RESEARCH ARTICLE

Connectivity of agroecosystems: dispersal costs can vary among crops

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Abstract Knowledge of how habitat heterogeneity affects dispersal is critical for conserving connectivity in current and changing landscapes. However, we generally lack an understanding of how dispersal costs and animal movements vary among crops characteristic of agroecosystems. We hypothesized that a physiological constraint, desiccation risk, influences movement behavior among crops and other matrix habitats (corn, soybean, forest, prairie) in *Ambystoma tigrinum* (tiger salamander) in Illinois, USA. In a desiccation experiment, salamanders were added to enclosures in four replicate plots of each matrix habitat, and water loss was measured every 12 h for 48 h. Changes in water loss were examined using a linear mixed model. Water loss varied among treatments, over time, and there was a significant treatment-time interaction. Water loss was greater in corn and prairie than in forest and soybean. To assess whether salamanders move through matrix habitats that minimize desiccation, we tracked movements of individuals released on edges between habitats for two treatment combinations: soybean–corn, and soybean–prairie. As predicted based on our desiccation experiment, movements were oriented towards soybean in both cases. Thus, variation in desiccation risk among matrix habitats likely influenced movement decisions by salamanders, although other factors such as predation risk could have contributed to habitat choice. We argue that conceptualizing dispersal cost as uniformly high in all crop types is too simplistic. Estimating crop-specific dispersal costs and movement patterns may be necessary for constructing effective measures of landscape connectivity in agroecosystems.

Keywords Agriculture · Amphibian · Connectivity · Cost-distance · Dispersal · Illinois · Landscape matrix · Least-cost · Salamander · Spatial ecology

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Introduction

Dispersal is an important life-history trait with consequences for individual fitness, population dynamics, and evolution (Clobert et al. 2001). Dispersal is also a key determinant of spatial population structure (Harrison and Taylor 1997), species persistence (Lande 1988), and potential distributional shifts in response to climate change

(Opdam and Wascher 2004). Metapopulation biology has become a dominant conservation paradigm for understanding the influence of dispersal on population processes in fragmented landscapes (Hanski and Gilpin 1997). Although metapopulation theory was historically neutral with respect to dispersal and matrix habitats (i.e., habitats between suitable patches), matrix heterogeneity is becoming an important component of metapopulation approaches (Wiens 1997; Ricketts 2001; Schooley and Wiens 2005; Prugh et al. 2008).

Despite recent integration of matrix heterogeneity into metapopulation models, we have a limited understanding of how matrix habitats influence dispersal and connectivity in agroecosystems. In many systems, models of landscape connectivity (e.g., least-cost models; Adriaensen et al. 2003) are based on expert opinion to estimate the resistance of matrix habitats to dispersal (Baguette and Van Dyck 2007; Beier et al. 2009; Janin et al. 2009). In agricultural systems, reliance on expert opinion often results in the assumption that all crops impose a uniformly high cost on dispersal (e.g., Schadt et al. 2002; Compton et al. 2007; Magle et al. 2009). Yet, agricultural crops can vary tremendously in vegetation structure and cover, associated predation risk, and resources such as food or refuge availability. Patterns of animal movement can vary among agricultural crops as well (Rizkalla and Swihart 2007), suggesting that a single, high dispersal cost does not apply equally to all crops. If crops differentially influence animal movement patterns, an evaluation of how dispersal costs vary among crops can inform models of landscape connectivity in agricultural systems.

Insight into how dispersal costs vary among agricultural crops and other matrix habitats may be gained by understanding the proximate physiological and behavioral factors that influence movement costs and decisions. In particular, pond-breeding amphibians are excellent model organisms to address how dispersers interact with matrix habitats within a physiological context. Risk of water loss should impose strong physiological constraints on juvenile dispersers due to their small bodies, permeable skin, and high surface area to volume ratio (Sinsch 1990; Rothermel and Semlitsch 2002; Chan-McLeod 2003; Mazerolle and Desrochers 2005; Semlitsch 2008). Using a field experiment, we tested the hypothesis that desiccation risk varies among agricultural crops

and matrix habitats that differ in canopy coverage, air temperature, and relative humidity for *Ambystoma tigrinum tigrinum* (eastern tiger salamander, Ambystomatidae) in northern Illinois. We predicted that desiccation risk would be greater in matrix habitats with less canopy coverage, higher air temperatures, and lower humidities at the soil surface. Next, we conducted a second experiment to test the hypothesis that matrix habitat influences movement decisions by juvenile dispersers. We predicted that salamanders would select habitats that minimize desiccation risk when given a choice, although other factors could contribute to movement decisions (e.g., predation risk). We discuss how an empirical, mechanistic understanding of dispersal costs and movement behavior may advance our conceptualization of landscape connectivity and enhance conservation efforts for species in agricultural ecosystems.

Methods

Study species

Ambystoma tigrinum is subterranean, using mammal burrows and excavated burrows in upland forests and prairies for refuge during most of the year. In Illinois, adults breed primarily in fishless ponds from February to April. Juveniles emigrate from ponds into upland habitats between July and September and become sexually mature within two years (Petranka 1998). Consistent with other pond-breeding amphibians (e.g., Phillips 1989), interpond dispersal for this species is greater for juveniles than adults (Church et al. 2007). Thus, we used juveniles in our desiccation and movement experiments.

We collected 78 *A. tigrinum* larvae for both experiments from 4 spatially independent wetlands in Lee County, IL. Individuals were collected and stored individually in plastic containers filled with 4-cm of well water between 22 June and 2 July 2009. To avoid capturing siblings within wetlands, we collected individuals of varying size classes from spatially segregated locations. Larvae were fed mealworms ad libitum until the start of metamorphosis. After metamorphosis, we stored salamanders individually in plastic containers lined with moist paper towels, and metamorphs were fed mealworms ad libitum.

Desiccation experiment

We conducted the desiccation experiment at a 9300-ha area in northern Illinois centered on the Richardson Wildlife Foundation property (West Brooklyn, IL; 41°42′26.6″N, 89°11′25.0″W). To address whether desiccation risk varies among crops and other matrix habitats, we subjected individuals to water loss in one of four treatments: corn, soybean, forest, and prairie. Treatments were chosen to represent the dominant habitats experienced by juvenile dispersers throughout the region. We used four replicate plots of each habitat. Experimental units were located in four spatially-disjunct blocks (average distance between blocks = 1260 m). Blocks were not chosen randomly, as we selected areas to minimize variation in soil characteristics. Treatments were assigned to a single experimental unit within blocks (4 treatments × 4 blocks = 16 total plots). Prairie vegetation was dominated by *Coreopsis lanceolata*, *Schizachyrium scoparium*, and *Sorghastrum nutans*, whereas forest plots were dominated by *Acer negundo*, *Prunus serotina*, *Quercus velutina*, and *Robinia pseudoacacia*.

We used 64 individuals in the desiccation experiment. Within each replicate plot, we installed four dehydration enclosures (modified from Rothermel and Luhring 2005). Each enclosure contained one salamander. We attached a 51 × 57-cm cylinder sleeve of fiberglass screening to a 25-cm section of 15-cm diameter polyvinyl chloride (PVC) pipe. We wrapped the fiberglass screening around the outside edge of each PVC pipe such that a 30-cm tall section of screening extended beyond the end of the pipe. Duct tape was used to fasten the fiberglass screening to the outside edge of each PVC pipe. We used 9.1-kg fishing line to sew together the ends of each section of cylindrical screening. The PVC was buried so that the top end of the PVC was at the soil surface, and only the 30-cm tall section of the screening was above ground. Enclosures were placed 2 m apart in a 2 × 2-m grid. Care was taken to minimize disturbance to the soil surface within each enclosure during installation.

The experiment was conducted between 12 August and 14 August 2009. We stopped feeding salamanders 2 days before the start of the experiment. On the first day of the experiment, individuals were placed in containers with 1-cm well water to fully hydrate for a minimum of 1.5 h. Before transferring salamanders to enclosures, we gently blotted individuals with a paper towel, and we measured their snout-vent-length (SVL) and mass to the nearest 0.01 g using a portable electronic scale (Ohaus Scout Pro Balance, Pine Grove, New Jersey, USA). We randomly assigned salamanders to enclosures. Individuals were placed on the soil surface within enclosures on 12 August between 1700 and 2100. We returned every 12 h for 48 h to measure salamander mass. Weight loss during this time was assumed to be due to water loss (Pough and Wilson 1970; Rothermel and Luhring 2005). We also measured air temperature and relative humidity at 10-min intervals throughout the experiment using a HOBO Pro v2 logger (Onset Computer Corp., Bourne, Massachusetts, USA). A single data logger was mounted 1–2 cm above the ground in the center of each 2 × 2-m experimental plot. Canopy cover was measured as % closed canopy at the soil surface in each enclosure using a spherical densiometer.

We used a linear mixed model using restricted maximum likelihood estimation (PROC MIXED—SAS version 9.1; SAS Institution Inc., Cary, North Carolina, USA) to test for effects of treatment, block, time, and all two-way interactions on water loss. Individual was used as a random effect. We chose the first-order autoregressive covariance structure, which assumes that observations on a given individual closer in time are more correlated than are observations separated by longer times. Individuals were nested within the treatment-block interaction. Mass at each time interval was used as the response variable, and initial mass was used as a covariate. In eight cases, fewer than four subsamples were available within experimental units due to escape (1 individual each missing after 12 and 24 h), mortality (2 individuals at 48 h), and an erroneous data record (1 individual at 48 h).

Finally, we used ANOVA to evaluate the effect of matrix habitat on canopy cover at the soil surface using PROC GLM in SAS. Canopy cover estimates were averaged across subsamples at the soil surface (Gotelli and Ellison 2004) and arcsin-transformed to reduce heteroscedasticity.

Movement orientation experiment

To evaluate the prediction that salamanders choose to move through matrix habitats that minimize desiccation risk, we released individuals on edges between habitats

used in our desiccation experiment. Short-term movements (<16 h) were recorded using radiotelemetry. Because we had a limited number of salamanders and radiotransmitters, we only assessed movement decisions for individuals released at two treatment combinations, soybean–prairie and soybean–corn, which provided clear expectations based on results of the desiccation experiment. The soybean–prairie plot was located at the Phillips Tract natural area in Urbana, IL (40°7′59.3″N, 88°8′56.9″W) and the soybean–corn plot was located at the South Farms research area in Champaign, IL (40°2′38.1″N, 88°14′5.8″W). The University of Illinois owns both sites. Treatment combinations and locations were chosen due to (1) presence of sharp, narrow (<1.5 m) boundaries with bare soil between habitats to motivate movement, and (2) absence of a visible elevation gradient, which could potentially bias movement decisions.

The experiment was conducted between 3 September and 27 September 2009. We established four 1 × 1-m release locations along edges at the soybean–prairie plot, and five 1 × 1-m release locations along edges at the soybean–corn plot. Our generalizations are restricted because there was only one plot per each treatment combination. However, the releases within a plot were considered independent, and release locations were ≥20 m from each other and established along boundaries with varying aspect orientations (i.e. north–south vs. east–west). We used 49 salamanders for this experiment, 40 of which were also used in the desiccation experiment. Juvenile salamanders were randomly assigned to treatments, release dates, and release locations within treatments, with the exception that each treatment combination received an equal number of individuals originally used in the desiccation experiment ($n = 20$). We released individuals only on days without measurable precipitation to avoid soil-surface temperature and humidity conditions being homogenized among matrix habitats by rain. Salamanders were fitted with radiotransmitters (Models A1015, A1025, and A1036, ATS, Inc., Isanti, Minnesota, USA) that weighed ≤8% body mass. Because we were primarily interested in short-term movements (<16 h), we affixed transmitters directly to the dorsal surface of each individual with cyanoacrylate (SuperGlue). Cyanoacrylate is commonly used to close skin incisions in amphibians (Gentz 2007), and it has been used to affix passive integrated transponder tags

externally to ambystomatid salamanders (Charney et al. 2009). On the day of releases, we affixed transmitters to individuals between 1400 and 1600 in the laboratory. Individuals were then transported to treatment plots and released between 1700 and 2000. We placed each salamander under a black bucket on a randomly assigned release location for two min of acclimation, and the bucket was removed with a 4-m rope. Salamanders were released at both plots on 6 of 11 release nights, and the average number of individuals released on any given night was 3. The time interval between releases at a given release location ranged from 1 to 10 days (median = 2). We released a total of 24 individuals in the soybean–prairie plot and 25 individuals in the soybean–corn plot.

We relocated and recovered radiomarked salamanders using an ATS R410 receiver (Isanti, Minnesota, USA) 12–16 h after release. Individuals were recovered with transmitters still affixed 82% of the time ($n = 40$ individuals). For each salamander that moved ≥1 m, we recorded total distance moved from the release location and the angle of movement (0° defined movement directly into soybean, 90° and 270° represented movement along ecotone). We included angles of movement for nine individuals for which only the transmitter was recovered, assuming that the transmitter location was representative of the individual's short-term movement orientation. Based on the desiccation experiment (see Results), our a priori prediction was that the mean direction of movement would be oriented towards soybean in both treatments. A V-test was used to test the null hypothesis that the distribution of angles was randomly distributed against the alternative that angles were clustered around 0° (Zar 1984). Statistical analyses were conducted in Oriana (version 3.13, Kovach Computing Services, Anglesey, Wales).

Results

Desiccation experiment

Individual mass varied among treatments and over time, and there was an interaction between treatment and time (Treatment: $F = 8.61$, $P = 0.0001$, df = 3, 47; Time: $F = 83.12$, $P < 0.0001$, df = 3, 163; Treatment × Time: $F = 18.86$, $P < 0.0001$, df = 9, 163). Individual mass at each time period also depended on

initial mass ($F = 456.81$, $P < 0.0001$, df = 1, 47). There were no significant block effects, either alone or in interaction with treatment or time (Block: $F = 1.09$, $P = 0.36$, df = 3, 47; Block $\times$ Treatment: $F = 0.94$, $P = 0.50$, df = 9, 47; Block $\times$ Time: $F = 0.94$, $P = 0.49$, df = 9, 163). Water loss was consistently low in forest and soybean plots and greatest in corn and prairie plots (Fig. 1a). Mass decreased over time in all habitats, with the exception of a slight increase in mass in soybean and prairie plots between 24 and 36 h. Overall, mass decreased faster in corn and prairie plots compared to soybean and forest plots. Two mortalities occurred in the prairie treatment between 36 and 48 h.

Differences in mass among treatments corresponded to variation in daytime air temperature (Fig. 1b) and humidity levels at the soil surface (Fig. 1c). Forest and soybean plots had lower daytime air temperatures and greater daytime humidities compared to corn and prairie plots. Variation in soil-surface air temperature and relative humidity among treatments was less pronounced at night than during the day. Canopy cover at the soil surface also varied significantly among treatments (ANOVA, $F = 25.43$, $P < 0.0001$, df = 3, 12; mean % closed canopy ± 1SE: corn = 83.56 $\pm$ 3.60, forest = 88.19 $\pm$ 5.63, prairie = 34.63 $\pm$ 17.52, soybean = 87.25 $\pm$ 2.52).

Movement orientation experiment

Of individuals moving ≥ 1 m after release (soybean–prairie: $n = 16$; soybean–corn: $n = 23$), the total distance moved averaged 16.7 m (range = 1.5–91.1 m; SD = 21.8 m) in the soybean–prairie treatment and 7.9 m (range = 1.3–40.0 m; SD = 8.0 m) in the soybean–corn treatment. Salamander movement directions were not randomly distributed in either treatment (V-test; soybean–prairie: $u = 1.61$, $P = 0.054$; soybean–corn: $u = 1.79$, $P = 0.037$), and movements were oriented towards soybean in both treatments (Fig. 2).

Discussion

Desiccation risk for *A. tigrinum* juveniles varied substantially among matrix habitats. Water loss was greater in open prairies than closed-canopy forests, supporting results from a previous desiccation study on pond-breeding amphibians (Rothermel and
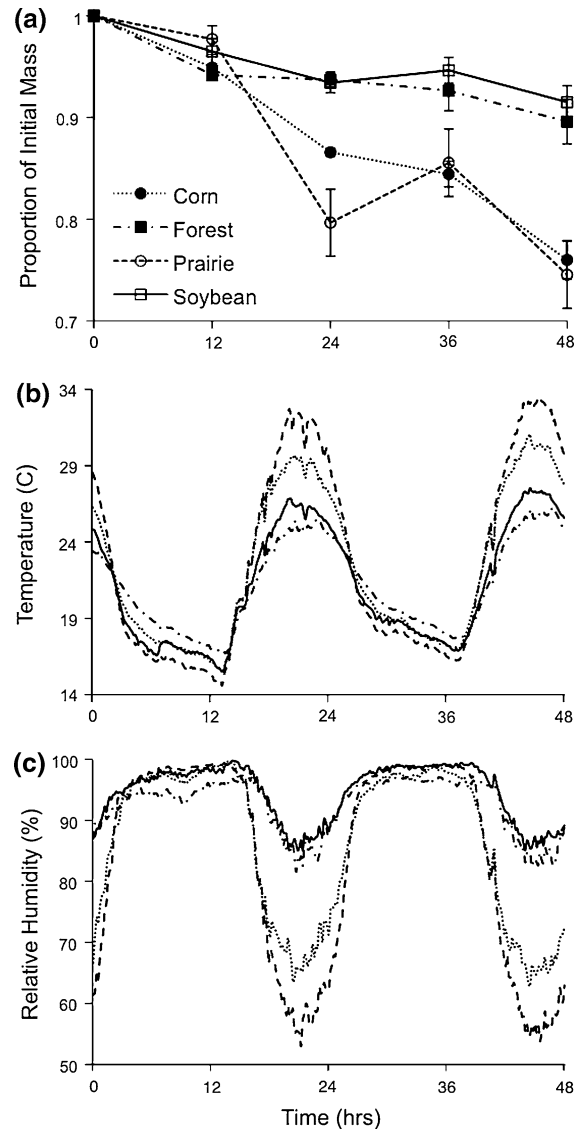

Fig. 1 Temporal patterns for (**a**) water loss (mean proportion of initial mass $\pm$ 1SE) for juvenile *A. tigrinum*, (**b**) air temperature, and (**c**) relative humidity at the soil-surface among corn, forest, prairie, and soybean treatments during a desiccation experiment in Illinois. Night intervals (1700–500) are 0–12 and 24–36 h, and day intervals (500–1700) are 12–24 and 36–48 h. Note that individual mass was used as the response variable in our analysis of water loss. Proportion of initial mass is presented for display purposes only

Semlitsch 2002). However, the two row crops dominating agricultural landscapes in the midwestern USA—corn and soybean—had different effects on desiccation. Water loss was equally low in forest and soybean, whereas it was high in corn and prairie.
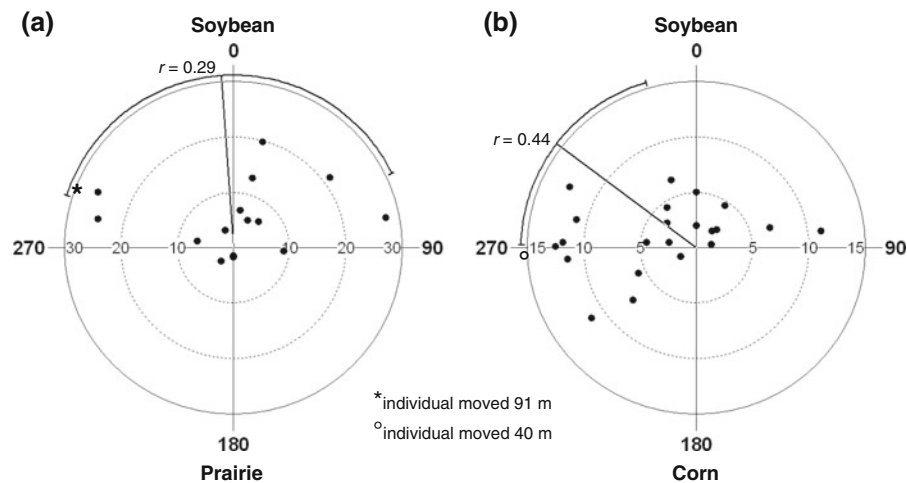
Fig. 2 Short-term (<16 h) angular orientations and linear distances moved for juvenile *A. tigrinum* released at edges between (**a**) soybean and prairie (*n* = 16), and (**b**) soybean and corn (*n* = 23) in Illinois. Orientation towards soybean was the a priori expectation based on a desiccation experiment (Fig. 1a). Direct movement into soybean was defined as 0°. *Black circles* represent both orientation and distance moved (m, represented by *concentric circles*) for individual salamanders. Mean vector and 95% confidence intervals are represented by *bold black lines*. Length of the mean vector (*r*) is also indicated

When individuals were given a choice to move between matrix habitats with variable desiccation regimes (soybean–prairie and soybean–corn), movements were oriented towards soybean, suggesting that (1) a physiological constraint influenced movement decisions, and (2) dispersal costs can vary significantly among crops in agricultural landscapes.

Dehydrated amphibians can be subject to greater predation risk (Rohr and Madison 2003) and lower survival (Rothermel and Luhring 2005; Rittenhouse et al. 2008, 2009) than hydrated animals. Negative consequences of dehydration on locomotor performance (Preest and Pough 1989) and habitat permeability during movement (Rothermel and Semlitsch 2002; Mazerolle and Desrochers 2005) have suggested that desiccation risk influences dispersal as well. Our results expand on this work by showing that *A. tigrinum* desiccation risk varies among common upland matrix habitats, and that juvenile salamanders orient movements toward low-risk habitat where dehydration should be reduced. Previous experimental studies on habitat choice at forest-clearcut boundaries indicate that many species prefer forested habitats, but these studies do not link movement decisions to measured desiccation risk (Chan-McLeod 2003; Rittenhouse and Semlitsch 2006; Stevens et al. 2006; Graeter et al. 2008). In our system, even

when given a choice between prairie and an agricultural crop, salamanders oriented towards soybean, which represented low desiccation-risk habitat. We cannot completely rule out the possibility that other factors confounded with matrix habitat (e.g., predation risk) influenced movement decisions, although we note that the only predation event during our experiment took place in soybean.

Variation in desiccation risk among habitats appears to be related to differences in air temperature and relative humidity levels at the soil surface, especially during the day (Fig. 1). Furthermore, these differences in microclimatic conditions may be related to canopy coverage at the soil surface, which varied significantly among treatments. Average canopy cover was greatest in corn, soybean, and forest, and lowest in prairie. Temperature and humidity differences between corn and soybean may be related to vegetation structure as well. In contrast to corn, soybean has dense, shrub-like foliage near the soil surface. Morning dew formation on soybean foliage was substantial, whereas dew formation was minimal in corn plots (B.J. Cosentino, personal observation). Dew formation on low-lying foliage may have kept daytime humidity levels high at the soil surface in soybean plots. Previous studies in forest-clearcut systems have shown that desiccation rate covaries

with daytime air temperature among habitats, but not with relative humidity (Rothermel and Semlitsch 2002; Rothermel and Luhring 2005). Soil moisture has also been correlated with amphibian desiccation in some cases (Rothermel and Semlitsch 2002), but not in others (Rothermel and Luhring 2005). Although surface movement occurs mainly at night when environmental conditions are relatively uniform, *A. tigrinum* movement can occur during the day (B.J. Cosentino, personal observation), and individuals using refuges are still exposed to variable daytime temperature and humidity conditions among habitats.

Of broad significance is the difference in *A. tigrinum* desiccation between corn and soybean, and the corresponding orientation of movements towards soybean when individuals were given a choice between corn and soybean. Agricultural landscapes represent 40.8% of land in the United States (USDA NASS 2007) and are composed of numerous crop types, but modeling and empirical studies of landscape connectivity have commonly treated agricultural land as a single, homogeneous land cover that is highly resistant to animal movement. We argue that this assumption can be too simplistic. Given previous work on effects of desiccation risk on movement rates and survival in amphibians (Preest and Pough 1989; Rothermel and Semlitsch 2002; Rothermel and

Luhring 2005; Rittenhouse et al. 2008, 2009), our results strongly suggest that crops can differentially influence movement decisions, habitat permeability, and individual survival. Such variation in dispersal costs among crops creates the potential for the spatial distribution and temporal rotation of crops to influence population processes.

When quantifying landscape connectivity, data on desiccation risk can inform the rank and magnitude of movement resistances for matrix habitats in least-cost (Adriaensen et al. 2003) or circuit theory (McRae et al. 2008) frameworks (Stevens et al. 2004; Rayfield et al. 2010). In our study area, a cost surface accounting for crop-specific desiccation risk varies greatly from a surface informed by expert opinion (Fig. 3). These surfaces represent alternative hypotheses on how landscape structure influences dispersal, and the relative support of connectivity metrics based on each cost surface can be evaluated using data on interpond movement, occupancy dynamics, or gene flow. Such an analysis would provide insight into how a key physiological constraint on amphibian movement—desiccation risk—scales up to influence metapopulation dynamics and population genetic structure.

Importantly, dispersal costs associated with desiccation risk in agricultural crops will vary temporally (Mazerolle and Vos 2006). Before planting,
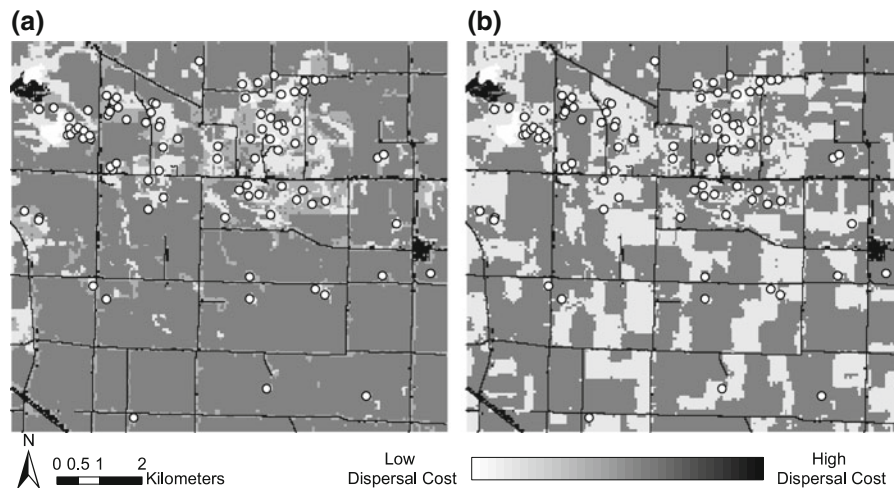

Fig. 3 Dispersal cost surfaces for *A. tigrinum* (**a**) representative of expert opinion and (**b**) based on empirical data on desiccation risk (Fig. 1a) for an agricultural landscape in northern Illinois, USA. The landscape is dominated by corn, soybean, forest, prairie, and developed areas. In the expert opinion surface, forest was assigned a lower cost than prairie, and costs were uniformly high among crops. In the surface based on empirical data, soybean and forest had lower costs than corn and prairie. Developed areas were assigned the highest cost in both surfaces. Cost values were fixed for each cover type. *Open circles* represent potential breeding wetlands used by *A. tigrinum*

agricultural fields are open and bare during spring in many parts of the United States. Thus, adults of spring-breeding amphibians may face a uniformly high risk of movement when migrating across agricultural fields. However, field-level tillage practices may influence desiccation risk. For example, the presence of old plant material in no-till fields may moderate desiccation risk by functioning as refuges, whereas tilled fields would be relatively barren at the soil surface. In a forested ecosystem, Rittenhouse et al. (2008) found that the presence of coarse woody debris in clearcuts moderates desiccation risk for anurans. In agricultural fields, desiccation risk likely declines as plant cover increases through the growing season, but we would expect greater among-crop variation in risk late in the growing season (July–September) when juveniles emigrate from ponds after metamorphosis. Finally, although crops such as soybean provide low desiccation risk-habitat, individuals emigrating during harvest may be susceptible to disturbance from agricultural machinery (Saumure et al. 2007).

When possible, we stress the utility of using experiments to understand how movement behaviors and decisions vary among matrix habitats encountered during dispersal. In this study, an experimental approach improved our understanding of how a physiological constraint was related to dispersal cost for *A. tigrinum* among matrix habitats, including agricultural crops. These results can inform resistance values in studies of landscape connectivity to assess how specific, proximate factors driving the disperser-matrix interaction scale up to influence landscape-ecological and evolutionary processes. Effective measures of spatial connectivity are needed to understand current distributions of species in agro-ecosystems and to predict responses to land-use change and climate shifts.

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