Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes

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Abstract. The dynamics of ecological communities emerge from the interplay of local and regional processes, but there are few long-term data on multiple interacting species across multiple sites to evaluate these processes. We report the population dynamics of two species of treefrogs, the spring peeper (*Pseudacris crucifer*) and the chorus frog (*P. triseriata*), in 37 ponds over 11 years. We examined the relation between larval traits of these species and responses to environmental change (a severe drought) at the local (pond) level, and the consequences to regional dynamics of the species. Consistent with experimental evidence, predators limited abundances of both species, competitive effects were undetectable, and pond hydroperiod and forest canopy cover affected species' presences and population sizes. The drought caused strong reductions in pond hydroperiods and predator densities, which led to increases in colonization probability and decreases in extinction probability for the chorus frog. These habitat dynamics resulted in the colonization of 15 new ponds and exponential growth in regional population size of the chorus frog. Colonization probability was positively related to pond connectivity. Pond occupancy rates for the spring peeper were relatively constant, but important source ponds on the landscape changed with the drought. Ponds with extensive forest canopy cover were sink habitats for both species, and high pond connectivity appeared to be necessary to maintain species' presences in these habitats. Landscape dynamics were responsible for changes in the fundamental spatial structure of species' populations, e.g., the chorus frog transitioned between approximations of a classic metapopulation and a patchy population over the course of the study. Many of these results were driven by the interplay of climate variation and spatial food web structure, indicating the importance of incorporating this interaction into metacommunity theory. Our results further indicate the crucial role of habitat (pond) heterogeneity to species persistence, i.e., moderating the potential Moran effects of spatially correlated weather conditions. Overall this study illustrates: (1) how natural systems constantly transition between metapopulation/metacommunity states typically treated as static in the literature, (2) the extensive interconnection of phenomena at different scales in ecology, and (3) the importance of habitat heterogeneity and landscape context for amphibian conservation strategies.

Key words: anurans; colonization; extinction; food webs; local and regional processes; long-term data; metacommunity; metapopulation; pond hydroperiod; predators; Pseudacris *spp.; sink habitats.*

Introduction

Ecological communities exist in a spatial and temporal context and, thus, there is an inevitable interplay between local species interactions and regional processes in generating and maintaining the structure of these communities. The clear challenge facing population and community ecologists is to develop a conceptual framework that synthesizes the influence of processes operating at these different scales. There have been significant advances incorporating these processes in theory and exploring the consequences of their interplay at both the population and community level (e.g.,

Hanski 1999, Leibold et al. 2004). While it is clear that the different conceptual models proposed (e.g., patchy vs. classic metapopulations, neutral vs. species sorting metacommunities) identify properties and processes that are relevant to natural systems, these systems inevitably exhibit a mosaic of characteristics of the models. Thus, there is a critical need for empirical work that evaluates the appropriateness of these different models, or indicates what synthesis of processes is most relevant. However, there are still relatively few systems for which there are long-term data on the dynamics of a number of interacting species on multiple sites to provide such inferences. Ideally, one would like to employ such data to understand the relation between species traits and their responses to environmental change or species interactions at the local level, and follow the conse-

quences of these to the spatial and regional dynamics of these species and the subsequent feedbacks to local dynamics.

Amphibian communities hold much promise for advancing a synthesis of local and regional processes in metapopulation and metacommunity biology (Werner et al. 2007a). Larval amphibians have provided a model system for the study of local species interactions (e.g., Wilbur 1997, Morin 1999), and considerable information exists on the nature of these interactions and the relation between species traits and performance. Additionally, amphibian populations are cited as prime candidates to exhibit metapopulation/metacommunity structure as larval interactions are restricted to ponds distributed over a terrestrial landscape (e.g., Sjogren-Gulve 1994, Alford and Richards 1999, Gamble et al. 2007). Because both amphibians and many of their larval predators have complex life cycles that facilitate dispersal between ponds (sites of larval interactions), it is likely that local pond communities will interact extensively through regional processes. However, considerable controversy exists regarding the nature of the spatial structure of amphibian populations, in part because of insufficient information on their dispersal capabilities and the fact that a "ponds as patches" abstraction fails to incorporate the role of the terrestrial habitat in juvenile/adult dynamics (as opposed to simply a matrix to be traversed in dispersing between ponds; Marsh and Trenham 2001, Smith and Green 2005). Thus, it seems clear that understanding the consequences of spatial structure will be key to predicting amphibian community structure and species persistence, but there is limited empirical evidence that sheds light on the actual nature of this spatial structure.

In this study, we monitored the dynamics of two species of treefrogs, the spring peeper (*Pseudacris crucifer*) and the western chorus frog (*P. triseriata*), and their potential predators and competitors in a large number of ponds over 11 years. Fortuitously, this monitoring included an ENSO (El Niño/Southern Oscillation) related drought, and this climate variation presented an uncommon opportunity to view the interaction of local and regional processes as the two species responded differently to landscape dynamics. In order to interpret species responses, we asked what local factors including predators, competitors, and pond characteristics were associated with species' performance in ponds, and how these factors were influenced by the drought. Of particular interest were those factors that were related to source–sink relations for these species. We then asked what role pond connectivity played in local and regional dynamics of species populations and the patterns in pond occupancy and maintenance of presences in sink habitats. Finally, we determined which of these local and regional factors were associated with the colonization/extinction dynamic of ponds for each species. In conjunction with detailed experimental studies that have elucidated the nature of local

interactions in these species (e.g., Smith 1983, Skelly 1995a, b, 1996, Smith and Van Buskirk 1995), our data permit a mechanistic interpretation of the factors responsible for trends locally in species' densities within ponds and how these changes then influence regional population sizes and pond connectivity and occupancy patterns. Our results clearly demonstrate the role of habitat diversity in maintenance of species populations in the face of temporal variation in local habitat characteristics, and provide insights on the role of spatial structure in amphibian populations.

The system and background experimental work

The spring peeper and chorus frog are small (adult size 20–30 mm snout–vent length [SVL]) congeneric hylid frogs that in Michigan breed in early spring and metamorphose from ponds two to three months later. Typically, the two species replace each other on the hydroperiod gradient from more ephemeral and largely predator-free ponds where chorus frogs dominate, to longer hydroperiod, predator-rich ponds where spring peepers dominate (Skelly 1996). After metamorphosis, juveniles move into lowland marshes, wetlands, and moist upland forests (Delzell 1958, Alexander 1965).

Experimental studies both in the laboratory and field have outlined the mechanistic basis for the differences in *Pseudacris* distributions on the hydroperiod gradient (Smith 1983, Skelly 1995a, b, 1996, Smith and Van Buskirk 1995). Larvae of the two species differ markedly in activity rates with chorus frogs being more active than spring peepers (e.g., Smith 1983, Smith and Van Buskirk 1995, Skelly 1996). Consequently, chorus frog larvae grow faster; Skelly (1996) reported that chorus frogs metamorphosed an average of 18 days earlier than spring peepers. Because it is more active, however, the chorus frog is more vulnerable to predators and typically inhabits shorter hydroperiod ponds, which are relatively predator-free. The reduced activity level of the spring peeper comes at a significant growth cost (requiring longer hydroperiod ponds), but enables it to maintain populations in the face of higher predator densities (Skelly 1996). Field experiments conducted with these two species confirm the strong influence of predators on their distribution and abundance, and in addition, suggest that interspecific competitive effects are weak or undetectable at natural densities (Skelly 1995a, b, Smith and Van Buskirk 1995). The differences in species' performance in different pond types thus revolve around an activity-mediated growth rate–predation risk trade-off (Werner and Anholt 1993).

In addition to pond hydroperiod and predator density, studies also have identified forest canopy cover over ponds as an important variable influencing performance of *Pseudacris*. Halverson et al. (2003) reported that pond occupancy, larval density, larval size, and developmental stage of spring peepers were positively correlated with pond light level in New England. Spring peepers transplanted into open- and

closed-canopy ponds grew 83% faster in open-canopy ponds. Periphyton production was nearly twofold higher in open-canopy compared to closed-canopy ponds, and laboratory experiments confirmed that resource levels were at least in part responsible for poorer performance in closed-canopy ponds (Skelly et al. 2002). The above studies thus provide an excellent foundation on which to interpret changes in local densities of *Pseudacris* as pond characteristics change, and how this should affect patterns of pond occupancy and regional population sizes.

METHODS

The monitoring program

We monitored the distribution and abundance of all amphibians and their predators over 11 consecutive years (1996–2006) in 37 water bodies on the University of Michigan's E. S. George Reserve (hereafter ESGR; see Werner et al. 2007*a*, *b*). The ESGR is a 525-ha tract located 40 km northwest of Ann Arbor, Michigan (42°28′ N, 84°00′ W). Areas of sampled ponds were obtained from either bathymetric maps (27 ponds, adjusted for drying when making total population estimates), or from aerial photographs (10 ponds; see Werner et al. 2007*b*). To estimate pond hydroperiods, we installed depth gauges in the fall of 1998, and water depths have been recorded at frequent intervals since that time. Prior to 1998, we have data on water levels for 22 of the ponds in the fall of most years between 1988 and 1997. Forest canopy cover over the ponds was quantified using a spherical densiometer (Halverson et al. 2003, Werner et al. 2007*b*).

We quantitatively sampled tadpoles and their predators by "pipe sampling" and dipnetting ponds during the third week in May (with the exception of 1996–1997 when we sampled late May–early June). The pipe sampler was a 76×36 cm section of aluminum pipe (fitted with handles), which sampled 0.1 m^2 of the sediments and associated water column. The sample was taken by quietly approaching an area and quickly thrusting the pipe through the water column and into the sediments to seal the sample area. Nets (22×27 cm; 1×2 mm mesh size) were employed to remove all animals from the sampled water column and the first few centimeters of the sediments. Circular sweeps of the net were taken until at least 10 consecutive sweeps were made without capture of any animals (see Mullins et al. 2004 for an evaluation of the technique). We took 20–40 pipe samples depending on pond size (except in two ponds <75 m^2 where we took 10 samples) haphazardly located at least 2 m apart and dispersed among the pond microhabitats. If pond area was much reduced due to drying, the number of pipe samples was reduced accordingly.

After pipe sampling, we employed the same nets to dipnet the ponds for the equivalent person-minutes as the number of pipe samples taken. In cases where density estimates were employed in analyses and the species was only obtained in the dipnet samples (12.7% of cases for spring peepers and 18.2% for chorus frogs), we estimated density from dipnet catch per unit effort (obtained from regressions of pipe density estimates against *Pseudacris* captured per person-minute dipnetting when individuals were captured by both techniques; see Werner et al. 2007*b*). There was a strong relationship between pipe densities and capture per unit effort dipnetting ($r = 0.92$, $F_{1,161} = 824.3$, $P \ll 0.001$). Based on this sampling effort, if larvae were binomially or Poisson distributed, our 95% detection threshold for a species occurred at densities on the order of 1 larva/3.3 m^2 in the larger ponds (see Werner et al. 2007*b*). In 2003–2004 we also dipnetted some of the ponds in the middle of June; these ponds filled late in those years so eggs would not have hatched by the time we sampled in May. We also conducted 10–15 anuran call-count surveys each year by approaching each pond between dusk and midnight during the breeding season and listening for about five minutes to identify the calling species and assign each species a calling intensity index (0, no callers; 1, 1–10 callers; 2, 11–50 callers; and 3, >50 callers). For all analyses, we employed the maximum chorus size recorded for a species that year in a pond.

In addition to the *Pseudacris*, all potential predators (including fish, salamander larvae, Odonata, Hemiptera, Coleoptera, Areaneae, Hirudinea) were collected from pipe and dipnet samples, preserved, and identified to species where reliable keys were available (most taxa), or to genus when this was not possible. Based on literature accounts, ultimate size, and our experience we considered the following invertebrate taxa potential *Pseudacris* predators: odonate nymphs of the families Aeshnidae, Cordulidae, Gomphidae, and Libellulidae, larval beetles of the larger dytiscids (*Dytiscus*, *Hydaticus*, *Colymbetes*) and hydrophilids (*Hydrochara*, *Dibolocelus*), and larger adult dytiscids (*Dytiscus*, *Hydaticus*, *Colymbetes*, *Acilius*, *Graphoderus*, *Agabus*, *Rhantus*, *Ilybius*). Other taxa included were Belostomatidae, Notonectidae, Nepidae, and the Megaloptera (only *Chauliodes*). All predators were measured and samples were dried to obtain length–dry mass regressions for predator biomass estimates. Anuran biomass estimates were obtained from biomass–SVL regressions (Werner et al. 2007*b*).

Statistical procedures

Regional patterns.—We first assessed the temporal patterns in regional population sizes (sum across ponds of mean larval densities × bathymetrically corrected areas, i.e., areas adjusted for dying on each sampling date) and pond occupancy rates (fraction of ponds occupied of those that ever contained the species) for these species. Because occupancy rates in open- and closed-canopy ponds have different implications (see *Statistical procedures: Local factors, canopy cover*) we assessed these separately. We then asked whether these patterns were consistent with the following hypotheses

concerning local and regional factors potentially affecting these species.

Local factors, predation.—Larvae of both *Pseudacris* species are small (e.g., typically <12 mm SVL at metamorphosis), and therefore vulnerable to a wide range of predator species. To assess predator effects we plotted larval densities of both species against estimated dry mass biomass of predators (fish, salamanders, and invertebrates) for all pond–year combinations. These plots resulted in triangular-shaped clouds of points in the lower left corner of the graphs. This pattern is expected if predation constrains species' densities under an upper boundary, and beneath that boundary other factors can further limit densities (e.g., Lessin et al. 2001). To estimate this upper boundary, we fit regressions to the highest values of the dependent variable in equal-width classes of the independent variable (Blackburn et al. 1992). We present the results for eight equal-width classes, which Blackburn et al. (1992) suggest provide the best estimate of the true slope of the relationship (we assessed stability of the results by comparing these results with those of all other equal-width classes between 6 and 12). We employed the curve fit function in SPSS to compare fits of linear, logarithmic, and exponential functions to the data.

Local factors, competition.—We next asked if there was evidence of competitive effects in patterns of larval size and developmental stage of these species. We constructed regressions of SVL and developmental stage (Gosner stage) vs. the biomass of conspecific or heterospecific treefrogs, or the biomass of all larva of anuran species in the pond. Because of potential differences in phenology across years, we first standardized SVL (Gosner stage) to the mean across all ponds that year. To account for the effects of extreme interannual variation in densities within ponds, we considered pond-years as independent data points (e.g., the coefficient of variation in total anuran larval biomass across years within a pond averaged over all ponds was 154% ± 10%). However, it is possible that ponds might exhibit unique (negative) size–density relationship while the aggregate across ponds showed no relationship, so we also examined each pond individually for potential relations between competitor biomass and standardized SVL across the 11 years.

Local factors, canopy cover.—Based on the literature, we hypothesized that pond canopy cover would have marked effects on these species. We classified ponds as open canopy if forest cover was <75% and closed canopy if cover was ≥75%. Werner et al. (2007b) found that anuran species richness declined precipitously in ponds with >75% cover, and the two *Pseudacris* also exhibited strong declines in densities in these ponds. To assess whether closed-canopy ponds were sink habitats for these species, we compared realized rates of population increase in open- and closed-canopy ponds following a colonization event. To do this we extracted all absence/presence/presence sequences from the data,

i.e., an absence in year 1 followed by a colonization in year 2 leading to an extant population in year 3, and compared the ratios of population sizes in years 3 and 2. We also compared mean and maximum densities of these species in open- and closed-canopy ponds. Finally, we compared the probability of detection of a larval population in open- and closed-canopy ponds given that a male chorus was detected in that pond in the spring.

The environmental driver and local factors.—The ESGR experienced a significant drought beginning in 1998. We hypothesized that the drought would affect these species through availability of ponds for oviposition, ability of the species to complete development, and effects on their predators. We assessed the impact of the drought by comparing the mean fraction of ponds that held water in October prior to 1998 (data for the years 1988–1991 and 1995–1997) vs. 1998–2006. We were able to do this for the 22 ponds where we had data on fall drying before the initiation of the current monitoring program in 1996. We also compared mean hydroperiod of ponds before and after initiation of the drought period where we had more complete data on drying times in all 37 ponds (i.e., post-1996).

To assess the impact of the drought on predator densities, we compared May biomass densities of predators for three categories of pond drying: ponds that (1) contained water continuously from at least midsummer of the previous year through spring of the current year, (2) dried in the fall of the previous year but contained water in the spring of the current year, and (3) dried in the fall of the previous year and were dry in spring of the current year but filled before the May sampling date (if ponds were dry in the spring they were always dry the previous fall). These analyses were conducted including all predator types; parallel analyses were also conducted on caudate and invertebrate predator biomass separately to assess whether different predator types were affected differentially by the drought.

Regional factors, pond connectivity.—We hypothesized that landscape or regional context in addition to local factors was important to dynamics of these species and therefore assessed patterns in pond connectivity. We employed the connectivity index for pond i, S_i, taking into account distances to all other ponds on the ESGR containing that species and their respective population sizes (reviewed in Moilanen and Nieminen [2002] and Winfree et al. [2005]):

$$S_i = \sum \exp(-\alpha d_{ij})N_j$$

where α scales the effect of distance to dispersal ($1/\alpha$ is the mean dispersal distance), d_{ij} is the distance (edge to edge) between ponds i and j, and N_j is the larval population size of the species in pond j (thus we assume larval population size is correlated with numbers of dispersing individuals). This index therefore accounts for spatial position and population densities of ponds

but is independent of intervening terrestrial habitat characteristics.

To employ this index, we need to know the time to reproductive maturity and the average dispersal distance for the two *Pseudacris* species. Time to first reproduction is required because we need to know when our measure of population density, the larval population in pond *j*, potentially influences the breeding adult population of pond *i*. Adult survivorship of these species is sufficiently low that the majority of individuals reproduce once (Collins 1975, Smith 1987). Average dispersal distance enables an estimate of α.

An overview of the literature suggests that individuals can return to breed the first spring after metamorphosis, and almost certainly in the second year. For chorus frogs, Smith (1987) found that marked individuals on Isle Royale returning the first year after metamorphosis were virtually all males with most females returning in their second year. This population is considerably north of the ESGR, with a shorter growing season and presumably slower juvenile growth rates than on the ESGR. Whitaker (1971) indicated that individuals in central Indiana could return in a year. Based on growth rates of chorus frog populations in our ponds the year following initial colonization (mean increase in population size in 13 ponds of 4.3 ± 1.3-fold where a larval population was detected after a three-year absence from the pond), it appears that a sizeable fraction of populations metamorphosing the previous summer returned to breed the following spring. For the spring peeper, Delzell (1958) concluded that some individuals of both sexes grew large enough to return the first year to breed at a site within 20 km of the ESGR. Lykens and Forester (1987) estimated most spring peepers do not breed until the second year based on skeletochronology. Taken together, these studies suggest that some weighting of population sizes the previous two years in neighboring ponds would constitute the most appropriate connectivity measure for a focal pond *i*. In the absence of definitive data on proportions of populations maturing in the first year, we simply employed a mean of the S_i values calculated for years $t - 1$ and $t - 2$ (i.e., all larval N_j populations that likely contributed adults to pond *i* in year *t*).

Average dispersal distances for these species appear to be quite short; Kramer (1973) marked adult chorus frogs with ^{60}Co and over four months all recaptures with the exception of two individuals were made within 150 m of the breeding pond and most within 100 m. Rittenhouse and Semlitsch (2007) construct dispersal kernels for a number of amphibians and estimate that 50% isopleths occurred at just under 100 m (183 m for frogs but these were larger species). Maximum dispersal distances have been reported to be 573 m for spring peepers (Delzell 1958) and 685 m for chorus frogs (Spencer 1964). Thus, it appears that mean dispersal distances for these two species are likely under 100–150 m. Johnson et al. (2007) also found that the mean distance from breeding ponds

for gray treefrogs (*Hyla versicolor*) was <100 m. We employed a mean dispersal distance of 100 m for both species, but also conducted analyses for mean dispersal distances from 75 to 300 m to assess the robustness of our conclusions.

Using these values, for each year we estimated the mean connectivity across all ponds that ever contained the specified species on the ESGR, and tested for differences in mean connectivity before and after the drought. We also determined the relation between pond connectivity and the presence and magnitude of male choruses for each species. Additionally, we compared the average connectivity of ponds that exhibited presence/presence sequences to those that exhibited absence/absence sequences. Finally, we examined relations between connectivity and larval densities. Because densities of these species were related to pond area, hydroperiod, and canopy cover, we examined the relation between connectivity and residuals of larval density from regressions of density against the first principal component extracted from pond area, hydroperiod, and canopy cover.

Dynamics, extinction and colonization probabilities.— To relate the above local and regional factors to the dynamics of these species on the ESGR landscape, we estimated extinction and colonization probabilities and employed logistic regression analyses.

We estimated extinction and colonization probabilities based on larval populations in a pond. Thus, we are using the terms colonization and extinction in a restricted sense; true extinction requires that the adult population associated with a pond disappears (see *Discussion*).

Larval extinction probability, p_e, was calculated between each pair of consecutive years (e.g., Gotelli and Taylor 1999) where:

$$p_e = [\text{number of ponds in which a presence (at time } t) \\ \text{was followed by an absence (at time } t + 1)] \\ \div (\text{number of ponds occupied in year } t).$$

Similarly, the probability of colonization, p_c, was:

$$p_c = [\text{number of ponds in which an absence (at time } t) \\ \text{was followed by a presence (at time t} + 1)] \\ \div (\text{number of ponds unoccupied in year } t).$$

In all cases we only included ponds in analyses that had been known to have had a presence of the species in question at least once during the 11 years. We also calculated extinction probabilities using the likelihood estimators suggested by Clark and Rosenzweig (1994). This procedure estimates extinction rates including those "hidden"; i.e., extinctions in a year followed by colonization the succeeding year so that the sample record actually exhibits a presence/presence sequence. Because literature accounts of these two species indicate that individuals can achieve reproductive status in 1–2 years, we also estimated parameters assuming that the

species had to be absent two consecutive years to constitute extinction, and that a colonization event could only occur if the pond was unoccupied the two previous years.

The above probabilities assessed region-wide patterns in colonization and extinction through time regardless of hydration status of the pond. In some pond-years, ponds lacked water during the breeding season or dried prior to our sampling in May precluding establishment of treefrog populations. We report the number of extinction events and ponds unavailable for colonization for each species due to drying, and then exclude these pond-years and explore what characteristics of ponds in addition to this catastrophic factor influenced the probability of extinction or colonization with logistic regression.

Dynamics, logistic regression.—For these analyses we employed multiple logistic regression with the following binary response variables: (1) an extant population in a pond in a given year went extinct in the following year or did not, and (2) a pond without that species in a given year was colonized or not in the following year. We chose predictor variables that we deemed likely to affect colonization and extinction probabilities. Predictor variables for models of extinction probability were: (1) proportion canopy cover over pond, (2) proportion days wet the previous summer, (3) connectivity, (4) population size the previous year, (5) competitor biomass in year $t - 1$, (6) competitor biomass in year t, (7) predator biomass in year $t - 1$, and (8) predator biomass in year t. Predictor variables for models of colonization probability included: (1) proportion canopy cover, (2) connectivity, (3) competitor biomass in the current year, and (4) predator biomass in the current year. Thus, the extinction models included variables from the previous year as these could affect extinction of a population, whereas the colonization model only included variables for the current year when the colonization potentially could occur. Variance inflation factors were computed for all correlations among predictor variables and none exceeded 1.7, indicating that multicollinearity was not a problem.

Overall evaluation of the full models was made by comparing their log-likelihoods with those of the corresponding reduced models (i.e., constant only, employing the log-likelihood ratio statistic and the G^2 test; e.g., Quinn and Keough 2002). This procedure tests the hypothesis that the logistic model was more effective than the null model at predicting response variables. Statistical significance of individual regression coefficients (H_0 that $\beta_i = 0$) was evaluated by fitting a series of reduced models omitting the specified factor and comparing the fit to the full model. If the G^2 test was significant, this indicated that inclusion of that factor made the full model a better fit to the data than the reduced model (Quinn and Keough 2002). Goodness of fit was assessed by the Hosmer-Lemeshow test. The initial spring peeper extinction model produced a very

poor fit to the data and a counterintuitive result (connectivity positively related to extinction). Examination of the data indicated that this result was due to an apparent extinction in one extremely highly connected marsh (separated from another large marsh by a low dam). Spring peepers called in this marsh and fortunately we had dipnet samples from June in that marsh (in addition to the May samples), which documented presence of spring peeper larvae. We corrected the datum for this marsh to a presence/presence sequence and present the analyses with the corrected datum. Significant variables were the same in the two models except for connectivity (became insignificant) and population size the previous year (became significant).

Dynamics, pond synchrony.—In order to assess the synchrony in population dynamics across ponds and responses to changing environmental conditions, we estimated the rate of change in population size for each pair of years for each species in all ponds. Rate of change was measured as: $[\ln(N_t) - \ln(N_{t-1})]/\ln(N_{t-1})$. Because colonization and extinction events represent positive and negative changes in population, respectively, we also plotted these on figures displaying synchrony among populations.

RESULTS

General patterns

Spring peepers and chorus frogs bred in a large array of ponds on the ESGR; presences of both species were recorded in 25 of the 37 ponds. There were four additional ponds where only spring peepers were recorded and three ponds where only chorus frogs were recorded. Densities of the spring peeper averaged 6.9 ± 1.7-fold greater than those of the chorus frog in ponds where the two were found coexisting.

The two species exhibited very different trends in regional population sizes over the study period (Fig. 1). Spring peeper regional abundance peaked in 2001–2002, but with the exception of these two years regional population sizes ranged between 400 and 1490 × 10³ larval individuals (Fig. 1). The number of ponds occupied by this species also was fairly constant over the study period (20.5 ± 0.9 ponds/yr). The occupancy rate of closed-canopy ponds was lower than that of open-canopy ponds (47.3% ± 6.3% vs. 82.2% ± 3.7%, respectively, mean ± SE, $t = 4.79$, df = 20, $P < 0.001$; Fig. 1).

Regional population sizes of the chorus frog, however, differed markedly between 1996–2000 and 2001–2006 (Fig. 1). The estimated regional population size of the chorus frog swelled from 48 500 in 2000 to 253 200 in 2001, and remained large through 2006 (mean 1996–2000; 24 000 ± 4100 individuals, and after 2000; 331 600 ± 62 600 individuals, t test, $t = 4.4$, $P = 0.002$). Correspondingly, pond occupancy rates increased dramatically in 2001. Over the study period, only one pond contained chorus frogs in every year, and the chorus frog averaged only 4.6 ± 0.8 occupied ponds between
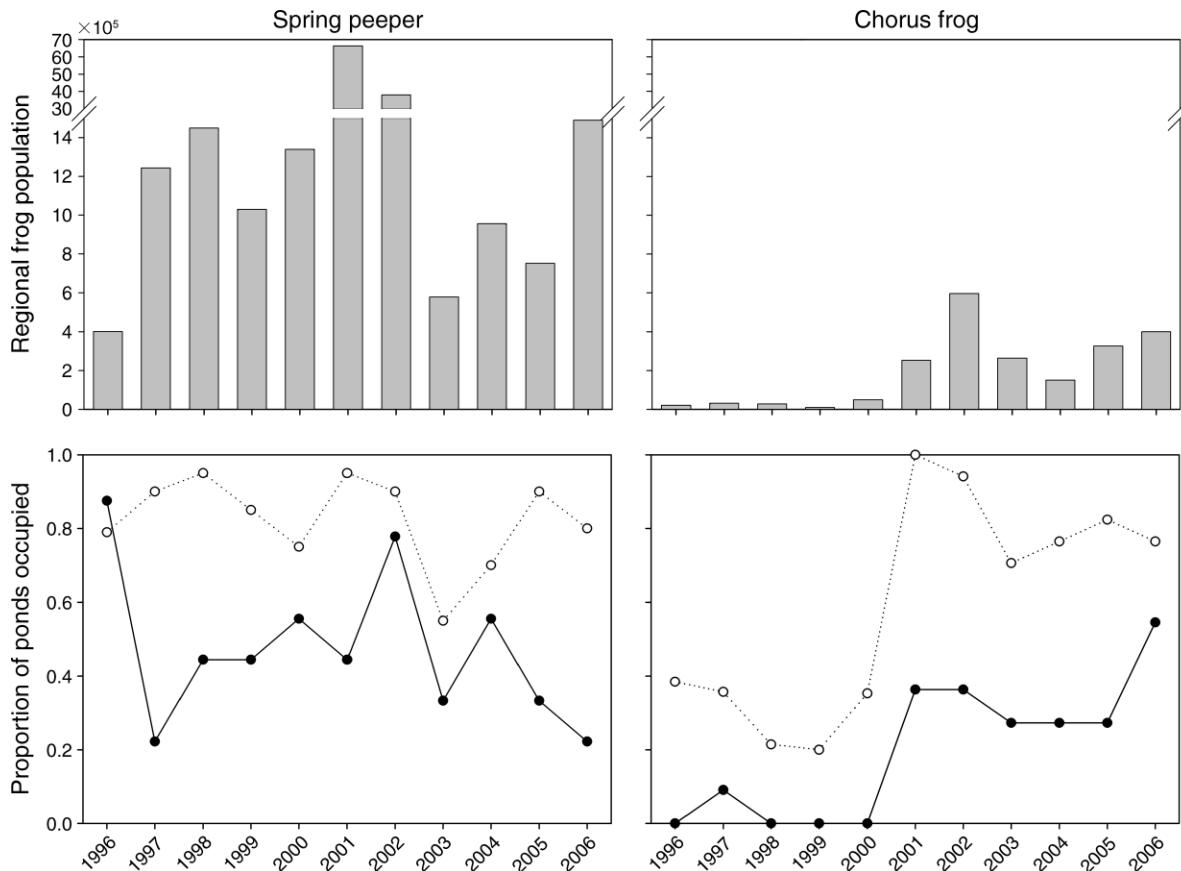
FIG. 1. Regional population sizes and fraction of available open-canopy (open symbols, dashed lines) and closed-canopy (solid symbols, solid lines) ponds occupied by the spring peeper (*Pseudacris crucifer*) and chorus frog (*P. triseriata*) on the E. S. George Reserve, near Ann Arbor, Michigan, USA, 1996–2006.

1996 and 2000, but 18.0 ± 2.4 occupied ponds after that (t test, $t = 11.3$, $P < 0.001$). In 2000 there were six extant populations of chorus frogs, and the following spring (2001) the chorus frog colonized 15 new ponds. Occupancy rate of closed-canopy ponds again was lower than (and largely parallel to) that of open-canopy ponds (19.8% ± 5.7% vs. 59.2% ± 8.9%, respectively, $t = 3.73$, df = 20, $P = 0.001$; Fig. 1).

Despite differences in overall population trends, both species exhibited explosive growth in regional population sizes in 2001–2002, and substantial declines in population in 2003 (Fig. 1). The declines in 2003 were due to spring drying in a number of the ponds that extended beyond the breeding period (in 2000 most ponds filled between 10 and 21 April, but in 2003 filling was delayed until 30 April to 4 May (which is the tail end of the breeding season). Consequently, the chorus frog was found in only 15 ponds in 2003 compared to 20 ponds in 2002, and the spring peeper in only 14 ponds as compared with 25 ponds the previous year.

Local factors

Predation.—Plots of species densities vs. predator biomass densities clearly suggested that predators constrained populations of both species (Fig. 2). Best fit upper boundary relations were nonlinear and highly significant for both species (Fig. 2). Maximal densities of predators with which species were ever associated are a crude estimate of the density of predators that would potentially exclude species from a pond. These values were just under 1500 mg/m^2 for the chorus frog and just over 4000 mg/m^2 for the spring peeper, indicating that the spring peeper was capable of tolerating a predator biomass over twice that of the chorus frog.

Competition.—There was little evidence of competitive effects influencing these species. There was a significant positive relationship between standardized SVL (hereafter simply SVL) and intraspecific biomass for the spring peeper ($F_{1, 177} = 47.6$, $P < 0.001$) and for the chorus frog ($F_{1,97} = 8.8$, $P = 0.004$, considering all pond-years as independent data points). Results were similar for interspecific effects between these species; there was a significant positive relationship between chorus frog SVL and spring peeper biomass, and spring peeper SVL was unrelated to chorus frog biomass (Fig. 3). If we considered potential interspecific effects from anuran larvae of all species, both species exhibited significant positive relationships between SVL and total
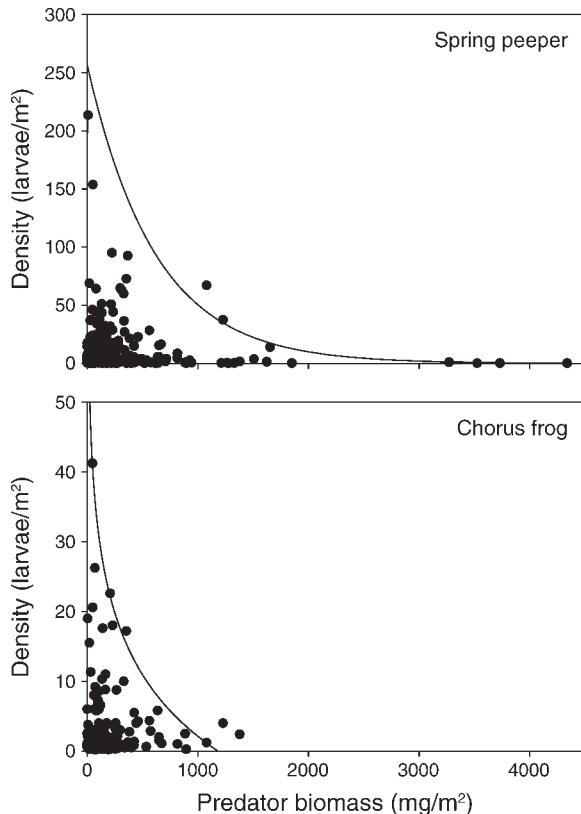
FIG. 2. Density of spring peeper and chorus frog larvae found in ponds as a function of predator biomass for all pond years combined. Lines are upper boundary fits. For the spring peeper, the exponential model provided the best fit (equal-width class of 8, $R^2 = 0.99$, $P < 0.001$), and regressions employing all equal-width classes (6–12) were significant (all $P < 0.005$). No slopes were more than 3.7% different than when using 8 classes. For the chorus frog, the logarithmic model provided the best fit (equal-width class of 8, $R^2 = 0.97$, $P < 0.001$), and again regressions for all equal-width classes were significant (all <0.001); no slopes were more than 5.4% different than when using eight classes.

biomass of larval anuran species in the ponds (Fig. 3). Results for all relationships were identical if developmental stage (standardized Gosner stage) rather than SVL was employed in the regressions.

Because relationships within individual ponds could be obscured in the global analyses, we also examined data for individual ponds across years. Intraspecific regressions for the spring peeper were significant in only four of 25 ponds and three of the four had positive slopes. For the chorus frog the regression for only one of 20 ponds was significant, and it also had a positive slope. Interspecific relationships were not significant for the spring peeper ($n = 19$ ponds), and only three of 18 regressions were significant for the chorus frog, and two of these three had positive slopes. The result was the same for SVL vs. biomass of all anuran larvae in the ponds. For spring peepers there were 25 ponds with multiple data points, and only three regressions were

significant and all were positive. Similarly, only one of 21 regressions was significant for the chorus frog and it also was positive. Thus, across all comparisons only two of 12 significant relationships exhibited negative slopes.

Canopy cover.—Closed-canopy ponds were sink habitats for these species. We extracted all absence/presence/presence sequences in ponds from the data, i.e., a colonization in year 2 followed by an extant population in year 3. In closed-canopy ponds, the mean ratio of population sizes in year 3 compared to year 2 (i.e., growth of the population) was 0.84 ± 0.30 for the chorus frog, and 0.43 ± 0.23 for the spring peeper. In contrast, newly established populations in open-canopy ponds exhibited population growth ratios of 4.23 ± 1.0 for the chorus frog and 2.80 ± 0.68 for the spring peeper. This pattern also was reflected in the fact that pond occupancy rates were lower in closed-canopy ponds (Fig. 1), and mean and maximum densities of these species were much higher in open-canopy ponds. Mean densities for spring peepers were fivefold, and for chorus frogs sixfold, higher in open-canopy ponds (*t* test for both species, $P < 0.001$), and the maximum densities achieved averaged 10.6-fold higher for spring peepers and eightfold higher for chorus frogs in open-canopy ponds (*t* test for both species, $P < 0.017$). Male calling intensities, however, were much more similar than larval abundances in open- and closed-canopy ponds. We compared the mean calling intensities for these species in ponds of comparable sizes (closed canopy, 340–2500 m² and open canopy, 198–2500 m²) after 2000. For the spring peeper calling intensities averaged 2.1 ($n = 12$) for open-canopy ponds and 1.7 ($n = 9$) for closed-canopy ponds. Similarly, for the chorus frog calling intensities were 1.7 ($n = 10$) and 1.3 ($n = 9$), respectively. However, the probability of detection of a larval population in May given presence of a male chorus in the spring also was lower in closed-canopy ponds, averaging only 49% (chorus frog) and 57% (spring peeper) of that for open-canopy ponds ($\chi^2 = 39.4$, $P \ll 0.001$ for spring peeper and $\chi^2 = 27.2$, $P \ll 0.001$ for chorus frog, on frequencies of presence/absence given calling in open- and closed-canopy ponds). This trend was nearly parallel across all calling intensity levels, suggesting that presence of calling males was less likely to result in establishment of a larval population in closed-canopy ponds. Finally, for both species 88% of the ponds on the ESGR that never produced a larval presence were closed-canopy ponds. Indeed, despite the fact that a number of closed-canopy ponds were occupied by these species (Fig. 1), across years the open-canopy ponds accounted for 97.7% ± 0.5% (spring peeper) to 99.1% ± 0.3% (chorus frog) of the regional populations of these two species. All of these patterns indicated that closed-canopy ponds were consistently sink habitats for these species.

The environmental driver and local factors

The ESGR experienced a significant drought beginning in the late summer of 1998; most ponds held water
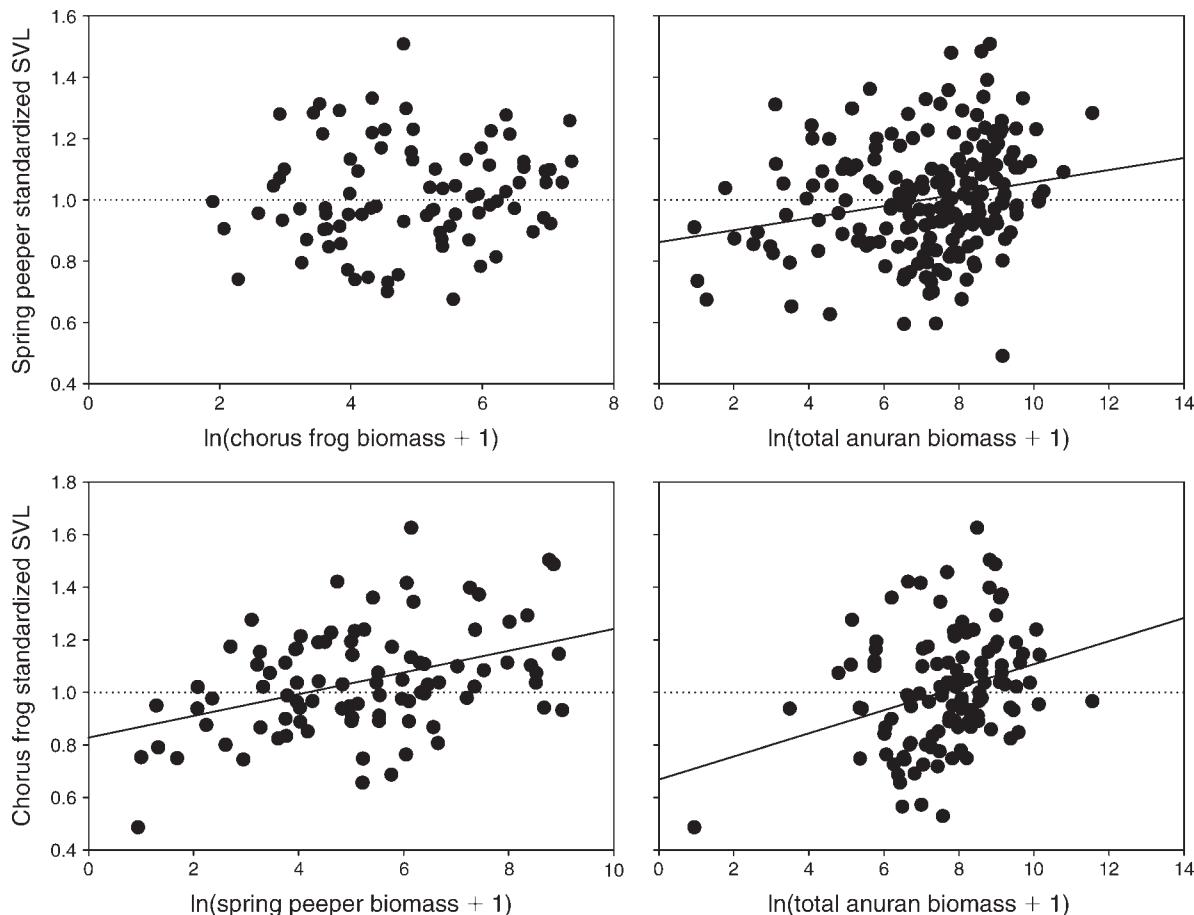
FIG. 3. Standardized mean snout–vent length (SVL) of spring peepers and chorus frogs as a function of log-transformed biomass of congeners and log-transformed sum of biomass of all species of anuran larvae (both originally measured as mg/m^2). The dotted line represents the standardized mean SVL. All significant relationships were positive: chorus frog vs. spring peeper biomass ($F_{1,91} = 19.1$, $P < 0.001$), spring peeper vs. total anuran biomass ($F_{1,198} = 9.6$, $P = 0.002$), and chorus frog vs. total anuran biomass ($F_{1,116} = 11.4$, $P = 0.001$).

in July 1998 but by the end of that fall nearly 80% of the ponds were dry. Drought conditions worsened into the fall of 1999 when 89% of ponds were dry in the fall, several of which had not dried for decades (three had contained reproducing fish populations; Werner et al. 2007b). Dry conditions persisted through 2006; the mean fraction of ponds holding water in October was significantly greater for the period prior to 1998 compared to 1998–2006 (0.69 ± 0.09 vs. 0.29 ± 0.02, respectively, for the 22 ponds sampled in both periods, t test, arcsine square-root transformed data, $t = 4.5$, df = 14, $P = 0.001$). Across all 37 ponds, 73% contained water in the fall of 1997; this number declined to a mean of 19% ± 2% during the falls of 1998–2006.

The drought thus strongly affected average hydro-period of ponds and this in turn had dramatic effects on predator densities in these ponds. For potential source (open-canopy) ponds, combined predator biomass was significantly different across drying categories for spring peeper ponds (Fig. 4). Predator biomass was threefold higher in ponds with continuous water than ponds that

had dried in the fall, and densities were 2.5-fold higher in ponds that had dried in the fall compared to those that were dry both in the fall and spring. Results were similar for the chorus frog (Fig. 4); predator biomass was 2.1-fold higher in ponds with continuous water than ponds that had dried the previous fall, and 2.5-fold higher in ponds that had dried the previous fall than those that were dry both in fall and spring. Thus, if ponds were dry the previous fall and into the spring, but the pond filled before breeding of the *Pseudacris*, these species experienced only 13–19% of the mean predator biomass found in a pond that held water continuously. We also repeated the previous analyses using data from only those ponds that experienced all three drying regimes at least once ($n = 12$ ponds). These ponds were utilized by both *Pseudacris* species. Mean predator biomass again differed among categories in these ponds (category 2 was 52% of category 1 and category 3 was 34% of category 2, $F_{2,33} = 12.3$, $P < 0.001$), and all categories differed significantly from each other.
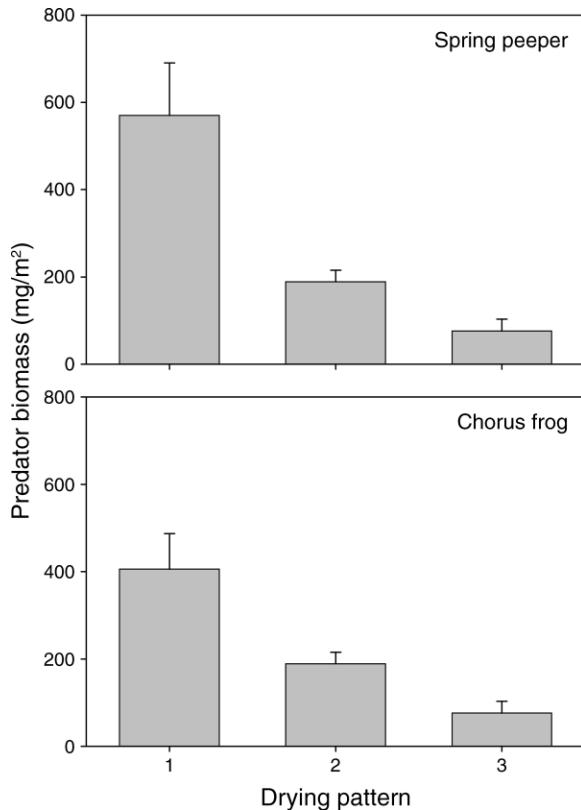
FIG. 4. Predator biomass (mean + SE) in May for spring peeper and chorus frog ponds conditional on whether the pond had held water continuously from midsummer the previous year until May of the current year (1), dried in the fall of the previous year (2), or dried in the fall of the previous year and was dry in the early spring of the current year (3). For analyses we employed all ponds in which the species in question was found during the 11-year study period: spring peeper, ln-transformed data, $F_{2,46} = 22.45$, $P < 0.001$; chorus frog, ln-transformed data, $F_{2,43} = 17.83$, $P < 0.001$. Post hoc tests (Tamhane's) indicated that all categories differed significantly from each other for both species.

As a consequence of these effects of drying, mean predator biomass across all spring peeper ponds was 2.7-fold higher before (1996–1998) compared to after (1999–2006) initiation of the drought (ln-transformed data, paired samples t test, df = 19, $t = 3.3$, $P = 0.004$) and 3.7-fold higher in chorus frog ponds ($t = 3.3$, df = 16, $P = 0.005$). All predator categories were affected by the drought. The impact of the drought on fish populations was clear; fish were extirpated from three ponds (Werner et al. 2007b). Caudate and invertebrate predators also were strongly affected by the pattern of drying that a pond experienced. Results for both of these groups were qualitatively identical to those presented in Fig. 4.

In summary, at the local (pond) level predator densities and canopy cover had strong impacts on the *Pseudacris,* and the drought had strong effects on pond hydroperiod and associated predator biomass levels. As a consequence of the drought, the ponds harboring a large fraction of the regional populations for both species changed. For example, fish were extirpated from three large marshes (see Werner et al. 2007b) and from 1996 to 1998 these ponds accounted for 0 and 1% of the regional populations of the chorus frog and spring peeper, respectively, whereas from 1999 to 2006 these ponds accounted for 31% and 60% of these populations, respectively.

Regional factors

Connectivity.—Average pond connectivity differed dramatically for the two species. For the spring peeper, the average pond on the ESGR exhibited consistently high connectivity over the period of the study ($>0.7 \times 10^4$; see Fig. 5), with a strong peak following the population increase in 2001–2002 (see Fig. 1). By contrast, mean pond connectivity for the chorus frog was very low prior to 2001 ($<0.4 \times 10^3$) but increased 23-fold after 2001 (t test, $P = 0.004$; Fig. 5). Further, connectivity for the spring peeper was always greater than that of the chorus frog: mean pond connectivity
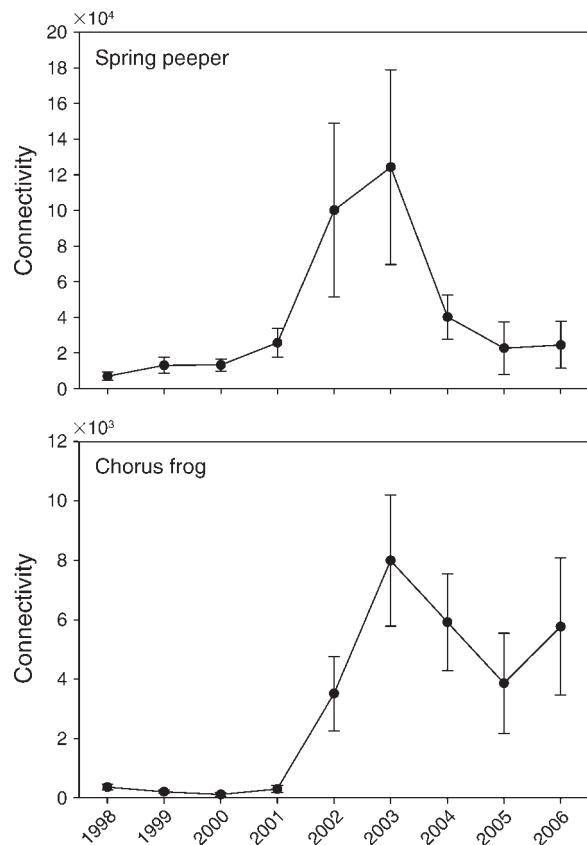

FIG. 5. Connectivity of ponds (mean ± SE) of the E. S. George Reserve across years for the spring peeper and chorus frog. Means are across all ponds that had ever contained the species in question over the 11-year study period and that contained water when sampled in May. Note that the scales on the ordinates differ; that for the spring peeper is an order of magnitude larger than for the chorus frog.

through 2001 was 66-fold greater than that of the chorus frog and 11-fold greater after 2001.

We estimated two indices of species' presence: male chorus size and larval density. The presence and magnitude of male choruses should be most directly related to connectivity of ponds. That is, there are many other potentially intervening variables between immigration of males (i.e., a chorus) to a focal pond and the actual presence or density of larvae in the pond when we sampled in May, e.g., whether females were attracted, predator levels, or freezing of eggs. Because the probability of detection of a larval population was very high (85%) and not different when the calling intensity index was 2 (11–50 callers) or 3 (>50 callers) for both species, we combined these classes in the analyses. Presence and magnitude of choruses was significantly related to pond connectivity for the chorus frog, but not for the spring peeper, though the trend was similar (Fig. 6).

Ponds where species were continuously absent were less connected than those where species were consistently present. For example, we compared connectivity of all possible presence to presence (PP) with absence to absence (AA) sequences for ponds that were known to have supported a population of the species in question at least once during the 11-year period. For both species, ponds that exhibited PP sequences were more highly connected than those that exhibited AA sequences (chorus frog, t test, $t = 4.0$, df $= 85$, $P < 0.001$; spring peeper, $t = 2.4$, df $= 166$, $P = 0.02$). There were no relations between connectivity and density residuals from regressions of density against the first principal component extracted from pond area, hydroperiod, and canopy cover, suggesting that while connectivity was important for colonization it does not appear to have a major influence on local density.

All of the above analyses were based on a mean dispersal distance of 100 m. There was little change in patterns if we employed mean dispersal distances between 75 and 250 m, but the patterns became less distinct using mean dispersal distances >300 m. The few data on dispersal for these species indicate that adults on average move much shorter distances than 250 m (see *Methods*).

The previous correlations indicated that connectivity was related to calling intensity and larval presences. However, such correlations are potentially confounded with the increase in regional population size over the study period (i.e., for chorus frogs many newly colonized ponds exhibited exponential population growth so there is an inevitable correlation between the increase in connectivity and local calling intensity). Ideally, to illustrate the effect of connectivity one would like passive sampling units on the landscape that were not actively participating in regional population increase. The closed-canopy ponds essentially meet these criteria; they are sinks and thus occupancy simply
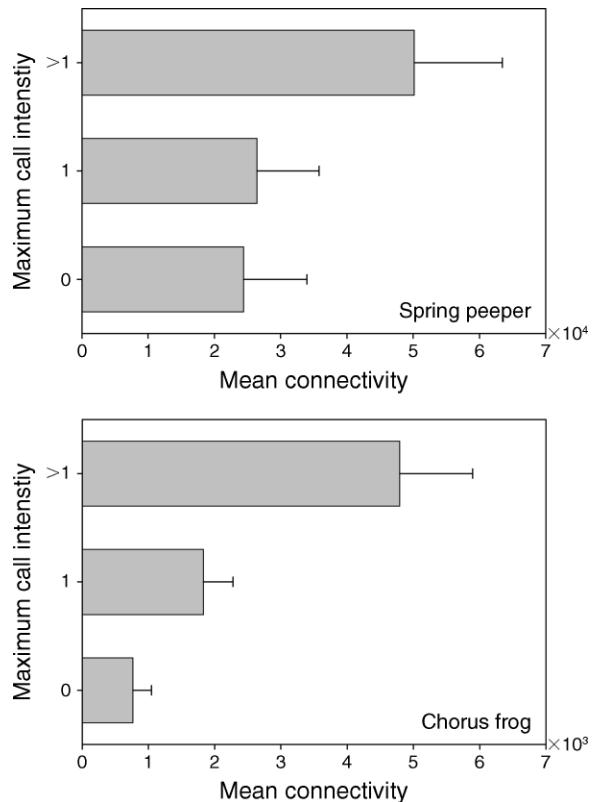

FIG. 6. Connectivity of ponds (mean + SE) for the spring peeper and chorus frog vs. maximum call intensity (chorus size). Categories are 0, no males; 1, 1–10 males, and >1, >10 males. Note that the scale is an order of magnitude larger for the spring peeper. Differences are significant for the chorus frog ($F_{2,182} = 4.7$, $P = 0.01$), and post hoc tests (Tamhane's) indicated that ponds with no chorus frogs calling did not differ in connectivity from those with <10 individuals calling ($P = 0.14$), but that the latter differed from ponds with >10 individuals calling ($P = 0.04$).

reflects colonization/rescue or mass effects from surrounding source ponds.

Consistent with expectations, the fraction of closed-canopy ponds with larval spring peeper populations was consistently relatively high (Fig. 1), parallel to the high connectivity of these ponds over the study period (Fig. 5). In contrast, when mean pond connectivity for the chorus frog was low (Fig. 5), virtually no closed-canopy ponds exhibited larval populations of this species (0 in 4 of 5 years; Fig. 1). Nonetheless, following the marked increase in average pond connectivity in 2001, a mean of 38% ± 4% of closed-canopy ponds exhibited larval chorus frog populations (Fig. 1). Thus, the contrast between species over time suggests an important role of the magnitude of dispersal enabling maintenance of populations in marginal habitats where they would not otherwise persist.

Dynamics

Extinction and colonization rates.—Employing the 1-yr extinction criterion (based on larval presences), mean

TABLE 1. Overall model evaluation for logistic regression analyses of extinction and colonization events for the chorus frog (*Pseudacris triseriata*) and spring peeper (*P. crucifer*) on the University of Michigan's E. S. George Reserve, near Ann Arbor, Michigan, USA.

Species' model	Model G^2	df	P	Hosmer-Lemeshow χ^2	df	P
Chorus frog extinction	28.32	8	<0.001	6.75	8	0.56
Chorus frog colonization	18.27	4	0.001	6.60	8	0.58
Spring peeper extinction	40.17	8	<0.001	10.70	8	0.22
Spring peeper colonization	19.70	4	0.001	8.72	8	0.37

colonization probability over the monitoring period for the spring peeper exceeded extinction probability, i.e., 0.39 ± 0.05 vs. 0.17 ± 0.04, respectively. There were no differences in colonization or extinction probabilities before and after inception of the drought (1996–1999 vs. 2000–2006, *t* test, colonization $P = 0.51$ and extinction $P = 0.58$). Employing the 2-yr extinction criterion resulted in similar values to the 1-yr criterion, i.e., 0.35 ± 0.08 and 0.09 ± 0.03 for colonization and extinction probabilities, respectively, and these also did not differ before and after the drought. Estimates of colonization and extinction probabilities based on the Clark and Rosenzweig (1994) method (1-yr criterion) were 0.39 ± 0.05 and 0.27 ± 0.05, respectively. The higher mean extinction probability was due to estimated "hidden" extinctions.

Colonization and extinction probabilities for the chorus frog reversed dramatically following the drought. In the three years prior to 2000, mean colonization and extinction probabilities were 0.10 ± 0.05 and 0.53 ± 0.10, respectively. During the seven following years these probabilities were 0.40 ± 0.08 and 0.19 ± 0.05, respectively. Both colonization and extinction probabilities differed significantly before and after the drought (*t* tests, colonization, $t = 3.2$, $P = 0.01$, and extinction, $t = 3.2$, $P = 0.01$). Employing the 2-yr extinction criterion gave similar results; pre-drought colonization and extinction probabilities were 0.06 ± 0.04 and 0.53 ± 0.10, respectively, and post-drought were 0.40 ± 0.11 and 0.08 ± 0.03, respectively. Again, both colonization and extinction probabilities differed significantly before and after the drought (*t* tests, colonization $P = 0.03$ and extinction $P = 0.04$). Using the Clark and Rosenzweig (1994) method, estimated colonization and extinction probabilities (1-yr criterion) before and after the drought were: 0.10 ± 0.05 and 0.60 ± 0.13 vs. 0.40 ± 0.08 and 0.34 ± 0.12, respectively.

Logistic regressions.—In this section we identify characteristics of ponds associated with colonization and extinction events. We can definitively identify the cause of extinction or lack of colonization in cases where the pond was dry in the spring precluding breeding or dried before we sampled extirpating populations. For the spring peeper there were 37 total extinction events, 14 (38%) of which were due to spring drying. For the chorus frog, there were 31 extinction events, 8 (26%) of which were due to spring drying. The number of pond years when a colonization was not possible due to spring

drying (i.e., the pond was unoccupied the year before and potentially could be colonized if it had held water) accounted for 17% of pond-years for spring peepers and 19% for chorus frogs. To assess factors in addition to catastrophic drying, we excluded all pond-years where spring drying occurred for the following analyses.

For both species, all logistic regressions were highly significant, and Hosmer-Lemeshow tests indicated that all provided good fits to the data (Table 1). For the spring peeper, comparisons with reduced models indicated that three factors gave statistically significant information concerning extinction probability: canopy cover, predator biomass in the previous year, and population size the previous year (Table 2a). Canopy cover and predator biomass were positively related to extinction probability, and population size negatively related to extinction probability. Proportion of days wet the previous summer (negative effect on extinction) was nearly significant ($P = 0.06$). Populations of spring peepers that went extinct the following year averaged 24% of those that did not (population sizes: 24 646 ± 15 740 vs. 100 728 ± 22 858 individuals, respectively; *t* test, $P = 0.007$).

For the chorus frog, three variables reduced predictive power of the extinction probability model if removed: population size of chorus frogs in the previous year and current-year competitor and predator biomass (the latter at the 0.06 level, Table 2c). Population size and competitors were negatively associated with probability of extinction, and predators were positively associated with probability of extinction. The negative correlation between current competitor density and extinction probability (Table 2c) was the opposite of the expectation for competitive effects, and thus appears to represent the fact that when conditions were favorable for the chorus frog in a pond, they also were favorable for other (potentially competing) species as well, and therefore extinction probability was lower. The negative correlation with population size indicated that probability of extinction was greater for smaller populations; populations of chorus frogs that went extinct averaged 22% of the size of those that did not go extinct (population sizes: 4292 ± 2319 vs. 19 466 ± 4275 individuals, respectively; *t* test, $P = 0.002$).

Colonization models for both species identified canopy cover as having negative effects on colonization probability. For the spring peeper, canopy cover and

TABLE 2.   Significance tests of individual regression coefficients in the logistic regression analyses.

Predictor variable	β	SE β	Reduced model G^2	df	P
a) Spring peeper extinction					
Proportion of canopy cover	4.1507	1.4002	11.29	1	0.001
Predator biomass, yr $t - 1$	0.0012	0.0005	5.87	1	0.015
Population, previous yr	−0.00004	0.00003	4.04	1	0.044
Proportion of days wet, previous summer	−2.1513	1.1437	3.42	1	0.064
b) Spring peeper colonization					
Proportion of canopy cover	−4.2672	1.5572	10.14	1	0.001
Predator biomass, yr t	−0.0007	0.0004	3.70	1	0.054
c) Chorus frog extinction					
Population, previous yr	−0.00016	0.00009	6.65	1	0.010
Predator biomass, yr t	0.00253	0.00138	351	1	0.061
Competitor biomass, yr t	−0.00020	0.00011	5.35	1	0.021
d) Chorus frog colonization					
Proportion of canopy cover	−2.1648	0.7629	8.20	1	0.004
Connectivity	0.0002	0.00009	7.30	1	0.007

current year predator biomass were the only factors that significantly reduced predictive power of the model if removed (Table 2b). Both had strong negative effects on colonization probability. Two factors significantly affected colonization probability for the chorus frog (Table 2d); proportion of canopy cover (negative) and connectivity (positive).

Synchrony.—Populations of these two species exhibited strong asynchrony in rates of population change across the ESGR landscape (Fig. 7). Ponds exhibiting positive and negative growth rates between years were evident in all 10 comparisons for the spring peeper and colonization and extinction events similarly both occurred in nine of the 10 between-year comparisons. The impact of widespread climatic events on rates of population change, however, was evident in average values (e.g., general trends for positive changes between 1999 and 2002, and negative changes between 2002 and 2003). Results for the chorus frog were similar; large scale Moran effects can be noted with populations generally increasing 1999–2002 and decreasing 2002–2003 and then again increasing 2003–2005, but with the exception of 2000 all years exhibited populations with positive and negative changes.

DISCUSSION

Examination of *Pseudacris* dynamics on the ESGR illustrates the interaction of local and regional processes determining metacommunity structure. The experimental work on the relation between species' traits and performance in this system provided mechanistic interpretations of species' responses to environmental change at the local level, which then had profound impacts on species' spatial population structure and regional dynamics. Climate variation (drought) altered breeding habitat qualities across the ESGR landscape, and the associated changes in identity of source and sink ponds highlights the importance of habitat (pond) heterogeneity to species persistence in the face of environmental change. Local responses led to changes in pond connectivity that had a strong influence on colonization–extinction dynamics, presences in sink habitats, and ultimately regional population sizes. Here we elaborate on these issues and the inferences they provide regarding the spatial structure of these anuran populations.

Extreme and/or cyclical climatic conditions can have dramatic effects on population dynamics and selection on species' traits (e.g., Grant and Grant 1989). The ENSO event in the South Pacific (Hoerling and Kumar 2003) had strong effects on the ESGR *Pseudacris*; the chorus frog transitioned from a relatively rare and narrowly distributed species to an abundant and widely distributed species as the drought transformed the ESGR landscape to one with more ephemeral, predator-poor ponds. In contrast, the spring peeper showed little change in overall pond occupancy rates, but did exhibit variation in regional population size and the position of source ponds. Such climatic events are frequent occurrences for these species; multiple-year droughts at least as severe as that of the 1998–1999 period (as measured by the Palmer Hydrological Drought Index) have occurred on average every 8.4 ± 2.5 years in Michigan (1895–2006 data from the National Climatic Data Center for Michigan division 10). We expect that relative abundance and pond occupancy rates of the chorus frog will again decrease as a wetter cycle ensues; i.e., as hydroperiods of ponds increase and predator populations build. Thus, these species are consistently confronted with a landscape (at least in terms of breeding pond characteristics) that is highly dynamic due to climate fluctuations. Our long-term data provide insight into the profound impact this variation has on regional population structure of these species.

The supporting body of experimental work (Skelly 1995*a*, *b*, 1996, Smith and Van Buskirk 1995) was crucial in making clear interpretations of the correlations in our data regarding changes in the *Pseudacris* populations. There was a clear causal relation between
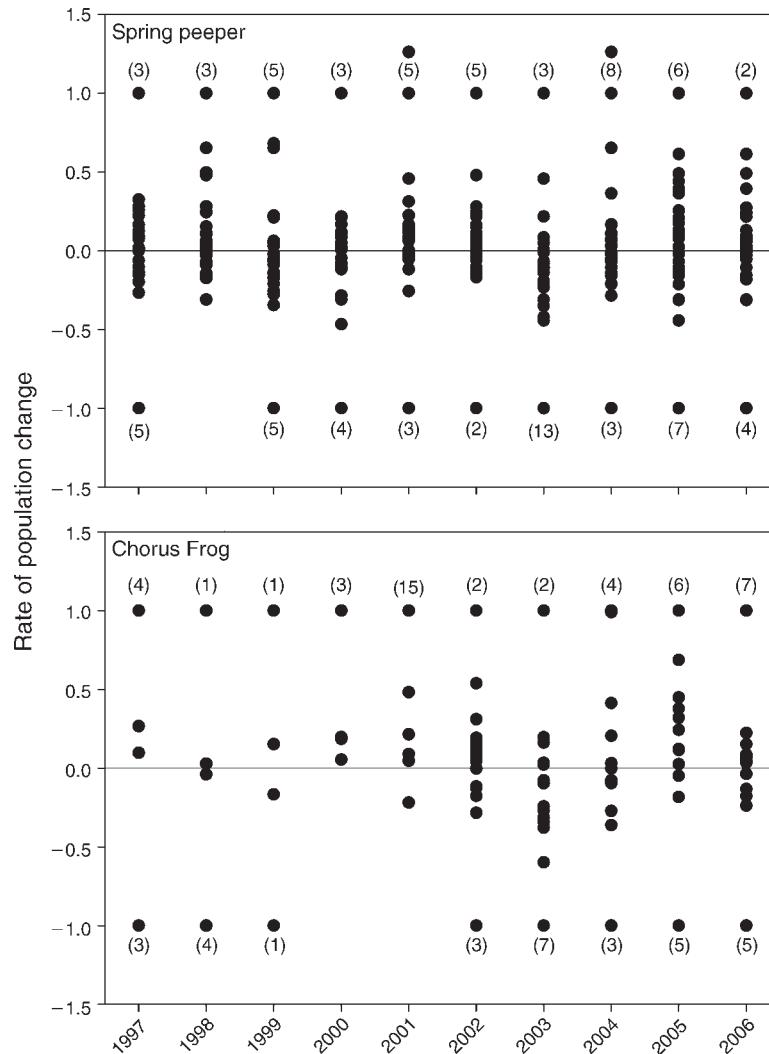
Fig. 7.   Rate of change for spring peeper and chorus frog populations across years. Points are the rate of change for a species in an individual pond between year t and $t - 1$. Colonization and extinction events are also noted on the graphs and are arbitrarily placed at $+1$ and -1, respectively, with the number of events in parentheses.

drought effects on pond hydroperiod, the consequent effects on predator densities, and how species traits (i.e., larval activity levels) were related to responses in local abundances of these species. Shortened hydroperiods resulted in extinctions, but affected the (less active, slower growing) spring peeper more (e.g., Table 2a), reflecting the fact that it has an average 18-day longer larval period on the ESGR than the chorus frog (Skelly 1996). There were positive associations between predator levels and the probability of extinction for both species, but the (less active) spring peeper tolerated higher predator biomass densities (more than twofold) than the chorus frog (Fig. 2). These differences are consistent with experimental work on activity differences and vulnerability of the two species to predators (Morin 1983, Lawler 1989, Skelly 1995a, b, 1996, Smith and Van Buskirk 1995). Thus, when predator densities

are high, ponds can be sink habitats for these species, especially for the chorus frog (i.e., predators can increase the risk of extinctions, see *Results: Dynamics: Logistic regression*). The lack of evidence for competitive effects also is consistent with experimental results; e.g., Skelly (1995a, b) found little evidence of competitive effects between the two species at natural densities on the ESGR. These inferences indicate the power of combining long-term data with experimental studies addressing species traits and their performance to understand local population dynamics.

In order for these climatic effects on local populations to have regional consequences, however, they must reverberate spatially through dispersal. The proximate evidence for the nature of this effect in our system was the role of pond connectivity. Pond connectivity was positively associated with number of males calling and

colonization probabilities for the chorus frog, and there was a trend in this direction for the spring peeper (Fig. 6). Extinction rates for the spring peeper were quite low throughout the study and likely both larger local population sizes (average sevenfold higher population densities than chorus frogs) and rescue effects due to high pond connectivity contributed. Following 2000 this also was the case for the chorus frog. Our data further indicated that closed-canopy ponds were sink habitats for both species, and canopy cover strongly affected colonization and extinction probabilities of these species (significant in three of the four logistic regressions; Table 2). Pond connectivity appeared critical in maintaining the high occupancy rates of closed-canopy sinks by spring peepers, and by the chorus frog after 2000. Despite the large body of theory on source–sink dynamics, there have been few empirical studies demonstrating the role of mass effects maintaining species in marginal or sink habitats for any taxon (Diffendorfer 1998, but see Caudill 2003, Johnson 2004). Werner et al. (2007a) also provide evidence that pond connectivity influenced turnover in amphibian species composition of the ESGR ponds. Thus, space plays a large role in determining how structure of these communities changes as climate varies.

It appears likely that the majority of colonization and extinction events as indexed by larval populations are actual colonizations and extinctions (absence of a larval population is not definitive evidence of an extinction given that adults may skip breeding or move to other ponds to breed under certain circumstances; Collins 1975, Petranka et al. 2004, Resetarits 2005). For example, colonization and extinction probabilities did not change substantially when we required that a species had to be absent from a pond for two years before an extinction or a colonization could occur. In addition, the fact that these species are short-lived, disperse short distances, and appear to show site fidelity as adults (e.g., M. F. Benard (*unpublished manuscript*) reported that out of 4100 individually marked adult *Pseudacris regilla*, only three were ever observed as adults at more than one pond), further suggests that absences likely represent extinctions.

Pond connectivity was assessed by distance to, and population size in, other occupied ponds on the ESGR, but this alone appears insufficient to fully characterize connection of ponds. For example, the colonization of 15 new ponds in 2001 by chorus frogs lagged behind the initiation of the drought in 1998–1999. Many of these were clearly true colonization events; 13 of these ponds had not contained larval chorus frog populations for the previous four years and all 15 had <10 males calling when colonized in 2001. It appears that a unique coincidence of factors enabled this explosive colonization. Between 1999 and 2001, regional population size of the chorus frog increased over fivefold annually (Fig. 1), but this increase basically occurred in a small set (three to six) of ponds. All six ponds the chorus frog inhabited

in 2000 dried the previous fall, and four of these ponds were dry in the spring before filling and permitting breeding by the chorus frog. These drying patterns would result in greatly reduced predator populations and enhance survival of the larval populations (Fig. 4). Optimal conditions for larvae in the ponds in 2000 then were fortuitously followed by the wettest June–August period between 1987 and 2006 (rainfall was 2.6 standard deviations greater than the mean; NOAA, National Climatic Data Center, COOP ID number 200230) creating moist terrestrial conditions that presumably would favor survivorship and movement of juveniles, and facilitate the extensive colonization of new ponds in 2001. Further, since 62% of the ponds on the ESGR dried in the fall of 2000, many of the new ponds encountered in 2001 contained fewer predators facilitating colonization. The spring peeper also exhibited a large increase in population size in 2001 presumably for many of these same reasons. Knapp et al. (2007) also found *Rana mucosa* colonization of lakes was correlated with an unusual three-week rainy period suggesting dispersal propensity and/or survival increased during dispersal. Thus, our data suggest that connectivity is a function not only of species densities and the spatial proximity of ponds, but variable microclimatic conditions in the matrix (or the complementary habitat for species with complex life cycles) as well.

Based on these results, what can we infer about the spatial structure of these two anuran species? Breeding ponds are the most convenient locale to sample and monitor amphibian populations, and to quantify habitat characteristics. In doing so, it is tempting to view these populations as metapopulations centered on the pond habitat, i.e., a "ponds as patches" conception (Marsh and Trenham 2001), and therefore to advance pond-based explanations of the phenomena that we have observed. However, because the life cycle of amphibians is biphasic, the terrestrial habitat is equally critical for maintaining juvenile and adult segments of populations, and not simply a matrix for dispersal between ponds. Nonetheless, if species are ultimately tied to a pond breeding site at some point in the life cycle and dispersal is limited, even in a continuous high quality terrestrial habitat sufficient isolation of ponds will effectively result in a nonequilibrium metapopulation structure. As ponds become closer together relative to dispersal capabilities, these populations will begin to approximate a classic metapopulation and then grade into a patchy population structure. Variance in size and quality of patches can create an orthogonal dimension (e.g., island/mainland–source/sink metapopulations; Harrison and Taylor 1997).

The *Pseudacris* system certainly exhibits aspects of metapopulation structure when viewed (sampled) from the pond perspective. Hanksi's (1999) four criteria for a classic metapopulation all are met to some extent. First, most ponds supported local breeding populations for some period. Second, few ponds or populations were

large enough to assure long-term survival (both species exhibited a large number of extinctions). Third, ponds clearly were not isolated enough to prevent recolonization. Fourth, there was abundant asymmetry in local population dynamics in ponds (Fig. 7). Further, an expectation of metapopulation structure is that a number of suitable habitats will lack populations at any given time. This appeared to be the case for the chorus frog early in the survey; employing a conservative maximum predator biomass threshold of 750 mg/m^2 (see Fig. 2), between 1996 and 2000 nearly 70% of low-predator, open-canopy ponds (63 pond-years) were not occupied by chorus frogs. This percentage dropped to 15% after 2000 (96 pond-years). On the other hand, these species simply could be patchy populations where the embedded breeding sites (ponds) were subject to temporal variation in quality, and concordance of pond populations with the above four criteria simply reflects variation in quality of breeding sites over time (see Petranka et al. 2004, Petranka and Holbrook 2006 for an example). That is, apparent extinctions represent occasional reproductive failures at a particular breeding site, but not extinction of the local panmictic population.

Our data suggest that the *Pseudacris* populations embodied characteristics of multiple metapopulation structures that changed over time due to the interaction of spatial population structure and a dynamic landscape (see also Hill et al. 1996, Nieminen and Hanski 1998, Dunham and Rieman 1999). The chorus frog, for example, appeared to transition from a population structure much closer to a classic metapopulation (or island/mainland metapopulation) early in the study, to one much closer to a patchy population after 2000. Early in the study the chorus frog inhabited only 3–6 ponds annually, occupied ponds averaged 702 ± 315 m apart (estimated maximum dispersal distance for this species is 685 m), and average pond connectivity and colonization rates were very low. Acceptable ponds (*n* = 11), at least in terms of predator density and canopy cover, went 2–4 years without populations. However, after 2001, ponds occupied by the chorus frog averaged 182 ± 46 m apart, and this species exhibited much higher colonization, and lower extinction, rates and maintenance of populations in closed-canopy sinks. Thus, spatial structure of this species appeared to change extensively along the gradients of classic metapopulation-island/mainland metapopulation to patchy population structure in response to the environmental driver.

In contrast, we interpret spring peeper populations as much closer to a patchy population structure with variation in the quality of embedded breeding sites. The high average pond connectivity for this species throughout the monitoring period, the consistently high occupancy rates for sink habitats, and the large regional population size are consistent with a patchy population view. There were extinctions associated with ponds but colonization rates were quite high and we suspect that hidden extinctions (i.e., ponds recolonized immediately

the next spring after an extinction; see Clark and Rosenzweig 1994) were fairly high. That is, reproductive failures occurred in ponds and major source ponds changed temporally, but this would not represent an extinction of the large highly connected regional population. It is unlikely, however, that even the spring peeper achieved the conceptual extreme of a patchy population; the fact that population growth rates in ponds were highly asynchronous and there was a suggestion of an effect of connectivity (Fig. 6) indicates that movement of individuals was not sufficient to fully synchronize populations everywhere.

The temporal dynamics of both species on the ESGR highlight the importance of spatial landscape heterogeneity in population transitions and the persistence of species. Spatially correlated weather conditions are a significant mechanism causing large-scale synchrony in population dynamics and potential extinctions of species (Hanski and Woiwod 1993, Ranta et al. 1998, Piha et al. 2007). However, habitat heterogeneity (here in aquatic breeding sites) can significantly mute the synchronizing (Moran) effects of climate variation, and enable or enhance the persistence of species (see also Weiss et al. 1988, Kindvall 1996, Hanski 1999). Ponds on the ESGR vary extensively in area, hydroperiod, presence of fish, and canopy type (Werner et al. 2007b), and these ponds responded heterogeneously to the drought (as evidenced by the asynchrony in population responses). Important source populations (ponds) changed over time for both species, and previously permanent ponds that had contained fish were important refuges for these species in years of severe drying. Both of the *Pseudacris* are short-lived, and dispersal to new source habitats is critical as drought changes the quality of ponds (Caldwell 1987, Lannoo 1998). Thus, the persistence of these species is dependent on availability of a diversity of pond types scaling the hydroperiod gradient within characteristic dispersal distances, i.e., preventing spatially correlated weather conditions causing large-scale synchrony and potential extinctions. Moreover, it is likely that these ideas in principle apply to the terrestrial environment as well. Piha et al. (2007) have argued that persistence of *Rana temporaria* was positively related to the heterogeneity of the surrounding terrestrial landscape during a drought. We know little about potential interactions between habitat heterogeneity in aquatic and terrestrial environments and environmental change on species with complex life cycles.

Environmental change affects performance through species' traits, and thus a common environmental perturbation can be "perceived" very differently by species as similar as the *Pseudacris* we studied. Because spring peeper life history traits enable it to use a wide variety of ponds and persist at higher predator levels, large variation in hydroperiod prompted less effect on its local abundance and overall pond occupancy rates than the chorus frog. The consequences of these trait differences can in turn influence selection on other traits.

For example, Johst et al. (2002) show theoretically that metapopulations in dynamic landscapes should experience selection for longer dispersal distances, and greater rates of population increase. Lehtinen and Galatowitsch (2001) indicate that chorus frogs colonized restored wetlands sooner than spring peepers suggesting somewhat longer dispersal distances. Mean rates of increase for the chorus frog in newly colonized ponds on the ESGR were higher than for spring peepers (4.25 vs. 2.80), and a substantial fraction of chorus frog populations evidently return to breed in one year. These patterns would be consistent with the predictions of Johst et al. (2002) if the chorus frog indeed does experience the landscape as more dynamic than the spring peeper with cyclic changes in weather conditions and average pond hydroperiod.

The two *Pseudacris* species do not appear to strongly interact competitively, but interact with, and potentially through, a diverse array of predators, i.e., they are embedded in a larger metacommunity. With dynamic changes in pond hydroperiod, predator taxa (e.g., odonates, dytiscid beetles, fish) will move differentially on the landscape relative to each other as well as to the amphibians (e.g., McCauley 2006). Shortened hydroperiods can have a greater impact on predators than the *Pseudacris* as many predators have longer larval periods and/or overwinter as larvae and lack temporal storage in adult forms like the amphibians. Thus climate variation can have large impacts on local trophic structure of ponds, and the interplay of climatic variation and spatial food web structure drove many of the *Pseudacris* responses on the ESGR. Chase and Knight (2003) similarly show that the effect of drought on population size of mosquitoes can be counterintuitively positive due to effects on pond food web structure (again due to reduction of predators). The majority of metacommunity theory explicitly models competitive interactions (reviewed in Amarasekare et al. 2004), and clearly the interplay of landscape dynamics and spatial food web structure is an important area to address (e.g., Holt and Hoopes 2005, Hoopes et al. 2005). A major challenge here will be to conceptualize the interactions of taxa that move over very different scales on the landscape and those with different temporal storage stages.

In conclusion, this study illustrates the strong interaction of processes at a number of different spatial and temporal scales in determining *Pseudacris* distribution and abundance. Our data reflect the influences of climate variation (due to an ENSO event) ranging down to local conditions in ESGR ponds and the feedbacks between these effects and regional population structures. The comparative dynamics of the two species revealed the signature of differences in species traits that had wide-ranging impacts as drought effects on local ponds were scaled up to regional population sizes, pond occupancy rates, and species relative abundances. The associated transitions in species' spatial structures are likely cyclic with climate variation, and have important

implications for windows of vulnerability to extinction or selection on species traits. Thus, it seems clear that attempts to classify the metapopulation structure of amphibians (e.g., Smith and Green 2005, Petranka and Holbrook 2006) or other groups largely will be counterproductive. It is well recognized that natural populations exhibit a mosaic of the characteristics of these simple conceptual models that will change over time and that it is more useful to focus on the relevant process operating at these different scales (e.g., Ovaskainen and Hanski 2004).

Amphibians are among the most threatened animal taxa (Houlahan et al. 2000, Collins and Storfer 2003, Stuart et al. 2004), and anthropogenic destruction and fragmentation of habitats and disruption of wetland hydrology, in particular, are a large element in their decline (Bradford 2005). From a conservation perspective, this study illustrates the critical need to: (1) maintain heterogeneity in habitat types, specifically breeding pond types, (2) ensure that the landscape incorporating these habitats enables movement of species as locations of source and sink habitats change with spatially correlated environmental perturbations, and (3) understand the impact of wetland restoration or management strategies on the spatial food web structures of ponds. It is likely that the long-term integrity of amphibian communities (and those of many other taxa) is intimately associated with this spatiotemporal structure in conjunction with habitat heterogeneity (e.g., Leibold et al. 2004, Urban 2004). A great deal of amphibian conservation work has focused on how much upland habitat is necessary to maintain a population at a single pond (Semlitsch 1998, Trenham and Shaffer 2005). The *Pseudacris* results suggest that this focus will be futile for many species in the long run, as without supporting heterogeneity in breeding site characteristics, climate variation inevitably will result in local extinction.

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