



Turnover in an amphibian metacommunity: the role of local and regional factors

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Ecologists have long realized that stable species richness values can mask rapid turnover in species composition. Because turnover occurs as a consequence of both local and regional processes, understanding the responsible factors provides insight on processes influencing community structure at different scales. Despite the insights to be gained from data on species turnover, they remain relatively uncommon. We present data on the interannual turnover in species composition of larval amphibian communities in 37 ponds over seven years. Species composition of a given pond community was highly dynamic; about half of the species that could be found breeding in a particular pond were actually present in a given year. All species participated in this community turnover, but to different degrees. Using a model selection approach, we show that a statistical model including local environmental factors (pond area, hydroperiod, and canopy cover) and pond connectivity on the landscape provided the best predictions of turnover. Averaged parameter estimates were significant for area, hydroperiod, and connectivity and these same variables were identified by hierarchical partitioning as having significant independent effects on turnover. Area and hydroperiod were negatively related to turnover, whereas connectivity was positively related to turnover. Additionally, the average fraction of years a species was present in a pond was positively correlated with average local population size, but even more strongly correlated with regional population size, suggesting both local and regional influences on turnover. Of the measured biotic factors (biomass of fish, invertebrate predators, anuran and caudate larvae), presence of fish was the only factor that significantly affected rates of turnover. Several mechanisms could be responsible for changes in species composition (species extinctions, skipped breeding and movement of choruses), but extinctions appear to be the major cause of turnover. These results have important implications to understanding long-term persistence of species on landscapes and the causes of patterns in species richness on environmental gradients.

Ecologists have a longstanding interest in the causes of patterns in species richness and composition of communities. Early observations suggested that, while species richness could be relatively stable in an environment, membership of the community could be dynamic. For example, theories of island biogeography and the effects of disturbance provided clear, early statements that a colonization/extinction dynamic may underlie relative stability in species richness across habitats that differ in characteristics such as area, isolation, or disturbance (MacArthur and Wilson 1967, Connell 1978). More recently, interest in the regional processes contributing to population persis-

tence and the structure of ecological communities (Hanski 1999, Hubbell 2001, Leibold et al. 2004) has further emphasized the importance of temporal turnover. This interest, however, also has highlighted the lack of long-term data from multiple habitats that could provide estimates of turnover rates in natural communities. Because changes over time in species composition at a site occur as a consequence of both local and regional processes, long-term data estimating turnover are central to developing a metacommunity theory incorporating processes operating at these different scales. Data on turnover also may provide inferences regarding the causes of patterns in species

diversity on productivity and other such environmental gradients (Steiner and Leibold 2004). Despite the obvious insights to be gained from such data, they rarely have been collected and the factors associated with turnover remain poorly documented.

Larval amphibian communities offer an excellent system to address the relationship between patterns in species richness and the dynamics of species turnover. These communities exhibit strong patterns in species richness across environmental gradients (Wilbur 1984, Werner et al. 2007), and yet long-term studies of single ponds indicate extensive temporal variation in the presence and breeding success of different species (Semlitsch et al. 1996, Trenham et al. 2003). Understanding the factors that affect this turnover in different habitat types therefore could provide important insights into processes responsible for structuring these communities. Pond breeding amphibians also are prime candidates for spatially structured populations due to their association with discrete breeding sites distributed over the terrestrial landscape (Sjogren-Gulve 1994, Marsh and Trenham 2001). Consequently, we might expect these species to participate in metacommunities assembled by the tension between local species-sorting and colonization–extinction (or mass effect) processes (Leibold et al. 2004). Further, in the case of amphibians long-term data on turnover are critical in differentiating background turnover from long-term declines that may reflect patterns in the world-wide decline of these species (Pechmann et al. 1991, Alford and Richards 1999, Houlahan et al. 2000, Skelly et al. 2003). That is, estimates of turnover can help interpret the inferences from static sampling regimes (Skelly et al. 2003), and knowing the factors associated with turnover can help shape management and conservation policies.

In this study, we estimated interannual rates of turnover in the species composition of 37 ponds over seven years. We have previously shown that the species richness of these communities exhibits strong and consistent patterns among ponds that differ in disturbance rate (hydroperiod), area, and productivity (canopy cover) (Wilbur 1984, Skelly et al. 1999, Werner et al. 2007). Our objective here was to ask what local and regional factors were associated with the variation in turnover rates among ponds, whether all species participated in this turnover, and how this turnover was related to patterns in species richness on environmental gradients. Using a model selection analysis, we determined the best supported set of factors for predicting turnover in the ponds formulated from local abiotic or biotic factors and pond connectivity on the landscape. These results enable us to determine the factors associated with turnover in these communities and infer potential mechanisms responsible. The results have important implications to understanding the causes of patterns in metacommunity dynamics and

species richness among different communities, and the factors affecting the long-term persistence of species on landscapes.

The system

We studied the larval amphibian communities inhabiting 37 water bodies on the Univ. of Michigan's E. S. George Reserve (hereafter ESGR). The ESGR is a 525 ha tract located about 40 km northwest of Ann Arbor, Michigan (42°28'N, 84°00'W) that has been fenced and administered as a restricted access preserve since 1930. The ESGR water bodies (hereafter termed ponds) range from small, temporary pools to large, permanent marshes. Seventeen amphibian species have been recorded breeding on the ESGR, including representatives of three frog and three salamander families (Appendix 1). Two species were not collected in our survey; *Plethodon cinereus* is entirely terrestrial and *Acris crepitans* went locally extinct on the ESGR in 1971 due to a drought (Collins and Wilbur 1979). Thus, our analysis was based on 15 of the 17 species. Of these 15, one was not distinguished from *Ambystoma laterale* (*A. tremblayi*, which is a gynogenetic triploid hybrid of the *A. jeffersonianum* complex and is quite difficult to distinguish based on external characteristics, Uzzell 1964, Wilbur 1971). Two species, *Rana palustris* and *Hemidactylum scutatum*, were rare in our collections.

Methods

We surveyed the amphibians of the ESGR ponds over seven years (1996–2002). We sampled larval amphibians twice each year (typically the third week in May and July) to estimate densities of both the spring and summer breeders. Samples were taken by “pipe sampling”, dipnetting and seining. The pipe sampler enclosed 0.1 m² of water column and sediments from which all animals were cleared with nets (22 × 27 cm with a 1 × 2 mm mesh size). Sampling effort varied with size of the pond and ranged from 20–40 pipe samples haphazardly distributed across representative microhabitats (with the exception of several ponds <100 m² where 10–15 samples were taken). Following completion of the pipe sampling, we dipnetted the pond for the equivalent person-minutes as the number of pipe samples taken (i.e. if 40 pipe samples were taken we dipnetted for 40 person-minutes) employing the same nets used to clear the pipes. In cases where density estimates were employed in analyses and species were only obtained in the dipnet samples, we estimated density from dipnet catch per unit effort obtained from regressions of pipe density estimates against individuals captured per person-minute dipnetting (Appendix 2).

In ponds with deeper water (>1 m, 5 water bodies), standard sampling was supplemented with two hauls of an 8-m bag seine in the deeper water (permitting us to sample areas that were too deep for the pipe samplers).

Analyses of species accumulation curves (Colwell and Coddington 1994) and estimates of detection thresholds indicated that the above sampling methods were very effective at characterizing the larval communities in the ESGR ponds (Werner et al. 2007 Appendix 2). Also, for one species, the wood frog, *Rana sylvatica*, we had egg counts; the probability that we detected a larval population given egg deposition averaged 0.96 ± 0.01 over years when eggs were not killed by drying (Appendix 2). Thus, although it is inevitable that there were detection errors in the data, we are confident that our estimates of species' presences in ponds were a very good approximation to the actual number of species.

Statistical procedures

We assessed interannual variation in the species richness of ponds in two ways. First, we compared the mean number of species found in a pond over the seven years to the cumulative number of species found in that pond. Second, we quantified interannual turnover by employing the complementarity index (Colwell and Coddington 1994, Koleff et al. 2003), which calculates the fraction of species distinct in two species lists. That is, we computed a β diversity in time as the proportion of amphibian species in a pond occurring in only one or the other of each two consecutive year period, and then averaged these values for the seven year data set ($n=6$ comparisons; Moreno and Halffter 2001). To address the question of whether specific species were differentially contributing to interannual turnover, we assessed the "reliability" of species presences in ponds. We defined reliability as the proportion of years a species was found in a pond given that it had been recorded in that pond at some point during the seven years of the survey (conditional on the presence of water in the pond when the species would breed).

Model formulation

We employed a model selection approach to identify the most appropriate statistical model for predicting turnover in amphibian species composition of the ponds (Burnham and Anderson 2002). We formulated models representing biologically plausible mechanisms or hypotheses by which local and regional factors could influence this turnover. Since there is little information on factors affecting turnover in different taxa of amphibians to guide a priori hypotheses, we included all species (i.e. anurans and caudates) in our analyses. The abiotic variables we measured were pond

hydroperiod, area and forest canopy cover. These three variables are known to be associated with the species composition and richness of amphibian communities and therefore could plausibly affect turnover (Skelly et al. 1999, Van Buskirk 2005, Werner et al. 2007). Pond areas ranged between 10 and 53 400 m², though the frequency distribution was skewed to smaller ponds (e.g. 73% <2500 m²). Average pond hydroperiod (% of days that a pond held water) ranged from 30 to 100% over the study period (across ponds $62.5 \pm 3.5\%$, Werner et al. in review). Canopy cover of the ponds ranged from <1 to 93% ($\bar{x}=59 \pm 5\%$, Werner et al. 2007). Local biotic variables (Appendix 2) included average biomass m⁻² of potential competitors of anurans (biomass of anuran larvae), predators (invertebrate predator biomass), and caudate biomass (which could index competitors or intraguild predators for caudates and predators for anurans).

To assess the role of landscape context (a regional factor) we employed the connectivity index, S_i , taking into account distances to all possible source ponds on the ESGR and their respective population sizes (reviewed by Moilanen and Nieminen 2002, Winfree et al. 2005):

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_j$$

where α scales the effect of distance to migration ($1/\alpha$ is the mean migration distance), d_{ij} is the distance (edge to edge) between ponds i and j , and N_j is the sum of the mean population sizes of all amphibian species in pond j over the seven years. N_j therefore weights each potential source pond by the average total population size of larval amphibians in the pond (thus we assume larval population size is correlated with numbers of dispersing individuals). Estimates of average dispersal distances for the amphibian species on the ESGR were not available. Data on dispersal distances for amphibians are sparse and typically reported as a maximum dispersal distance (Marsh and Trenham 2001, Smith and Green 2005). Semlitsch (1998) reported mean dispersal distances of six species of ambystomatid salamanders (which are less mobile than anurans) to range between 30 and 250 m. Smith and Green (2005) reviewed studies reporting maximum distances moved for 90 species of amphibians (<1 km for 56% of anurans and 94% of salamanders). Because mean distances moved will be considerably less than these estimates, we employed an average value of 750 m in analyses. To assess the sensitivity of conclusions to this value we also calculated S_i over a range of mean migration distances between 100 and 3000 m.

We formulated a series of models that postulated local abiotic variables, local biotic variables, or regional connectivity individually were the best predictors of

Table 1. Akaike model selection results for predicting turnover.

Model	Number of parameters	n	Residual SS	AIC _c	Δ _i	W _i
Abiotic variables	5	32	0.35	-132.6	10.0	0.007
Biotic variables	5	32	0.61	-114.3	28.3	0.000
Connectivity	3	32	0.64	-118.1	24.4	0.000
Abiotic+biotic	8	32	0.33	-124.1	18.5	0.000
Abiotic+connectivity	6	32	0.23	-142.6	0.00	0.979
Biotic+connectivity	6	32	0.43	-122.3	20.3	0.000
Global model	9	32	0.21	-134.1	8.5	0.014
R ² of the best model =0.71						

Model-averaged parameter values. Bold values are those where 95% confidence intervals excluded 0.

Parameter	Area	Canopy cover	Hydroperiod	Invertebrate predators	Caudate biomass	Anuran biomass	Connectivity
Estimate	-0.051	-0.055	-0.323	-0.0002	-0.0002	0.0000	0.027

turnover. We then constructed models incorporating combinations of these groups of variables (Table 1). The global model included all seven of the local and regional variables. The models were formulated for ponds without fish (or years without fish). Only two ponds contained fish for all seven years, and the impact of fish renders many relationships on environmental variables quadratic that are otherwise linear (Werner et al. 2007). We further excluded three ponds where turnover was not applicable (no presences) or poorly estimated because of rare presences, leaving 32 ponds in the analyses.

We employed AIC_c, a bias-corrected version of Akaike's information criterion, to rank models according to the strength of support from the data (Burnham and Anderson 2002). The best model is that with the lowest AIC_c value, and we employed Akaike weights to assess the likelihood of alternative models. Akaike weights also were used to estimate parameter values and their variances employing a model averaging approach (Burnham and Anderson 2002). Model averaged estimates and SE's were calculated and 95% confidence intervals employed to assess the magnitude of the effect. We concluded that there was an effect if the confidence interval excluded 0.

The Akaike model selection procedure seeks the single best supported predictive model, but this approach does not identify those variables most likely to influence variation in the response variable (turnover in our case). Abiotic and biotic predictor variables were often significantly intercorrelated (Werner et al. 2007), and this multicollinearity makes it difficult to identify variables that have independent effects on the response variable. To address this problem, we employed hierarchical partitioning (Mac Nally 2002,

Quinn and Keough 2002). Hierarchical partitioning employs goodness of fit measures (R² in a multiple regression setting) and averages the incremental improvement in fit by the addition of a given variable to all of the possible models (2^k models for k predictor variables) with that variable compared to the equivalent models without that variable. Using this method one can partition explanatory power for each predictor variable into independent effects and those due to joint effects with other variables (i.e. those that cannot be unambiguously associated with the variable in question). We further employed a method randomizing the data suggested by Mac Nally (2002) to statistically evaluate which predictor variables should be retained (analyses conducted in R, Anonymous 2006).

Results

Interannual turnover in amphibian species composition

Interannual turnover in species composition of the ESGR ponds can be illustrated by comparisons of their mean and cumulative species richness (Fig. 1). Cumulative species richness of a pond averaged 6.0 ± 0.4 species with a range from 0 to 10. In contrast, mean species richness of a pond was considerably less, averaging 3.3 ± 0.3 species. Thus, mean richness of a pond averaged only 54% of cumulative richness, with 92% of the values across ponds lying between 30 and 75%. This fraction was unrelated to the cumulative number of species found in a pond (excluding two ponds, one with no species and one that had one species in one year, R²=0.04, F_{1,33} = 1.5, p = 0.24). The average interannual turnover (measured using the

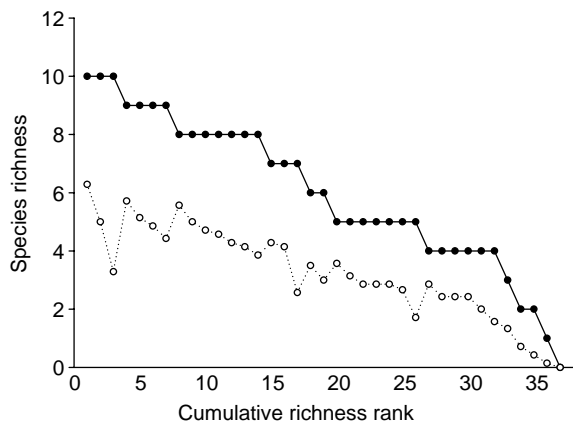


Fig. 1. Mean (open symbols) and cumulative (solid symbols) amphibian species richness for the E. S. George Reserve ponds rank ordered by their cumulative richness.

complementarity index and hereafter referred to as turnover) underlying the pattern in Fig. 1 was 0.52 ± 0.03 . That is, ponds on average only experienced 48% of species in common in two consecutive years.

Reliability of individual species' presences

The reliability of different species' presences in a pond varied considerably, ranging from 14 to 87%, with a mean of $50 \pm 6\%$ (Fig. 2). Thus, all species participated in the interannual turnover, but to different degrees. These results indicated that species differed in reliability, but the values do not tell us how important various species were to the actual turnover events that occurred. For example, a species with low reliability would not contribute much to the realized turnover if it were a rare species, or conversely a species found in a large number of ponds with fairly high reliability could contribute significantly to the turnover events. The percent contribution of the different species to the total number of turnover events (i.e. a presence to an absence plus an absence to a presence) ranged between 0.6 and 18%, with the six most abundant species contributing between 8 and 18% of the turnover events.

Model selection and the factors associated with interannual turnover

The best supported model for predicting turnover (ponds without fish, $n=32$) by the Akaike criterion included both abiotic variables and pond connectivity ($R^2=0.71$, Table 1). The Akaike weight for this model was 0.98 indicating that the model had a 98% chance of being the best model given the data. The biotic

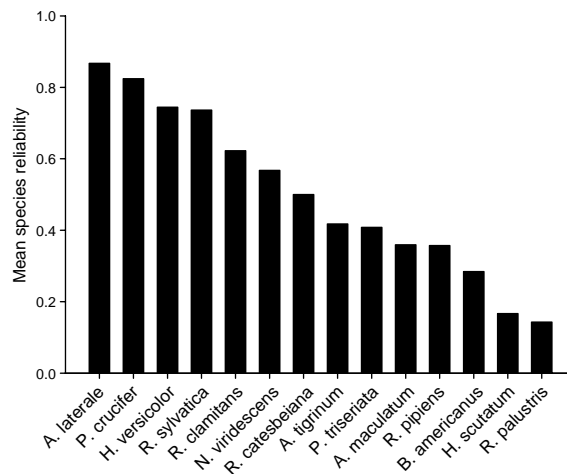


Fig. 2. Mean reliability for species found in the E. S. George Reserve ponds. See Appendix 1 for a species list of the Reserve.

model by comparison had an R^2 of only 0.24. Although connectivity alone did not account for a large amount of the variation in turnover ($R^2=0.2$), it markedly improved predictive capabilities when added to the abiotic model (Table 1), suggesting that it captured aspects of variation not accounted for by the abiotic variables. Model averaged parameter estimates indicated that area, hydroperiod, and connectivity were different from 0 (Table 1).

It is not clear from the model selection analysis whether all of these variables independently contribute to variation in species richness, or if variables are included in the model because they contribute to the overall best fit due to correlations with causal variables. For example, the three environmental variables were moderately collinear (variance inflation factors ranging from 2.1–4.5, Werner et al. 2007), whereas connectivity was not significantly related to any of these variables. Further, it is not clear if all independently contributing variables are included in the selected models. We employed hierarchical partitioning to identify the extent to which each of the seven variables was independently correlated with turnover. The results of this analysis strongly reinforced those of the model selection exercise (Table 2). Area, hydroperiod and connectivity all contributed between 22 and 32% of the summed independent effects of all variables on turnover, and were significant according to the randomization test (i.e. the same variables identified by the model averaging procedure as having significant parameter values). In contrast, biotic factors accounted for only 1–8% of the independent effects. As noted earlier, connectivity appears to be unique in having modest total effects, but a much higher ratio of independent to joint effects than any of the other variables included in

Table 2. Hierarchical partitioning of variance for the seven predictor variables for turnover.

Anurans			
Variable	Independent	Joint	Total
Area	0.24*	0.29	0.53
Hydroperiod	0.17*	0.18	0.35
Connectivity	0.16*	0.04	0.20
Canopy cover	0.08	0.21	0.29
Invertebrate predators	0.06	0.14	0.20
Caudate biomass	0.02	0.03	0.05
Anuran biomass	0.01	0.03	0.04

Asterisks indicate values significant by the randomization procedure.

the best supported model (Table 2). Simple correlations between turnover and each of the three significant variables with turnover are presented in Fig. 3

There also were population characteristics of individual species that in addition to connectivity suggested an influence of regional processes. One might expect species' reliability to be related to the population size in a pond (i.e. small populations would be more vulnerable to extinction). Indeed, the relation between \ln mean local population size of a species (the density of larvae \times pond area, averaged across ponds and years) and their average reliability was positive and marginally non significant ($R^2 = 0.27$, $F_{1,10} = 3.7$, $p = 0.08$). If we estimated regional population size (average density \times pond area, summed over ponds on the ESGR and averaged across years), however, the relationship between species' reliability and \ln regional population size was highly significant and accounted for twice the variation in reliability (Fig. 4, $R^2 = 0.55$, $F_{1,10} = 12.2$, $p = 0.006$).

There was little evidence of an important effect of biotic factors on turnover from the above analyses. However, these analyses excluded ponds with fish, of which there were five prior to 1998–99 on the ESGR, and two thereafter (Werner et al. 2007). There does appear to be a strong impact of fish on turnover in these communities. We computed turnover for the five ponds in years when they had fish, and average turnover was 2.6 ± 0.4 fold higher than predicted values for the best supported model in Table 1 (i.e. for ponds with equivalent area, hydroperiod, canopy cover and connectivity). Four of the five values lie outside the 95% confidence intervals for predicted values. Moreover, for the three ponds that lost fish during the survey due to drought, turnover values averaged 3.3 ± 1.4 fold higher when they contained fish than when fish were absent.

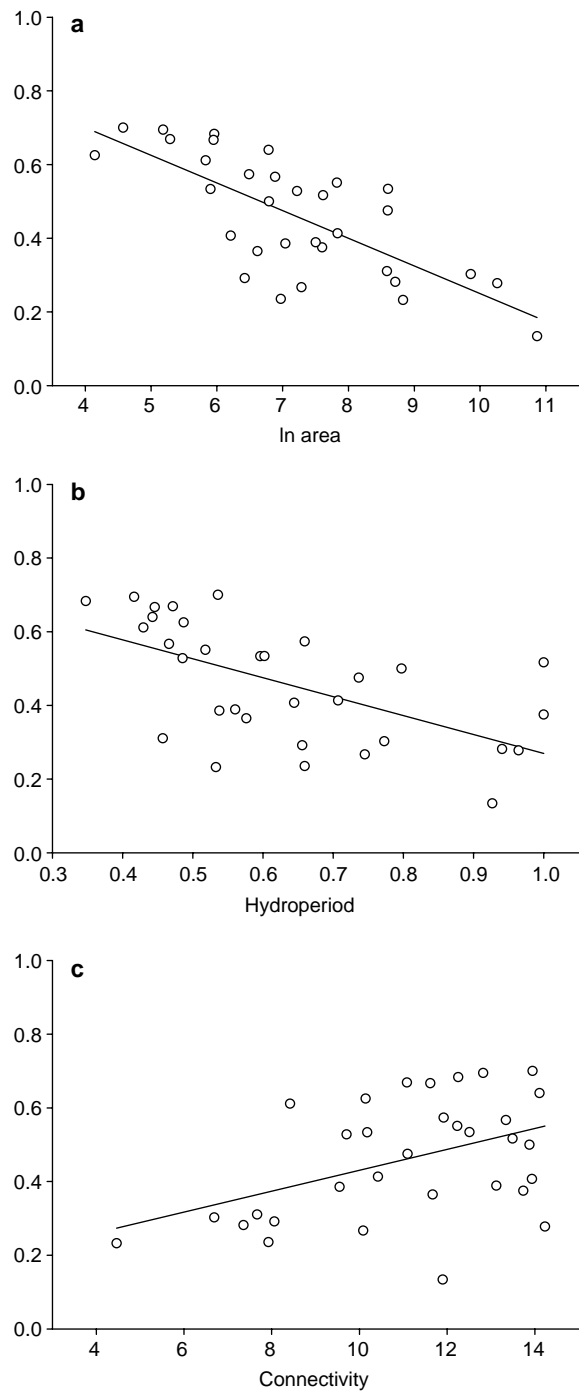


Fig. 3. Mean turnover (complementarity) of the E. S. George Reserve ponds as a function of, (a) \ln area, (b) hydroperiod, and (c) connectivity ($S_i \times 10^{-5}$). Connectivity for the relationship portrayed was calculated based on a mean dispersal distance of 750 m.

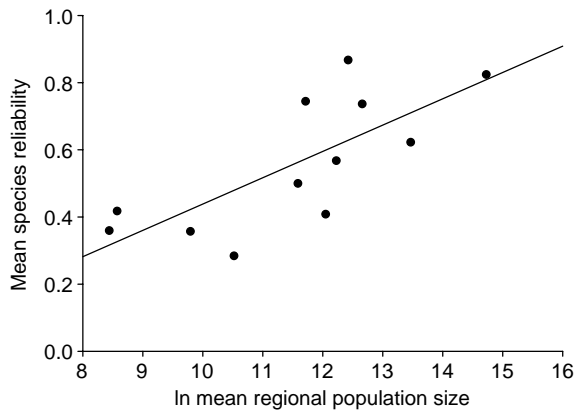


Fig. 4. Mean species reliability as a function of ln of mean regional (larval) population size for the species on the E. S. George Reserve.

Discussion

Both local and regional factors contributed to turnover in the species composition of these larval amphibian communities. At the scale of the entire ESGR (540 ha), amphibian species composition has been stable for at least 30 years (one species went locally extinct following a drought in 1971, Collins and Wilbur 1979). Further, there are strong patterns in the species richness of these ponds with environmental characteristics (Collins and Wilbur 1979, Skelly et al. 1999, Werner et al. 2007). However, our data on the relation between mean and cumulative richness of ponds, turnover rate, and species reliability all point to very large interannual turnover in the species composition of ESGR ponds. Across a wide range of pond types and communities of different richness, only about half of the species found in a pond across seven years were actually present in any given year. These data suggest that the patterns in species richness are underlain by dynamic processes associated with this turnover. For example, ponds that have high cumulative species richness can exhibit a wide range in characteristic mean annual richness (Fig. 1).

The high rates of turnover we report are not an artifact of our focus on larval populations (e.g. as opposed to calling surveys of adults). High rates of temporal turnover appear to be characteristic of amphibian communities (Hecnar and M'Closkey 1996, Semlitsch et al. 1996, Skelly et al. 1999, Pechmann et al. 2001, Marsh and Trenham 2001, Petranka et al. 2003), and estimated turnover rates for individual species also suggest that other systems may experience similar community turnover. For example, we compared turnover of *Rana clamitans*, *R. sylvatica*, *Pseudacris crucifer* and *Hyla versicolor* with those estimated by Trenham et al. (2003) and Hecnar and M'Closkey (1996). Estimates of turnover (mean pro-

portional gains and losses in detections for the four species) for all studies were very similar: 0.18 ± 0.13 and 0.18 ± 0.07 , respectively (Trenham et al. 2003), 0.23 ± 0.1 and 0.24 ± 0.05 , respectively (this study), and those of Hecnar and M'Closkey fell between these values. Thus, despite the very different sampling protocols (and life history stages assessed) among the three studies, estimates of rates of individual species turnover were similar.

In larval amphibian communities, turnover may be the result of several different mechanisms. Turnover can arise from sampling error, from species going extinct in a pond, from species that are present at the pond (as adults) but did not breed (skipped breeding, Semlitsch et al. 1996), or from adult breeding congregations that moved between ponds (Collins 1975, Petranka et al. 2004). These mechanisms each have different implications to pond community structure, and the factors correlated with turnover could provide clues as to the actual causes behind turnover (which inform issues from individual breeding strategies to metacommunity dynamics).

The weight of the evidence suggests that the majority of the turnover we report represents local extinctions. Evidence in the literature for skipped breeding and movement of breeding congregations is limited, and typically associated with drying (or imminent drying) of breeding ponds or other site disturbances such as fish addition or deletion from ponds (Collins 1975, Petranka et al. 2004, Resetarits 2005). If we exclude all cases where a pond was dry when we sampled in either survey period (or fish presence changed), the estimated turnover only declines from 0.52 to 0.46. Thus, nearly 90% of the turnover that we recorded occurred when these factors would not limit species breeding or prompt chorus movement. Second, the most abundant species on the ESGR are short lived (the exception is a salamander) and the majority of individuals in these populations likely only breed once (Collins 1975, Smith 1987, Berven, pers. comm.). Consequently, it is not likely that these species would skip breeding more than one year. During the seven years of sampling, half (103/201) of the "extinction" events resulted in species' absences from the pond for ≥ 2 years, and nearly one-third (70/201) of these events were ≥ 3 years. Literature surveys also suggest that site fidelity in adults is strong in the amphibian species found on the ESGR (with perhaps the exception of *Bufo*, Marsh and Trenham 2001, Smith and Green 2005). For example, Vasconcelos and Calhoun (2004) followed *R. sylvatica* and *A. maculatum* (abundant species on the ESGR) at three human-constructed ponds within 200 m of one another; fidelity to a breeding site was 88% to 98% in *R. sylvatica* and 100% in *A. maculatum*. Berven and Grudzien (1990) found that *R. sylvatica* in five ponds exhibited 100% pond

fidelity, and Benard (2005) reported that out of 3500 individually marked adult *Pseudacris regilla*, only two were ever observed as adults at more than one pond. Thus, though multiple factors may contribute to turnover, it appears likely that the majority of turnover events here represent local extinctions.

Local abiotic characteristics and connectivity accounted for 71% of the variance in turnover of the ESGR ponds (Table 1). Numerous studies have indicated that extinctions are correlated with local environmental factors (Hanski 1999), so the relation with abiotic factors is not unexpected. Area had the largest independent and total effect on turnover (Table 2). One would expect an increase in extinction rates (or decreases in viability of sink populations) as populations decrease in size in smaller ponds (contributing to higher turnover in these ponds). Reflecting this effect, species reliability decreased as mean population size decreased, and extinction rates of individual species on the ESGR are negatively related to local population size (Werner et al. 2007). A large number of studies on numerous taxa demonstrate that extinctions are negatively correlated with area (reviewed by Hanski 1999), though other important habitat variables collinear with area are not often measured.

Pond hydroperiod also was an important factor associated with turnover in ESGR amphibian species. The role of hydroperiod in limiting the distribution of amphibian species across ponds has been a prevailing paradigm in amphibian ecology (Wilbur 1984, Wellborn et al. 1996, Urban 2004). These conceptualizations have emphasized the constraints that hydroperiod places on the larval period of amphibians and/or the particular predators or competitors a species faces in these ponds. This is largely a static representation emphasizing that the patterns arise due to the accumulation of species with traits that can achieve positive fitness at different points along the hydroperiod gradient. However, unlike canopy cover or area, hydroperiod varied over the time scale of our study (Semlitsch et al. 1996). Smaller ponds with shorter mean hydroperiods exhibited a nonlinear increase in the coefficient of variation in hydroperiod (as would be expected on statistical grounds alone) and this variance was elevated over the survey period due to a significant drought beginning in the late summer of 1998 (Hoerling and Kumar 2003, Petranka et al. 2003, Werner et al. 2007). This variance in hydroperiod clearly would contribute to mean turnover in ponds. Thus, the patterns in species richness along the hydroperiod gradient appear to be driven in part by this variation and the consequent effects on the dynamics of species turnover. Reinforcing this view, in open-canopy ponds (where there was a large range in areas) there was no relation between pond area and cumulative species richness, whereas there was a strong

positive relation between pond area and mean species richness (Werner et al. unpubl.). That is, the increasing variation in hydroperiod (along with small population effects) would contribute to the increasing disparity between mean and cumulative richness in smaller ponds.

Our data indicate little evidence of the role of biotic factors in species turnover, with the exception of the presence of fish. Population densities of amphibians were much lower with fish than in their absence (e.g. in three ponds that lost fish due to the drought, the average increase in total amphibian density was 19.8 ± 7.2 fold), and undoubtedly the vulnerability of most amphibians to fish contributed to the turnover of species in these ponds. Higher turnover in these ponds also may have occurred because few ponds on the ESGR were permanent with fish, and even those species that are not vulnerable to fish and limited to permanent ponds (e.g. bullfrogs, Werner and McPeck 1994), have exhibited small populations on the ESGR for the period of the survey. Therefore, rescue effects that arise from large regional populations would be lacking for these species.

Unlike the analyses of local factors, we do not have replicated units (suites of ponds) embedded in different landscapes to examine in a parallel fashion the influence of regional context on interannual turnover in ponds. However, we were able to explore the impact of space (pond connectivity) on turnover rates. Connectivity can influence turnover through enhanced colonization rates, rescue effects and the maintenance of sink populations by source ponds, and the feasibility of movement of breeding congregations. There was a positive relationship between turnover and connectivity of ponds (this relation was significant for simulated average dispersal distances between 500 and 3000 m). Because smaller ponds exhibited higher turnover and higher connectivity (since large marshes containing large amphibian populations were always incorporated in their connectivity), a large number of the smaller ponds were found in the upper portion of Fig. 3c. To assure that the relation in Fig. 3c was not an artifact of these size differences, we also examined the relationship between turnover and connectivity limiting focal ponds to those $\leq 2600 \text{ m}^2$ (24 ponds). Thus, larger marshes were part of each of these focal pond's environments, and the focal ponds should be similar in their propensity to attract or be discovered by dispersing amphibians. The relationship between turnover and connectivity remained strongly positive (though R^2 and significance levels decreased, $R^2 = 0.14$, $F_{1,22} = 3.5$, $p = 0.08$).

It is likely that the general relationship between annual turnover and connectivity is unimodal. That is, because very isolated ponds would receive few dispersers, turnover rates would be relatively low in these ponds. However, with increases in connectivity potential

turnover is greater as populations that wink out of existence can be recolonized relatively quickly. Thus, over some range of connectivity values one would expect a set of habitats to exhibit a positive relation between connectivity and turnover. However, as connectivity continues to increase, ponds experience increasingly larger mass effects that could maintain marginal populations (rescue small or sink populations) or cause turnover to be cryptic (i.e. an extinction followed by colonization before the next sampling data, Clark and Rosenzweig 1994), so extinctions would be infrequent and turnover would again decrease.

Our findings suggest that the ESGR ponds occupy a region of moderate spatial proximities for amphibians where connectivity serves to promote turnover. Further, the reliability data indicate that a substantial fraction of this turnover is due to the regionally abundant and widespread species on the ESGR (and, of course, these species contribute disproportionately to connectivity values). Dispersal of these abundant species would enable recolonization of ponds that go extinct due to variation in pond quality over time or small population effects. Consequently, it is likely that the potential for this turnover results in the maintenance of overall average higher species richness in more connected ponds. Though application of the connectivity index to an entire community is rather crude, taken together all analyses suggest an important role of landscape context in influencing amphibian community structure.

Context appears to influence reliability at the scale of the individual species as well. There was a positive association between reliability and average local population size in the ponds, which one would expect given that the likelihood of extinction is related to the size of the local population. Reliability, however, exhibited an even stronger positive correlation with regional population size on the ESGR. Evidently, species that were widespread with large regional populations were able to sustain pond populations through rescue or mass effects, and thereby exhibit higher average reliabilities. That is, both community and individual species patterns suggest an important role of dispersal between ponds.

On the surface these two patterns may appear contradictory; i.e. for the local pond community connectivity positively affected turnover whereas when considering individual species, regional population size (which typically should increase connectivity of ponds) positively affected reliability (therefore less turnover). However, as noted earlier the 6 most abundant and reliable species each contributed between 8 and 18% of the turnover events, i.e. in the aggregate account for the majority of events. Given the large interannual variability in pond characteristics (especially hydroperiod) and small population sizes that can lead to higher extinction rates, mass effects originating with these

abundant species would enable expression of turnover in species composition, even though on average it may increase individual species' reliability through rescue effects.

The patterns we uncovered lead us to conclude that interconnections among ponds are critical to the dynamics in any particular pond. As an example, it is highly unlikely that especially the smaller ponds, which exhibit greater variation in local characteristics, would support many species without the landscape connection to counter high extinction rates, both on the time scale that we have examined here, and at a decadal scale where other factors contribute to the variation in local characteristics that influence species composition (e.g. canopy cover, Skelly et al. 1999). Metapopulation theory reinforces the idea that the persistence of species is highly sensitive to dynamics in patch quality (e.g. due to succession, Hanski 1999, Amarasekare and Possingham 2001, Ellner and Fussmann 2003, Biedermann 2004), and that patch quality can supersede patch geometry in explanations of metapopulation dynamics (Fleishman et al. 2002). Thus, transient changes in patch quality are likely to have very important effects on regional population trends, and Urban (2004) has suggested that this shifting mosaic of habitat suitability over time may result in these metacommunities being relatively resilient to spatially synchronous disturbance.

The extensive temporal variation in pond quality and species composition also has implications to the evolution of species traits. Coevolution of fixed species traits due to interactions with other species is less likely given the great variation in selective context generated by the variable presence of these species. Thus, it is not surprising that amphibian larvae have been found to exhibit extensive phenotypic plasticity, e.g. in timing and size at metamorphosis, morphology, physiology and behavior in response to both the physical environment and the presence of predators and competitors (Benard 2004, Relyea 2004, Van Buskirk and Arioli 2005). Further, factors leading to turnover likely result in selection for some level of dispersal in amphibians (and an ability to assess breeding sites, Resetarits 2005, Resetarits et al. 2005). Though amphibian adults have been reported to be highly philopatric (Berven and Grudzien 1990, Smith and Green 2005, but see Petranka et al. 2004), most at least have more extensive juvenile dispersal phases (reviewed by Marsh and Trenham 2001, Smith and Green 2005). This dispersal fundamentally enables spatial storage effects (Chesson et al. 2005) that would be critical in a dynamic landscape, and there are obvious advantages for species with substantial temporal storage in the adult phase as well (Warner and Chesson 1985). In light of the apparent importance of connectivity and dispersal, observations of population divergence suggesting localized adaptation among nearby ponds on the ESGR (Relyea 2002) and

elsewhere (Skelly 2004) are somewhat paradoxical. Understanding the tension between dispersal (gene flow) and local adaptation in these species will shed considerable light on both their ecology and evolution (Urban and Skelly 2006).

There are relatively few long-term data on multiple, interacting communities of organisms that enable us to estimate the magnitude of, and factors affecting, rates of temporal turnover in communities. Such data are critical to understanding the relation between local and regional factors, isolating the important role of landscape dynamics in metapopulation and metacommunity processes (Hanski 1999, Amarasekare and Possingham 2001, Ellner and Fussmann 2003), interpreting life history strategies of species, and evaluating census data for management or conservation issues (Skelly et al. 2003). The extensive community turnover that we have estimated in the ESGR ponds is in line with studies of other taxa showing similarly high rates of turnover at local sites (e.g. birds, Boulinier et al. 2001, Doherty et al. 2003, Bennett et al. 2004; insects, Krauss et al. 2003), suggesting that it will be important to conceptualize species assemblages as metacommunities and explore the interaction of these processes mediated through the movement of individuals between habitats. Our data suggest that dispersal-assembly plays a role in the ESGR amphibian community (Hubbell 2001), but there also are striking patterns in the association of species traits with different environments, i.e. a great deal of species sorting or niche assembly is also occurring (Collins and Wilbur 1979, Skelly et al. 1999, Werner et al. 2007). It is critical that we address the interaction of these processes occurring at different scales in order to provide a predictive framework for community assembly and effective management strategies for the conservation of species.

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Appendix 1

Amphibian species reported on the E. S. George Reserve.

Family	Species	Common name
Bufo	<i>Bufo americanus</i>	American toad
Hylidae	<i>Acris crepitans</i>	cricket frog
	<i>Hyla versicolor</i>	gray tree frog
	<i>Pseudacris crucifer</i>	spring peeper
Ranidae	<i>P. triseriata</i>	chorus frog
	<i>Rana catesbeiana</i>	bullfrog
	<i>R. clamitans</i>	green frog
	<i>R. pipiens</i>	leopard frog
	<i>R. sylvatica</i>	wood frog
Ambystomatidae	<i>R. palustris</i>	pickrel frog
	<i>Ambystoma laterale</i>	blue-spotted salamander
	<i>A. maculatum</i>	spotted salamander
	<i>A. tigrinum</i>	tiger salamander
Plethodontidae	<i>A. tremblayi</i>	Tremblay's salamander
	<i>Hemidactylium scutatum</i>	four-toed salamander
	<i>Plethodon cinereus</i>	red-backed salamander
Salamandridae	<i>Notophthalmus viridescens</i>	eastern newt

Appendix 2

Sampling efficacy

We assessed sampling efficiency by first examining species accumulation curves (Colwell and Coddington 1994) and associated statistics employing EstimateS, ver. 7 (<http://viceroy.eeb.uconn.edu/estimates>). All individuals were pooled from the pipe, dip and seine samples for a pond in a given year, and species accumulation curves constructed based on the distribution of species among individuals (sampling effort). We employed the Chao2 bias-corrected richness estimator to estimate “true” species richness of ponds from the distribution of species among individuals we obtained.

We also computed 95% detection threshold curves as a function of sampling effort and hypothetical larval density. Since both pipe sampling and dipnetting

contributed to detection ability, we can obtain a standardized total effort (pipe equivalents) by employing regressions to predict numbers of individuals collected per unit effort dip netting. These regressions were obtained by plotting pipe density estimates against individuals captured per person-minute dipnetting for all cases where individuals of a given taxon were captured by both techniques in a pond. That is, we used all dates where we went to a pond and where we had a density estimate (from pipe samples) and a catch per unit effort from the dipnetting for that taxon on that date as an individual datum. Because of the highly episodic nature of amphibian populations, we had enormous variation in density estimates for each family within a pond across sampling dates so data points from a pond are not clustered at any position on the density/catch per unit effort graph (i.e. density estimates are not confounded with sampling effort, pond characteristics, etc.). To ensure adequate sample sizes and ranges for these relationships, we grouped species by family. Regressions were constrained to go through the origin and were highly significant (ambystomatids: $R^2 = 0.72$, $p < 0.001$, hylids: $R^2 = 0.88$, $p < 0.001$, ranids: $R^2 = 0.76$, $p < 0.001$, newts: $R^2 = 0.88$, $p < 0.001$) with the exception of that for the American toad where sample sizes were small ($R^2 = 0.26$, ns). The mean slope of the four significant relationships (weighted by number of species in each family) was 0.85 ± 0.1 indicating that the number of individuals collected per min of dipnetting was equivalent to the number typically collected in 1.2 pipe samples. Since person-minutes dip netting was always equivalent to the number of pipe samples taken, this means that our effective sampling effort was just over twice that represented by the number of pipes (i.e. if we took 40 pipe samples, the effective sampling effort was essentially 88 pipe equivalents). We could therefore use pipe equivalents to estimate detection probabilities.

As a further indication of sampling efficiency, we examined the relationship between the reliability with which we sampled species in a pond and sampling effort in that pond. We computed reliability as the fraction of years each species was sampled in a pond given that it was collected in that pond at least one year. Species' reliability for a pond was the average across all species found in the pond. We then regressed this reliability value against the ln of pond area/no. of pipe samples taken to determine if there was a relation between reliability and this measure of sampling effort.

Results of the above analyses are as follows. Estimators of species richness from sampling effort typically converge on the observed species number when all species are represented by two or more individuals in the collection (Colwell and Coddington

1994). This was the case in 64% of our 219 pond-year combinations. The remaining cases therefore contained one or more singletons (species represented by a single individual in the sample). Cases with singletons that are adequately sampled versus inadequately sampled can look substantially the same (Colwell and Coddington 1994), so in these cases we employed the Chao2 richness estimator in EstimateS to estimate the true species richness of the pond that year. In only 14% of cases where one or more singletons were represented in the sample did the theoretically estimated number of species exceed the actual number sampled by >0.5 , or in 5% of the total number of pond-year combinations represented in the dataset. Further, there was no relation ($R^2 = 4 \times 10^{-6}$) between the fraction of records in a pond that were singletons and the sampling effort in that pond (measured as pond area/no. of pipe samples taken, which varied over a 212 fold range because we were unable to sample very large marshes with the same effort as small ponds). Also, using ponds $>100 \text{ m}^2$ (i.e. that usually contained amphibians) regressions of reliability against sampling effort were not significant and only explained 9% of the variation. Thus, there was no evidence that sampling intensity influenced the reliability with which we documented presence of a species in a pond given that we knew that it was found there at least one of the seven years. And, as noted in the text for the wood frog where we had egg counts the probability that we detected a larval population given egg deposition averaged 0.96 ± 0.01 over years when eggs were not killed by drying. Finally, the detection threshold analysis indicated that if larvae were assumed (as a first approximation) to be binomially or Poisson distributed, our 95% detection threshold for a species occurred at densities on the order of 1 larva per 3.3 m^2 in the larger ponds. Thus, although there are inevitable detection errors in the data, we are confident that our estimates of species richness of ponds provide an excellent approximation to the number of species present there.

Estimation of biotic variables

Amphibians in the samples were identified to species, snout-vent length measured, and Gosner stage recorded. All potential predators of amphibians (including fish, Odonata, Hemiptera, Coleoptera, Araneae, Hirudinea) were identified to species where reliable keys were available (most taxa), or to genus when this was not possible (e.g. a number of dytiscid beetle larvae), and measured (length or head width depending on taxon). For analyses of predator effects, we selected a subset of the invertebrates that we expected to be important predators on amphibian larvae based on literature accounts, ultimate size, and our experience. Among the odonates we included all members of the Aeshnidae, Cordulidae, Gomphidae and Libellulidae. We also included the Belostomatidae, Notonectidae, Nepidae and the Megaloptera. Finally, among the beetles we included larvae of the larger dytiscid (*Dytiscus*, *Hydaticus*, *Colymbetes*) and hydrophilid species (*Hydrochara*, *Dibolocelus*), and the larger adult dytiscids (*Dytiscus*, *Hydaticus*, *Colymbetes*, *Acilius*, *Graphoderus*, *Agabus*, *Rhantus*, *Ilybius*).

We employed predator biomass in analyses in order to scale the presence of larger predators in accord with their abilities to prey on a wider size range, and to consume more, of the amphibian larvae. Samples of invertebrate predators were dried (at 60°C for 24 h) to obtain length-dry weight regressions. Due to the small number of specimens available for some taxa, or lack of adequate keys, we in some cases lumped species into broader taxonomic and/or morphologically similar categories (usually family-level). Length-weight regressions also were obtained for ambystomatid salamanders (Yurewicz unpubl.), the newt (Fauth unpubl.), and anuran larvae (individual species regressions were so similar that a composite regression was used for all species; $R^2 = 0.99$, $F_{1,156} = 18,670$, $p \ll 0.001$). We employed these regressions to calculate biomass densities of invertebrate predators, caudates and anuran larvae in ponds for use in the model selection analyses.