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Forecasting climate change impacts on the distribution of wetland habitat in the Midwestern United states

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Abstract

Shifting precipitation patterns brought on by climate change threaten to alter the future distribution of wetlands. We developed a set of models to understand the role climate plays in determining wetland formation on a landscape scale and to forecast changes in wetland distribution for the Midwestern United States. These models combined 35 climate variables with 21 geographic and anthropogenic factors thought to encapsulate other major drivers of wetland distribution for the Midwest. All models successfully recreated a majority of the variation in current wetland area within the Midwest, and showed that wetland area was significantly associated with climate, even when controlling for landscape context. Inferential (linear) models identified a consistent negative association between wetland area and isothermality. This is likely the result of regular inundation in areas where precipitation accumulates as snow, then melts faster than drainage capacity. Moisture index seasonality was identified as a key factor distinguishing between emergent and forested wetland types, where forested wetland area at the landscape scale is associated with a greater seasonal variation in water table depth. Forecasting models (neural networks) predicted an increase in potential wetland area in the coming century, with areas conducive to forested wetland formation expanding more rapidly than areas conducive to emergent wetlands. Local cluster analyses identified Iowa and Northeastern Missouri as areas of anticipated wetland expansion, indicating both a risk to crop production within the Midwest Corn Belt and an opportunity for wetland conservation, while Northern Minnesota and Michigan are potentially at risk of wetland losses under a future climate.

Keywords: artificial neural network, climate projections, isothermality, midwest, modeling, wetlands, WorldClim

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Introduction

Wetlands play an important role in mitigating the impacts of flooding on a landscape scale (Hey & Philippi, 1995) and effective management of these habitats requires knowing where conditions will continue to support their creation or maintenance as the climate changes. Climate change is anticipated to bring about shifts in the pattern and timing of rainfall for the Midwestern United States, yielding increases in the frequency and intensity of severe storms during the growing season and an increase in seasonal flooding from snow melt (USGCRP (U.S. Global Change Research Program), 2009; Wuebbles & Hayhoe, 2004). Wetlands generally act as buffers to severe flooding by diverting and retaining floodwaters (Farber, 1987; De Laney, 1995), but a majority of wetlands within the conterminous United States have been degraded; an estimated 59% of freshwater wetland area was filled, dredged, or otherwise altered within the last 200 years (Bedford, 1999; Bridgham *et al.*, 2006). Economic impacts of flooding have risen over the past century, not only as a function of increasing development and infrastructure along waterways and coastlines but also because of a decline in buffering capacity afforded by wetland ecosystems (Hey & Philippi, 1995). Climate change has the potential to degrade wetlands in some regions, and facilitate their formation in areas where wetlands are not particularly prevalent (Johnson *et al.*, 2005), threatening what buffering capacity remains in a time when flooding is anticipated to become more frequent and severe (Bronstert, 2006).

Wetlands respond rapidly to shifts in hydrology (Keddy, 2002), a property that is controlled by climate at both regional and landscape scales (Erwin, 2009). For example, the boundaries of lacustrine wetlands shift with lake water levels, which are intricately connected to precipitation and temperature via recharge and evaporation rates (Keddy & Reznicek, 1986; Mortsch, 1998; van der Valk Arnold, 2005). Increasing rainfall totals and accumulation of snow can yield larger lakes

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with a wider fringe of associated lacustrine wetlands (Keddy, 2002). Aridification and water table stabilization tend to reverse this process (Kroes & Brinson, 2004), and can result from climate (e.g. decrease rainfall totals or seasonality) or local factors (e.g. reservoir-controlled discharge *sensu* Dynesius & Nilsson, 1994). Coastal wetlands respond dynamically to flooding and sediment accretion from tidal processes, tropical storms, and river discharge (Poff *et al*., 2002; Nicholls, 2004). Riverine wetlands retain floodwaters or form in oxbows where flooding deposits fresh sediment (Keddy, 2002). Finally, blanket bogs are dependent upon ample precipitation and low temperatures with very little hydrologic connectivity to the surrounding landscape (Heathwaite, 1993; Bragg & Tallis, 2001). As a result, both the expansion and disappearance of bogs are reported to have strong associations with shifting temperature and precipitation patterns (Mauquoy & Yeloff, 2008).

The wetland–climate connection is fairly direct for some habitat types (ombrotrophic bogs), but often subject to innumerable landscape and local influences (Burkett & Kusler, 2000) making it difficult to predict how any particular wetland will respond to a changing climate. This leaves managers with unclear conservation targets, especially when climate forecasts predict many historic norms to be untenable in the near future (Harris *et al*., 2006; Zedler *et al*., 2012).

Geographically explicit modeling offers a powerful option for evaluating wetland response to climate change. Taking advantage of freely available geodatabases, such models can derive correlations between the prevalence of wetlands on a regional scale with current climate, and use these associations to predict responses to forecasted climates. Fine-scale geographically explicit datasets are available that quantify both the distribution of wetlands and many of the major drivers of wetland ecosystem formation. The USGS National Wetland Inventory provides geographic extents for wetlands of multiple classifications (USFWS (United States Fish & Wildlife Service), 2001). Models incorporating drainage networks (Simley & Jr Carsell, 2009), elevation (USGS, 2005a, 2012), and climate surfaces (Kriticos *et al*., 2012) have the potential to predict long-term hydrologic variation. On the ground and remotely sensed data shed light on land-cover types, and the degree of anthropogenic disturbance, which when paired with fine-scale applications of global circulation models (Kriticos *et al*., 2012) provide the opportunity to predict shifts in the broad-scale distribution of wetland types under future climates. Forecasted wetland distributions may be used to focus conservation efforts on maintaining wetlands where the climate is projected to threaten their existence and to facilitate wetland creation in areas where shifting hydrologic regimes necessitate flood mitigation.

We developed a system of geographically explicit models to evaluate the connection between climate and the distribution of two major wetland types (emergent and forested). These models represent the beginning of a process to further resolve wetland compositional differences on a landscape scale, because the emergent vs. forested wetland dichotomy represents one of the broadest scale distinctions between wetland vegetation types. Wetland type is primarily determined by the frequency and severity of flooding (Keddy, 2002). Emergent wetland communities are resilient to or even require frequent or persistent floods that occlude more competitive upland species (Keddy, 2002). Forested wetlands are characterized by low-frequency flooding, as woody species are generally less tolerant of prolonged inundation than herbaceous species (Toner & Keddy, 1997; De Jager *et al*., 2012; Deng *et al*., 2013). These ecosystems host fundamentally different communities and yield different goods and services (Weisberg *et al*., 2013).

In this study, we tested the hypothesis that wetland distribution remains associated with climate on a regional scale despite pervasive anthropogenic modification and we explored the implications of this association for projecting wetland area into the coming century. We tested the hypothesis that modeled wetland area would increase for the Midwest when climate change scenarios were applied, because of a predicted increase in flooding frequency/intensity on the regional scale [Strzepek *et al*., 1999; Wuebbles & Hayhoe, 2004; USGCRP (U.S. Global Change Research Program), 2009] would lead to net gains in wetland area. Finally, we explored the geographic distribution of forecasted changes in wetland area and we discuss the implications of such a model as a management tool for the region.

Materials and methods

Study area and datasets

The study area comprised the majority of the Midwest [as defined by the USGCRP (U.S. Global Change Research Program) (2009)], where wetland distributions were recorded by the USFWS (United States Fish & Wildlife Service) (2001). The inclusive study area comprises 960,000 km^2, 6.9% of which was classified as forested or shrub dominated wetlands and 1.9% as emergent marsh by the USFWS NWI. Freshwater ponds, lakes, and rivers, though considered wetlands by the NWI, were not included as predictor or response variables in the model described herein. This omission was made to isolate the role of climate on wetland formation, and to avoid generating a model that simply describes the hydrologic connectivity between emergent or forested wetlands with surrounding water bodies. Shapefiles from the NWI (USFWS (United States Fish & Wildlife Service), 2001) were compiled into a single geodatabase for the US states included in the study area. The NWI contains polygons designating the boundaries of wetlands throughout most US counties and provides broad and specific classifications. Broad classifications include forested/scrub-shrub, freshwater emergent, or ponds and rivers, while specific classifications indicate hydrogeomorphic type, substrate, and major vegetation classes (Cowardin *et al*., 1979). The state of Wisconsin wetland inventory followed a modified sampling protocol (Johnston & Meysembourg, 2002) and does not provide public access to the entirety of the wetland inventory for their state, and was therefore left out of the analysis (Fig. 1).

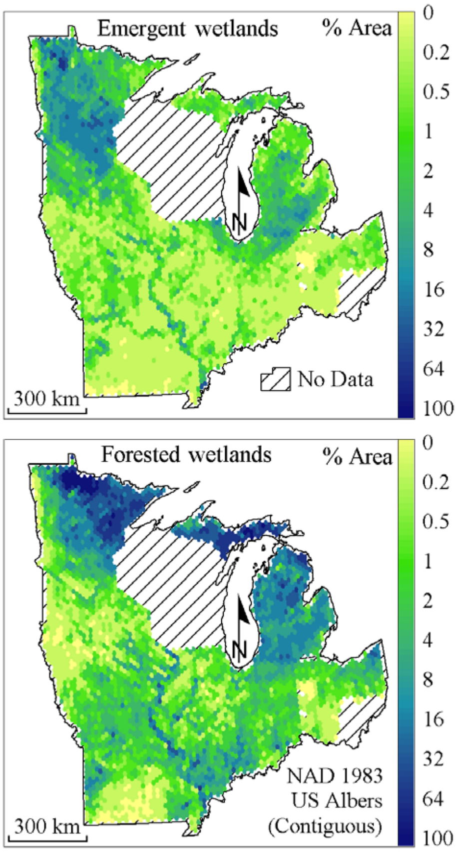

Fig. 1 Forested and emergent wetland types are represented as percent area within 260 km^2 hexagons (n = 4307). The National Wetland Inventory lacks publically accessible records for Wisconsin (upper middle) and for southeastern Ohio (lower right corner) and these regions were not included in the analysis. Hexagons expressing the maximum wetland area tend to be in the northern portions of the study area, or along major drainage basins. Moving northward through Minnesota and Michigan, freshwater emergent marshes become less prevalent as forested wetlands increase in area.

Bioclimatic surface layers were extracted from CliMond global climate products (Kriticos *et al*., 2012) representing current and projected conditions based on historic climate records and two Global Circulation Models from the IPCC 4th assessment (Solomon, 2007). These bioclimatic layers represent 35 variables that are nearly evenly distributed among metrics related to temperature, precipitation, solar radiation, and soil moisture (Table 1) and are intended to encapsulate components of climate that are most relevant to biological functions (Nix, 1986; Beaumont *et al*., 2005).

'Current' conditions represent climate summaries for the period 1975–1990 calculated from products in the WorldClim database (Hijmans *et al*., 2005) that were reformatted following the procedure outlined by Kriticos *et al.* (2012). Projected climate surfaces for 2100 were used [CSIRO Model for A1B and A2 emissions scenarios (Nakicenovic *et al*., 2000)] to develop climate differential surfaces (future conditions−current conditions) (Table 1) and to apply the model described below to predict wetland compositional shifts throughout the study area.

A series of additional pertinent datasets were also included in the models to quantify their relative impact on wetland area and to control for their effects when projecting future wetland distributions under different climate scenarios (Table 2). National Land-Cover classes (200 m resolution) were extracted from the 1992 database (USGS, 2005b) and included as model variables to account for landscape-level variation in major land uses and habitat types. The Global Human Footprint Index (Sanderson *et al*., 2002; WCS & CIESIN, 2005) was also included to quantify the degree of landscape-level habitat alteration directly related to anthropogenic factors. The Human Footprint Index indicates areas of human influence on ecosystems by combining anthropogenic land-cover types with human population, nighttime lighting, and transportation networks. Finally, components of elevation and hydrology were summarized from the National Elevation Dataset (100 m resolution)(USGS, 2012) and the US National Hydrography Dataset (Simley & Jr Carsell, 2009) to describe topographic variability and landscape position of each sampling unit.

Compatibility and data processing

All metrics were summarized using a grid of 260 km^2 hexagons distributed over the 960 000 km^2 study area (n = 3638). This method provided a consistent means of summarizing the above datasets using coincident points and represents a compromise among the spatial scales at which the component metrics vary. A hexagonal grid was used rather than the traditional square tiled grid to optimize visualization of connective elements at the landscape scale. As many wetlands in the study area follow linear features (streams, rivers, and pond fringes), the hexagonal grid was deemed a more appropriate technique for preserving these spatial relationships (Birch *et al*., 2007). The 260 km^2 hexagonal grid represents an upscaling of all component metrics to varying degrees based on the input data scale. All upscaling was performed after first projecting shapefiles (or rasters in the case of climate surfaces) using US Contiguous Albers Equal Area Conic projection.

Table 1 Climate variable descriptions (from Xu & Hutchinson, 2011) and means calculated for the inclusive study area (N = 3638). Current values represent means for the period 1970–1990, while A1B and A2 indicate the magnitude and direction of change under these IPCC emissions scenarios as calculated by from the WorldClim database (Hijmans *et al.*, 2005). Wet, dry, warm, or cold refer to values calculated for the wettest, driest, warmest, or coldest quarter (1/4) or week (1/52). Seasonality is represented as the coefficient of variation

Description	Current	A1B	A2
Temperature (°C)			
Annual (μ)	12.02	13	14.2
Diurnal Range (μ)	12.02	11.1	10.8
Isothermality	0.29	0.3	0.3
Seasonality	0.04	0	0
Max Warm 1/52	28.74	33.1	34.3
Min Cold 1/52	−12.54	−3.9	−2.7
Annual Range	41.29	37.1	37
Wet 1/4	18.93	19.5	19.9
Dry 1/4	−4.46	5.2	8.3
Warm 1/4	20.86	25.1	26.2
Cold 1/4	−5.03	1.4	3.1
Radiation (W m^{-2})			
Annual (μ)	133.6	133	132.9
Max 1/52	217	232.6	237.6
Min 1/52	51.6	44.7	42.8
Seasonality	0.43	0.5	0.5
Wet 1/4	196.6	194.3	193.2
Dry 1/4	72.05	78.8	85.8
Warm 1/4	202.8	210.4	212.2
Cold 1/4	68.5	57.4	55
Precipitation (mm)			
Annual (μ)	872.2	893.3	898.9
Wet 1/52	24.69	27.5	28.6
Dry 1/52	7.88	8.5	8.1
Seasonality	0.34	0.3	0.4
Wet 1/4	301.4	312.4	318.4
Dry 1/4	126	140.1	140.8
Warm 1/4	289.8	274	268.4
Cold 1/4	127.2	146.8	151.8
Soil Moisture Index			
Annual (μ)	0.84	0.8	0.8
Max 1/52	0.99	1	1
Min 1/52	0.62	0.5	0.4
Seasonality	0.14	0.2	0.3
Wet 1/4	0.96	1	1
Dry 1/4	0.67	0.5	0.5
Warm 1/4	0.69	0.6	0.5
Cold 1/4	0.9	0.9	0.9

Table 2 Variables summarizing landscape context calculated for the inclusive Midwestern United States (N = 3638). Descriptions for land-cover classes are truncated from the original 1992 published dataset (USGS, 2005b)

Category	Description	Mean
Land-Cover Class (% Area)	Urban	1.45
	Dry Cropland	38.43
	Crop/Grassland	15.45
	Crop/Woodland	17.98
	Grassland	0.3
	Savanna	0.54
	Deciduous Forest	13.57
	Evergreen Forest	0.76
	Mixed Forest	10.09
	Water Bodies	1.39
Human Footprint Index (0–100)	Mean	39.55
	Minimum	17.04
	Maximum	88.19
	SD	14.56
Elevation (m)	Mean	288.6
	Min	249.13
	Max	332.37
	SD	15.57
Hydrology (km)	Closest Major River	8.72

Wetland inventory data were summarized (upscaled) as the cumulative percent total acreage of each broad wetland class for each hexagonal sampling unit. Climate data (originally at a 30 s or 0.86 km^2 resolution) were standardized by averaging values for the inclusive area within hexagons. Proportional area for each land-cover class was recorded for hexagons as a measure of landscape-level coverage type and mean and coefficient of variation for the Human Footprint Index (originally 1 km resolution) were calculated. Finally, the distance to the nearest persistent river or coastline was calculated for each hexagon as a measure of broad-scale connectivity to these hydrographic networks. Rather than including all possible stream classes, which would overlap all hexagons, only major rivers were included as defined by the US National Hydrography Dataset (Simley & Jr Carsell, 2009). All hexagons that intersected a major river or a shoreline of one or more of the Great Lakes received a score of 0 for this metric.

Model development

Predictor and response metrics were first compiled into a single geodatabase. Partial Mantel tests (Smouse *et al.*, 1986; Fortin & Gurevitch, 2001) were used to determine whether the multivariate distance matrix for climate was significantly associated with that of wetland composition while controlling for space and contextual fixed factors (land cover, human footprint, distance to major rivers, and elevation). The partial Mantel tests performed here describe relationships between multivariate distance matrices rather than individual component variables and can have insufficient power if sample sizes are low or the spatial relationships being tested are complex (Fortin & Gurevitch, 2001). The sample sizes presented here were sufficient to resolve the complexity of the spatial relationships at the scale of the Midwest, but similar analyses for subsections of the study area may be prone to type II error. All distance matrices were generated using Bray–Curtis coefficients (Bray & Curtis, 1957) with the exception of location, which incorporated Euclidean coefficients.

A simple linear model incorporating all independent variables was inappropriate to make predictions due to severe predictor multicollinearity and the variety of distributions for predictor variable classes. Artificial Neural Networks (ANN) have been proposed as a means to circumvent these issues (Zhang *et al.*, 1998) to assess the relationships between individual predictors and responses (Lek & Guégan, 1999), though producing complex equations that obscure potentially useful mechanistic relationships. As a compromise, a linear model paired with collinearity reduction techniques was used to explore the strength and direction of relationships between predictor variables/classes and response variables, while an ANN-based model was applied to more reliably predict the effects of future climate scenarios. Similar approaches have been applied to understand and forecast long-term rainfall patterns (Mekanik *et al.*, 2013) and atmospheric ozone (Sousa *et al.*, 2007).

Linear model

Linear models were developed to describe the connection between climate variation and wetland prevalence and major vegetation types (forested vs. emergent). Two models were constructed using all 54 independent variables (Tables 1 and 2) to separately predict freshwater emergent wetland and forested/scrub-shrub percentages using the 'lm' function in R (R Core Team, 2013). Forward and reverse search functions were used to minimize Akaike Information Criterion (AIC) for each of the two models using the 'scale' function in R (Hastie & Pregibon, 1992; Venables & Ripley, 2002; R Core Team, 2013) and revised linear models were then generated using these variable subsets. Model residuals were tested for normality (Shapiro–Wilks test) and mapped to assess spatial patterns in model prediction error. Regional and local cluster analyses were conducted using Moran's I (Moran, 1950) and Anselin's Local Moran's I (Anselin, 1995), respectively, to assess the significance of spatial clustering of residuals, and identify localities with nonnormal residual distributions. Predictor variables were sequentially removed to reduce multicollinearity and generate coefficients for each variable whose signs and magnitudes could be interpreted. This was achieved through variance inflation factor (VIF) reduction, which was performed by constructing a model that incorporated all candidate predictor variables (post-AIC reduction) and recording VIF for each variable. The predictor variable with the largest VIF was removed from subsequent models and this process is iterated until all independent variables expressed a VIF <10 (Hair *et al.*, 1992). T-statistics were generated for each independent variable, assigning a magnitude, direction, and importance to each predictor-response pair.

Model coefficients were applied to climate projections for the year 2100 under the A2 SRES while holding all remaining factors constant. Model predictions for the current wetland distribution were subtracted from the 2100 projections to yield projected differences in wetland area. Modeled current conditions were used instead of observed current conditions to evaluate the degree of change projected by the model, independent of model bias. These differences were mapped to assess patterns in climate leveraging and cluster analyses were performed to delineate regions where wetland area is predicted to expand or contract.

Artificial neural network

An Artificial Neural Network (ANN) was constructed using the inclusive set of predictor variables derived from the AIC reduction technique applied for the linear models to predict the magnitude and spatial variation in potential wetland area for the Midwestern United States. Artificial Neural Networks are used primarily for pattern recognition in complex datasets where there are many predictor variables (Cheng & Titterington, 1994). The core topology of the Artificial Neural Network (hereafter called ANN Model, or simply ANN) consisted of a single layer of six hidden nodes calculated using the hyperbolic tangent activation function (Zhang *et al.*, 1998). Multilayer topologies did not perform appreciably better than a single-layer network, and these approaches were discarded in favor of the simplest model architecture. Gradient boosting was applied ($n = 7$ iterations yielding a total of 42 hidden nodes) to improve forecasting accuracy (Friedman, 2001) and the learning rate was set at 0.1 to reduce the likelihood of overfitting. A weighted decay function was incorporated into the model, as this approach is recommended to improve model performance and avoid overfitting when importance varies among predictor variables [SAS Institute Inc., Cary, NC, USA (2012)]. Model training was performed using 67% of the dataset, where the remaining data constituted a random holdback for model validation. Residual means were tested for significant deviation from zero (t-tests), as network construction does not constrain residuals to zero and directional bias in mean residuals can affect forecasting accuracy (Hyndman & Athanasopoulos, 2013). Diagnostic tests of the model residuals were performed as described for the linear models (above). Model coefficients were applied to climate projections for the year 2100 under the A2 SRES while holding all remaining factors constant.

This predictive framework isolates the modeled effects of climate on projected wetland area, but it is unrealistic to expect the constituent covariates to remain static. United Nations estimates project a 62% increase in the US population from the year 2000 to 2100 (United Nations, 2012). It is reasonable to assume that this will lead to an increase in the intensity of land use and human impact even if stringent sustainability measures and green technologies are implemented. In addition to the projections described above, the ANN model was applied to model projections for 2100 that, in addition to A2 climate projections, incorporated a 25% increase in the human footprint index and a 62% increase in urban and dry cropland (LCVR1 and LCVR2) cover classes (with concomitant and uniform decreases in remaining land-cover classes, so that land-cover totals were constrained at 100%). A 62% increase in both urban and dry cropland reflects a simplified land use scenario, where urban centers expand proportionally with population size and cropland area per capita is maintained at historical levels (but see Ramankutty *et al.*, 2002). A 25% increase in the human footprint index (paired with a 62% rise in population) reflects a 23% decrease in per capita human impact on the landscape scale that could be achieved through urban planning, development of green technologies and widespread efforts to recover ecosystem functions (Gaston, 2010).

Though analyses were primarily focused on the 2100 projected climate for the A2 SRES, the ANN model was also applied to the A1B SRES for comparison of the projected % change in wetland distributions for 2100.

Results

Mantel tests

A partial Mantel test (Smouse *et al.*, 1986; Fortin & Gurevitch, 2001) indicated that the (3638X3638) distance matrices generated for climate (35 variables) and wetland acreage (forested vs. emergent) were significantly associated (Mantel $r = 0.17$, $P = 0.001$, based on 999 permutations) when controlling for geographic distance among hexagon centers. A second partial Mantel test indicated that the distance matrix for wetland acreage (forested vs. emergent) was significantly associated with climate (35 variables) when controlling for an additional distance matrix comprising contextual fixed factors including geographic distance, land use, land cover, elevation, and distance to major tributaries (Mantel $r = 0.17$, $P = 0.001$, based on 999 permutations). Finally, a partial Mantel test indicated little association between environmental context and wetland area when controlling for climate at the 260 km^2 scale (Mantel $r = -0.05$, $P > 0.05$, based on 999 permutations).

Current conditions

The simultaneous forward and reverse step function successfully reduced AIC and the predictor dataset from 56 to 40 variables for emergent and 33 variables for forested wetlands. The resulting linear models were highly significant (emergent $F_{39,3598} = 128.3$, $P < 0.0001$, forested $F_{32,3605} = 320.7$, $P < 0.0001$), encapsulating a majority of the variation in wetland area for both habitat types at the 260 km^2 scale (emergent $R^2 = 0.58$, forested $R^2 = 0.74$). These models still incorporated variables with unacceptably high VIF scores (>10), indicating that though useful for prediction, individual variable coefficients are not interpretable (Table S1). Sequential variable removal for VIF reduction further limited the number of predictor variables to 19 for emergent and 17 for forested wetlands (emergent $R^2 = 0.47$, forested $R^2 = 0.57$)(Table 3).

The linear model identified a negative association between wetland area and isothermality that was highly significant ($P < 0.0001$) and independent of wetland type (Table 3). Isothermality represents thermal 'stability' or 'evenness' relative to annual variations in temperature (O'Donnell & Ignizio, 2012). Moisture index seasonality was identified as a key factor (based on coefficient magnitudes) distinguishing between emergent and forested wetland types where high values were associated with forested wetlands and low values were associated with emergent wetlands (Table 3).

The ANN model produced an overall generalized $R^2 = 0.96$, predicting a majority of the variability in emergent ($R^2 = 0.72$) and forested ($R^2 = 0.84$) wetland areas. The reported R^2 values represent the proportion of variation explained by the model for those data not included in the training set. Model projections incorporating increases in human footprint and land-cover change did not differ significantly from those of the A2 Scenario (emergent $t = -1.25$, $P = 0.2$, forested $t = 1.48$, $P = 0.1$)(not shown).

Residuals for the linear model differed significantly from zero ($\mu_{emergent} = 0.6$, $t = 13.5$, $P < 0.001$, $\mu_{forested} = -2.4$, $t = -17$, $P < 0.001$) indicating an overestimation of forested wetland area. Mean residuals for the Artificial Neural Network also differed significantly from zero ($\mu_{emergent} = -0.15$, $t = -4.3$, $P < 0.001$, $\mu_{forested} = -0.42$, $t = -5.2$, $P < 0.001$), but the effect size of the model bias was considerably smaller (<0.5%). Residual frequency distributions were all significantly nonnormal (Shapiro–Wilk $P < 0.001$) though the sample size ($n = 3638$) was sufficiently large to make normality testing oversensitive.

Model residuals were significantly spatially clustered ($P < 0.0001$), indicating regions of model over/underestimation (Fig. 2). The most striking and consistent model underestimations were for areas with atypically high proportions of wetlands. These included the Mississippi river, northern Minnesota, and central Michigan where the abundance of surface water from tributaries and lakes likely contributed to an increase in wetland area that was uncharacterized by the model variables.

Forecasted response to climate change

With the exception of linear model projections for emergent wetland area (one-sample $t = -0.09$, $P = 0.9$), all models forecasted significant increases in area conducive to emergent and forested wetland formation for the year 2100 (Fig. 3). Projected forested wetland area was 3.5% greater for the linear model than that of the ANN model, while the ANN model forecasted a 2% increase in emergent wetland area ($t = 9.3$, $P < 0.0001$) (Fig. 3a). The ANN model forecasted significant increases in both emergent and forested wetland area

Table 3 Linear model coefficients and significance following variable reduction to minimize AIC and to restrict all variables to VIF scores <10

	Emergent					Forested				
Variable	Est	StErr	t	VIF	Sig	Est	StErr	t	VIF	Sig
Intercept	14	0.7	21	NA	***	6.4	1.1	6	NA	***
Longitude	–					0	0	−1	7	
z (μ)	0	0	−3	3	***	–				
z (min)	–					0	0	2	3	
z (σ)	0	0	−7	2	***	0	0	−10	2	***
% Urban	0.7	0.1	5	1	***	−3	0.3	−11	1	***
% Dry Cropland	–					−2.9	0.1	−31	5	***
% Crop/Grassland	0.5	0.1	10	1	***	−2	0.1	−16	2	***
% Crop/Woodland	0.6	0	15	2	***	−2	0.1	−20	3	***
% Savanna	−0.7	0.4	−2	1		–				
% Decid. Forest	0.4	0	8	3	***	-2.2	0.1	−18	5	***
% Mixed Forest	0.1	0.1	2	2	*	–				
HF (max)	0	0	−8	2	***	0	0	2	2	
HF (σ)	0	0	6	2	***	0	0	−5	2	***
Isothermality	−10	1	−11	8	***	−28	1.7	−17	6	***
T Wet 1/4 (μ)	−0.1	0	−6	5	***	−0.2	0	−14	3	***
P wet 1/52	0	0	5	4	***	0	0	3	6	*
☼ Wet 1/4	0	0	8	6	***	–				
☼ Dry 1/4	0	0	2	3	*	0	0	−6	3	***
☼ Warm 1/4	0	0	−12	5	***	–				
Min 1/52 MI	−3.7	0.2	−16	4	***	–				
MI (CoV)	−3.9	0.5	−8	8	***	13.5	1	14	8	***
MI Warm 1/4 (μ)	–					6.2	0.4	16	2	***

Variable codes: z = elevation (m), % = percent land cover within sample units, HF = human footprint index (0–100), ☼ = radiation (W m-2), T = temperature (°C), P = precipitation (mm), MI = Moisture Index. Wet/dry/warm/cold refer to values calculated for the wettest/driest/warmest/coldest quarter (1/4) or week (1/52)
Significance codes: 0>'***' <0.001, 0.01> '*' <0.05 .

for the year 2100 under the A2 and A1B SRES (one-sample *t*-test, $P < 0.0001$) (Fig. 3b). The A1B Emissions Scenario (Nakicenovic *et al.*, 2000) yielded significantly greater increases in wetland area when compared to the A2 SRES for forested, but not emergent wetlands ($t_{\text{forested}} = 6.6$, $P < 0.0001$, $t_{\text{emergent}} = 1.87$, $P = 0.06$) (Fig. 3b). Further application of the ANN model predicted increases in wetland area when altering human impact and land-cover variables to reflect increases in anthropogenic land use. However, model projections incorporating increases in human footprint and land-cover change did not differ significantly from those without these alterations under the A2 SRES ($t_{\text{forested}} = 1.48$, $P = 0.1$, $t_{\text{emergent}} = -.25$, $P = 0.2$).

Though there was considerable agreement between the LM and ANN models in total wetland area changes for the study region, the linear models were considered less suitable for spatially explicit forecasting than the ANN model (owing to a greater dispersion of residuals, reduced percentage variance explained, and lack of robustness to multicollinearity). As a result, the spatial distributions of forecasted wetland changes for the ANN and LM approaches are not expressly compared, though linear model forecasts are provided in the supplementary material (Figure S1).

Artificial neural network model projections for 2100 (A2 SRES) were significantly spatially clustered (Moran's I $P < 0.001$) (Fig. 4) yielding increases in conditions conducive to wetland formation throughout the majority of the study area. Projected wetland area differences fell along a latitudinal gradient for the ANN model, with wetland losses occurring in the northernmost portions of the study area, and wetland gains occurring primarily in the south. The ANN model predicted declines in both emergent and forested wetland area for the Agassiz and Tamarack Basins as well of the central lakes wetland ecological units of Minnesota (MDNR, 1997) and Michigan's Upper Peninsula, where some of the region's largest peat-accumulating and mineral soil wetland complexes are found. These areas are also the least impacted by humanity in the Midwest

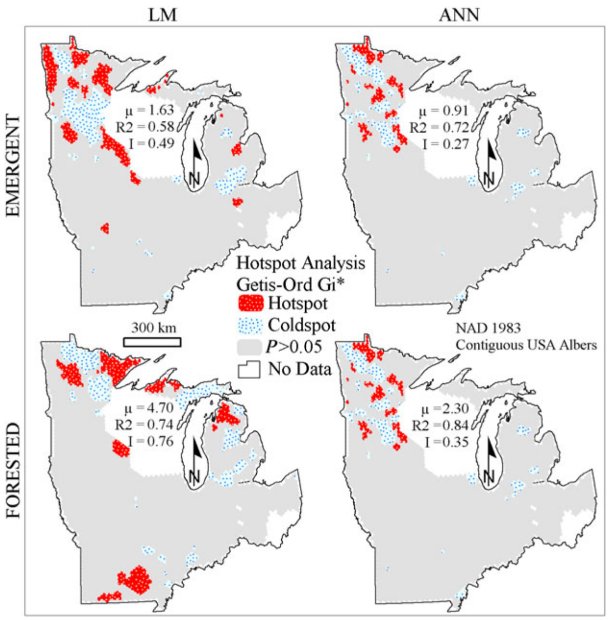

Fig. 2 Model residuals for linear models (LM)(Left) and the constructed Artificial Neural Network (ANN)(right) for both Emergent (top) and Forested (bottom) wetland habitat types. (μ) indicates the average deviation of model predictions from observed values (% area). Reported R2 values represent the proportion of variation in 2001 wetland areas explained by each model. Moran's I values are reported for global cluster analyses. Clustering of low and high values ($|Z| > 1.96$) are mapped using z-scores calculated for the Getis–Ord Gi* statistic (Getis & Ord, 2010). Hotspots and coldspots represent significant high/low-value clustering (Getis–Ord Gi* $|Z| > 1.96$), indicating model over/underestimation of current wetland area.

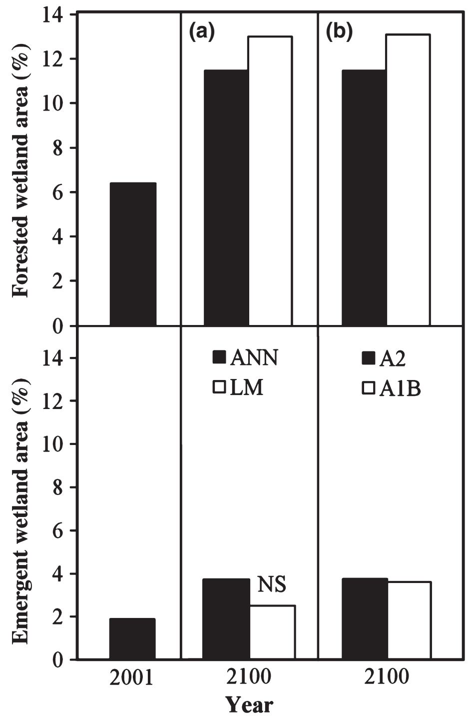

Fig. 3 Wetland % area forecasts for the year 2100. (a) Presents linear model (LM) and artificial neural network (ANN) projections for the CSIRO model of the A2 emissions scenario for the year 2100. (b) Presents a comparison of ANN model projections for the A2 and A1B emissions scenarios. NS indicates nonsignificance (two-tailed *t*-test, $P > 0.05$).

(Human Footprint Index = 19, vs. remainder of study area = 42).

Discussion

The observed associations between wetland area and climate were consistent with other geographic surveys that suggest climate plays a critical role in determining wetland distribution (Erwin, 2009). This indicates that even though human activity has converted a majority of wetlands in the Midwest for other purposes (Bridgham *et al.*, 2006), the prevalence of remaining habitat depends largely on climate and historic conditions.

Linear models identified climate factors that were associated with total wetland area and with the relative prevalence of major vegetation types. Isothermality, which represents the thermal 'stability' or 'evenness' of a region relative to annual variations in temperature (O'Donnell & Ignizio, 2012), exhibited a strong negative association with current wetland area. Isothermality likely affects wetland formation and maintenance indirectly by influencing seasonal hydrologic cycles. Seasonal flooding occurs as a result of spring snow melt in portions of the study area exhibiting low isothermality (particularly Minnesota and Michigan). This diurnal instability may lead to an increasing rate of snow melt in the spring, while increases in winter precipitation will produce larger daily runoff totals. Consequently, decreasing isothermality works in tandem with increasing winter precipitation to generate a more variable hydrograph with an increased frequency of soil saturation and/or inundation in northern portions of the study area.

Moisture index seasonality was identified as a key factor distinguishing between emergent and forested wetland types. Emergent wetlands were associated with water tables that were relatively constant through time (low values), while forested wetlands were associated with greater seasonal variation (high values). This model assembly reinforces the consensus that hydrology is a key determinant of wetland community composition (Mortsch, 1998; Keddy, 2002) and that the intensity/frequency of flooding determines not only whether a wetland exhibits woody or herbaceous vegetation (Toner & Keddy, 1997) but

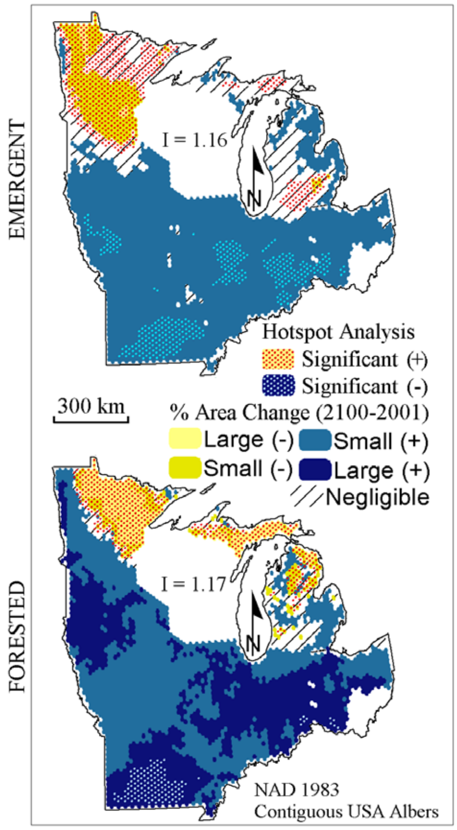

Fig. 4 Forecasted changes in wetland area for 2100 based on WorldClim CSIRO model of the A2 emissions scenario. Artificial Neural Network (ANN) forecasts are reported for both emergent (top) and forested (bottom) wetland types. Percent area change is represented as large (>10%), small (2–10%), or negligible (<2%). The reported hotspot analysis represents clustering of low and high differentials (points) using the Getis–Ord Gi* statistic ($|Z| > 1.96$). Significant low-value clustering indicates forecasted declines in wetland area, while significant high value clustering indicates future conditions conducive to wetland area expansion. Global Moran's I values are reported within the Wisconsin void.

also the relative prevalence of these habitat types on a regional scale as well.

Climate means never emerged as the best predictors of wetland area. Rather, climate extremes and measures of variability accounted for a greater proportion of variation in wetland area. This emphasizes an important and often overlooked distinction for wetland vegetation. Wetland plants are characterized by their tolerance of inundation (Menges & Waller, 1983; Blom & Voesenek, 1996; Jackson & Colmer, 2005; Luo *et al.*, 2008). Inundation functions more to restrict incursion of nonwetland species than to promote wetland species per se (Mitsch *et al.*, 2009). As a result, extremes in soil moisture likely indicate the restriction of upland species, where hydrophytes are capable of persisting. Soil moisture and precipitation means may be very similar for upland and wetland areas, but measures of variability or extremes encapsulate the frequency and intensity of this important source of stress. This highlights an historic overemphasis on climate means as drivers of ecological change as identified by Smith (2011) and supports explicitly addressing climate variability in both experimentation and modeling (*sensu* Thibault & Brown, 2008).

Model projections incorporating increases in human footprint and land-cover change did not differ significantly from those of the A2 SRES, indicating that the ANN Model construct did not heavily weight land cover or the human footprint index as wetland area predictors. This is likely due to the relatively coarse scale of observation (260 km^2) and pervasive land use in the region (Table 2) which may have yielded insufficient examples of unmodified landscapes – with the possible exception of the northernmost extents of Minnesota and Michigan. Projected wetland area increases should therefore be interpreted as increases in area conducive to wetland formation, which can alternatively be interpreted as an increased incidence of flooding or soil saturation within a predominantly agricultural landscape. A total of 38.43% of the Midwestern land surface was classified as unirrigated cropland as of 1992 (USGS, 2005b). The majority of this area is concentrated in the Corn Belt, a band stretching Northwest–Southeast which coincides with significant clusters of both forested and emergent wetland increases. This suggests, as predicted by Strzepek *et al.* (1999) and Rosenzweig *et al.* (2002, 2004), that crop production in the Corn Belt will be at an increased risk of waterlogging or flooding stress under a future climate (especially in the westernmost extent). This may be ameliorated somewhat by the concurrent predicted 175 km northeastern shift in the Corn Belt with increasing temperature (Newman, 1980). However, this shift may lead to an increase in economic demands to reclaim existing wetlands north of the existing Corn Belt for crop production. Hydrologic control will become more difficult within the current Corn Belt, requiring management strategies that account for increases in soil saturation and runoff on a landscape scale. Missouri and Iowa may well become hotspots of wetland restoration and construction, where runoff retention becomes a much needed ecosystem service that wetland creation/expansion can provide (Hey & Philippi, 1995) and the climate yields conditions that make wetland creation and maintenance less costly. It is also worth noting that as crop demands lead to intensification of land use on existing farms (Ramankutty *et al.*, 2002), repurposing of surrounding lands for wetland creation may not be considered tenable in the near term. Although regulations exist to protect existing wetland habitat (Lewis, 2001), increasing crop demands and losses due to flooding may put wetland conservation increasingly at odds with agriculture (*sensu* Lemly *et al.*, 2000). Regulators and managers will be required to take up strategic flexibility (Tietenberg, 2003) and coordination among jurisdictions on a regional scale to orchestrate wetland redistribution in a manner that is sustainable with respect to the prevailing climate while avoiding undue strain on agriculture. In addition, wetland area losses are projected for the northernmost portions of the study area as a function of climate change. In the absence of proactive management, the most valuable wetlands in terms of habitat connectivity, biodiversity, and carbon sequestration will be exchanged for recently created wetlands in a largely fragmented agricultural landscape.

Restoration and conservation of wetlands have not traditionally made explicit considerations for a changing climate on management practices (Erwin, 2009). These models, and others like them, can serve to help revise regional targets for wetland creation and mitigation, incorporating climate resiliency into plans to preserve wetland ecosystem services in the future. Moreover, wetland distribution modeling has the added benefit of identifying regions of future hydrologic instability and provides the opportunity to proactively avert losses in food production, infrastructure and human life by mitigating increasing flood severity before it is realized on a regional scale.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Linear Model forecasted changes in wetland area for 2100 based on WorldClim CSIRO model of the A2 emissions scenario. Linear models are reported for both emergent (top) and forested (bottom) wetland types. Percent area change is represented as large (>10%), small (2–10%), or negligible (<2%). The reported hotspot analysis represents clustering of low and high differentials (points) using the Getis–Ord Gi* statistic ($|Z| > 1.96$). Significant low-value clustering indicates forecasted declines in wetland area, while significant high value clustering indicates future conditions conducive to wetland area expansion. Global Moran's I values are reported within the Wisconsin void.
Table S1. AIC-reduced OLS model coefficients and significance following variable reduction to minimize AIC without VIF reduction (N = 3638).