

Rowland Freya Elizabeth (Orcid ID: 0000-0002-1041-5301)

Journal: Ecology

Manuscript type: Article

Asynchrony, density dependence, and persistence in an amphibian

FREYA E. ROWLAND^{1,6}, ELIZABETH S. SCHYLING¹, L. KEALOHA FREIDENBURG¹, MARK C. URBAN², JONATHAN L. RICHARDSON³, A.Z. ANDIS ARIETTA¹, SUSAN B. RODRIGUES⁴, ADRIANA D. RUBINSTEIN¹, MICHAEL F. BENARD⁵, AND DAVID K. SKELLY^{1,4}

¹School of the Environment, Yale University, 370 Prospect St., New Haven, CT 06511 USA

²Department of Ecology and Evolutionary Biology and Center of Biological Risk, University of Connecticut, Storrs, CT 06269 USA

³Department of Biology, University of Richmond, VA 23173 USA

⁴Yale Peabody Museum of Natural History, Yale University, New Haven, CT 06511 USA

⁵Department of Biology, Case Western Reserve University, 10900 Euclid Ave., Cleveland, OH 44106 USA

⁶Corresponding author: frowland@usgs.gov

Received 26 April 2021; revised 15 November 2021; accepted 14 January 2022

Handlign Editor: Daniel E. Schindler

Open research: Data (Rowland, et al. 2022) are available on Dryad at <https://doi.org/10.5061/dryad.0cfxpnw3r>. Code (Rowland, 2022) is available on Zenodo at <https://doi.org/10.5281/zenodo.5903388>.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1002/ecy.3696](https://doi.org/10.1002/ecy.3696)

This article is protected by copyright. All rights reserved.

Abstract. Understanding drivers of metapopulation dynamics remains a critical challenge for ecology and conservation. In particular, the degree of synchrony in metapopulation dynamics determines how resilient a metapopulation is to a widespread disturbance. In this study, we used 21 years of egg mass count data across 64 nonpermanent freshwater ponds in Connecticut, USA to evaluate patterns of abundance and growth and to assess regional as well as local factors in shaping the population dynamics of wood frogs (*Rana sylvatica* = *Lithobates sylvaticus*). In particular, we asked whether a species known to undergo metapopulation dynamics exhibited spatial synchrony in abundances. With the exception of a single year when breeding took place during severe drought conditions, our analyses revealed no evidence of synchrony despite close proximity (mean minimum distance < 300 m) of breeding ponds across the 3213 ha study area. Instead, local, pond-scale conditions best predicted patterns of abundance and population growth rate. We found negative density dependence on population growth rate within ponds as well as evidence that larger neighboring pond populations had a negative effect on focal ponds. Beyond density, pond depth was a critical predictor; deeper ponds supported larger populations. Drought conditions and warm winters negatively affected populations. Overall, breeding ponds vary in critical ways that either support larger, more persistent populations or smaller populations that are not represented by breeding pairs in some years. The infrequency of spatial synchrony in this system is surprising and suggests greater resilience to stressors than would have been expected if dynamics were strongly synchronized. More generally, understanding the characteristics of systems that determine synchronous population dynamics will be critical to predicting which species are more or less resilient to widespread disturbances like land conversion or climate change.

Key words: amphibian; anuran; climate; competition; habitat; landscape; metapopulation; population ecology; spatial ecology

INTRODUCTION

Do populations rise and fall independently in response to local factors or are they synchronized in space? Spatial synchrony can emerge when populations are connected by dispersal (Ranta et al. 1995) or when an external driver simultaneously affects populations across a region (Moran 1953; A. Liebhold, Koenig, and Bjørnstad 2004). Although common across a wide range of taxa (A. Liebhold, Koenig, and Bjørnstad 2004), we still know relatively little about what characteristics of species, ecosystems, and disturbances drive synchrony. This information is critical for assessing the vulnerability of metapopulations to widespread disturbances like land-use or climate change and ultimately for predicting species extinction risks (Abbott 2011; Fox et al. 2017).

Metapopulations are an ensemble of populations connected by dispersal that experience population turnover, extinction, and establishment of new populations (Hanski and Gilpin 1991). The degree to which metapopulation synchronize (i.e., temporal correlation in population sizes) depends on the interplay between local factors such as dispersal and demographic stochasticity (Kendall et al. 2000) and regional factors such as disturbances and landscape heterogeneity (Haydon and Steen 1997; Lande, Engen, and Sæther 1999; Briggs and Hoopes 2004). Metapopulations better connected by dispersal tend to be more synchronized (Larsen et al. 2021), as are metapopulations experiencing synchronous disturbances such as regional weather events (Kahilainen et al. 2018). Although dispersal can synchronize populations (Abbott 2011), this effect can be significantly diminished by density-dependent dispersal (Ims and Andreassen

2005). This complexity of metapopulation synchrony means understanding how local- and regional-level characteristics determine synchrony is not yet well understood.

When metapopulation theory was developed, pond-breeding amphibians were among the first organisms to be considered as candidate taxa (Alford and Richards 1999) because of their high dispersal rates among breeding ponds. While adults tend return to the same breeding pond, juvenile dispersal rates can be as high as 20% of metamorphs (Gamble, McGarigal, and Compton 2007; Wang and Shaffer 2017). Drift fence data show up to 18% of juvenile wood frogs permanently move to a new breeding pond (Berven and Grudzien 1990). A second factor which may contribute to synchronization in amphibians is the influence of interannual variation in weather (Piha et al. 2007). The absolute dependence of many species on nonpermanent wetlands for breeding means that drought conditions can restrict the availability of breeding habitat. Low rainfall can lead to premature drying of pond basins stranding entire larval cohorts (RAYMOND D. Semlitsch et al. 1996; Alford and Richards 1999). More generally, soil moisture and humidity levels are important to the survival and activity patterns of terrestrial amphibian stages (T. A. G. Rittenhouse et al. 2008). Yet, given their biology, few amphibians have been evaluated for spatial synchrony of population abundances (Petranka, Smith, and Floyd Scott 2004; Piha et al. 2007; Cayuela et al. 2020) in part owing to the rarity of long-term, multi-population datasets.

In this study, we take advantage of a 21-year record of wood frog (*Rana sylvatica* = *Lithobates sylvaticus*) egg mass counts from 64 nonpermanent freshwater ponds in Connecticut, USA to explore spatial synchrony and drivers of population dynamics in amphibians.

MATERIALS AND METHODS

Data collection

Wood frogs breed in early spring in freshwater wetlands. Females typically lay their egg masses in concentrated areas of a few meters over several days. Most female wood frogs mature after two years (Berven 1990; 2009; Sagor et al. 1998). Each female lays one egg mass in a given year, and most show high (~100%) site fidelity after first breeding, although a small portion of juveniles disperse up to 2000 m away from their natal site before their first breeding season (Berven and Grudzien 1990). The lifespan of wood frogs depends on latitude (Bastien and Leclair 1992), but they rarely live longer than five years.

From 2000 to 2020, we monitored 64 freshwater nonpermanent wetlands (hereafter ponds) in the 3213 ha Yale-Myers Forest in northeastern Connecticut, USA (Fig 1). Ponds varied in surface area (average = 2642 m², range = 24–41361 m², CV = 252), canopy closure (i.e., global site factor; average = 52%, range = 0–98%, CV = 68), depth (average = 52 cm, range = 22–118, CV = 46), and egg mass counts (average = 71, range = 0–1113, CV = 130). Every spring we censused each pond for wood frog egg masses. If egg masses were found, we estimated the total number of masses as the average of two independent counts. As each female only lays one egg mass per year (i.e., only produces one clutch) and site fidelity is high (Berven and Grudzien 1990), egg mass counts offer an accurate proxy for the number of breeding females within a pond in a given year. Previous work indicates egg mass counts are an accurate and precise technique for monitoring wood frog populations (Crouch and Paton 2000).

Pond-level variables

Attributes of ponds in our models included maximum pond depth and canopy closure. Depth was recorded at the time of egg mass surveys. Most ponds have a permanent depth gauge so measurements are standardized across years, otherwise depth was recorded as the deepest

point in the pond. Pond canopy closure was measured as in Arietta et al. (2020) by using five hemispherical photographs taken along the shore at each cardinal point and at the center of each pond during leaf-off and leaf-on seasons. We estimated average leaf-on and leaf-off global site factor (GSF; the ratio of above-canopy radiation to under-canopy radiation) (Anderson 1964) and used a weighted GSF value integrated over the duration of wood frog embryonic and larval life cycle (Halverson et al. 2003). GSF is scaled between 0–1, and we report it here as a percentage.

Regional-level variables

We included air temperature and Palmer Drought Severity Index as regional-scale variables. Here we define regional factors as those affecting multiple breeding populations simultaneously. We downloaded daily temperature records from the National Climatic Data Center of the National Oceanic and Atmospheric Administration (NOAA) observing station at the Windham Airport in Willimantic, Connecticut, approximately 19 km south of the study area. We estimated winter thaw as the number of days between 1 October and 30 March above freezing in the winter prior to breeding (i.e., winter thaw_(t-1)). This date range gives an estimate of the fall and winter conditions for juveniles and adults and aligns winter temperature with the hydrologic water year that begins 1 October each year.

The Palmer Drought Severity Index (hereafter drought severity) uses temperature, precipitation, and soil information to estimate the departure of moisture supply from the norm (Palmer 1965). We downloaded historical monthly drought severity data for Connecticut from the National Centers for Environmental Information division of NOAA (available at <https://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/psi/200011-202010>). Drought severity typically ranges between -4 and 4, although more extreme values are possible. A drought severity value around zero indicates normal conditions, whereas a value ≤ -4 indicates

extreme drought and a value ≥ 4 extremely wet conditions. We used an average monthly drought severity value from 1 March to 30 September to represent the moisture conditions that breeding adults, tadpoles, and new metamorphs would experience from the highest pond levels (early spring) to lowest levels in late summer and early fall. To test if larval and juvenile conditions affected females during their first breeding year, we also tested a two-year lag in drought severity (i.e., drought severity_(t-2)) corresponding to the first year of maturity. We did not explore other time lags (e.g., t - 3, t - 4) as the vast majority of females only breed once and female survival beyond two years is extremely low (Berven 1990).

Estimating density dependence

Females typically take two years to reach sexual maturity, so the effect of larval intraspecific competition within a focal pond on a breeding female was defined as the density of egg masses (i.e., egg masses / pond area) two years prior.

The effect of neighboring ponds (a proxy for terrestrial density dependence) was estimated using the egg mass data neighboring pond egg mass counts weighted by distance (Eq 1).

$$\text{Eq. 1: } \sum e^{-\theta d_{ij}} (\text{egg masses}_j)$$

Where θ is 1/maximum distance from pond considered to be within a relevant range, d_{ij} is the distance between the focal pond_i and neighboring pond_j, and egg masses_j is the number of egg masses counted in pond_j in a given year. These values are then summed to estimate the weighted effect of neighboring conspecifics, where closer ponds are given greater weight in generating the estimate. Although genetic data estimate wood frog dispersal distance based on microsatellite markers is 1000 m, only ~18% of juveniles disperse and adults rarely or never disperse (Berven

and Grudzien 1990). Furthermore, radio tracking estimates indicate the 95% of the isopleth for wood frog movement is within 300 m of natal ponds and 50% of the isopleth is within 133 m (T. A. Rittenhouse and Semlitsch 2007), so a decay function with a maximum dispersal distance of 500 m would capture nearly all likely dispersal. We set $1/\theta$ at 500 m to represent half of the maximum genetic dispersal distance and twice the minimum average distance between ponds as a conservative estimate of competition from surrounding ponds.

Data analysis

All statistical analyses were run in R v4.0.2 (R Core Team 2020). To examine potential spatial autocorrelation, we used the package *ape* (Paradis and Schliep 2019). We used latitude and longitude coordinates from the center of each pond to generate a distance matrix, then took the inverse of matrix values and replaced diagonal values with zero. We used the ‘Moran.I’ function on each year’s egg mass count data vs. inverse distance matrix and scaled the Moran’s I estimates to between -1 and 1. To explore patterns in synchrony across time and space we used the multivariate spline (cross-)correlogram function ‘spline.correlog’ in the *ncf* package (Bjornstad 2020). The function requires multiple observations at each location and estimates spatial dependence as a continuous function of distance. We used 5000 resamples to estimate 95% confidence envelopes.

We explored influences of pond, climate, and intraspecific density on population size (i.e., egg mass counts) and population growth rate. We defined population growth rate (hereafter growth rate) as the number of breeding females over a generation time of two years (Eq 2):

$$\text{Eq. 2: } \ln\left(\frac{\text{egg masses}_t + 1}{\text{egg masses}_{(t-2)} + 1}\right)/2$$

Where t is the number of egg masses in the survey year, $t-2$ is the number egg masses two years prior, and the entire function is divided by the number of years between measurements. This approach normalizes high and low values for better comparison across ponds.

We estimated multilevel/partially pooled Bayesian hierarchical models of two response variables (average egg mass counts and population growth rate) in relation to the scaled and centered predictors, which included pond depth, canopy closure, density, drought severity, a two-year lag in drought severity, and winter thaw days. We fit the regressions using *rstanarm* (Goodrich et al. 2020), which automatically scales and centers predictors and adjusts the scales of priors during the run. For each regression we used weakly informative normal prior distributions with a mean of zero and standard deviation of 2.5 for predictions, ran four chains for 10,000 iterations, and discarded the first half as a warm-up to obtain 20,000 simulations for analysis. We confirmed convergence using Gelman–Rubin statistic ($R_{\text{hat}} < 1.01$) and by examining trace plots. None of the models had influential outliers as assessed by leave-one-out cross-validation (“loo”) in the ‘rstan’ package (Stan Development Team 2020). Four ponds that had egg masses in zero or only one year of survey were not included in statistical analyses. We fit the average egg mass count models using both normal and log-normal distributions and did not find any differences in fit or which slopes overlapped zero (Appendix S1: Table S1), so we use the normal distribution for ease of interpretation.

We examined the relative importance of pond, climate, and population variables using Bayesian variable selection in the *Bvs* function of the ‘BayesVarSel’ package (Garcia-Donato and Forte 2018). ‘BayesVarSel’ calculates Bayes factors in linear models and provides formal Bayesian answers to variable selection problems as posterior probabilities. For both population size and population growth rate, we examined the following equation:

Eq. 3: average egg mass counts OR population growth rate

$$= \text{Depth} + \text{Canopy} + \text{Density}_{(t-2)} + \text{drought severity} \\ + \text{drought severity}_{(t-2)} + \text{Winter thaw}_{(t-1)}$$

We used robust priors and kept the top ten most likely models.

RESULTS

General trends

As is typical for amphibians, population sizes varied widely over time (Appendix S1: Fig. S1). Average egg mass counts within each pond ranged from 0–271, with an overall average of 71 egg masses pond⁻¹ yr⁻¹ (Fig. 1). There was high variation in egg mass counts through time within ponds (average CV_{pond} = 130, range = 39–447), but less variation across years over the entire metapopulation (average CV_{year} = 71, range = 60–88).

Over the 21 years of survey, four populations became extirpated (Little Thing and YM-33) or near-extirpated (S3 and Borrow Pit 1; Appendix S1: Fig. S1). Seven ponds (Dentist, E1, S4, X7, YM-02, YM-14, and YM-24) rebounded from near population collapses (Appendix S1: Fig. S1). Nine populations appeared to increase over time (A10, Boulder, C3, Kealoha's, Laurel, Mill, T5, YM-04, and YM-47), and nine populations decreased in size (Atwood, Blacksmith, Borrow Pit 2, Centre Pike, D1, E8, Greenbriar, YM-14, and YM-32; Appendix S1: Fig. S1). Twenty-three of the 64 ponds surveyed supported egg masses every year of survey (Appendix S1: Fig. S1).

Population growth rates did not reveal any obvious trends over time (Appendix S1: Fig. S2). With the exception of ponds that are rarely (F4, W4, YM-54) or never occupied (X2), all ponds experienced both positive and negative growth rates, depending on the year (Appendix S1: Fig. S2). Across all ponds, the average growth rate was positive but highly variable (average_{ponds}

= 0.014, $\text{stdev}_{\text{ponds}} = 0.099$). More than half of the surveyed ponds had an overall positive growth rate ($n = 33$ ponds), and slightly fewer had a negative overall growth rate ($n = 25$ ponds).

Spatial autocorrelation and synchrony

Generally, the relationship between inter-pond distance and egg mass counts (Fig. 2) was weak. Of the 21 years of egg mass counts evaluated, just one year, 2016 (Moran's $I = 0.103$, Bonferroni-adjusted $P = 0.019$) exhibited strong spatial autocorrelation (Fig. 2a). We did not detect any synchrony in egg mass counts at any distance up to 6 km (Fig. 2b).

Factors affecting population size

Neighborhood egg masses (weighted counts within a 500 m radius of the focal pond) had a weak negative effect and lagged drought severity_{t-2} had a weak positive effect on focal pond egg mass counts (Fig. 3a,c; Table 1). Drought severity_t (Fig. 3b), density of conspecifics two years prior (Fig. 3e), pond depth (Fig. 3f), and pond canopy (Fig. 3g) closure had a strong positive effect on egg mass counts (Table 1), suggesting wetter years, higher densities two years prior to survey, deeper ponds, and greater canopy closure increased population size. The number of days in the preceding winter above freezing (winter thaw; Fig. 3d) had a negative effect on egg mass counts, suggesting that winter thaws could negatively affect either survival or breeding outcomes if females skipped a breeding year.

Bayesian variable selection indicated that the top supported model for egg mass counts included density_(t-2) and pond depth (posterior prob = 0.433). Both the highest posterior probability and median probability models included density_(t-2) and pond depth only. The second most supported model also included drought severity_t (posterior prob = 0.154; Appendix S1: Table S1). The next two top models included density_(t-2), depth, and then either drought severity_t (posterior prob = 0.075) or neighborhood egg masses_(t-2) (posterior prob = 0.070). All of the top

ten models included density_{t-2} and depth, five included drought severity_t, whereas canopy (3/10 models), neighborhood egg masses_(t-2) (3/10 models), winter thaw (2/10 models), and drought severity_(t-2) (1/10 models) were included in fewer than half of the top 10 models. Both density_(t-2) and pond depth were fixed (posterior probability of inclusion = 1.0), but the model indicated the highest support for a model that included three or more covariates. Drought severity_t (posterior inclusion prob = 0.36) and neighborhood egg masses_(t-2) (posterior inclusion prob = 0.26) had stronger support for inclusion than canopy (posterior inclusion prob = 0.13), winter thaw (posterior inclusion prob = 0.11), and drought severity_(t-2) (posterior inclusion prob = 0.09).

Factors affecting population growth rates

The conspecific density two years prior depressed growth rates strongly (Fig. 4e, Table 1). Population growth rates were not related to neighborhood competition two years prior (Fig. 4a), drought severity_t (Fig. 5b), drought severity_(t-2) (Fig. 4c), nor winter thaw in the previous winter (Fig. 4d; Table 1). The effect of pond depth (Fig. 4f) and canopy closure (Fig. 4g) on population growth rates overlapped zero as well (Table 1).

Population growth rates were only predicted by density_(t-2) (posterior prob = 0.699) in the highest posterior model and the median probability model. Besides the density_{t-2} only model, the other top supported models had less than 10% probability (Appendix S1: Table S2). Density_(t-2) was retained in all of the models; depth, drought severity_t, and neighborhood egg masses_(t-2) were in three of the top ten models, and the other parameters only in one of the top ten each. Density_(t-2) had a fixed inclusion probability (posterior inclusion probability = 1.0) indicating that it was supported in every model iteration. All other variables had low support. The next highest inclusion probabilities included depth (posterior inclusion prob = 0.12) and neighborhood egg masses_(t-2) (inclusion prob = 0.10). The other four variables were relatively unlikely to be

included in the model: drought severity_t (inclusion prob = 0.07), winter thaw (inclusion prob = 0.05), and canopy and drought severity_(t-2) (both inclusion probs = 0.03).

DISCUSSION

In one of the few long-term studies of its kind on pond breeding amphibians, we failed to detect spatial synchrony in population dynamics in all but a single year. We studied a large number of potential breeding sites ($n = 64$) over a period of more than two decades representing 7–10 generations of wood frogs. This result is surprising both because wood frogs are well known to disperse among breeding populations as juveniles and because the species is sensitive to climate variables such as precipitation that might be expected to have a regional influence on populations. Population sizes had high variability during the study, but there was only a single year out of 21 with evidence of synchrony. It is possible that the association observed during 2016 is a random occurrence, but by the time wood frogs bred in the spring of 2016, northeastern Connecticut was in a severe drought (drought severity < -3.0) and had been under moderate or severe drought conditions for the previous 12 months. This event was the most intense drought that had been experienced in the northeastern United States since the mid 1960's — which inspired Palmer to create the drought severity index (Palmer 1965) — and led to early pond drying (Nagel et al. 2021).

Our finding of synchrony in only one year suggests that extreme climate variation could create conditions that synchronize breeding habitats. In 2016, ponds were approximately 16 cm shallower than the long-term average, and the average population declined by 13% compared with the long-term average. Our populations experienced other years of drought (e.g., 2017) as well as very damp conditions (e.g., 2019) over the run of the study, but none of these other years were associated with synchrony. This result may indicate that extremes in weather patterns

Accepted Article
induce synchrony in otherwise asynchronous metapopulations and deserves further exploration as extreme events such as heavy precipitation, flooding, and heat waves are becoming more frequent with climate change (Ummenhofer and Meehl 2017).

Metapopulation synchrony is widespread in nature, occurring within taxa as different as ungulates (Post and Forchhammer 2002), birds (Koenig and Liebhold 2016), insects (A. M. Liebhold, Haynes, and Bjørnstad 2012), and trees (LaMontagne et al. 2020) separated by several hundred to a thousand kilometers. Our study augments a small but growing body of literature documenting asynchrony in amphibian populations assessed at larger spatial scales. Five populations of the great crested newt (*Triturus cristatus*) located up to several hundred kilometers apart lacked synchrony (Cayuela et al. 2020), and forty populations of the common frog (*Rana temporaria*) exhibited synchronous population declines across distances of 50-100 km only during extreme drought (Piha et al. 2007). At our 3213 ha study site, none of the ponds are more than 2 km and most are < 1 km from the nearest neighbor (avg. minimum distance = 270 m), meaning they share temperature and precipitation conditions and are within the maximum known movement distance for our species (2.5 km; Berven and Grudzien 1990). For these reasons, we expected to see spatial synchrony in the population dynamics of this species. While it is possible, or even probable, that some of our occupied breeding ponds do not represent demographically distinguishable populations (Petranka, Smith, and Floyd Scott 2004), we expect that describing connected sites as separate populations would inflate synchrony, but that was not what we observed. Future research is needed to quantify dispersal rates and their variation among populations over time.

The lack of synchrony in this study implies a role for local factors in driving population dynamics. We found that density dependence was pervasive. Egg mass density two years prior

Accepted Article

within a pond (i.e., focal pond intraspecific competition) was associated with strong negative density dependence. This two-year period represents the average age of first breeding for female wood frogs, and hence is a proxy for cohort size in this species with limited overlapping generation time for females (Berven 1990; 2009). Intraspecific competition among larvae has been demonstrated in field experiments with wood frogs (D. K. Skelly, Freidenburg, and Kiesecker 2002) and other species (David K. Skelly 1995). We cannot rule out a role for terrestrial competition given the nature of our data. Outdoor enclosure experiments (Altwegg 2003; Harper and Semlitsch 2007; Benard and Middlemis Maher 2011) and long-term field studies (Berven 2009; Kissel, Tenan, and Muths 2020) have found negative density dependence in terrestrial stages of wood frogs and other amphibians. Evidence for terrestrial density dependence in our study is supported by the finding that neighborhood wood frog density had a negative effect on focal population growth rate. The most likely explanation for this pattern is competition among juvenile and/or adult wood frogs. Such interactions have been frequently assumed for pond breeding amphibians (Wilbur 1980) but have proven difficult to detect and study (Pechmann 1995).

We also discovered evidence for variation in the capacity of breeding ponds to support populations. A positive effect of prior density on current egg mass counts suggests that large populations tend to stay large while smaller populations tend to remain small. While the factors driving variation among ponds will require further study, pond depth emerged as one important variable; deeper ponds tend to have larger populations. Pond depth is only weakly correlated with area in our system ($r = 0.17$), but it is possible that larger ponds have higher larval-stage carrying capacities. Additionally, pond depth is often related to the timing of drying in nonpermanent ponds, and hydroperiod can be a strong determinant of wood frog and other

Accepted Article

anuran presence (David K. Skelly, Werner, and Cortwright 1999; Nagel et al. 2021). Early drying is an important cause of mortality in pond breeding amphibians (Raymond D. Semlitsch 1987) and may provide an explanation for this association. In addition to direct mortality effects from drying, it is also possible that breeding adults could avoid shallow ponds (Crump 1991; Rudolf and Rödel 2005).

Our analyses uncovered a negative influence of warmer winters on wood frog population size. This finding may appear counterintuitive for an ectotherm, but likely relates to the unique overwintering biology of the species. Wood frogs partially freeze each winter, and the process of freezing and thawing is energetically and physiologically intensive (Storey and Storey 1984; Sinclair et al. 2013). Warmer winters are likely to yield more freeze-thaw cycles and may affect overwinter survival and deplete energy stores that could be used in breeding. For example, female wood frogs produce smaller clutches following warmer winters compared to colder winters (Benard 2015). As our study region continues to warm (Arietta et al. 2020), this mechanism could become an increasingly important issue for the species. Research on many organisms focuses much more on the active seasons rather than dormant seasons. Our findings emphasize the importance of understanding winter conditions when trying to determine the overall impacts of climate change on organisms (Williams, Henry, and Sinclair 2015).

Our data help position efforts to manage species that are in decline. Although density dependence had the strongest effect on population size and population growth rate, we suggest that preserving ‘good’ ponds with high population sizes of the amphibian of interest misses a large portion of the life cycle that influences population dynamics. Maintaining pond and habitat heterogeneity in a network of ponds is best for management of amphibians (Raymond D.

Semlitsch 2000) as it buffers years of reduced breeding (McCaffery et al. 2014), high predation (Holyoak 2000), drought (Piha et al. 2007), and diseases such as ranavirus (Earl and Gray 2014).

Metapopulation synchrony declines as the strength of local density-dependence increases (Kendall et al. 2000). Here we show that strong local regulation of populations (i.e., density dependence) can override regional environmental variability in most years resulting in asynchronous fluctuations that enhance metapopulation resilience (Fox et al. 2017). The infrequency of spatial synchrony our system suggests greater resilience than previously expected. Yet even in metapopulations with strong local regulation we detected synchrony in drought and a negative effect of winter temperatures. As weather patterns alter with climate change, understanding the characteristics of systems that determine asynchronous and synchronous population dynamics will be critical to predicting which species are more or less resilient to widespread disturbances.

ACKNOWLEDGMENTS

We thank the many lab members past and present who helped collect data. This work was funded by grants from the National Science Foundation, the Yale Institute for Biospheric Studies (YIBS), and by support from Yale University. FER was supported by a YIBS Donnelley Postdoctoral Fellowship. Animal handling was approved by Yale University IACUC (2004-10361, 2006-11024, 2007-10361, 2019-10361, 2009-11024, 2009-11040, 2010-10361, 2013-10361, and 2016-10361) and field surveys were conducted with permission from Yale Myers Research Committee (SKE01).

AUTHOR CONTRIBUTIONS

Accepted Article

FER, ESS, LKF, MCU, JLR, SBR, AZAA, ADR, and DKS contributed to data collection and field study. FER performed the analysis. DKS and MFB conceived of the study. FER and DKS wrote the manuscript with input from all coauthors.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

LITERATURE CITED

- Abbott, Karen C. 2011. "A Dispersal-Induced Paradox: Synchrony and Stability in Stochastic Metapopulations: Dispersal-Induced Paradox in Metapopulations." *Ecology Letters* 14 (11): 1158–69. <https://doi.org/10.1111/j.1461-0248.2011.01670.x>.
- Alford, Ross A., and Stephen J. Richards. 1999. "Global Amphibian Declines: A Problem in Applied Ecology." *Annual Review of Ecology and Systematics* 30 (1): 133–65. <https://doi.org/10.1146/annurev.ecolsys.30.1.133>.
- Altwegg, Res. 2003. "Multistage Density Dependence in an Amphibian." *Oecologia* 136 (1): 46–50. <https://doi.org/10.1007/s00442-003-1248-x>.
- Anderson, Margaret C. 1964. "Light Relations of Terrestrial Plant Communities and Their Measurement." *Biological Reviews* 39 (4): 425–81.
- Arietta, A Z Andis, L Kealoha Freidenburg, Mark C Urban, Susan B Rodrigues, Adriana Rubinstein, and David K Skelly. 2020. "Phenological Delay despite Warming in Wood Frog *Rana Sylvatica* Reproductive Timing: A 20-year Study." *Ecography* 43 (12): 1791–1800.

- Bastien, Heloise, and Raymond Leclair. 1992. "Aging Wood Frogs (*Rana Sylvatica*) by Skeletochronology." *Journal of Herpetology* 26 (2): 222.
<https://doi.org/10.2307/1564868>.
- Benard, Michael F. 2015. "Warmer Winters Reduce Frog Fecundity and Shift Breeding Phenology, Which Consequently Alters Larval Development and Metamorphic Timing." *Global Change Biology* 21 (3): 1058–65. <https://doi.org/10.1111/gcb.12720>.
- Benard, Michael F., and Jessica Middlemis Maher. 2011. "Consequences of Intraspecific Niche Variation: Phenotypic Similarity Increases Competition among Recently Metamorphosed Frogs." *Oecologia* 166 (3): 585–92. <https://doi.org/10.1007/s00442-010-1896-6>.
- Berven, Keith A. 1990. "Factors Affecting Population Fluctuations in Larval and Adult Stages of the Wood Frog (*Rana Sylvatica*)." *Ecology* 71 (4): 1599–1608.
<https://doi.org/10.2307/1938295>.
- . 2009. "Density Dependence in the Terrestrial Stage of Wood Frogs: Evidence from a 21-Year Population Study." *Copeia* 2009 (2): 328–38. <https://doi.org/10.1643/CH-08-052>.
- Berven, Keith A., and Thaddeus A. Grudzien. 1990. "Dispersal in the Wood Frog (*Rana Sylvatica*): Implications for Genetic Population Structure." *Evolution* 44 (8): 2047–56.
<https://doi.org/10.1111/j.1558-5646.1990.tb04310.x>.
- Bjornstad, Ottar N. 2020. *Ncf: Spatial Covariance Functions* (version R package version 1.2-9).
<https://CRAN.R-project.org/package=ncf>.
- Briggs, Cheryl J, and Martha F Hoopes. 2004. "Stabilizing Effects in Spatial Parasitoid–Host and Predator–Prey Models: A Review." *Theoretical Population Biology* 65 (3): 299–315.

- Cayuela, Hugo, Richard A Griffiths, Nurul Zakaria, Jan W Arntzen, Pauline Priol, Jean-Paul L na, Aur lien Besnard, and Pierre Joly. 2020. “Drivers of Amphibian Population Dynamics and Asynchrony at Local and Regional Scales.” *Journal of Animal Ecology* 89 (6): 1350–64.
- Crouch, William B., and Peter W. C. Paton. 2000. “Using Egg-Mass Counts to Monitor Wood Frog Populations.” *Wildlife Society Bulletin (1973-2006)* 28 (4): 895–901.
- Crump, Martha L. 1991. “Choice of Oviposition Site and Egg Load Assessment by a Treefrog.” *Herpetologica*, 308–15.
- Earl, Julia E., and Matthew J. Gray. 2014. “Introduction of Ranavirus to Isolated Wood Frog Populations Could Cause Local Extinction.” *EcoHealth* 11 (4): 581–92.
<https://doi.org/10.1007/s10393-014-0950-y>.
- Fox, Jeremy W., David Vasseur, Morgan Cotroneo, Lilian Guan, and Franz Simon. 2017. “Population Extinctions Can Increase Metapopulation Persistence.” *Nature Ecology & Evolution* 1 (9): 1271–78. <https://doi.org/10.1038/s41559-017-0271-y>.
- Gamble, Lloyd R., Kevin McGarigal, and Bradley W. Compton. 2007. “Fidelity and Dispersal in the Pond-Breeding Amphibian, *Ambystoma Opacum*: Implications for Spatio-Temporal Population Dynamics and Conservation.” *Biological Conservation* 139 (3–4): 247–57.
<https://doi.org/10.1016/j.biocon.2007.07.001>.
- Garcia-Donato, Gonzalo, and Anabel Forte. 2018. “Bayesian Testing, Variable Selection and Model Averaging in Linear Models Using R with BayesVarSel.” *The R Journal* 10 (1): 155–74.
- Goodrich, B, J Gabry, I Ali, and S Brilleman. 2020. *Rstanarm: Bayesian Applied Regression Modeling via Stan* (version R package version 2.21.1). <https://mc-stan.org/rstanarm>.

- Halverson, MA, DK Skelly, JM Kiesecker, and LK Freidenburg. 2003. “Forest Mediated Light Regime Linked to Amphibian Distribution and Performance.” *Oecologia* 134 (3): 360–64.
- Hanski, ILKKA, and MICHAEL Gilpin. 1991. “Metapopulation Dynamics: Brief History and Conceptual Domain.” *Biological Journal of the Linnean Society* 42 (1–2): 3–16.
<https://doi.org/10.1111/j.1095-8312.1991.tb00548.x>.
- Harper, Elizabeth B., and Raymond D. Semlitsch. 2007. “Density Dependence in the Terrestrial Life History Stage of Two Anurans.” *Oecologia* 153 (4): 879–89.
<https://doi.org/10.1007/s00442-007-0796-x>.
- Haydon, Daniel, and Harald Steen. 1997. “The Effects of Large–and Small–Scale Random Events on the Synchrony of Metapopulation Dynamics: A Theoretical Analysis.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 264 (1386): 1375–81.
- Holyoak, Marcel. 2000. “Habitat Patch Arrangement and Metapopulation Persistence of Predators and Prey.” *The American Naturalist* 156 (4): 378–89.
<https://doi.org/10.1086/303395>.
- Ims, Rolf A, and Harry P Andreassen. 2005. “Density-Dependent Dispersal and Spatial Population Dynamics.” *Proceedings of the Royal Society B: Biological Sciences* 272 (1566): 913–18.
- Kahilainen, Aapo, Saskya van Nouhuys, Torsti Schulz, and Marjo Saastamoinen. 2018. “Metapopulation Dynamics in a Changing Climate: Increasing Spatial Synchrony in Weather Conditions Drives Metapopulation Synchrony of a Butterfly Inhabiting a

Fragmented Landscape.” *Global Change Biology* 24 (9): 4316–29.

<https://doi.org/10.1111/gcb.14280>.

Kendall, Bruce E., Ottar N. Bjørnstad, Jordi Bascompte, Timothy H. Keitt, and William F.

Fagan. 2000. “Dispersal, Environmental Correlation, and Spatial Synchrony in

Population Dynamics.” *The American Naturalist* 155 (5): 628–36.

<https://doi.org/10.1086/303350>.

Kissel, Amanda M., Simone Tenan, and Erin Muths. 2020. “Density Dependence and Adult

Survival Drive Dynamics in Two High Elevation Amphibian Populations.” *Diversity* 12

(12): 478. <https://doi.org/10.3390/d12120478>.

Koenig, Walter D., and Andrew M. Liebhold. 2016. “Temporally Increasing Spatial Synchrony

of North American Temperature and Bird Populations.” *Nature Climate Change* 6 (6):

614–17. <https://doi.org/10.1038/nclimate2933>.

LaMontagne, Jalene M., Ian S. Pearse, David F. Greene, and Walter D. Koenig. 2020. “Mast

Seeding Patterns Are Asynchronous at a Continental Scale.” *Nature Plants* 6 (5): 460–65.

<https://doi.org/10.1038/s41477-020-0647-x>.

Lande, Russell, Steinar Engen, and Bernt-Erik Sæther. 1999. “Spatial Scale of Population

Synchrony: Environmental Correlation versus Dispersal and Density Regulation.” *The*

American Naturalist 154 (3): 271–81. <https://doi.org/10.1086/303240>.

Larsen, Stefano, Lise Comte, Ana Filipa Filipe, Marie-Josée Fortin, Claire Jacquet, Remo

Ryser, Pablo A. Tedesco, et al. 2021. “The Geography of Metapopulation Synchrony in

Dendritic River Networks.” Edited by Mikko Heino. *Ecology Letters* 24 (4): 791–801.

<https://doi.org/10.1111/ele.13699>.

- Liebhold, Andrew, Walter D Koenig, and Ottar N Bjørnstad. 2004. “Spatial Synchrony in Population Dynamics.” *Annu. Rev. Ecol. Evol. Syst.* 35: 467–90.
- Liebhold, Andrew M, Kyle J Haynes, and Ottar N Bjørnstad. 2012. “Spatial Synchrony of Insect Outbreaks.” *Insect Outbreaks Revisited*, 113–25.
- McCaffery, Rebecca M., Lisa A. Eby, Bryce A. Maxell, and Paul Stephen Corn. 2014. “Breeding Site Heterogeneity Reduces Variability in Frog Recruitment and Population Dynamics.” *Biological Conservation* 170 (February): 169–76.
<https://doi.org/10.1016/j.biocon.2013.12.013>.
- Moran, Patrick AP. 1953. “The Statistical Analysis of the Canadian Lynx Cycle.” *Australian Journal of Zoology* 1 (3): 291–98.
- Nagel, Leah D., Stacy A. McNulty, Matthew D. Schlesinger, and James P. Gibbs. 2021. “Breeding Effort and Hydroperiod Indicate Habitat Quality of Small, Isolated Wetlands for Amphibians Under Climate Extremes.” *Wetlands* 41 (2): 22.
<https://doi.org/10.1007/s13157-021-01404-x>.
- Palmer, Wayne C. 1965. “Meteorological Drought.” Research Paper No. 45. Washington, D.C: Office of Climatology, U.S. Weather Bureau. <https://www.ncdc.noaa.gov/temp-and-precip/drought/docs/palmer.pdf>.
- Paradis, E, and K Schliep. 2019. “Ape 5.0: An Environment for Modern Phylogenetics and Evolutionary Analyses in R.” *Bioinformatics* 35: 526–28.
- Pechmann, Joseph HK. 1995. “Use of Large Field Enclosures to Study the Terrestrial Ecology of Pond-Breeding Amphibians.” *Herpetologica*, 434–50.

- Petranka, James W, Charles K Smith, and A Floyd Scott. 2004. “Identifying the Minimal Demographic Unit for Monitoring Pond-breeding Amphibians.” *Ecological Applications* 14 (4): 1065–78.
- Piha, Henna, Miska Luoto, Markus Piha, and Juha Merilä. 2007. “Anuran Abundance and Persistence in Agricultural Landscapes during a Climatic Extreme.” *Global Change Biology* 13 (1): 300–311. <https://doi.org/10.1111/j.1365-2486.2006.01276.x>.
- Post, Eric, and Mads C Forchhammer. 2002. “Synchronization of Animal Population Dynamics by Large-Scale Climate.” *Nature* 420 (6912): 168–71.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing* (version 4.0.2). Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Ranta, Esa, Veijo Kaitala, Jan Lindström, and Harto Linden. 1995. “Synchrony in Population Dynamics.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 262 (1364): 113–18.
- Rittenhouse, Tracy A. G., Elizabeth B. Harper, Leland R. Rehard, and Raymond D. Semlitsch. 2008. “The Role of Microhabitats in the Desiccation and Survival of Anurans in Recently Harvested Oak–Hickory Forest.” *Copeia* 2008 (4): 807–14. <https://doi.org/10.1643/CH-07-176>.
- Rittenhouse, Tracy AG, and Raymond D Semlitsch. 2007. “Distribution of Amphibians in Terrestrial Habitat Surrounding Wetlands.” *Wetlands* 27 (1): 153–61.
- Rowland, F. 2022. freyarowland/WoodFrogCode: (v1.1). Zenodo. <https://doi.org/10.5281/zenodo.5903388>
- Rowland, F., E. Schyling, L. K. Freidenburg, M. Urban, J. Richardson, A. Z. A. Arietta, S. Rodriques, A. Rubinstein, M. Benard, and D. Skelly. 2022. Data from: Asynchrony,

density dependence, and persistence in an amphibian. Dryad, data set.

<https://doi.org/10.5061/dryad.0cfxpnw3r>

Rudolf, Volker HW, and Mark-Oliver Rödel. 2005. "Oviposition Site Selection in a Complex and Variable Environment: The Role of Habitat Quality and Conspecific Cues."

Oecologia 142 (2): 316–25.

Sagor, Eli S, Martin Ouellet, Evelynne Barten, and David M Green. 1998. "Skeletochronology and Geographic Variation in Age Structure in the Wood Frog, *Rana Sylvatica*." *Journal of Herpetology*, 469–74.

Semlitsch, Raymond D. 1987. "Relationship of Pond Drying to the Reproductive Success of the Salamander *Ambystoma Talpoideum*." *Copeia* 1987 (1): 61.

<https://doi.org/10.2307/1446038>.

———. 2000. "Principles for Management of Aquatic-Breeding Amphibians." *The Journal of Wildlife Management* 64 (3): 615. <https://doi.org/10.2307/3802732>.

Semlitsch, RAYMOND D., DAVID E. Scott, JOSEPH H.K Pchmann, and J. WHITFIELD Gibbons. 1996. "CHAPTER 9 - Structure and Dynamics of an Amphibian Community: Evidence from a 16-Year Study of a Natural Pond." In *Long-Term Studies of Vertebrate Communities*, edited by MARTIN L. Cody and JEFFREY A. Smallwood, 217–48. San Diego: Academic Press. <https://doi.org/10.1016/B978-012178075-3/50010-6>.

Sinclair, Brent J., Joseph R. Stinziano, Caroline M. Williams, Heath A. MacMillan, Katie E. Marshall, and Kenneth B. Storey. 2013. "Real-Time Measurement of Metabolic Rate during Freezing and Thawing of the Wood Frog, *Rana Sylvatica* : Implications for Overwinter Energy Use." *The Journal of Experimental Biology* 216 (2): 292–302. <https://doi.org/10.1242/jeb.076331>.

- Skelly, D. K., L. K. Freidenburg, and J. M. Kiesecker. 2002. "Forest Canopy and the Performance of Larval Amphibians." *Ecology* 83 (4): 983–92.
[https://doi.org/10.1890/0012-9658\(2002\)083\[0983:FCATPO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0983:FCATPO]2.0.CO;2).
- Skelly, David K. 1995. "Competition and the Distribution of Spring Peeper Larvae." *Oecologia* 103 (2): 203–7. <https://doi.org/10.1007/BF00329081>.
- Skelly, David K., Earl E. Werner, and Spencer A. Cortwright. 1999. "Long-Term Distributional Dynamics of a Michigan Amphibian Assemblage." *Ecology* 80 (7): 2326–37.
[https://doi.org/10.1890/0012-9658\(1999\)080\[2326:LTDDOA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2326:LTDDOA]2.0.CO;2).
- Stan Development Team. 2020. *RStan: The R Interface to Stan* (version R package version 2.21.2). <http://mc-stan.org/>.
- Storey, Kenneth B., and Janet M. Storey. 1984. "Biochemical Adaption for Freezing Tolerance in the Wood Frog *Rana Sylvatica*." *Journal of Comparative Physiology B* 155 (1): 29–36.
<https://doi.org/10.1007/BF00688788>.
- Ummenhofer, Caroline C., and Gerald A. Meehl. 2017. "Extreme Weather and Climate Events with Ecological Relevance: A Review." *Philosophical Transactions of the Royal Society B: Biological Sciences* 372 (1723): 20160135. <https://doi.org/10.1098/rstb.2016.0135>.
- Wang, Ian J., and H. Bradley Shaffer. 2017. "Population Genetic and Field-ecological Analyses Return Similar Estimates of Dispersal over Space and Time in an Endangered Amphibian." *Evolutionary Applications* 10 (6): 630–39.
<https://doi.org/10.1111/eva.12479>.
- Wilbur, H M. 1980. "Complex Life Cycles." *Annual Review of Ecology and Systematics* 11 (1): 67–93. <https://doi.org/10.1146/annurev.es.11.110180.000435>.

Williams, Caroline M., Hugh A. L. Henry, and Brent J. Sinclair. 2015. "Cold Truths: How Winter Drives Responses of Terrestrial Organisms to Climate Change: Organismal Responses to Winter Climate Change." *Biological Reviews* 90 (1): 214–35.
<https://doi.org/10.1111/brv.12105>.

TABLES

Table 1. Slope estimates from the regression models. Bolded parameters indicate that there is a 95% or greater probability that the slope is non-zero. CRI = credible interval

response	slope parameter	mean	std dev	2.5% CRI	97.5% CRI
Egg mass counts	Neighborhood competition _{t-2}	-0.03	0.03	-0.09	0.03
	Avg drought severity_t	4.18	1.75	0.69	7.58
	Avg drought severity _{t-2}	3.02	1.56	-0.05	6.06
	Winter thaw days	-0.70	0.26	-1.22	-0.18
	Pond competition_{t-2}	186.50	51.65	82.83	286.79
	Pond depth	0.45	0.18	0.09	0.80
	Pond canopy	0.67	0.31	0.05	1.26
	Population growth rate	Neighborhood competition _{t-2}	-1.89 x 10 ⁻⁴	1.29 x 10 ⁻⁴	-4.41 x 10 ⁻⁴
Avg drought severity _t		0.016	0.012	-0.008	0.039
Avg drought severity _{t-2}		-0.005	0.012	-0.029	0.019
Winter thaw days		-1.77 x 10 ⁻³	2.08 x 10 ⁻³	-5.90 x 10 ⁻³	2.32 x 10 ⁻³
Pond competition_{t-2}		-5.71	1.25	-8.35	-3.46
Pond depth		5.65 x 10 ⁻⁴	7.90 x 10 ⁻⁴	-9.72 x 10 ⁻⁴	2.12 x 10 ⁻³
Pond canopy		7.09 x 10 ⁻⁵	6.94 x 10 ⁻⁴	-2.18 x 10 ⁻³	1.43 x 10 ⁻³

FIGURE CAPTIONS

Fig. 1. We surveyed 64 ponds over 21 years at Yale-Myers Forest (3213 ha; dark green area) in northeastern CT, USA. Annual average egg mass counts changed across time, but not effort (symbol size). Red lines connect ponds within 500 m of each other (i.e., ponds that are included in a focal pond's neighborhood competition metric).

Fig. 2. Spatial autocorrelation between (A) annual egg mass counts and year of survey. Points with Bonferroni-adjusted $P \leq 0.05$ are highlighted in red. (B) Spline cross-correlogram of multivariate spatial data with Moran's I vs. distance and 95% confidence envelope. All Moran's I values were scaled between -1 and 1.

Fig. 3. Egg mass count regressions. Each panel shows pond-specific regressions (gray lines, $n = 60$ ponds) and the overall regression (thick black lines) between egg mass counts within a given year and (A) number of egg masses within a 500 m radius of focal pond two years prior weighted with an exponential decay function such that closer ponds have a higher proportional effect than those farther away; (B) Palmer Drought Severity Index (drought severity) in survey year; (C) drought severity two years prior to survey year; (D) winter days above freezing; (E) conspecific density two years prior to survey year; (F) pond depth (cm); and (G) pond canopy closure as GSF.

Fig. 4. Population growth rate regressions. Each panel shows pond-specific regressions (gray lines, $n = 60$ ponds) and the overall regression (thick black lines) between population growth rate within a given year and (A) number of egg masses within a 500 m radius of focal pond two years

prior weighted with an exponential decay function such that closer ponds have a higher proportional effect than those farther away; (B) Palmer Drought Severity Index (drought severity) in survey year; (C) drought severity two years prior to survey year; (D) winter days above freezing; (E) conspecific density two years prior to survey year; (F) pond depth (cm); and (G) pond canopy closure as GSF. Panels without visible pond-specific regressions indicate that pond-specific and overall regressions were roughly equivalent and weak predictive ability.







