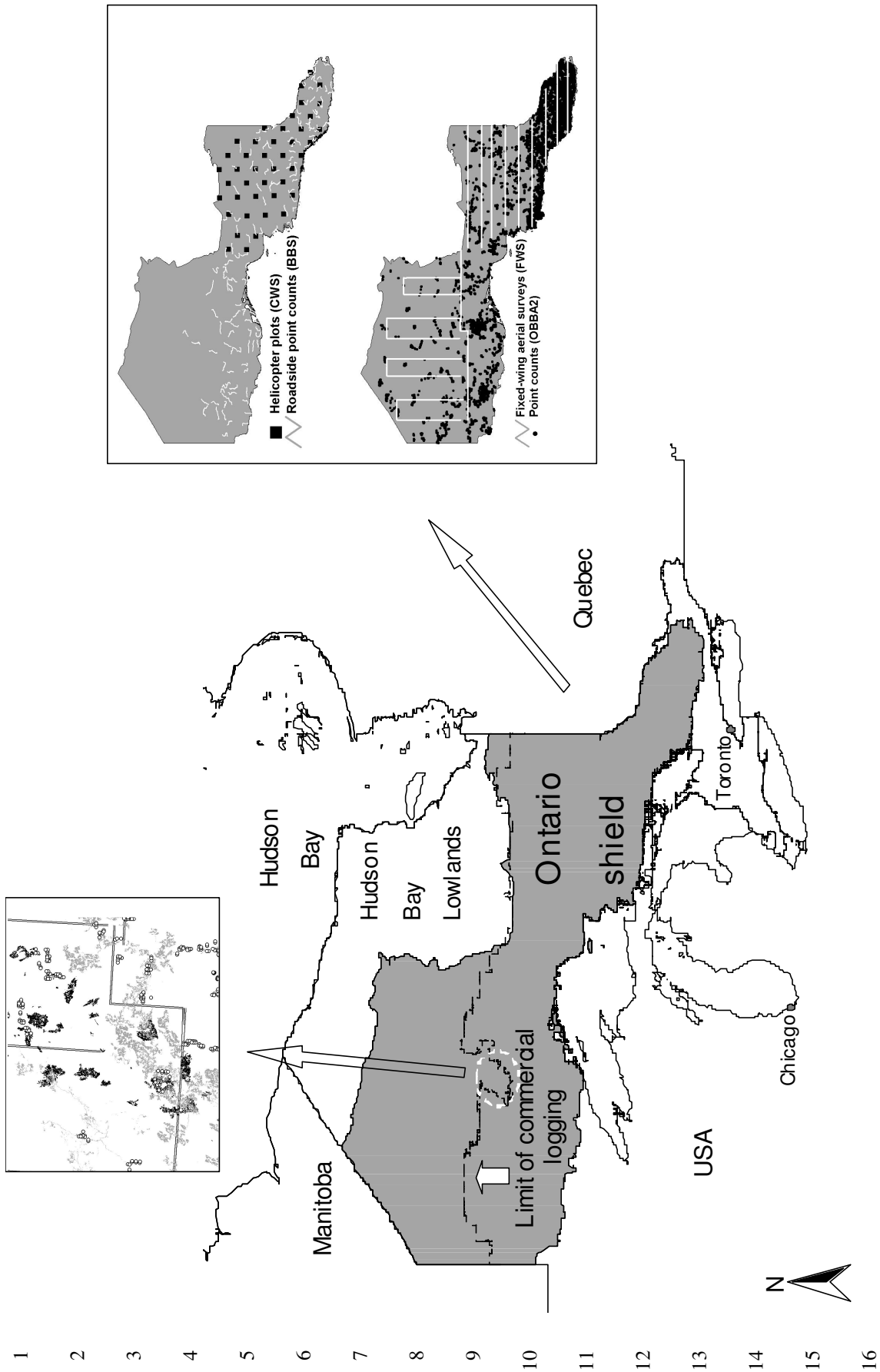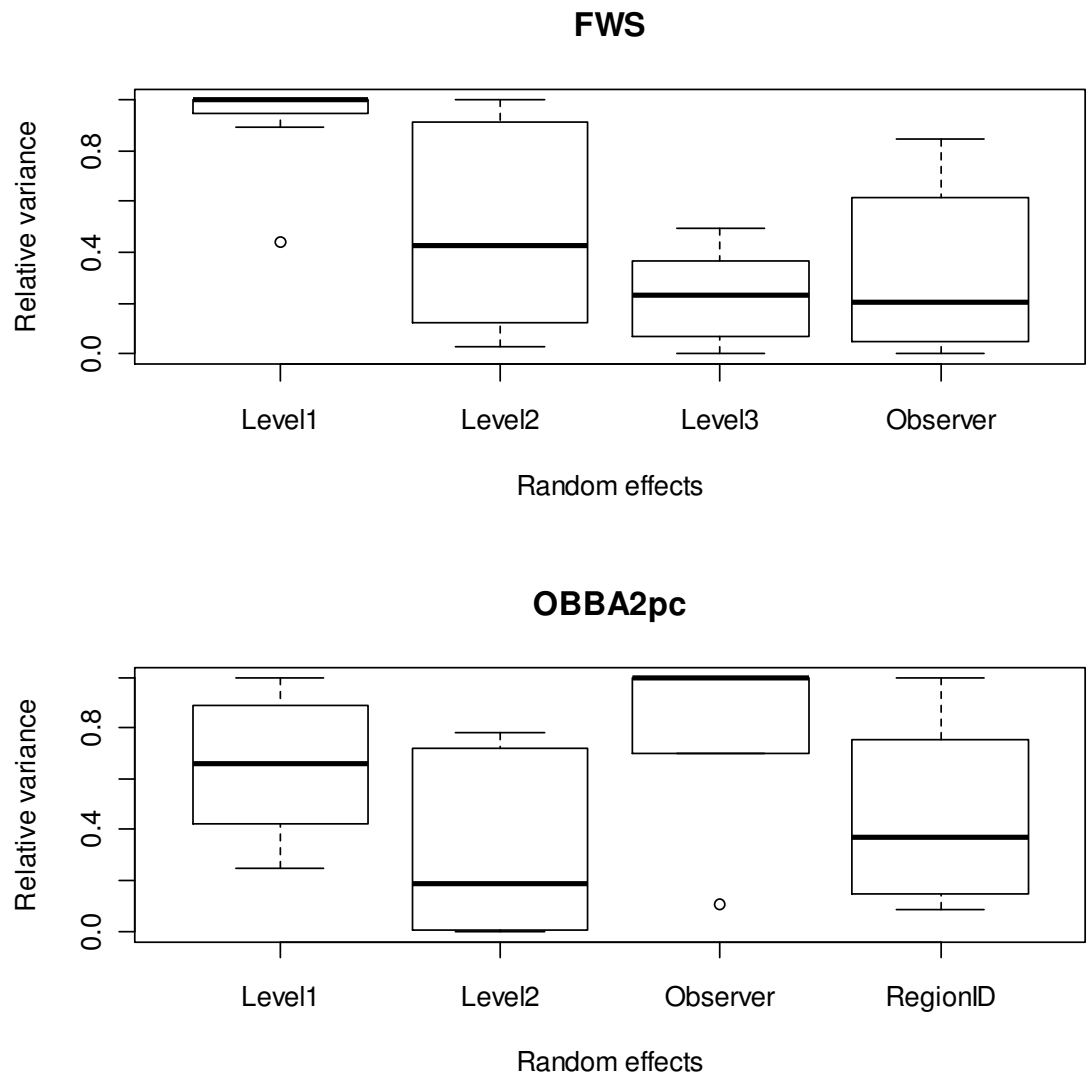
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20 Figure 1

Börger et al. Modeling Distribution Dynamics

Figure 2

FWS

OBBA2pc

1

2

3   Figure 3

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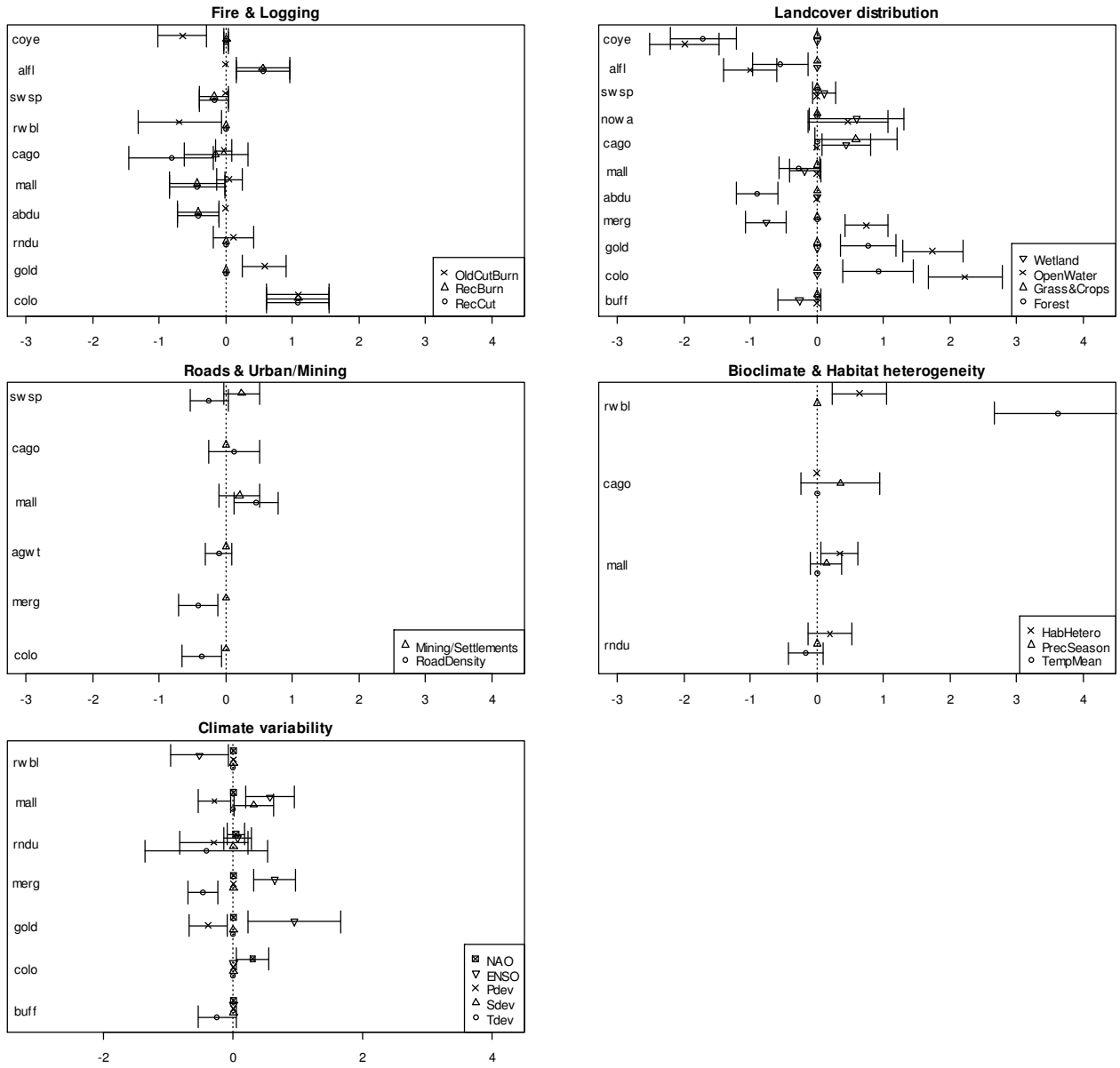
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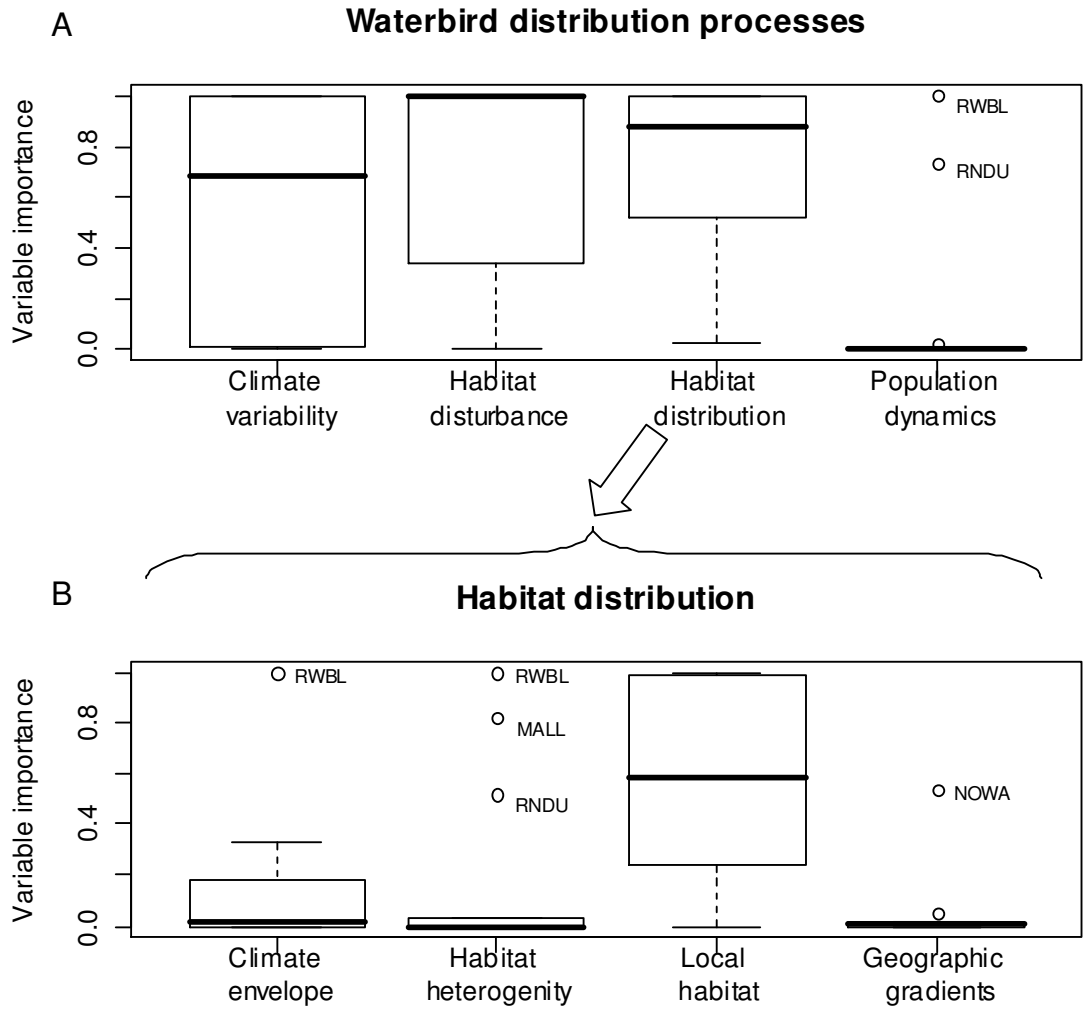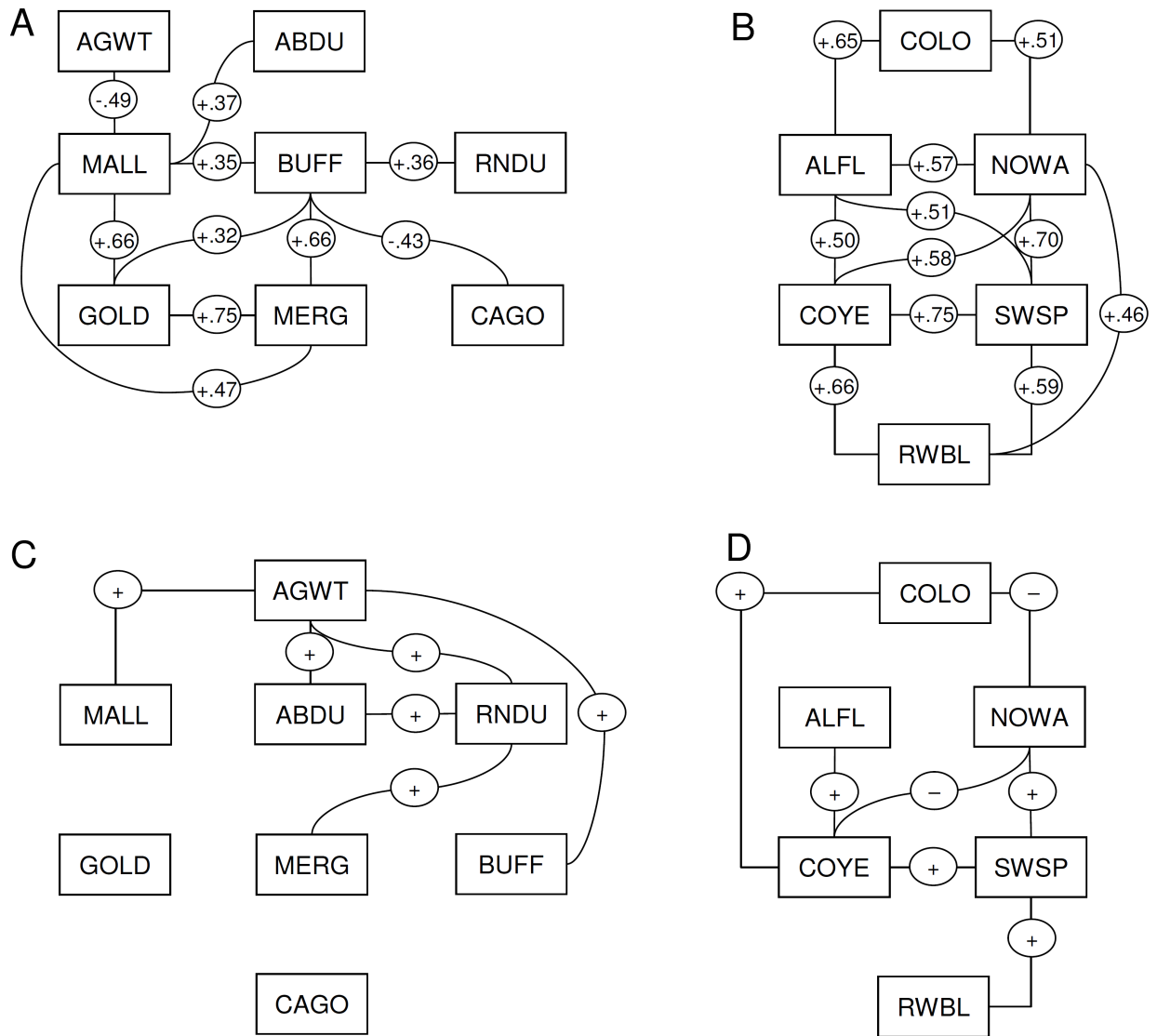
20   Figure 4

log odds of occupancy

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4   Figure 5

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3   Figure 6