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GIS-BASED ESTIMATES OF FORMER AND CURRENT DEPRESSIONAL WETLANDS IN AN AGRICULTURAL LANDSCAPE

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Abstract. Before European settlement, 23% of Illinois (3.2 million of 14 million ha) was covered by wetlands. It is estimated that 90% of those wetlands were lost during conversion of the landscape to agriculture and urban use. Champaign County was one of the most extensively drained counties in Illinois, with 39–60% of original county area estimated to have been drained. Current and future efforts to conserve and restore wetlands would benefit from information on the number and distribution of former wetlands. We used GIS to estimate the spatial extent, density, pattern, and sizes of former and extant depressional wetlands in Champaign County. We derived several models of former wetlands; all models used hydric soils but varied by using Digital Raster Graphics (DRG), 30-m Digital Elevation Models (DEM), or Digital Orthophotography Quarter Quadrangles (DOQ). We also combined the DRG and DEM models, and we conducted visual field surveys for saturated or ponded conditions to test the models. The DRG model was conservative: it identified fewer and larger wetlands than the DEM model (the DOQ model was judged inadequate). Depending on the model selected, we estimated that 1077–4090 depressional wetlands formerly existed in the county, and that 78.6–91.6% were drained, accounting for 1108–2777 ha of lost wetland habitat in Champaign County alone. Thus, depressional wetlands accounted for the vast majority of historical wetland loss and should be a priority for wetland restoration efforts. Spatial pattern among wetlands also changed: an organism adapted to the former landscape had >50% probability of reaching another wetland within 260 m: today that same species faces a 7.8% probability at that distance. The modern landscape of Champaign County (and others like it) poses potential risk for remaining wetland metapopulations, and GIS models of precise former wetlands locations can be a valuable initial tool for wetland conservation and restoration efforts.

Key words: agriculture landscape; depressional wetlands; Digital Elevation Model; Digital Orthophoto Quarter Quads; Digital Raster Graphics; GIS; Illinois (USA); isolated wetlands; metapopulations; temporary ponds; wetland loss.

INTRODUCTION

Before European settlement (hereafter ''settlement''), the Midwestern United States had ample wetland area. For example, 23% of Illinois (3.2 million ha) was covered in wetlands (Suloway and Hubbell 1994). While seasonally inundated landscape resisted European settlement, subsequent wetland drainage is well documented (Bogue 1951, 1959, McManis 1964, Winsor 1975, Herget 1978, Whitney 1984, Prince 1997, Vileisis 1997). As a result, only 3.5% (505 000 ha) of Illinois is now covered in wetlands, a loss of 90% of the number of the state's wetlands (Suloway and Hubbell 1994). Given the flat to gently rolling topography, many of the lost habitats may have been depressional wetlands.

Depressional wetlands

We define depressional wetlands as areas with hydric soils that occur in an area of lower elevation, surrounded by higher elevation, so that surface outflow is not sufficient to drain the area. A hydric soil is ''a soil formed under conditions of saturation, flooding, or ponding long enough during the growing season to develop anaerobic conditions in the upper part'' (Hurt et al. 2003).

Depressional wetlands provide ''ecosystem services,'' by contributing to species diversity and genetic diversity in a landscape (Semlitsch and Bodie 1998). The loss or alteration of isolated wetlands can reduce the number of sites at which some species can reproduce and recruit juveniles and increase the distance between neighboring wetlands, so that extirpated populations are less likely to be renewed by a neighboring source population (Semlitsch and Bodie 1998).

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The lack of exact locations of former wetlands means that attempts to restore wetlands in the now-agricultural landscape must operate without knowledge of presettlement conditions. Original land survey and drainage district data may provide some records of former wetland locations, but are not readily accessible to planners and are not clearly uniform or wholly intact. We address this deficiency by developing a reliable model of former depressional wetlands in a heavily drained county of Illinois, based on a Geographic Information System (GIS). Specifically, we use GIS and field verification to estimate the spatial extent, density, pattern, and sizes of former and extant depressional wetlands in Champaign County, Illinois, USA. In addition, we evaluate several forms of GIS data for accuracy by comparing model results to field observations.

METHODS

Study area

We focused on Champaign County, Illinois (Appendix A), as it was one of the most extensively drained counties in the state. It is estimated that 40–61% of the county was once covered by wetlands; today that number has dropped to 0.9%. This transition represents a conversion of 39–60% of the original county area and a loss of 98% of the historical wetlands in the county (Suloway and Hubbell 1994).

We developed three models, using different publicly available data sets, to depict the locations of former depressional wetlands. Digital Raster Graphics (DRG), Digital Elevation Models (DEM), and Digital Orthophotography Quarter Quadrangles (DOQ) were each overlaid with digital hydric soils to develop a model of former depressional wetlands. Current depressional wetlands were also modeled for comparison, and all four models were tested by visual observation of sites. Finally, a combination of the DRG and DEM models was derived.

Hydric soils

Detailed digital soils for the county were obtained from the U.S. Department of Agriculture (USDA), Natural Resource Conservation Service (NRCS) Soil Survey Geographic Database (SSURGO). Hydric soils and soils with hydric inclusions were both used in the analyses. Hydric soils covered 48.6% of the county, and both soil types covered 92.3% of the area in Champaign County (Appendix B). We used both soil types because hydric inclusions commonly occur in moderately well drained and somewhat poorly drained soils, are often found in depressions or along drainage ways (Natural Resources Conservation Service 2003, *available online*)[4] and were intermingled with hydric soils in Champaign County.

[4] ⟨http://www.ct.nrcs.usda.gov/hydric-windham.html⟩

Digital raster graphic (DRG) model

The DRG data set is a digital version of the U.S. Geological Survey 7.5′ topographic maps (ISGS 1997). The paper maps from which the digital versions were created ranged in date from 1960 to 1975. To create the DRG model, all of the depressions shown on the county digital topographic map were digitized into polygons and overlaid with the hydric soils. Depressions that intersected hydric soils were selected to create the DRG model for former depressional wetlands. It should be noted that highway borrow pits with angular shapes and roadside locations were excluded from this model a posteriori, based on the assumption that they did not represent former depressional wetlands.

Digital elevation model (DEM) model

During development, DEMs are categorized as Level 1 and Level 2, where Level 2 models attain better quality of data (U.S. Geological Survey [USGS] 1998). Digital elevation models are developed from digital topographic maps (DRGs); ideally, a model of depressional wetlands based on Level 2 DEM data should match the corresponding model based on DRG data, given that DEMs are derived from DRGs. Champaign County DEMs were acquired as Level 2 models with 30-m resolution (i.e., each grid represents a 30 × 30 m area), and were developed in two ways. One portion of the county was developed from 10-m resolution grids that were extrapolated to 30-m resolution (D. Luman, *personal communication*). In principle, the DEMs derived as 10-m resolution grids should be more accurate than those based as 30-m grids, even after conversion to a uniform, 30-m resolution. DEMs of low-relief terrain, as is present in Champaign County, are generated from maps with contour intervals of 3.048 m or less, and the vertical accuracy is equal to or better than 15 m (USGS 1993).

Depressions in elevation were found using the SINKS command in ARC/INFO (Environmental Systems Research Institute [ESRI], Redlands, California, USA). A sink is defined as an endorheic cell or a depression in elevation into which water can flow but which has no outflow (ESRI 2001), and is fully consistent with our definition of a depressional wetland. The SINKS command is typically used to remove depressions in watershed and stream network calculations to ensure proper drainage mapping (ESRI 1996). The NRCS digital soils survey was intersected with the sinks, and the combined sinks and hydric areas were selected to produce the DEM model of former depressional wetlands.

The procedure described above has two potential errors. Current elevations (per USGS DEM [USGS 1998]) could miss some presettlement wetlands due to subsequent, unknown filling of depressions, and results in an underestimate of former depressional wetlands. Conversely, if some constructed stream channels (e.g., ditches, swales) include elevational depressions that did not exist in presettlement times, the method would produce an overestimate. The first potential error cannot be corrected, but is of less concern because it contributes to a conservative estimate. The second potential error can be partially corrected by removing polygons that intersect with streams. Sinks that intersected streams or a buffer equivalent to their horizontal accuracy in the DEM data (streams coverage for Illinois is 1:100 000 with a horizontal accuracy of 50.9 m) were removed and not considered as former depressional wetlands.

Digital orthophotography quarter quadrangles (DOQ) model

The DOQ data layer is aerial photography (the majority of the photos were taken in March and April of 1998, 1999, and 2000, before crops mask bare soils) that has been rectified and georeferenced to produce digital raster images for use in remote sensing and GIS (USGS 2000). This imagery was used to identify areas in which the soil appeared to be darker than the surrounding soils. These subjectively identified ''wet areas'' were marked with a central point in the GIS and overlaid with the hydric soils. Points that intersected hydric soils were selected to become the DOQ model of the former depressional wetlands.

Combined models

We combined the DRG and DEM models, because both models had high accuracy rates in the field but low overlap (see Results below). To combine models, we identified wetlands with each model, excluded the DEM wetlands that overlapped with DRG wetlands, to avoid double counting. DEM overlapping wetlands were removed because the DRG areas tended to be more representative of actual shapes that appeared in the landscape.

Current depressional wetlands

Extant depressional wetlands were identified with the DRG, DEM, and combined models, overlaid with the National Wetlands Inventory (NWI) data layer for Champaign County (U.S. Fish and Wildlife Service et al. 1996). This model yielded an estimate of presettlement depressional wetlands that had persisted through the intensive landscape changes of the settlement period. NWI in Illinois was created from 1:58 000 color infrared photographs taken from 1980 to 1987. Though NWI data were not expected to serve as a perfect reference for comparison to the other models, NWI was the only other resource available for an entire county. In addition, palustrine wetlands identified in the NWI corresponded closely to the Wisconsin Wetlands Inventory (Johnston and Meysembourg 2002).

Field testing of GIS models

The DRG, DEM, and DOQ models were tested by observing sites following precipitation events, where saturated soils and/or standing water without apparent drainage (e.g., ditches, swales) were considered positive evidence for a former depressional wetland (Appendix C). Only potential wetlands that were observable from roads were visually evaluated. A total of 219 sites distributed along >200 km of Champaign County roads were judged over three years and after six separate rain events.

Statistical analyses

The GIS-based models yielded data on the density, sizes, and spatial configuration of former and current depressional wetlands. The distance between wetlands was analyzed by nearest neighbor analyses to consider the potential effects of large-scale drainage on metapopulation dynamics of wetland-dependent species. The spatial distribution of wetland sizes (ha) was analyzed with the expectation that wetland size distribution is important for regional biodiversity of wetland-dependent species. Based on model results, we analyzed spatial patterns for the DRG, DEM, and combined (DRG + DEM) models only. Spatial statistics were calculated using CrimeStat 2.0 (Ned Levine and Associates, Houston, Texas, USA).

Nearest neighbor distances were found using the ARC/INFO POINTDISTANCE command, where each polygon in the former and current depressional wetlands models was assigned a label point at the center of the polygon and the distance was found from each polygon center to its nearest neighbor. Polygon centers were used because depressional wetlands are typically seasonal, and boundaries change depending on hydrology. A nearest neighbor index (NNI) was calculated for both former and current models, where NNI = (average nearest neighbor distance between wetlands)/(expected random distance). Nearest neighbor distances were adjusted to account for edge effects in the rectangular Champaign County: if a wetland was closer to the border than to a measured nearest neighbor distance, then the distance to the border was used as the adjusted nearest neighbor distance. This may underestimate the distances for edge wetlands but we feel this is minimal in a large dataset. Frequency distributions of nearest neighbor distances were also computed to compare former and current landscapes.

Wetland areas of former and current landscapes were analyzed by: frequency distributions; global Moran's I, for which a value significantly greater than the randomly expected $I = 0.0$ indicates wetlands were spatially autocorrelated (clustered); and Geary's C, for which a value significantly less than the randomly expected $C = 1.0$ indicates wetlands were clustered. Moran's I ranges from -1 to $+1$ and measures covariation among different geographic points, similar to a product moment correlation coefficient. The alternative, Geary's C, is based on paired comparisons between different point locations and can range from 0 to 2 (in the program CrimeStat 2.0). Observed values were sta-

TABLE 1. GIS-based model results of former and current depressional wetlands in Champaign County, Illinois, USA.

	Former landscape		Current landscape		Former − current (difference)		Former − current (difference, %)		Estimated annual loss†	
Model	No. sites	Area (ha)	No. sites	Area (ha)	No. sites	Area (ha)	No. sites	Area (ha)	No. sites	Area (ha)
DRG	1077	1108	231	284	846	824	78.6	74.4	8.5	8.2
DEM	3401	1884	125	107	3276	1777	96.3	94.3	32.8	17.8
Combined‡	4524	2870	335	336	4189	2504	92.6	87.2	41.9	25.0
DOQ§	4779		141		4638		97.0		46.4	

Notes: Model abbreviations stand for Digital Raster Graphics (DRG), Digital Elevation Models (DEM), DRG + DEM (Combined), and Digital Orthophotography Quarter Quadrangles (DOQ). Estimated numbers of wetlands and areas are based on field-verification accuracy rates of each model (DRG, 95%; DEM, 89%; DOQ, 44%), and the net (91.5%) accuracy of the combined (DRG + DEM) model.

† Estimated annual loss assumes a 100-yr (1850–1950) interval.

‡ The combined model excluded the slight (11.3% of DEM sites) overlap between the DRG and DEM models, but we considered it likely that the combined model provides an overestimate due to features of the DEM data (see *Results* for further details).

§ Wetland areas were not estimated by the DOQ model.

tistically tested against random expectations by *Z* tests; Moran's *I* and Geary's *C* tests were adjusted for small distances to prevent excessively large values for nearby wetlands: therefore, analyses are conservative. In addition, local Moran's I statistics for former and current wetland areas were calculated and mapped across the county to evaluate the changes in spatial patterning of wetland sizes.

RESULTS

Of the three models tested (DRG, DEM, DOQ), the DRG-based model was found to be conservative but the most reliable: 95% of the depressional wetlands predicted to exist by the DRG model were observed in the field tests (Table 1). Therefore, elevational depressions in hydric soils continue to correspond well with original topographic mapping surveys. This model was conservative, in that DRG-predicted wetlands were larger (average = 1.03 ± 2.02 ha [mean ± SD]) and fewer than those detected in the DEM-based model (average = 0.55 ± 1.57 ha). After accounting for field-testing accuracy, the DRG-based model identified 1077 wetlands covering 1108 ha (Fig. 1), which was less than the other models (Table 1).

Despite being ostensibly based on DRG data, the DEM model predictions did not match those of the DRG model: only 11.4% of former depressional wetlands identified by the DEM model overlapped with DRG-identified depressional wetlands (Table 1). We found the DEM model to be 89% accurate in the field, yielding 3401 former depressional wetlands covering 1884 ha (Fig. 2). Thus, many potential wetlands were identified with the DEM model that were not identified with the DRG model. Since many of these wetlands were smaller than those identified with the DRG model, the SINKS command in ARC/INFO appeared to be more sensitive in detecting depressions than original topographic surveys. This was borne out by our difficulty in visually detecting many of the DEM-based depressions during field testing: we found the DEM depressions were less obvious than those identified by the DRG model. An important clue about the DEM model is revealed in Fig. 2, which shows the portions of the county modeled with 30-m resolution vs. 10-m resolution that was converted to 30-m resolution during DEM production. The 30-m resolution portions typically have greater density of depressional wetlands, suggesting a number of false positives. Thus, the DEM model identified three-fold more depressional wetlands than the DRG model, but had a slightly lower field-testing accuracy rate because in the 30-m resolution parts of the county, it did not correspond well with the DRG model.

Because both models appeared fairly accurate but different, we also developed a combined (DRG and DEM) model. This combined model (with a net field accuracy of 91.5%) estimated 4524 former depressional wetlands (2870 total ha) in Champaign County (Table 1).

The DOQ model was based on ''wet areas'' identified in aerial photographs, and it produced several thousand more wetlands than the other models (Table 1). However, field testing revealed a low accuracy rate (44.2%), and we did not include the results of this model in further analyses.

Current depressional wetlands were identified with each of the DRG, DEM, and combined models and National Wetlands Inventory data (Table 1). Only 231 current depressional wetlands were estimated in Champaign County by the DRG model (Fig. 1); the DEM and combined models bracketed this number (Table 1). Depending on the model, 79–96% of the former depressional wetlands have been lost, accounting for 74–94% loss of depressional wetland area (Table 1).

The loss of so many wetlands shifted the spatial distributions over time, so that average nearest neighbor distances (center to center) were increased two- to threefold, depending on the model (Table 2). However, nearest neighbor index values remained significantly different from random, indicating that current wetlands continue to retain some clustering within the county

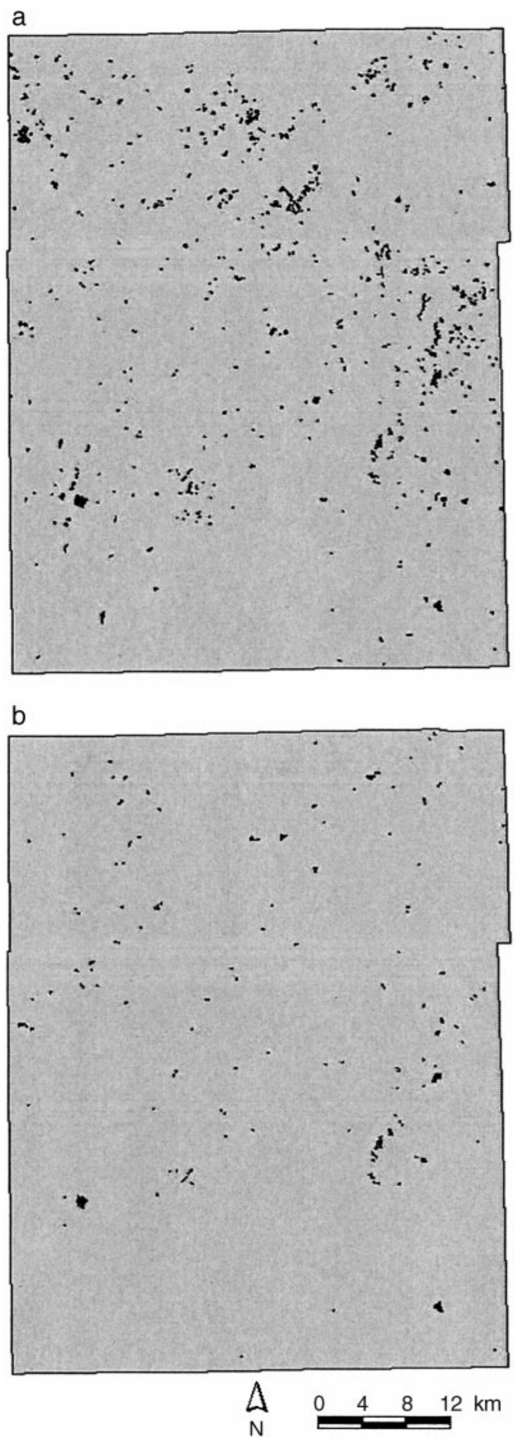

FIG. 1. (a) DRG (Digital Raster Graphics) model of former depressional wetlands and (b) DRG model of current depressional wetlands within Champaign County, Illinois, USA.

(Table 2). Because the GIS models provide precise locations, the details of drainage-driven spatial distributions can be considered. For example, if the former and current nearest neighbor distances of the DRG model are expressed as a percentage of the former distribution, the relative isolation of current wetlands is apparent (Fig. 3). Fifty percent of the former nearest neighbor distances (center to center) occurred within 259 m: today only 7.8% of current wetlands occur within that distance. In other words, organisms adapted to disperse among wetlands of the former landscape had >50% chance of locating another wetland if they could travel 260 m. Note that our estimate is conservative: edge-to-edge dispersal distances would be smaller and so encounter probabilities would be greater. Similar results were obtained with the DEM model.

Spatial structure of former depressional wetlands depended on both the model and statistic considered (Table 2). Wetland areas of the former landscape in the DRG model were significantly clustered according to Moran's *I*, but that spatial structure (clustering of wetland sizes) was lost after drainage. The DEM model (with its apparent false positives) did not detect such a change in spatial structure as measured by Moran's *I*, and the combination (DRG + DEM) model was a compromise between the two (Table 2). By contrast, Geary's *C* uniformly indicated significant spatial structure for all models, suggesting that it was insensitive to the substantial landscape change that has occurred. Thus, the global spatial autocorrelation statistic Moran's *I* indicated a homogenization of spatial pattern in wetland sizes for the DRG model, and this trend is supported by maps of local Moran's *I* values in former and current Champaign County (Fig. 4). Though some spatial pattern in wetland sizes remains, much of the pattern has been lost, and current pattern seems to depend on chance co-occurrence of a few, similar-sized, isolated wetlands.

DISCUSSION

We found that GIS-based models can accurately predict former and current depressional wetlands, if DRG or DEM models are applied. These two GIS-based models may be complementary and when combined may yield an accurate model with the advantages of both models. The resulting estimates of former depressional wetland locations, including distance and size distributions, yield more precise estimates of net loss than previously possible (Dahl 1990, Suloway and Hubbell 1994). However those wishing to apply this approach to other regions must be careful to understand the GIS data being used and the assumptions that necessarily ensue. Also, GIS estimates of former depressional wetland locations should be followed by detailed field investigations.

Earlier estimates of wetland loss based on soil types and historical data (Dahl 1990, Suloway and Hubbell 1994) report only total area lost. Our GIS-based ap-

TABLE 2. Spatial statistics of former and current depressional wetlands in Champaign County, Illinois, USA.

Model	Nearest neighbor index	Distance			Global Moran's I	
		Mean ± SD (m)	Z	P	I (area)	Spatially random I ± SD
Digital Raster Graphics (DRG)						
Former landscape	0.5922	442.2 ± 514.7	−26.27	0.0001	0.0047	−0.0009 ± 0.0014
Current landscape	0.5442	878.0 ± 1080.0	−13.59	0.0001	0.0063	−0.0041 ± 0.0074
Digital Elevation Model (DEM)						
Former landscape	0.7849	323.4 ± 261.9	−25.44	0.0001	0.00001	−0.0003 ± 0.0004
Current landscape	0.5613	1162.2 ± 1522.4	−9.97	0.0001	−0.0118	−0.0071 ± 0.0128
Combined (DRG + DEM)						
Former landscape	0.7928	300.5 ± 227.0	−26.66	0.0001	0.0016	−0.0002 ± 0.0008
Current landscape	0.5886	807.9 ± 1009.0	−14.40	0.0001	0.0302	−0.0030 ± 0.0177

FIG. 2. DEM (Digital Elevation Model) model of former depressional wetlands within Champaign County, Illinois, USA. Delineated portions of the county include 10-m resolution converted to 30-m resolution (light gray) and 30-m resolution DEM data (dark gray).

TABLE 2. Extended.

Moran's *I*		Geary's *C*			
Z	*P*	*C* (area)	Spatially random $C \pm$ SD	*Z*	*P*
3.88	0.0001	0.9444	1.0000 ± 0.0071	−7.83	<0.0001
1.50	0.067	0.8200	1.0000 ± 0.0212	−8.47	<0.0001
0.76	0.22	0.8430	1.000 ± 0.0039	−39.80	<0.0001
−0.38	0.36	0.9346	1.000 ± 0.0262	−2.50	0.006
2.52	0.0059	0.8723	1.0000 ± 0.0041	−30.79	<0.0001
1.87	0.0307	0.6772	1.0000 ± 0.0357	−9.05	<0.0001

proach yields overall estimates consistent with the estimate of Suloway and Hubbell (1994) and enables estimates of the numbers, spatial extent, and locations of depressional wetlands under both current and former landscapes. Such information is valuable for wetland conservation and restoration efforts.

Efforts to mitigate further wetland losses have been recently criticized (National Research Council 2001). Some wetland mitigation planning efforts may be improved by identifying and selecting former wetland sites which are far more likely to function properly when restored than a site without natural wetland geomorphology and soils. If planned at the landscape scale, wetland mitigation efforts could also replicate natural spatial configurations. Assuming metapopulation and metacommunity dynamics (Hanski 1999) are important for wetland biodiversity, wetland restoration that is consistent with historical landscape patterns should better fulfill wildlife habitat functions. For example, an appropriately patterned cluster of wetlands is more likely to enable a viable amphibian metapopulation than an isolated site.

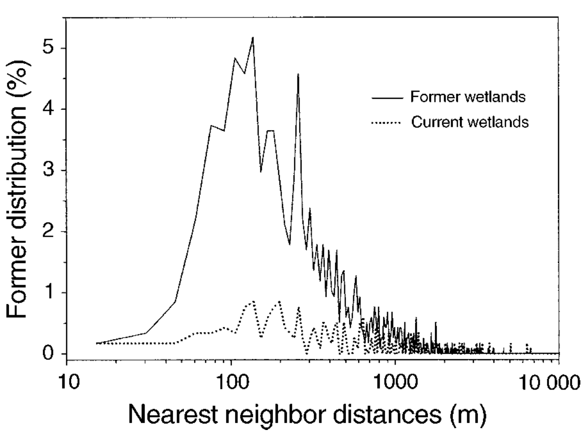

FIG. 3. Nearest-neighbor frequency distribution for the DRG model. Drainage of the prairie severely affected distances between depressional wetlands, which in turn probably affects metapopulation dynamics for extant wetland-dependent organisms. Note that the distance axis is log transformed.

Metapopulation and metacommunity dynamics among central Illinois wetlands evolved in a landscape that has since been largely replaced with row crops: the effects of this thorough and rapid change (approximately 100 years) on relict wetland-dependent systems must be part of the context for understanding more basic ecology. For example, according to our results (Fig. 3), organisms adapted to disperse among wetlands of the former landscape had >50% chance of locating another wetland if they could travel 260 m. Assuming that organisms have not yet fully adapted to the modern landscape, those same species have severely limited metapopulation dynamics today.

The approach we employed and its results are relevant to spatial ecology, including studies of metapopulation, metacommunity, and metaecosystem ecology (Wilson 1992, Hanski 1999, Loreau et al. 2003), dispersal kernels (Clark et al. 1999, Nathan and Müller-Landau 2000), and the effects of wetland loss and fragmentation on freshwater biodiversity (Wilcove et al. 1993, Ricciardi and Rasmussen 1999, Gibbs 2000, Jenkins et al. 2003). Spatial ecology often focuses on extant (e.g., Hanski et al. 1995) or interconnected habitats (e.g., Cottenie et al. 2003): the landscape of nonconnected depressional wetlands offers a different system in which to study spatial ecology, and should yield valuable insights in comparison to other landscapes.

Differences and combinations among models

We found that some publicly available GIS data sets are better suited than others to the identification of former or current depressional wetlands. We discarded our DOQ-based model due to the subjective nature of choosing a ''wet area'' from aerial photography. This experience may serve as a caution to others interested in applying aerial photography (and digital versions; DOQs) to wetland identification and delineation in regions with relatively low topographic relief and loess soils (often hydric).

Digital elevation models (DEMs) are created from topographic maps, but our models based on digital topographic maps (DRG) and DEMs did not coincide.

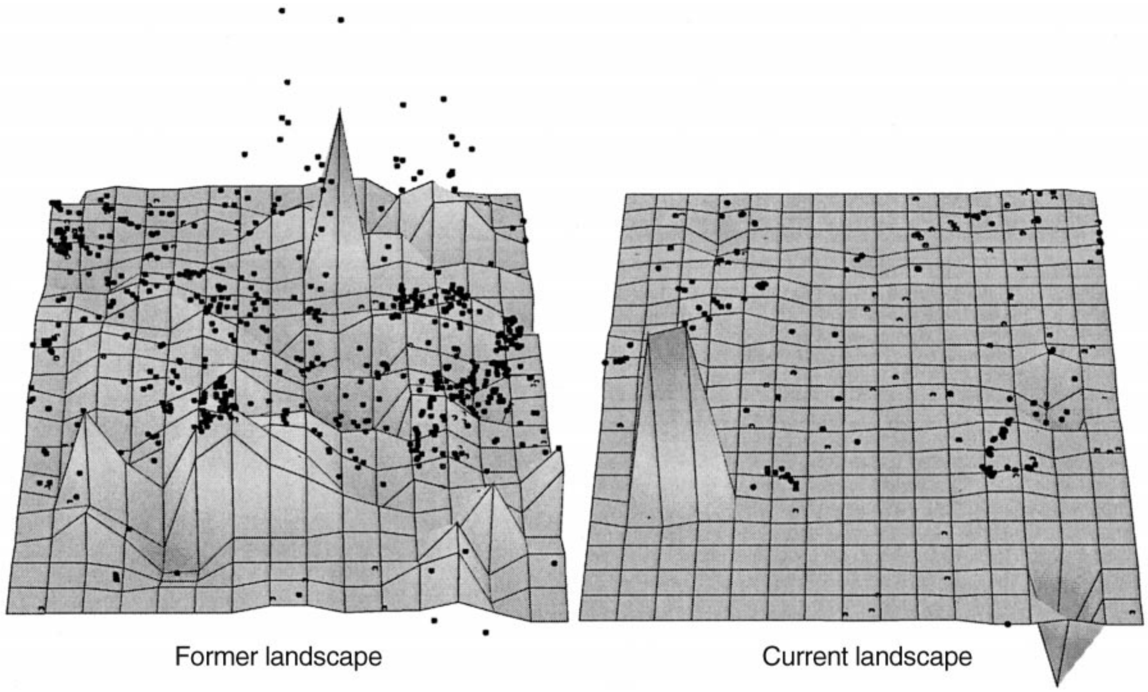

FIG. 4. Local Moran's *I* statistics, mapped across Champaign County, Illinois, for both the former and current landscapes, according to the DRG model. Both surface texture and shading are used to demonstrate smoothed values of local Moran's *I* statistics; black dots represent the position (*x* and *y* coordinates) and local Moran's *I* (*z* coordinate) of each wetland. Positive spatial autocorrelation indicates that wetland areas are similar, and negative spatial autocorrelation indicates that wetland areas differ. Each grid represents Champaign County, looking north.

The DRG model was most accurate, but it conservatively estimated the number and sizes of former depressional wetlands. Depressions shown on topographic maps and therefore digitized for the DRG model tended to be larger, more distinct depressions: the more subtle, smaller depressions were often not mapped, similar to approaches employed in mapping ephemeral streams (Mark 1983). Conversely, the DEM model identified many more and smaller wetlands, but was slightly less accurate. The lower accuracy rate of the DEM model could be due to several factors, including two different methods originally used to create the DEM data, with different underlying accuracies and the low topographic relief in the study area. Finer resolution data (10 m) identified fewer wetlands, indicating that the 30-m resolution basis generated false positives. Others attempting a similar approach should attempt to obtain 10-m resolution data; otherwise, models may be slightly generous in the numbers of wetlands identified. Also, the DEM model tended to have greater accuracy in areas of the county with greater topographic relief. It is likely that other regions with greater topographic relief will be modeled with even greater accuracy than that obtained in this effort.

For these reasons, we expect that the actual number of former, current, and lost depressional wetlands are intermediate between the estimates generated by the DRG and combined models. Also, the near concordance of our loss estimates with Suloway and Hubbell's (1994) estimate of 90% loss of wetland area for the state indicates that most wetlands lost were depressional wetlands. Finally, our estimates suggest that wetland restoration efforts in the region should focus on restoring depressional (often ephemeral) wetlands, rather than generating permanent water bodies.

Conservation applications

The spatial pattern of depressional wetlands in the former and current landscapes of Champaign County, Illinois may be instructive for conservation efforts of wetland species, based on three assumptions. First, Willman and Frye (1970) argued that the topography of Illinois existed essentially intact since the end of the Pleistocene glaciation, given that vegetation soon stabilized the soils. If so, then we can assume that the spatial array of depressional wetlands existed circa 10 000–12 000 years before settlement. Second, let us assume that organisms inhabiting depressional wetlands were adapted to conditions of those wetlands, including the ability to disperse requisite distances among wetlands for long-term persistence. Third, let us assume that the human transformation of the landscape was too rapid (circa 100 years) for substantial adaptation to changed dispersal distances (and intervening obstacles such as roads) to occur.

Given these assumptions, organisms adapted to the former landscape face a dramatically different dispersal regime in the current landscape. Modern dispersal distances may be very improbable for some species, which may then bear an extinction debt (Tilman et al. 1994, Jenkins et al. 2003) as isolated populations dwindle. For conservation purposes, it becomes essential to learn the typical dispersal distributions of focal species, and to plan for preservation or restoration of multiple wetlands within those distance limits. This strategy prescribes a different approach than preservation of individual habitats with little value assigned to the proximity of other such habitats. An improved strategy would seek to preserve or restore complexes or neighborhoods of depressional wetlands, consistent with former wetland distributions. For example, Johnson and Semlitsch (2003) observed *Hyla versicolor* adults dispersing 200 m during a breeding season. If a goal for a wetland was to restore a declining *H. versicolor* population, a wetland planner may seek to restore former wetlands (and their terrestrial buffers) within 200 m of the declining population to support metapopulation dynamics.

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APPENDIX A

A map showing the location of Champaign County, Illinois, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* A015-033-A1.

APPENDIX B

A diagram showing hydric soils and including solid with hydric inclusions is available in ESA's Electronic Data Archive: *Ecological Archives* A015-033-A2.

APPENDIX C

Photographs of typical sites identified as former depressional wetlands and visually verified in the field are available in ESA's Electronic Data Archive: *Ecological Archives* A015-033-A3.