
Consequences of Prairie Wetland Drainage for Crustacean Biodiversity and Metapopulations

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Abstract: *Much of Illinois was once wet prairie, dotted with ancient (ca. 10,000-year-old) ephemeral wetlands. Most wetland habitat (85%) was converted to agriculture over a span of about 100 years (ca. 1850-1950). The consequences of this severe habitat fragmentation on wetland communities and metapopulations are unknown. We studied crustacean communities (weekly stovepipe samples throughout hydroperiods) for 3 years in a set of extant ephemeral wetlands in Illinois. We generated species-sites curves by rarefaction and extrapolated those curves to conservatively estimate that 83-85 crustacean species may have inhabited approximately 4 million ephemeral wetlands that once existed in Illinois; 8-9 crustacean species were driven to extinction in Illinois during drainage; and 75-76 crustacean species are extant in the few remaining ephemeral wetlands of Illinois. We also conducted cellular automata simulations to examine the potential effects of habitat fragmentation on the genetic structure of extant crustacean metapopulation. Simulations indicated that conversion of the former wet prairie to agriculture may have reduced crustacean metapopulations to isolated populations that are more vulnerable to future habitat loss. Despite severe habitat fragmentation, curvilinear species-sites relationships suggest that the greatest extinction rates have yet to occur for ephemeral wetland crustaceans. However, selection for limited dispersal during habitat fragmentation may contribute to extinction debt for extant species. Conservation programs can preserve much of the historical biodiversity of ephemeral wetlands, but future wetland biodiversity will depend heavily on the success of those efforts. The consequences of historical wetland loss and the importance of wetland conservation efforts to agriculture in the United States should be instructive for other regions.*

Consecuencias del Drenado de Praderas de Humedales para la Biodiversidad y Metapoblaciones de Crustáceos

Resumen: *Una gran parte de Illinois fue una vez una pradera húmeda, dotada de antiguos humedales efímeros (ca. 10,000 años de edad). La mayoría del hábitat de humedal (~85%) fue convertido en tierras de agricultura en un tiempo aproximado de 100 años (ca. 1850-1950). Las consecuencias de esta severa fragmentación del hábitat sobre las comunidades y metapoblaciones se desconocen. Estudiamos las comunidades de crustáceos (muestras semanales tomadas con tubos a lo largo de los hidroperíodos) por 3 años en un juego de humedales efímeros existentes en Illinois. Generamos curvas de especies-sitios por enrarecimiento y extrapolamos estas curvas para estimar, de manera conservadora, que 83-85 especies de crustáceos podrían haber habitado aproximadamente los 4 millones de humedales efímeros que alguna vez existieron en Illinois; 8-9 especies de crustáceos terminaron en la extinción en Illinois durante el drenado; y 75-76 especies de crustáceos existen en unos cuantos humedales efímeros remanentes de Illinois. También llevamos a cabo simulaciones celulares autómatas para examinar los efectos potenciales de la fragmentación del hábitat en la estructura genética de una metapoblación existente de crustáceos. Las simulaciones indican que la conversión de la antigua pradera húmeda en agricultura pudo haber reducido las metapoblaciones de crustáceos en poblaciones aisladas que son más vulnerables a la pérdida futura de hábitat. A pesar de la severa fragmentación del hábitat, las relaciones curvilíneas especies-sitios sugieren que las tasas más grandes de extinción de crustáceos de humedales efímeros podrían ocurrir todavía. Sin embargo, la selección por disper-*

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sión limitada durante la fragmentación del hábitat puede contribuir a la deuda de extinción de especies existentes. Los programas de conservación pueden preservar gran parte de la biodiversidad histórica en humedales efímeros, pero la biodiversidad futura de humedales dependerá en gran medida del éxito de estos esfuerzos. Las consecuencias de la pérdida histórica de humedales y la importancia de los esfuerzos de conservación de humedales para la agricultura de los Estados Unidos deberán servir de ejemplo para otras regiones.

Introduction

Much of the midwestern United States is often referred to as the corn belt because of the prevalence of intensive agriculture. The corn belt's prominence in crop production came at a price for the former wet-prairie ecosystem and the habitat it presumably provided for aquatic organisms. Conversion of wet prairie to cropland was primarily a governmentally promoted, large-scale, and intensive change in hydrology of the landscape that is well documented (Bogue 1959; McManis 1964; Winsor 1975; Whitney 1984; Prince 1997). However, the loss of aquatic habitat and aquatic diversity went largely undocumented. After most wetland habitats were already lost, some public awareness and governmental actions have turned to the modern landscape: conservation of soil, water, and wildlife (primarily fish and waterfowl); economic pressures in agriculture; and agricultural chemicals in runoff (Prince 1997). All these problems have prompted modern efforts to conserve and restore some wetlands within the corn belt.

However, wetland conservation and restoration efforts conducted without knowledge of the former natural landscape may aim for an unknown target. Effective conservation of biodiversity and single species in prairie wetlands must begin with an understanding of the historical transformation of the landscape to its modern, artificial form, and the effects of that habitat fragmentation on biodiversity and metapopulation dynamics. Therefore, we summarized the history of wetland loss in Illinois, studied crustacean communities in a set of extant ephemeral wetlands, and modeled metapopulation dynamics. We extrapolated observed community structure to estimate the former and extant crustacean diversity of ephemeral wetlands in Illinois and modeled the effects of habitat fragmentation on extant crustacean metapopulations in those wetlands. We focused on crustacean communities because they are typically diverse and ecologically important in ephemeral wetlands.

Wetland Loss in the Corn Belt

The term *corn belt* dates to the 1880s (Warntz 1957) and is used in modern ecoregion classifications (Omerik 1995). The corn belt typically includes the states of Iowa, Illinois, Indiana, and Ohio, plus portions of neigh-

boring states. Illinois is consistently encompassed in the corn belt, and we use it as a case study of the corn belt.

Most Illinois soils are loess (fine-grained, poorly draining, aeolian deposits) overlying Wisconsinan or Illinoian drift and were deposited during the Wisconsinan glacial retreat (Willman & Frye 1970). In addition, much of Illinois is level to gently rolling, so that precipitation or snowmelt can form ephemeral wetlands without rapid runoff. Given that vegetation cover developed early and held soils in place after the Wisconsinan retreat (Willman & Frye 1970), ephemeral wetlands that formed on those soils have likely been present for about 10,000 years.

Tallgrass prairie, including many wetland species (McClain 1986), dominated much of the region prior to settlement by Europeans and their descendants (Transeau 1935; Sears 1981). The dominance of prairie vegetation rather than forest makes the area resilient to spring flooding, summer drought, strong winds, and occasional fires (Prince 1997).

The agent of the prairie's demise provides the best evidence that Illinois was once dominated by wet prairie. In 1870 and 1880, malaria caused almost 30 deaths per 100,000 persons in Illinois (Winsor 1975). By contrast, malaria is unknown in Illinois today. Historians have analyzed settlers' writings and described life in the wet prairie (e.g., Bogue 1959; Whitney 1984; Winsor 1987; Prince 1997). Charles Dickens (1850:354) visited the wet prairie of central Illinois in 1842 and wrote the following description:

We had a pair of very strong horses, but traveled at the rate of little more than a couple of miles an hour, through one unbroken slough of black mud and water. It had no variety but in depth. Now it was only half over the wheels, now it hid the axle-tree, and now the coach sank down in it almost to the windows. The air resounded in all directions with the loud chirping of frogs On either side of the track, if it deserves the name, was the thick 'bush'; and everywhere was stagnant, slimy, rotten, filthy water.

Coincident with settlement was a large-scale effort to distribute and then drain the vast wetlands, known then as swamp land. The U.S. Swamp Land Act of 1850 distributed federally owned wetlands to states. Illinois distributed lands to counties, which in turn sold them to individuals (Bogue 1951). Drainage districts were authorized by state law (in 1865 in Illinois) to organize the installation of ditches and branching networks of subsurface

drainage pipes ("drain tiles"). From 1880 to 1895, nearly 190,000 km of drain tiles were placed in Illinois alone (Prince 1997), at an average rate of over 12,600 km/year, or the equivalent of an annual trip from Chicago to Hong Kong. Large-scale efforts to drain wetlands continued at least into the mid-1900s, and many drain tiles (plus their modern, plastic equivalents) continue to function today.

The net result is that almost 2.8 million ha of Illinois wetland were lost within approximately 100 years (Dahl 1990). Almost all (90–99%) wetlands in some Illinois counties have been lost (Suloway & Hubbell 1994). Across Illinois, about 15% of pre-drainage wetland area still exists, but most of this area is now concentrated in riparian zones. Ephemeral wetlands of the former tallgrass prairie were rapidly and permanently replaced by surface and subsurface drainage in agricultural watersheds.

Historical wetland loss in Illinois preceded ecological understanding of those systems. For example, the Illinois Natural History Survey was formed in 1917, after much of the drainage had already been set in place, and early research focused on the Illinois River floodplain (Schneider 2000); the locations of former prairie wetlands went largely unrecorded. Illinois wetlands were inventoried as part of the National Wetland Inventory (NWI), but "most original wetlands that are now farmland were not classified as wetlands in the NWI" (Suloway & Hubbell 1994). Because 60% of Illinois is cropland (Luman et al. 1995), substantial numbers and the areal extent of former wetlands remain undocumented a century after they were drained.

The result of this socioeconomic, historical sequence is that the biodiversity and ecology of ephemeral wetlands in Illinois are virtually unknown, including the effects of historical habitat fragmentation. Therefore, we studied a local set of ephemeral ponds, extrapolated results to the former conditions in Illinois, and then estimated loss of species from that extrapolation. Finally, we conducted computer simulations to gain insight into the effects of this severe habitat fragmentation on extant metapopulation structure.

Methods

Study Area

We studied 13 ephemeral ponds near Bluff Springs, Illinois (Cass County). The ponds varied in hydroperiod—days with surface water present—and interconnections, depending on location, annual precipitation, and morphology. All ponds were shallow (maximum observed depth of 95 cm). Three of the 13 ponds were isolated from all other ponds by topography. Ten ponds were formed in shallow depressions within generally level terrain and were isolated in drier years (e.g., 1997). In wet-

ter years (e.g., 1996, 1998, 1999), these 10 ponds may be more appropriately described as sets of slightly deeper areas within a shallow, seasonal swamp. Climatic variation and subtle topography within the site contribute to complex patterns of flooding and hydroperiod among the ponds, and in some years (e.g., 2000) ponds may not form at all. Most ponds dried completely by midsummer, although the deepest pond could have a hydroperiod of more than a 1 year, given sufficient precipitation.

Crustacean Community Sampling

We sampled crustaceans weekly for 3 consecutive years (1996–1998) throughout hydroperiods in the 13 ponds. We placed a stovepipe sampler at a random location in each pond each week. The sampler (a cylinder 61 cm high \times 40 cm wide) was forced into the sediment, and all water within the cylinder was sieved on 35- μ m mesh (1996) or 74- μ m mesh (1997, 1998). Collected organisms were rinsed off the sieve and preserved with 4% buffered formalin, and the sampled volume of water was recorded. Pond depths were recorded, and hydroperiods were estimated from field notes and sampling intervals.

We first processed samples for large branchiopods (Anostraca, Conchostraca) by rinsing preserved samples on a sieve (same mesh sizes as above) and then into a pan. Anostracans and conchostracans were identified and enumerated, and the remaining sample was transferred back to the sample bottle. We then mixed the sample and quantitatively subsampled it in triplicate to identify and enumerate microcrustaceans (Cladocera, Copepoda, Ostracoda, and juvenile Anostraca and Conchostraca) with both stereo and compound microscopes. We identified species using the taxonomic keys of Pennak (1989), Edmondson (1959), and Hebert (1995).

Crustacean Community Data Analyses

Data collected in 1998 were analyzed for α , β and γ diversity (Whittaker 1960) and rarefaction curves (Hurlbert 1971; Colwell & Coddington 1994). The longest hydroperiods were observed in 1998, enabling a better estimate of crustacean species diversity than in 1996 or 1997. Beta diversity, which is overall diversity (i.e., γ diversity) divided by local diversity (α), provides an estimate of the change in species number among ponds. Rarefaction analyses provide estimates of the number of species expected with increasing sample numbers and were conducted with Biodiversity Pro (McAleece et al. 1997), which calculates the estimated species richness per sample, $E(S_n)$. We excluded densities of unidentifiable organisms (e.g., copepod nauplii) in rarefaction analyses, and the randomization function of rarefaction analyses pooled samples in random order (50 random

sorts on each pass). Rarefaction estimators used were the species accrual (hereafter, species), Chao 1, Chao 2, and first-order jackknife (hereafter jack 1) functions (for a full description of these estimator functions, see Colwell & Coddington 1994).

Extrapolations of Species Richness to Illinois

In the absence of information on crustacean communities of predrainage ephemeral wetlands in Illinois, we extrapolated Bluff Springs rarefaction curves to estimate potential crustacean species in the wet prairies of Illinois before drainage. We made several important assumptions. First, the small, relatively undisturbed Bluff Springs wetlands represent predrainage conditions. McClain (1986) estimated that 8.9×10^6 ha of Illinois prairie existed in 1820, whereas <930 ha remain intact today, and Dahl (1990) estimated that wetlands covered 22.8% of Illinois in the 1780s. Therefore, we assumed that 22.8% of the former Illinois prairie was wet (i.e., ephemeral wetlands), yielding 2.0×10^6 ha of ephemeral wetlands. Third, we assumed that the surface area of the average ephemeral wetland is 0.5 ha, based on an analysis of former depressional wetlands in Champaign County, Illinois (McCauley 2001). Thus, 4 million ephemeral wetlands would have been contained in the former prairie of Illinois. This estimate is conservative, because ephemeral wetlands were probably more common in the prairie than other parts of Illinois and because many wetlands were likely smaller than 0.5 ha in size.

Another important assumption for extrapolation is that β diversity among a set of 13 local wetlands represents β diversity among 4 million wetlands across Illinois. In reality, we expected local β diversity to be less than regional β diversity, so this assumption also contributed to conservative estimates of species richness.

Simulations of Metapopulation and Habitat Fragmentation

We used a cellular model (ISLANDS: Interactive Simulated LANDScape) to conduct computer simulations for a "crustacean" metapopulation (Hanski & Simberloff 1997). We developed the model to provide spatially explicit population dynamics in a patchy landscape. Cellular (also known as neutral) models enable simulation of population dynamics in each cell (hereafter, "site") and interactions among sites via dispersal. We used crustacean-like population parameters for a single species (described below), and we conducted a factorial experiment in which we varied (1) the rate of random habitat loss in the lattice and (2) the dispersal rate of the species among neighboring sites. Others have used cellular models to consider the effects of habitat loss on populations but have done so for pairs of competing species (e.g., Dytham 1994, 1995) or without considering the effects

of dispersal rate on metapopulation survival (Bascompte & Solé 1996) and have not selected population parameters to represent a taxon. Similar to the cellular models of Travis and Dytham (1998, 1999), our model considered different dispersal rates as genotypes and employed no tradeoff in dispersal rate and competition.

Cellular models typically assume short-distance dispersal by using nearest-neighbor interactions: sites that share a border can exchange organisms. This approach is reasonable for a model of passively dispersed crustaceans in wetland habitat patches. Crustaceans clearly disperse over long distances given geological time scales (Stemberger 1995). In Illinois wetland loss occurred within about 100 years, however, so dispersal in ecological time is relevant here.

Our simulation was intended to mimic habitat loss rates comparable to historical loss rates that occurred in Illinois and the corn belt but should not be construed as an accurate representation of that undocumented process. Instead, our simulation was an experiment to test for the effects of variation in an important feature (dispersal) of a hypothetical crustacean metapopulation undergoing habitat fragmentation. We experimentally varied overall rates of habitat loss to generate habitat fragmentation in the lattice, although we did not quantify fragmentation with fractal dimensions or percolation-theory scores (e.g., With & Crist 1995). We expected that dispersal among wetlands would modify metapopulation extinction risk in the face of habitat fragmentation and that high dispersal rates would be disadvantageous at greater rates of habitat fragmentation (Travis & Dytham 1999).

In each site (30×30 grid), the following process occurred in each time step (year) and was intended to represent a generic crustacean:

- (1) Adults produced dormant eggs and then died (as when an ephemeral wetland dries). For simplicity, we assumed that each adult produced 10 eggs and that this reproduction rate was uniform across all sites (i.e., that it was species-specific).
- (2) A dormant egg either stayed in the site or was randomly dispersed to one of the eight surrounding sites at a rate that we experimentally varied among 11 genotypes (ranging from 0 to 100% of produced eggs in increments of 10%). Dispersal rate was uniform for all sites per genotype, as though it was heavily dependent on genotype-specific traits (e.g., spines, hydrophobicity). Ten percent of dispersing eggs did not survive because of some hazard in transit, such as decomposition or predation.
- (3) Eggs (both those produced on site and immigrants) hatched: those that survived to adulthood reproduced clonally, and the cycle repeated. Each site had its own randomly determined probability of survival to adulthood. This probability incorporates local egg and juvenile survival, establishes the

patchiness in the landscape, and reaches a maximum value of 20% (average = 10%). This low probability to survival is counterbalanced by a high reproductive rate and mimics a Type III survivorship curve. Population in a site could reach a carrying capacity of 1000.

We considered the probability of surviving to reproductive age in a site as a fixed value, similar to the static pattern of habitat availability used by Travis and Dytham (1999). This decision reflects the importance of (1) hydroperiod, which depends in large part on the topography, soils, and vegetation of a site and (2) egg banks, which mitigate the effects of interannual variation in hydroperiod on long-term population viability. Temporally autocorrelated variation in survival rate could be introduced to represent interannual variation in precipitation but would unnecessarily complicate simulations for our current purposes. Instead, we considered local survival probability to represent a long-term average, consistent with an Illinois topography that existed since the last glaciation (Willman & Frye 1970) and organisms adapted to ephemeral wetland conditions. Therefore, favorable sites in our model developed a large population (as in a suitable wetland with an egg bank) and were unlikely to undergo repeated extinction/colonization events. Those sites were likely to serve as a source to other sink habitats.

A progressive and permanent habitat fragmentation occurred in our model, similar to the ephemeral wetland habitat loss during development of the corn belt. Once a site was "drained," it became uninhabitable, and eggs subsequently dispersed there could not survive. We varied habitat fragmentation in increments of 0, 0.125%, 0.25%, 0.5%, and 1.0% of sites lost in each year. Habitat fragmentation was enacted in the model by random site selection, followed by conversion to zero of site-specific probabilities of survival to reproductive age.

Each combination of habitat loss rate and dispersal rate was simulated in 100 iterations, and we considered each iteration to have reached an asymptote when 5 consecutive "years" occurred with no state changes in any of the 900 sites. States were defined by population size, as follows: 0, 1–250, 251–500, 501–750, 751–950, 951–1000. With progressive habitat fragmentation, additional state changes beyond the asymptote could occur, but these changes were trivial relative to general conclusions.

Results

Bluff Springs Crustacean Communities

Hydrology of the ephemeral ponds varied considerably among years. Ponds formed late (mid-April) in 1996, and most were dry by midsummer. In 1997 ponds formed early (early February) but dried early (ranging from mid-

February to late May). In contrast, ponds formed early in 1998 (mid-January), and some persisted into late summer (August). Pond hydrology affected species composition, as indicated by the distribution of species among ponds through the years (Table 1). Annual species richness (S) significantly increased with longer hydroperiod each year and overall (Fig. 1).

Twenty-nine crustacean species were observed in Bluff Springs ponds in 1998 (γ diversity), and α diversity ranged from 5 to 21 (mean = 11.8 ± 4.8 SD). Beta diversity ranged from 1.4 to 5.8 (mean = 3.0 ± 1.5 SD), indicating that roughly 3 additional species were observed with each additional pond sampled.

The 1998 data averaged 16.9 samples per pond (SD = 3.0). Rarefaction analyses are in units of number of species per sample. We expressed data as the number of species per pond, assuming 17 weekly samples collected per pond to characterize species diversity. The

Table 1. Crustacean diversity of the Bluff Springs ponds, 1996–1998.

Species	Number of wetlands inhabited		
	1996	1997	1998
<i>Acanthocyclops vernalis</i>	0	0	9
<i>Alonella diaphana</i>	0	0	3
<i>Alona guttata</i>	0	0	2
<i>Alona monacantha</i>	0	0	1
<i>Attheyella</i> sp.	6	0	5
<i>Bryocamptus/Cantbocamptus</i> sp.	12	11	8
<i>Ceriodaphnia reticulata</i>	0	2	11
<i>Chydorus sphaericus</i>	0	0	3
<i>Cryptocyclops bicolor</i>	3	0	6
<i>Cyclops exilis</i>	0	0	1
<i>Cyclops haueri</i>	2	0	6
<i>Cyclops navus</i>	12	1	8
<i>Cyclops nearcticus</i>	2	12	2
<i>Cypridopsis</i> sp.	7	0	5
<i>Cyprois</i> sp.	8	6	3
<i>Daphnia laevis</i>	0	0	6
<i>Daphnia obtusa</i>	12	10	13
<i>Eubranchipus serratus</i>	5	7	13
<i>Eucyclops speratus</i>	0	0	1
<i>Eucypris</i> sp.	0	9	8
<i>Eurycercus</i> sp.	0	0	1
<i>Kurzia latissima</i>	0	0	1
<i>Lynceus brachyurus</i>	8	9	9
<i>Moina micrura</i>	0	1	0
<i>Onychodiptomus sanguineus</i>	1	3	1
<i>Osphranticum labronectum</i>	3	1	9
<i>Pleuroxus denticulatus</i>	0	0	5
<i>Pleuroxus striatus</i>	1	1	0
<i>Prinocypris/Megalocypris</i> sp.	0	0	1
<i>Scapholeberis mucronata</i>	4	1	9
<i>Simocephalus exspinosus</i>	8	4	0
<i>Simocephalus serratus</i>	3	0	0
<i>Simocephalus vetulus</i>	0	0	5
Annual number of species	17	15	29
New species/year	—	3	13

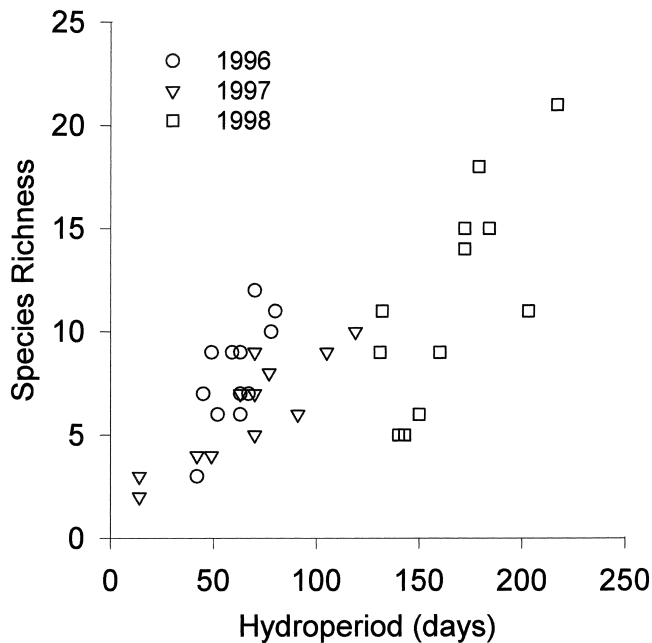


Figure 1. Crustacean species richness (S) as a function of annual hydroperiod (H) in the Bluff Springs ponds, 1996–1998. Regressions: $S_{1996} = -0.698 + 0.143H$, $R^2 = 0.49$; $S_{1997} = 1.629 + 0.071H$, $R^2 = 0.76$; $S_{1998} = -11.651 + 0.142H$, $R^2 = 0.56$; $S_{1996-1998} = 3.106 + 0.057H$, $R^2 = 0.55$.

species and Chao 1 functions were very similar and served as a lower boundary of species accrual among ponds, reaching 29 species in 13 ponds (Fig. 2). Chao 2 and jack 1 provided similar trajectories to an estimated total of 33 species present in the 13 ponds (Fig. 2). Therefore, 4 additional crustacean species may inhabit the Bluff Springs ponds than were observed in 1998 (in fact, 33 have been recorded during 1996–1998; Table 1), and weekly sampling during one year with long hydroperiods should represent 88% of total diversity. We selected species and jack 1 rarefaction curves as lower and upper bounds for $E(S_n)$, respectively, to be fit to an equation for subsequent predictions.

Extrapolations of Species Richness to Illinois

The species-area power function ($S = CA^z$, where S is species number, A is area, and C and z are constants) of Preston (1962) bears a rich history and provided adequate fits to the species and jack 1 curves of Fig. 3 ($R^2 = 0.913$ and 0.875 , respectively). However, the large-scale extrapolation required greater accuracy. We used a modified power curve of the form $E(S_n) = E(S_0) + kP^z$, where $E(S_n)$ is estimated species number, $E(S_0)$ is the intercept, P is the number of wetlands, and k and z are constants. This slight modification improved extrapolation accuracy (species, $R^2 = 0.962$; jack 1, $R^2 = 0.907$)

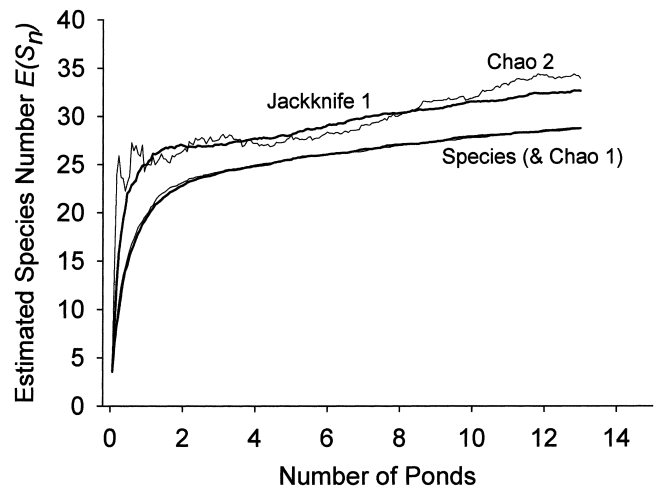


Figure 2. Rarefaction estimates of crustacean species number in the Bluff Springs ponds from 1998 samples. Species and Chao 1 estimators reach the actual total (29) collected in 1998. Other curves (Chao 2, jackknife 1) provide alternate estimates (for detailed explanations of these rarefaction estimators, see Colwell & Coddington 1994). Species and jackknife 1 were used for subsequent extrapolations.

while maintaining use of the power function (Fig. 3). Given the assumptions above, the two extrapolated regressions predicted similar crustacean diversity in the former Illinois prairie wetlands: 83–85 crustacean species may have inhabited the 4 million ephemeral wetlands of predrainage Illinois (Fig. 3).

How many Illinois crustacean species may have been driven to extinction during drainage of the wet prairie? If we assume that loss of crustacean species is proportional to loss of habitat, and given that 85% of Illinois wetlands have been lost (Dahl 1990), then extrapolated rarefaction curves indicate that 8–9 crustacean species may have become extinct in Illinois during conversion of wet prairie to agriculture (Fig. 3). Conversely, 75–76 crustacean species—about 90% of original diversity—may still exist in the few remaining ephemeral wetlands across Illinois, and the Bluff Springs ponds may be habitat to over 40% of Illinois' ephemeral wetland crustaceans.

Simulations of Metapopulation and Habitat Fragmentation

When little or no habitat loss occurred, a broad range of dispersal genotypes maintained similar large metapopulations (Fig. 4a). This result suggests that polymorphism of genetically determined dispersal rate would exist when prairie wetland habitat was intact, as was presumably the case in predrainage Illinois. However, modeled genotypes with greater dispersal rates were increasingly selected against as greater habitat fragmentation occurred. As habitat loss rate approached 1% per year, dis-

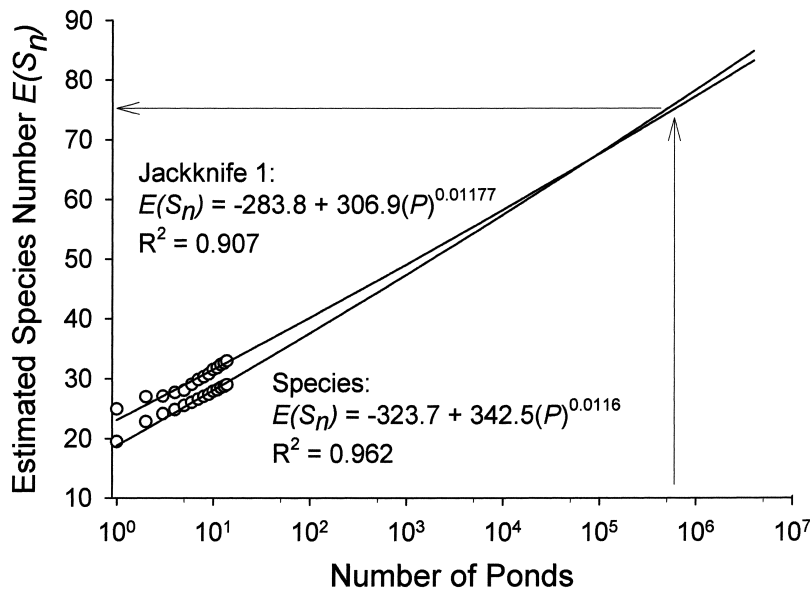


Figure 3. Crustacean species accrual and jackknife 1 estimators of species richness in Bluff Springs ponds, extrapolated to the former wet prairie of Illinois. Extrapolation regressions are in the form of a modified power equation: $E(S_n) = E(S_0) + kP^z$, where $E(S_n)$ is the estimated species number, $E(S_0)$ is the intercept, P is the number of wetlands, and k and z are constants. Equations shown are extended to 4 million wetlands based on estimates of former prairie and wetland prevalence in Illinois (open circles, Bluff Springs data; arrows, estimates after 85% wetland loss [Dahl 1990]).

persal rate became the main determinant of metapopulation size.

The modeled proportion of habitats occupied was much more sensitive to habitat fragmentation than to dispersal effects: <20% of sites were occupied when habitat loss occurred at 0.5% per year, regardless of dispersal genotype (Fig. 4b). Less than 5% of sites were inhabited by a low-dispersing genotype (10.0% of eggs dispersed per year) when habitat loss was 1.0% per year, yet that metapopulation experienced only a modest decline in size. Given habitat fragmentation and the consequent selection for low dispersal rates, sites tended to be either occupied by large populations or unoccupied (cf. Figs. 4a & 4b). Low-dispersing genotypes maintained large populations in extant sites, and as habitat loss progressed, those extant sites became more isolated.

Simulations were most dynamic (required more time to approach steady state) for genotypes with intermediate dispersal rates and moderate habitat-loss rates, as evidenced by the average time to reach the asymptotic stop point (Fig. 4c). At one extreme—very low habitat-loss rates—metapopulations for most dispersal genotypes quickly stabilized at large sizes and were distributed among many sites. At the other extreme—high dispersal rates across most habitat-loss rates—metapopulations rapidly declined to extinction.

Finally, we conducted a separate simulation to evaluate the sensitivity of our results to the selected life-history traits. We repeated the simulation experiment (above) with traits intended to represent a Type I survivorship curve (longer lived and lower reproductive rate). Maximum local survival rate to adulthood was set at 1.0, which yielded an average rate of 0.5. Half of all adults survived the “dry season” and reproduced again in the second “wet season,” and their reproductive rate was 2.0. Results of this Type I simulation were essentially

identical to those of the original Type III simulation, with one difference: metapopulation size was not depressed by high dispersal rates when no habitat fragmentation occurred, as was the case for the Type III simulation. The presence of long-lived adults counterbalanced the “dilution” effect of high egg dispersal on local populations.

Discussion

Historical conversion of wet prairie to agriculture in the midwestern United States occurred during about a century, it is responsible for >85% loss of wetlands in the former prairie region (Dahl 1990), and it occurred at a rate similar to that estimated for current tropical deforestation (Myers 1988). The regional landscape is now artificial and is built on a vast network of underground plumbing and ditches, draining into both channelized and natural streams. Also, this rapid habitat loss occurred on a landscape that had developed since the last glaciation (approximately 10,000 years ago). This natural history of the landscape needs to be recognized more fully if wetland conservation and restoration efforts are to be effective.

The consequences of wetland drainage on biodiversity in the corn belt are largely unknown. Without historical records of diversity in prairie wetlands, we can examine wetland communities only in extant, isolated fragments. One such fragment, the Bluff Springs ponds, appears to be relatively rich in crustacean species and spatially patterned, suggesting that larger-scale diversity may also have been high. Based on our computer simulation and extrapolations of data from this small-scale system to the once-vast wet prairie, we hypothesize the following for Illinois: (1) about 4 million ephemeral wetland habitats

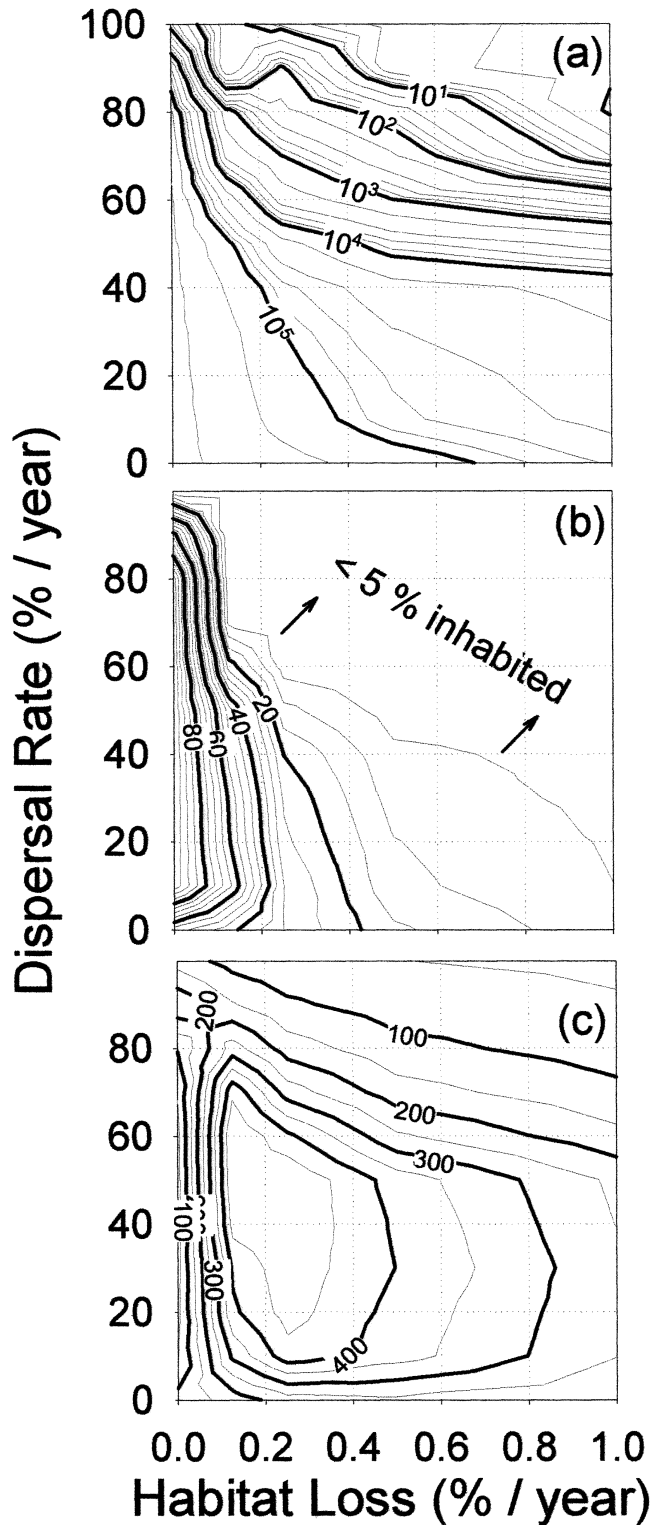


Figure 4. Metapopulation dynamics of crustaceans and results of habitat fragmentation simulation. Each graph can be visualized as a topographic map, with contour lines depicting average state at the steady-state asymptote for each parameter: (a) metapopulation size (N) at varying rates of habitat loss and dispersal; (b) percentage of sites inhabited at varying rates of habitat loss and dispersal; (c) time to asymptote at varying rates of habitat loss and dispersal.

may have existed before conversion of wet prairie to agriculture, and over 80 crustacean species likely inhabited those wetlands; (2) the surviving crustacean species (approximately 75 species by our conservative estimate) have been selected for limited dispersal and are reduced to isolated relict sites with little metapopulation dynamics among sites; and (3) the limited dispersal that may have enhanced species survival during habitat loss renders remaining species all the more vulnerable to further habitat loss.

How do our estimates of predrainage crustacean diversity compare to other studies of regional crustacean diversity in ephemeral wetlands? Mahoney et al. (1990) recorded 130 crustacean species in only 23 Carolina Bays. Morton and Bayly (1977) identified 60 microcrustacean species in 53 ephemeral ponds across eastern Victoria, Australia, and King et al. (1996) found 67 crustacean species in 58 ephemeral ponds along a 200-km transect (based on their Fig. 1) in California. Species-accrual curves based on the presence/absence data of Morton and Bayly (1977) and King et al. (1996) predicted far more extant species than did our smaller-scale study (Fig. 5) because of greater β diversity among ponds (means = 13.3, 13.0, respectively). Finally, we extrapolated the Morton and Bayly (1977) and King et al. (1996) rarefaction curves (Fig. 5) to 4 million wetlands with the power function used above ($R^2 = 0.999$ and 0.996 , respectively). The Morton and Bayly (1977) curve predicted 698 species, and the King et al. (1996) curve predicted 702 crustacean species. By comparison, our extrapolations of crustacean diversity in ephemeral wetlands in Illinois appear conservative, and it seems reasonable to assume that over 80 crustacean species inhabited the large wet-prairie archipelago that once dominated Illinois.

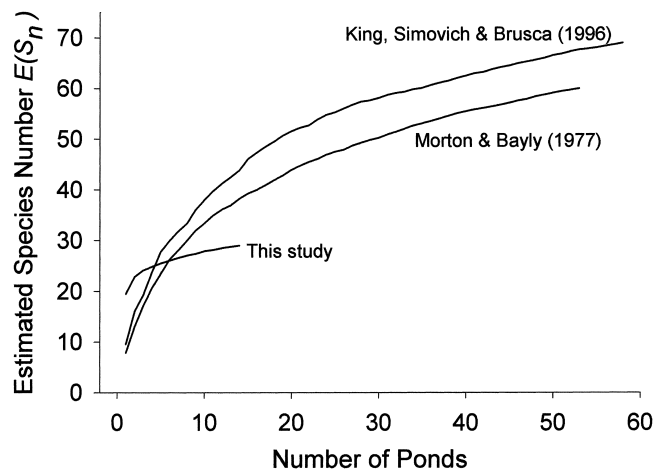


Figure 5. Crustacean species accrual curves for the studies of Morton and Bayly (1977), based on their Table 2, and of King et al. (1996), based on their Appendix B. The curve shown for this study is the same as the species curve in Fig. 3.

Given estimates of wetland loss, the extrapolated rarefaction curves for Illinois indicated that eight or nine crustacean species may have been driven to extinction in Illinois during drainage of the wet prairie. This estimate is conservative, given that most habitat loss occurred in areas dominated by wet prairie (Suloway & Hubbell 1994) and that the rarefaction curves are based on low β diversity. Clearly, estimates of crustacean diversity losses in former ephemeral wetlands of the corn belt are uncertain in the absence of historical data. However, an important insight emerges regardless of the extrapolation details: a curvilinear species-sites rarefaction curve dictates that relict ephemeral wetlands are especially valuable for extant diversity. For example, we estimated that about 90% of original crustacean diversity might still exist in the few remaining ephemeral wetlands of Illinois (<15% of original). This perspective does not excuse the regional extinction of species; instead it argues for active preservation of the remaining species-rich habitats with relatively high β diversity among sites.

Simulation offers an additional way to consider the effects of historical and severe habitat fragmentation on ephemeral wetland crustaceans that may still exist in the corn belt. Our simulation suggests that populations were polymorphic for dispersal rate when prairie wetland habitat was intact. After drainage, only genotypes with low dispersal rates are likely to have survived progressive loss of the corn belt habitat, consistent with the effects of habitat fragmentation on some insects (Van Dyck & Matthysen 1999). Given that 85% of Illinois wetlands have been lost (Dahl 1990) and that this loss occurred in about 100 years (approximately 1850–1950), habitat loss occurred at an average rate of about 0.85% per year. Examining Fig. 4 at that value shows that the remaining metapopulation of our model crustacean inhabits <10% of original habitat and is primarily composed of low-dispersing genotypes. Passive dispersal that occurs at high rates dilutes the few relict crustacean populations existing amid a drained landscape, consistent with the modeling results of Travis and Dytham (1999).

Second, crustaceans that have survived extensive habitat loss may be caught in a dispersal dilemma. Low dispersal rates have helped the species avoid extinction so far, but low dispersal may also limit metapopulation interactions that foster viability in a fragmented landscape. Selection for limited dispersal during habitat fragmentation may contribute to extinction debt (Tilman et al. 1994; Loehle & Li 1996), which implies a greater need for current and future wetland conservation efforts.

Finally, crustaceans that exist in relict wetlands of the corn belt today are likely disjunct isolates of former large metapopulations that were more interactive within a vast network of numerous, proximate wetlands. This vicariance biogeographic effect (Wiley 1988) may have led to greater genetic differences among extant popula-

tions than existed before drainage occurred. This effect contrasts in process to but may be similar in outcome to the persistent founder effects proposed for crustaceans in the Arctic (Boileau et al. 1992), and the overall genetic diversity of remaining species is probably diminished.

Simple questions about wetland biodiversity in the U.S. corn belt remain unanswered. For example, how many wetland invertebrate species exist in Illinois? How are those species distributed? Is the genetic structure of extant species in isolated ephemeral wetlands consistent with vicariance biogeography? Our extrapolations (hypotheses) should be tested. What role do egg banks have in ephemeral wetlands and former ephemeral wetlands and in the potential to restore these wetlands? Do interhabitat distances now exceed probable dispersal distances, and does this differ among species? How can wetland habitat best be restored to maximize regional biodiversity? Answers to these basic questions will be useful for management of aquatic habitats and biodiversity in the corn belt, and may indicate what lies ahead for other developing regions.

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