

Species interactions and the effects of climate variability on a wetland amphibian metacommunity

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Abstract. Disentangling the role that multiple interacting factors have on species responses to shifting climate poses a significant challenge. However, our ability to do so is of utmost importance to predict the effects of climate change on species distributions. We examined how populations of three species of wetland-breeding amphibians, which varied in life history requirements, responded to a six-year period of extremely variable precipitation. This interval was punctuated by both extensive drought and heavy precipitation and flooding, providing a natural experiment to measure community responses to environmental perturbations. We estimated occurrence dynamics using a discrete hidden Markov modeling approach that incorporated information regarding habitat state and predator–prey interactions. This approach allowed us to measure how metapopulation dynamics of each amphibian species was affected by interactions among weather, wetland hydroperiod, and co-occurrence with fish predators. The pig frog, a generalist, proved most resistant to perturbations, with both colonization and persistence being unaffected by seasonal variation in precipitation or co-occurrence with fishes. The ornate chorus frog, an ephemeral wetland specialist, responded positively to periods of drought owing to increased persistence and colonization rates during periods of low-rainfall. Low probabilities of occurrence of the ornate chorus frog in long-duration wetlands were driven by interactions with predators due to low colonization rates when fishes were present. The mole salamander was most sensitive to shifts in water availability. In our study area, this species never occurred in short-duration wetlands and persistence probabilities decreased during periods of drought. At the same time, negative effects occurred with extreme precipitation because flooding facilitated colonization of fishes to isolated wetlands and mole salamanders did not colonize wetlands once fishes were present. We demonstrate that the effects of changes in water availability depend on interactions with predators and wetland type and are influenced by the life history of each of our species. The dynamic species occurrence modeling approach we used offers promise for other systems when the goal is to disentangle the complex interactions that determine species responses to environmental variability.

Key words: amphibian communities; climate; metacommunity; multispecies occupancy; species interactions; wetland dynamics.

INTRODUCTION

Studies of community ecology are often motivated by a desire to explain patterns of species occurrence across a landscape. Occurrence, or the presence of a species at a particular location, depends on (1) species interactions (i.e., predator–prey or inter- and intraspecific competition; Ives 1995, Gilman et al. 2010, Zarnetske et al. 2012) and (2) characteristics of the physical environment that define habitat suitability for each species (Pounds and Crump 1994, Kupferberg 1996, Brooks 2004, Todd

et al. 2009). Each of these components is dynamic across space and time, particularly when driven by dynamic processes, such as climate (Falke et al. 2012, Miller et al. 2012). Patterns in species occurrence are scale dependent and can be used to inform species' distributions and serve as indicators of local habitat quality (Leibold et al. 2004, Yackulic et al. 2015). Metapopulation and metacommunity concepts provide a framework and set of tools that link species dynamics across these multiple spatial scales to account for interactions (via dispersing individuals) among populations or communities, respectively (Hanski 1999, Leibold et al. 2004).

Despite this, current approaches to understanding and predicting changes in species' distributions often rely on static representations of community structure and habitat

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suitability across the landscape (Falke et al. 2012, Miller et al. 2012, Yackulic et al. 2015). These approaches can limit the ability to draw definitive conclusions about the impact of environmental change on communities and our capability to preemptively manage for these impacts as well (Franklin 2010, Dormann et al. 2012, Yackulic et al. 2015). To enhance our ability to predict how climate change will impact species' distributions, we must first relate changes in species interactions and interactions between climate and the physical environment to species occurrence patterns within a single modeling framework. Accomplishing this in practice requires methods that can estimate the direct effects of species interactions (MacKenzie et al. 2011, Falke et al. 2012, Miller et al. 2012) and which can be used to ask how environmental perturbations affect communities rather than just individual species (Ives 1995, Urban 2004, Gilman et al. 2010).

In wetland systems, a major determinant of community structure is hydroperiod, which can range from highly ephemeral wetlands that remain inundated for short periods of time to permanent wetlands (Pechmann et al. 1989, Snodgrass et al. 2000a, Semlitsch et al. 2015). Habitat suitability for individual species is influenced by interactions between the physical characteristics of the wetland (i.e., soil composition, geomorphology, hydrology) and climate (Kupferberg 1996, Pounds et al. 1999, Brooks 2004, Jackson et al. 2014). The occurrence of wetland breeding amphibians is therefore driven by tradeoffs between the abiotic constraints of wetland hydroperiod and life history characteristics primarily related to fecundity, dispersal and development (Wilbur 1987, Pechmann et al. 1989, Snodgrass et al. 2000a, b, Babbitt et al. 2003, Baber et al. 2004). For instance, species adapted to highly ephemeral wetlands tend to develop rapidly and employ conspicuous feeding strategies as larvae, which increases the probability of metamorphosis prior to wetland desiccation (Wellborn et al. 1996). In contrast, species occupying permanent wetlands are more likely to experience increased predation and competition pressures and, as such, are often slow developing and cryptic (Snodgrass et al. 2000a).

Predation is a particularly strong biotic driver in the structuring of some amphibian communities (Wilbur 1987, Jackson and Semlitsch 1993). The presence of predators in wetlands generally excludes species that do not exhibit behavioral (i.e., microhabitat selection, activity reduction) or morphological (i.e., toxicity, unpalatability) adaptations to cope with predation pressure (Semlitsch and Reyer 1992, Snodgrass et al. 2000a). The effect of aquatic predators on larval amphibians is twofold. In addition to direct predation, non-lethal effects, such as changes in larval growth rate (Skelly and Werner 1990, Werner 1991, McCollum and Leimberger 1997), activity patterns, and habitat use (Skelly and Werner 1990, Werner 1991, Skelly 1992, Laurila et al. 1998) have been observed. These direct and indirect effects of co-occurrence with predators have been shown to exist in the presence of fishes, which can be particularly voracious predators of

larval amphibians (Babbitt et al. 2003, Binckley and Resetarits 2003, Hamer and Parris 2013). Few studies, however, have demonstrated that these effects differ among amphibian species in natural systems and are structured, in part, by the environment in which these interactions occur (though see Skelly 1992, Adams 1999). Given this, we focused our study on the predator-prey interactions between fishes and three amphibian species that occupy wetlands of different hydroperiod.

Fishes are generally incapable of persisting in wetlands that dry with some frequency or colonizing isolated wetlands without human- or climate-facilitated dispersal events (Wilbur 1987, Babbitt et al. 2003). During times of flooding and increased waterway connectivity, for instance, dispersal-limited species, such as fishes, can be introduced to wetlands from which they were previously absent. This is of concern for freshwater wetland systems, given that the frequency and intensity of extreme events (i.e., cyclonic storms), or other high rainfall events, for example, is projected to increase with climate change (Blaustein et al. 2010, Walls et al. 2013a). Changes in the presence, abundance and composition of fish predators, as a result, are likely to influence amphibian populations that were once isolated or limited in their exposure to fish predators.

We examined how predator-prey interactions and the physical environment interact to shape the outcomes of environmental perturbations on different amphibian species within a wetland-breeding assemblage. To achieve this, we focus specifically on a coastal wetland breeding amphibian assemblage. We present findings from a 6-year (2009–2014) study of occurrence dynamics for three amphibian species at St. Marks National Wildlife Refuge (SMNWR) in Florida, USA. The study occurred during a period of high environmental variability that included both severe drought and extensive flooding, providing a natural experiment to determine how the community responded to changing conditions. We analyzed occurrence dynamics using multistate occupancy models to investigate how metapopulation dynamics of amphibians and predators responded to environmental stochasticity, while simultaneously accounting for changes in habitat state (MacKenzie et al. 2011, Falke et al. 2012, Miller et al. 2012). Using an integrated approach that measured occurrence dynamics (state-dependent colonization and persistence) allowed us to retrospectively examine the mechanisms by which species were affected by extreme weather events to predict how communities might be affected by future changes in water availability.

METHODS

Study system and data collection

St. Marks National Wildlife Refuge is located near Apalachee Bay of Florida's northwest panhandle. We sampled 60 wetlands in the refuge's Panacea Unit from 2009 to 2014 for occurrence of three amphibian

species from the Coastal Plain of the southeastern United States that span the gradient in responses to wetland hydroperiod: the ornate chorus frog (*Pseudacris ornata*), which breeds exclusively in ephemeral wetlands (Caldwell 1987); the mole salamander (*Ambystoma talpoideum*), a species that breeds in wetlands of seasonal or semi-permanent nature (Semlitsch 1985); and the pig frog (*Rana grylio*), an abundant generalist species that most commonly inhabits permanent bodies of water (Lamb 1984, Ugarte et al. 2007, Hammerson et al. 2008).

Larvae of the ornate chorus frog develop rapidly (e.g., within 90 d in Louisiana) and have few adaptations to deal with high predation pressures from fishes or aquatic invertebrates (Caldwell 1987, Dundee and Rossman 1989). Larvae metamorphose in the late spring or early summer and were thus never observed during the fall sampling season at SMNWR. The mole salamander typically breeds from November to January throughout its range in the southeastern United States and exhibits high site fidelity, with individuals returning to the same wetlands to breed (Semlitsch 1985, Semlitsch and Gibbons 1985, Hammerson 2004). Individuals of this species can also persist in wetlands as paedomorphic adults and, thus, can be detected in wetlands during fall and spring seasons (Patterson 1978, Semlitsch 1985, Jackson and Semlitsch 1993, Doyle and Whiteman 2008). Similarly, the pig frog has a breeding season that spans approximately 6–7 months and its larvae require at least one year to complete development (Lamb 1984). As such, this species could also be detected in wetlands during both fall and spring sampling occasions at SMNWR. Despite being locally abundant in some locations, the pig frog is a species of concern throughout parts of its distribution and large knowledge gaps remain in our understanding of its ecology (Lamb 1984, Ugarte et al. 2007, Hammerson et al. 2008). Because species traits have an important role in defining optimal conditions for each species (Wilbur 1987, Pechmann et al. 1989, Skelly et al. 1999, Paton and Crouch 2002, Babbitt et al. 2003, Anderson et al. 2015, Semlitsch et al. 2015), they are also likely important in understanding the effects of changing climate. We hypothesized that differences in the habitat requirements of the ornate chorus frog, mole salamander, and pig frog would therefore provide insight into their responses to environmental perturbations.

From 2010 to 2011, an extreme drying event occurred at SMNWR, with low rainfall leading to reduced hydroperiod or drying of wetlands that typically hold water year-round (Walls et al. 2013b). Then, in 2012, Tropical Storm Debby impacted the Florida panhandle, completely flooding many wetlands throughout SMNWR, leading to changes in hydroperiod and colonization of previously isolated wetlands by fishes. An additional flood in 2013 maintained high fish colonization. Thus, we examined fish occurrence to test for the effects of predators on patterns of amphibian occupancy. Given that wetland colonization by many species occurred simultaneously, we were unable to disentangle the effect

of the 16 individual fish species detected during this study. We therefore focused on whether fishes of any species were present in a wetland (see Appendix S4 for complete list of species).

We surveyed wetlands during the spring (March–April) and fall (September–October) from 2009 to 2014. We monitored 45 wetlands from 2009 to 2011 and extended our sampling to include 15 additional wetlands in the spring of 2012. We assigned wetlands to one of two categories based on mean observed hydroperiod, hereafter referred to as short- and long-duration wetlands. Short-duration wetlands were observed to dry on average ≥ 1 time per year ($n = 25$). Long-duration wetlands included semipermanent and permanent wetlands that, on average, went >365 days ($n = 35$) between drying events. Categorization of wetlands was determined using a combination of instrumental records (27 wetlands were instrumented with HOBO 13 Foot Fresh Water Level Data Loggers, Onset, Bourne MA, USA) and observations on wetland size and depth during sampling (J. W. Riley et al., *unpublished manuscript*). This allowed us to quantify general differences among wetland basins that differed in potential water-holding capacity.

A combination of modified commercial crayfish, aluminum screen funnel, and minnow traps were used for a total of 8 trap nights per site per season from 2009 to 2010, 16 trap nights per site per season in 2011, and 20 trap nights per site per season from 2012 to 2014 (Walls et al. 2013b). All amphibians and fishes captured in our aquatic traps were recorded daily and subsequently released. For amphibians, these data reflect the presence of any life stage (larva, sub-adult, or adult) in the wetland at the time of sampling. This methodology, however, was insufficient for extremely ephemeral sites that dried prior to spring sampling, thus making them unsuitable for our aquatic trapping techniques. However, these sites may have still been suitable for species such as the ornate chorus frog, which prefer highly ephemeral wetlands, if water was present in the basin prior to our spring sampling occasions. Thus, we supplemented detection histories for this species with data from recordings of calling adult males using automatic recording units (ARU, Models SM1 and SM2, Wildlife Acoustics, Inc., Maynard, MA, USA) at a subset of 26 of the 60 sites from 2009 to 2014. The detection of calling adults at a site was assumed to indicate site suitability for the ornate chorus frog even if it was unsuitable for other species during spring sampling occasions. We assumed perfect detection for the ARU data, given that these devices were recording throughout the breeding season (recorded for 5 min on the hour from 18:00 to 06:00 EST; deployed for 50 d in 2009 and 2010, >100 days in 2011–2014). Daily detection probabilities indicated the probability of a false negative were negligible.

Dynamic multispecies occupancy model

We estimated occurrence dynamics for each amphibian species individually by fitting the integrated habitat and

multi-species occurrence model described by Miller et al. (2012) and summarized here. The approach simultaneously accounted for the presence or absence of the focal amphibian species, fishes, and whether a wetland was inundated with water. During any given sampling period, a wetland could belong to one of five states: (1) habitat was unsuitable (no water in the basin); (2) habitat was suitable and unoccupied; (3) habitat was suitable and occupied by amphibian species; (4) habitat was suitable and occupied by fishes but not by the amphibian; (5) habitat was suitable and occupied by fishes and amphibian species (Miller et al. 2012). Under our robust design framework, sites were assumed to remain in the same state during a given sampling period. We then estimated changes in wetland state from one season to the next (time t to time $t + 1$) so that a site either remained in the same state or transitioned to any of the four other states at time $t + 1$. As already detailed, the biology of each species necessitated the modeling of state transitions across years for the ornate chorus frog and across seasons for the mole salamander and pig frog. Transitions between states were modeled as a first-order Markov process, so that the probability a site occurred in a given state at time $t + 1$ was only conditional on the site's state at time t (MacKenzie et al. 2009, Miller et al. 2012). Higher order Markov processes were not modeled, but longer term effects were accounted for through the use of our climate covariates, which integrated up to 2 yr of rainfall, and the separation of wetlands into long- or short-duration, which controlled for heterogeneity that might influence site-level responses (i.e., recovery time after wetland drying) to changes in precipitation.

By simultaneously examining the dynamics of amphibians, fishes, and habitat using this multi-state approach we were able to examine how transitions in state variables were affected by predator-prey interactions and the interaction between weather and the physical environment (Miller et al. 2012). Transition probabilities among the five states were decomposed into several sub-parameters (Table 1) (MacKenzie et al. 2004, 2011, Miller et al. 2012). Colonization probabilities (γ) reflected the probability that amphibians or fishes occupied a site at time $t + 1$ that was unoccupied at time t . We allowed colonization probabilities of fishes and amphibians to depend on whether the other was present and whether a site was previously dry. If a site was dry in the previous season, colonization was only possible given a wetland also transitioned from unsuitable to suitable (ω). As an example, the probability a wetland transitioned from state 1 to state 3 was the product of the probability that (1) the wetland became suitable, (2) amphibians colonized a wetland previously unoccupied by fishes ($\gamma^{A,f}$), and (3) the wetland was not colonized by fishes given amphibians were not previously present ($1 - \gamma^{F,a}$). The full transition probability is given by: $\phi^{1,3} = \omega \times \gamma^{A,f} \times (1 - \gamma^{F,a})$. Similarly, persistence of the amphibian or fishes in a wetland (ϕ) was the probability that an occupied site at time t remained occupied at time

TABLE 1. Sub-parameters for the dynamic integrated-habitat occupancy model.

Parameter	Description
η	probability a wetland remains suitable between seasons
ω	probability a dry, unsuitable wetland becomes suitable
$\gamma^{A,d}$	probability of amphibians colonizing a wetland that was dry the previous season
$\gamma^{A,f}$	probability of amphibians colonizing a wetland that was unoccupied by fishes the previous season
$\gamma^{A,F}$	probability of amphibians colonizing a wetland that was occupied by fishes the previous season
$\gamma^{F,d}$	probability of fishes colonizing a wetland that was dry the previous season
$\gamma^{F,a}$	probability of fishes colonizing a wetland that was unoccupied by amphibians the previous season
$\gamma^{F,A}$	probability of fishes colonizing a wetland that was occupied by amphibians the previous season
$\phi^{A,f}$	probability of amphibians persisting at a wetland in the absence of fishes
$\phi^{A,F}$	probability of amphibians persisting at a wetland in the presence of fishes
$\phi^{F,a}$	probability of fishes persisting at a wetland in the absence of amphibians
$\phi^{F,A}$	probability of fishes persisting at a wetland in the presence of amphibians
$p^{A,f}$	probability of detecting amphibians when fishes are not present
$p^{A,F}$	probability of detecting amphibians when fishes are present
$p^{F,a}$	probability of detecting fishes when amphibians are not present
$p^{F,A}$	probability of detecting fishes when amphibians are present

$t + 1$, and again was allowed to vary depending on whether the other species was present. As such, persistence was conditional on a wetland remaining suitable between seasons (η). As another example, the probability a wetland remained in state 3 between seasons was the product of the probability that (1) a wetland remained suitable, (2) a given amphibian species persisted at the wetland ($\phi^{A,f}$), and (3) the wetland was not colonized by fishes ($1 - \gamma^{F,A}$) between seasons, so that: $\phi^{3,3} = \eta \times \phi^{A,f} \times (1 - \gamma^{F,A})$.

Parameter estimation and model selection

We fit models using the maximum likelihood estimator for dynamic multistate occupancy models in R and selected among different model parameterizations based on AIC (MacKenzie et al. 2011, Miller et al. 2012, R Core Team 2014). We used a sequential approach to fit models, as the full model included a large-number of parameters. We first chose among climate indices to determine the covariate that best predicted seasonal variation in the proportion of unsuitable wetlands during each sampling period. We assumed that the covariate that best predicted how many wetlands were dry would best describe

season-to-season climatic variation as it relates to amphibian and fish dynamics in wetlands that were not dry during the survey period but may have dried between seasons. We used logistic regression to choose among 11 climate indices related to water availability to determine the index that best predicted this seasonal variation. These indices included the Palmer Hydrological Drought Index (Karl 1986, Guttman 1991), the Palmer Drought Severity Index (Palmer 1965, Alley 1985), the Palmer Z-index, the Keetch-Byram Drought Index, and Standardized Precipitation Indices calculated for various time intervals (1 month, 2 months, 3 months, 6 months, 9 months, 12 months, and 24 months; Guttman 1998). All indices were calculated on a monthly basis and then averaged across the 2-month sampling period for each season (March–April for spring and September–October for fall).

We then selected among parameterizations of the full occupancy model, which included parameters for detection probabilities, initial occurrence probabilities, and among season transition probabilities to determine how transitions were influenced by wetland basin type (i.e., short or long duration), temporal variation in weather (i.e., the climate index), wetland dynamics (i.e., was the wetland dry during the previous season), and co-occurrence among species (e.g., how did amphibian persistence change when fishes were present and vice versa). We fit model components in the following order: (1) detection probabilities, (2) initial state distribution, (3) habitat transition probabilities, (4) amphibian and fish persistence probabilities, and (5) amphibian and fish colonization probabilities. The model set for component 2 (initial amphibian occupancy) was fit using the best-fit parameterization for component 1 (species detection), but the most general parameterization for components 3–5. We report estimates and standard errors from the overall best-fit model.

The full set of candidate models can be found in Appendix S1. The same set of models was considered for each of the three amphibian species, with the exception of the detection component. For detection probabilities, we considered whether amphibian detection was influenced by fish presence (and vice-versa), and whether detection varied by time or depended on mean hydroperiod (short- or long-duration). Pig frogs were poorly detected in 2009 and 2010, when commercial crayfish traps were the primary trapping method. Preliminary analyses also indicated that there was little temporal variation within or between seasons in detection for this species. As such, we ultimately modeled pig frog detection probabilities as a function of trap type (i.e., commercial crayfish, screen funnel or minnow trap) rather than time (Appendix S1: Table S2). For the initial state vector (i.e., the proportion of sites at the start of the study in each of the five states) we considered whether amphibian occurrence depended on fish presence and mean hydroperiod. For wetland transition probabilities we examined the influence of mean hydroperiod and our annual climate index. When

considering models for persistence of fishes and amphibians we considered mean hydroperiod and the climate index. We also examined whether persistence of one taxonomic group (e.g., amphibians) depended on whether the other was present (e.g., fishes). For fish colonization we considered effects of mean hydroperiod, amphibian presence, and the climate index. We also included an effect for whether a major flood event occurred to capture the effect of the flood events in 2012 and 2013 that increased waterway connectivity at our study site. For amphibian colonization, we considered effects of mean hydroperiod, fish presence, and the climate index.

Sensitivity analyses

We also conducted sensitivity analyses to quantify how amphibian and fish occurrence probabilities were expected to respond to changes in transition probabilities (Table 1; Miller 2012). Sensitivity measures the rate of change in a system state with respect to changes in underlying parameters (Miller 2012). As an example, we were interested in how the overall proportion of sites occupied by our amphibian species would respond to increases in fish colonization probabilities, as might occur if the frequency of flooding events changed. Sensitivity is then calculated as the derivative of the proportion of sites in states 3 and 5 (amphibian present) with respect to changes in the probability a site previously unoccupied by fishes is colonized in a given season. We used parameter values from our best-fit model to calculate sensitivities and followed procedures outlined in Miller (2012). For this study, we were interested in understanding how sensitive amphibian and fish occurrence (i.e., the total proportion of sites occupied by each) were to changes in the probability that (1) dry sites remained dry in the following time step, as expected if drought frequency increased; (2) wet sites remained inundated, as expected, if drought frequency decreased; (3) amphibians colonized a site; (4) amphibians persisted at a site; (5) fishes colonized a site, as expected if flooding events increased; and (6) fishes persisted at a site, as expected if drought decreases. We made separate calculations for short- and long-duration wetlands.

Additionally, we conducted a prospective analysis to examine how changes in the frequency of drying and flooding events could be expected to affect community composition in the future. A full description of the methods and results can be found in Appendix S2.

RESULTS

Of the 11 climate indices tested, the Standard Precipitation Index (SPI) for a two-month time period best explained the proportion of dry wetlands in a given season ($R^2_{McFaydden} = 0.56$; see Appendix S1: Fig. S1). Detection probabilities for the ornate chorus frog differed among occasions, by mean hydroperiod and

co-occurrence with fishes. Detection of the mole salamander differed among occasions and by mean hydroperiod, but was not influenced by the presence of fishes. Pig frog detection differed by trap type, mean hydroperiod, and whether they co-occurred with fishes (Appendix S1: Table S2).

The best supported model for initial chorus frog occupancy varied by mean hydroperiod, whereas mole salamander occurrence probabilities initially depended on the presence of fishes and mean hydroperiod. The best model for initial occurrence of pig frogs did not yield reasonable estimates due to sparse data in 2009 (Welsh et al. 2013). Therefore, all analyses were run with the next best-fit model that produced reliable estimates, which modeled the initial distribution as a function of fish presence (Appendix S1: Table S3).

Wetland inundation in a given season was best explained by whether it was inundated in the previous season, the two-month SPI, and, as expected, its classification as short- or long-duration. Short-duration wetlands were more likely to dry and remain dry, whereas <2% of long-duration wetlands went dry between any two seasons. Approximately 40% of wetlands dried during the drought of 2010–2011 (Appendix S1: Table S4).

Mean hydroperiod and two-month SPI best predicted the probability ornate chorus frogs persisted in wetlands, but persistence was not influenced by fishes. The highest probability of persistence occurred during Spring 2011 (0.99 ± 0.0002 and 0.86 ± 0.10 in short- and long-duration wetlands, respectively [mean \pm standard error]; Fig. 1a; Appendix S3: Table S1). Mole salamander persistence was positively related to two-month SPI but did not depend on the fish presence. Persistence in long-duration wetlands was lowest during observed drought conditions (0.51 ± 0.13 ; Fig. 1b; Appendix S3: Table S1). Pig frog persistence was constant across all seasons regardless of presence of fishes or mean hydroperiod (0.68 ± 0.04 ; Fig. 1c; Appendix S3: Table S1). The probability fishes persisted in a wetland was heavily influenced by mean hydroperiod. Persistence was higher and less variable overall in long- (0.99 ± 0.01) than in short-duration (0.68 ± 0.06) wetlands (Appendix S4: Table S2).

The proportion of unoccupied sites colonized by fishes depended on two-month SPI, amphibian occurrence, mean hydroperiod, wetland suitability in the previous season, and whether flooding occurred. Fishes were less likely to colonize wetlands that were dry or unoccupied by chorus frogs in the previous season. The opposite pattern held true when mole salamanders were present: fishes were more likely to colonize long-duration wetlands previously unoccupied by mole salamanders. Fish colonization did not depend on whether pig frogs were present but increased substantially during 2012 and 2013 flood events (Fig. 1h; Appendix S4: Fig. S1).

Colonization of short-duration wetlands by ornate chorus frogs was inversely related to two-month SPI; wetlands were more likely to be colonized during periods of drought (Fig. 1d). The ornate chorus frog never colonized

long-duration wetlands occupied by fishes whereas short-duration wetlands with fishes were more likely to be colonized (on average 0.39 ± 0.14) when compared to short-duration wetlands unoccupied by fishes (on average 0.20 ± 0.09) or previously dry wetlands (0.00 ± 0.003 ; Fig. 1e; Appendix S3: Table S2). Mole salamanders were most likely to colonize long-duration wetlands unoccupied by fishes (0.36 ± 0.08), colonized <1% of wetlands occupied by fishes and were never observed in long-duration wetlands that were dry in the previous season (Fig. 1f; Appendix S3: Table S2). Pig frog colonization was constant regardless of mean hydroperiod, fish presence, or previous habitat state (0.38 ± 0.04 ; Fig. 1g; Appendix S3: Table S2).

We used parameter estimates to calculate the proportion of wetlands in each state over the study period. The proportion of short-duration wetlands occupied by the ornate chorus frog peaked following the drought of 2010–2011 and overall chorus frog occurrence was higher in short-duration wetlands. Chorus frogs and fishes co-occurred with a non-negligible probability in both short- and long-duration sites, although chorus frog occupancy decreased in short-duration wetlands following flood events and the resultant increase in fish occurrence (Fig. 2a, b). Mole salamanders never occurred in our short-duration wetlands. Occurrence in long-duration wetlands decreased during the drought and continued to decrease as fish occurrence increased (Fig. 2c, d). Pig frog occurrence remained relatively constant throughout the study period in both short- and long-duration wetlands. Although co-occurrence of fishes and pig frogs increased over time, pig frogs appeared to be unaffected by changes in fish occurrence (Fig. 2e, f).

Ornate chorus frog occurrence was most sensitive to changes in the frequency of wetland drying. Positive changes in occurrence of this species are expected when (1) the probability that long-duration wetlands dry increases, (2) fish persistence in long-duration wetlands is reduced, and (3) when the probability that short-duration wetlands will remain inundated between years is increased (Fig. 3a). Mole salamander occurrence was most sensitive to changes in fish occurrence and habitat dynamics. In long-duration wetlands, occurrence is expected to increase when fish persistence is reduced and when drying becomes more frequent, due to the negative effect of habitat drying on fish persistence. Occurrence is also expected to decrease as the frequency of fish colonization increases, but to a much lesser extent than changes in persistence (Fig. 3b). Pig frog occurrence is relatively insensitive to changes in any model parameters, but is most affected by drying of both short- and long-duration wetlands (Fig. 3c). As expected, fish occurrence is expected to decrease in long-duration wetlands as the frequency of drying increases (Fig. 3d; Appendix S4: Fig. S2).

DISCUSSION

Predicting how communities will respond to climate change requires a strong understanding of the role that

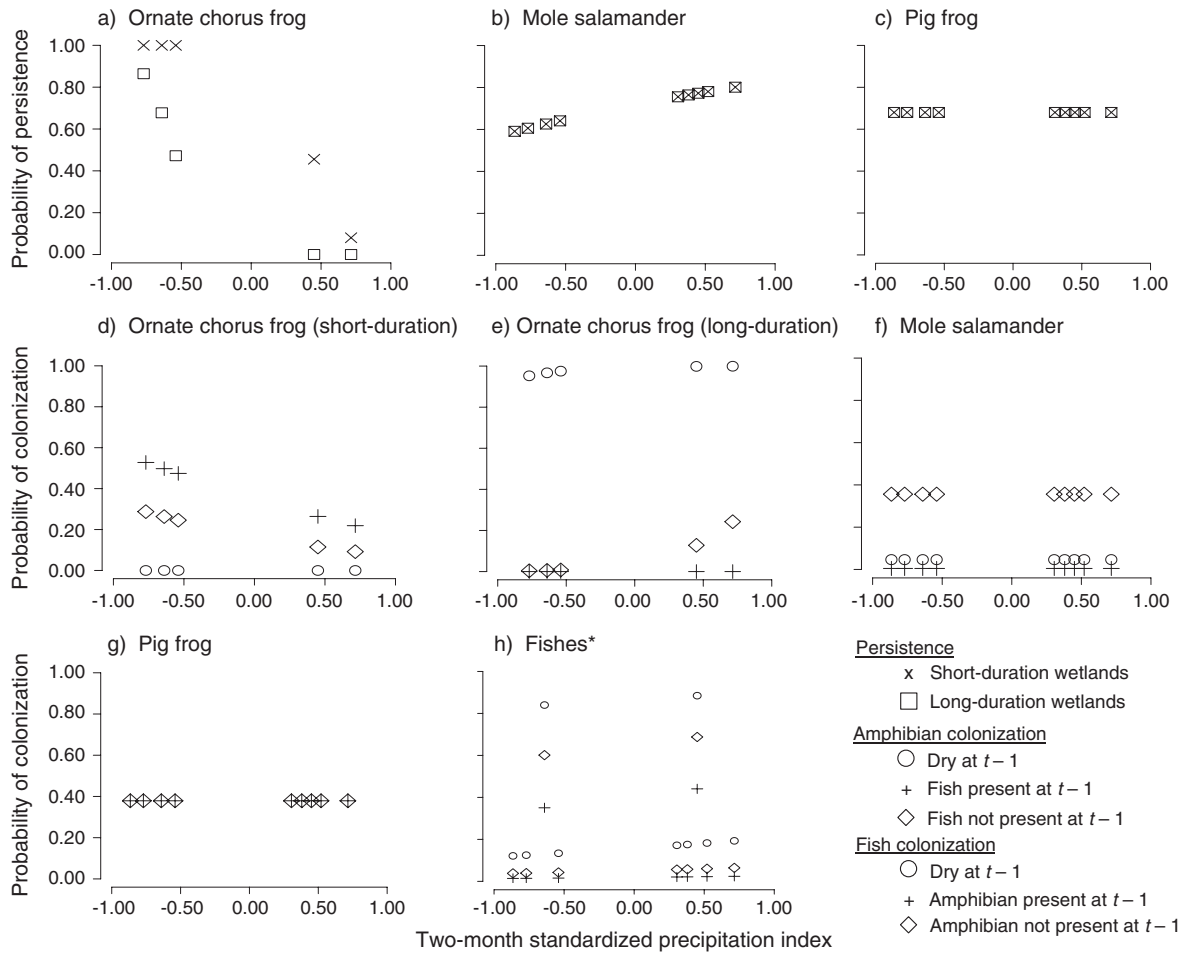


FIG. 1. Mean parameter estimates for occurrence dynamics vs. two-month standardized precipitation index (SPI). SPI values < 0 represent less-than-average precipitation. Species responses to changes in SPI over the study period were also structured by mean hydroperiod and the presence of fishes. Fish colonization of long-duration wetlands, as depicted here, was estimated using the mole salamander database (see Appendix S4: Fig. S1 for other parameterizations). The two peaks in fish colonization correspond to the two flooding events in 2012 and 2013.

species traits and species-interactions have in structuring responses (Ives 1995, Urban 2004, Gilman et al. 2010, Zarnetske et al. 2012, Anderson et al. 2015). Our results provide a direct demonstration of why it is important to consider these interacting components and provide a template for estimating interaction strengths in occurrence time-series data. Rather than a consistent response across species (e.g., more water leads to more wetland breeding amphibians that rely on water), we found that responses to changes in water availability varied among species. These differences likely emerge because of species-specific traits that affect how populations respond to changes in hydrology and predation pressure. These interactions with habitat and predators are the key determinant as to whether climatic variability affects the occurrence of each species.

Metacommunity processes explain the climate-mediated predator-prey interactions we observed in our system. Dispersal limitation and disturbance frequency

can allow for regional species coexistence in metacommunities of species that would not persist under direct interactions (Chesson 2000, Leibold et al. 2004). As a result, the rate at which predators exclude sensitive species is mediated by the frequency of disturbance and facilitated dispersal events (Chesson 2000, Kneitel and Miller 2003, Amarasekare et al. 2004, Leibold et al. 2004). In our coastal wetland system, precipitation determines the frequency with which wetlands dry, excluding fish predators, and facilitates colonization of fishes to isolated wetlands during flooding events. These changes in fish distributions have profound implications for amphibian species that are sensitive to the presence of fishes, such as the mole salamander.

These effects appear to be especially important in long-duration wetlands, which rarely dried during our study, even during periods of severe drought, and were therefore unlikely to lose fish predators once colonized. This insensitivity of long duration wetlands to periods of low-rainfall

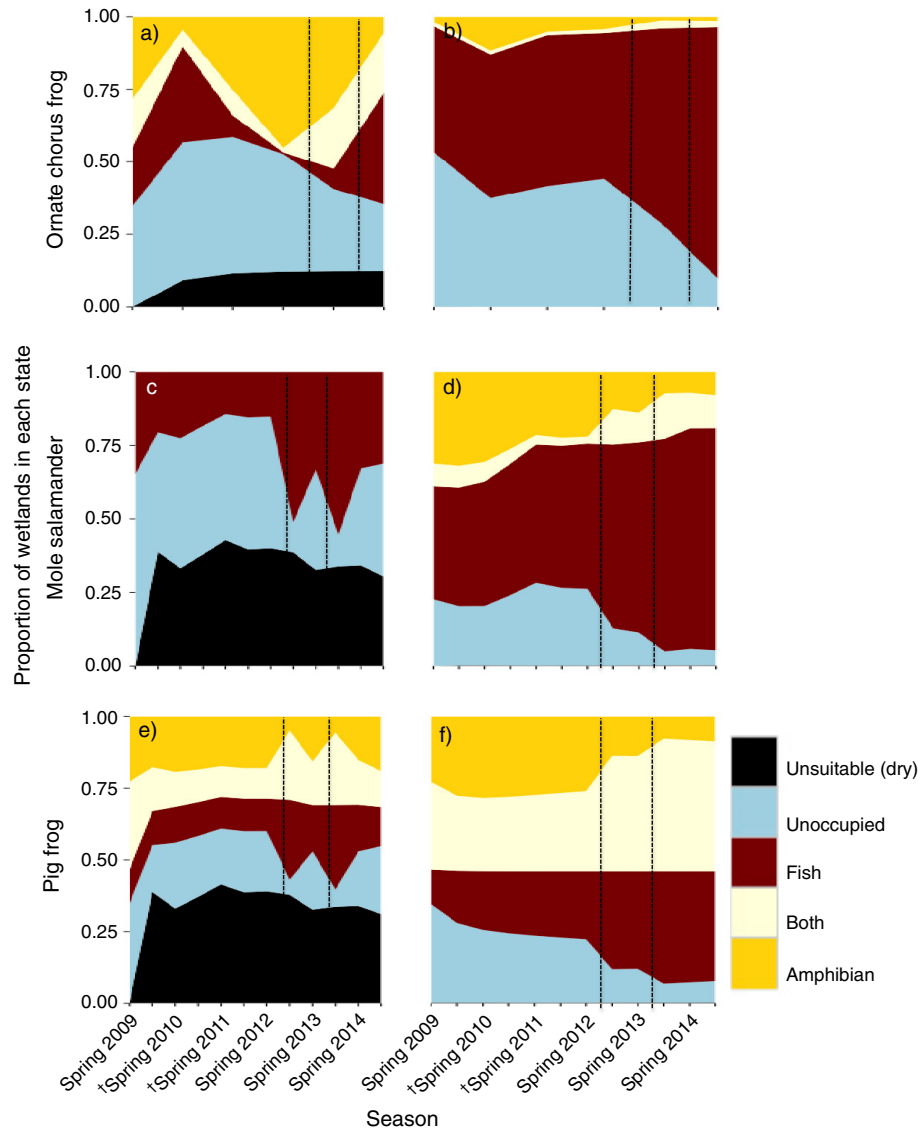


FIG. 2. Proportion of sites in each state for ornate chorus frog in (a) short- and (b) long-duration wetlands; for mole salamander in (c) short- and (d) long-duration wetlands; and for pig frog in (e) short- and (f) long-duration wetlands from 2009 to 2014. Daggers (†) indicate seasons in drought and vertical dashed lines indicate the timing of the two flood events.

leads to high persistence of these predators; i.e., fishes, once established in these wetlands, are likely to remain for long periods of time. These wetlands then serve as source populations that can increase the probability that refugia wetlands are colonized by wetlands during future flood events. Even small flooding events can shift the dynamics of wetlands for species sensitive to fishes that depend on isolated long-duration wetlands free from such large aquatic predators. Changes in the frequency of flooding in coastal systems, either as a result of sea-level rise or more frequent extreme weather events may have negative effects on species that rely on this habitat type.

These metacommunity effects play out very differently for species such as the ornate chorus frog, which are also sensitive to fish presence but able to successfully reproduce

in short-duration wetlands. Occurrence in long-duration wetlands for the chorus frog was rare in this study and these habitats largely serve as refugia during periods of drought. Colonization of chorus frogs did not occur in long-duration wetlands with fishes and was largely limited to occasions after a wetland dried. Similarly, chorus frogs only persist in long-duration wetlands during dry years. Instead, the ability of ornate chorus frogs to use short-duration wetlands allowed them to be decoupled from fish invasions after the flooding events.

Specific species responses

Species traits have been shown to play an important role in responses to disturbance; this has been

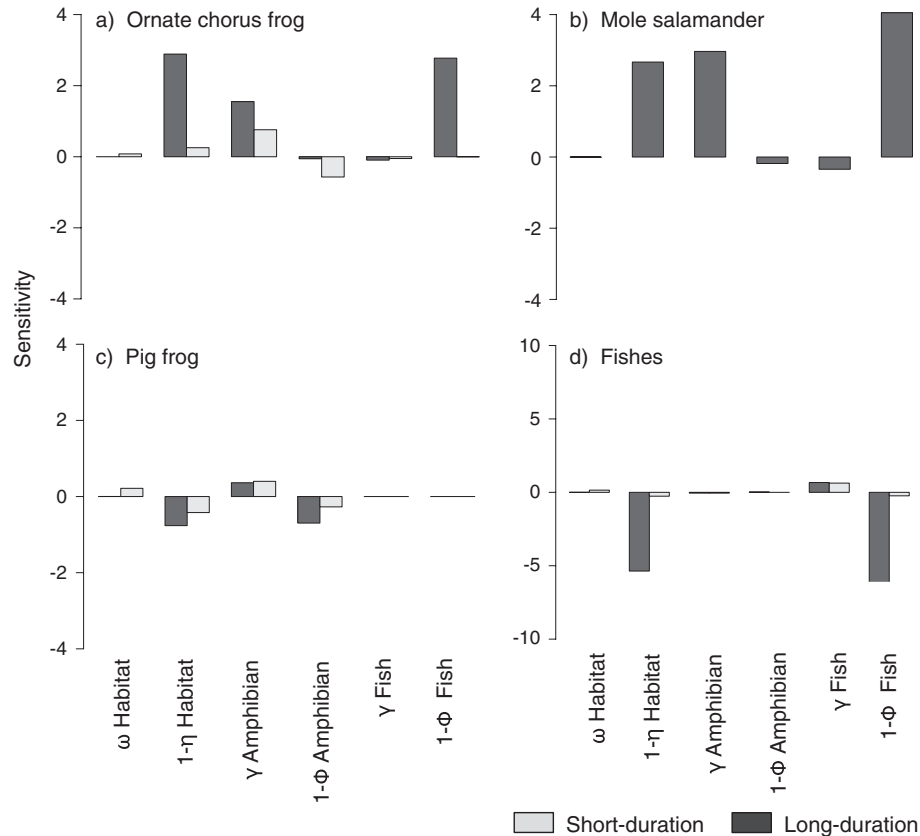


FIG. 3. Sensitivity analyses for occupancy of (a) ornate chorus frog, (b) mole salamander, (c) pig frog, and (d) fishes. Sensitivity analyses shown here for fish occupancy were performed using the mole salamander database; analyses were nearly identical between the three amphibian databases, but differed slightly due to different model parameterizations (see Appendix S4: Fig. S2). Ornate chorus frog occupancy was most sensitive to changes in habitat drying ($1 - \eta$ Habitat) and the removal of fishes ($1 - \phi$ Fish) from long-duration wetlands. Mole salamander occupancy was most sensitive to the removal of fishes from long-duration wetlands, while pig frog occupancy was relatively insensitive to changes in fish occurrence. Fish occupancy was only sensitive to the loss of suitable long-duration wetlands. Parameters are defined in Table 1.

demonstrated, for example, in assemblages of forest plants (Halpern 1989), infaunal polychaetes (Levin 1984), stream fishes (Schlosser 1990), and lentic freshwater communities (Wellborn et al. 1996). Life history characteristics can be important predictors of how communities organize and assemble. In the case of wetland breeding amphibian species, life history trade-offs that maximize fitness structure communities along a hydroperiod gradient (Snodgrass et al. 2000a, Babbitt et al. 2003, Baber et al. 2004). Here we show that differences between species across the wetland hydroperiod gradient can also predict responses to environmental perturbations.

Amphibians that breed in highly ephemeral wetlands are thought to be particularly vulnerable to changes in precipitation (Blaustein et al. 2010, Walls et al. 2013a). Our research highlights this by demonstrating that occurrence for the ornate chorus frog was strongly tied to annual habitat dynamics. Increases in colonization and persistence probabilities led to increased site use during periods of drought, consistent with a preference for sites that dry frequently (Dundee and Rossman 1989). In fact,

our simulations (see Appendix S2) indicate that this species prefers environments with a high frequency of disturbance events, which would ultimately serve to decouple occurrence of the ornate chorus frog from fish predators and create more suitable wetlands for this species to colonize.

Mole salamander occurrence responded negatively to environmental fluctuations, with occupancy steadily decreasing from 2009 to 2014. Mole salamanders rarely colonized wetlands previously occupied by fishes. Given that fishes persisted in the long-duration wetlands to which mole salamanders are restricted, even infrequent flood events are likely to have long-lasting consequences for this species. Fish removal from long-duration wetlands may prove beneficial for persistence of mole salamanders at SMNWR. However, any benefits would be short-lived if flooding continues to occur at the frequency observed in this study. Our simulations suggest that, if the variability observed in our study continues, mole salamander occupancy will decrease to <5% of wetlands at equilibrium (see Appendix S2). It is important to note

that our analysis does not look at the occurrence of individual fish species or the abundance of fish predators, which will also likely influence dynamics of sensitive amphibian species. While this would be particularly useful for management or fish eradication initiatives, we could not isolate species-specific differences due to the high correlation among fish species in colonization and extinction events.

The pig frog, our most generalist species, was largely unaffected by environmental perturbations (Ugarte et al. 2007). With a breeding season of 6–7 months and a larval development period of 365–730 d, this species is well adapted to successfully recruit from wetlands with high predation pressures (Wright 1932, Wright and Wright 1949, Lamb 1984, Dundee and Rossman 1989). Our sensitivity analyses indicated that species occurrence is most sensitive to changes in habitat dynamics, which suggests that this species may respond negatively under prolonged drought. However, this species may exhibit phenotypic plasticity in response to a decrease in hydroperiod by metamorphosing at a smaller body size (Ugarte et al. 2007).

Dynamic distribution models

Dynamic models can be powerful tools for disentangling the processes that lead to changes in species distributions (Franklin 2010, Yackulic et al. 2015). Characterizing the underlying colonization and extinction processes that determine metacommunity dynamics can provide key insights into how changes in environmental and climatic variability are likely to impact amphibian occurrence on the landscape (Miller et al. 2012, Semlitsch et al. 2015). By capturing such changes over time, we were able to understand the processes that shape amphibian occurrence in this coastal wetland system. For example, observing responses of amphibians to the introduction of fishes to some, but not all, wetlands during flooding events provided a natural experiment for asking how persistence of each species was influenced by the introduction of predators. This ability to reliably estimate dynamic processes at the community level provides a better understanding of natural systems and guidance for future management actions to combat species' decline (MacKenzie et al. 2009, Semlitsch et al. 2015). Large natural perturbations, such as the drought and flooding events that occurred on SMNWR, are particularly useful for measuring species' responses and allowed us to gain insight into species' interactions, wetland dynamics and the link between climate and the physical environment in which a species lives (Werner et al. 2009).

Climate change is predicted to further increase hydrologic variability of wetlands, thereby directly impacting amphibian communities (Pounds and Crump 1994, Kiesecker et al. 2001, McMenamin et al. 2008, Blaustein et al. 2010, Walls et al. 2013a). The persistence of amphibian assemblages is dependent on processes that occur at the local and landscape-level scale and will

require the preservation of wetlands that span the hydroperiod gradient (Paton and Crouch 2002, Phillips et al. 2002, Babbitt et al. 2003, Baldwin et al. 2006, Todd et al. 2009, Werner et al. 2009). Our work suggests that responses will vary among species and that these responses will be driven, at least in part, by interactions between changes in hydroperiod and shifts in the frequency of predatory interactions. Importantly, our research does not address complex interactions within the amphibian community assemblage (see Fauth and Resetarits 1991, Fauth 1999) or the influence of non-fish predators (e.g., birds, mammals, aquatic invertebrates; Relyea 2000, 2001). These interactions are likely influential and also affected by changes in water availability, but could not be adequately addressed in our study.

Linking large-scale ecosystem drivers, such as climate, to individual species responses is a recurrent theme in ecology, but rarely have these drivers been linked to community-wide responses. Understanding processes at the community level, however, is essential to predicting changes in biodiversity and implementing efficient strategies to combat species declines. Our simultaneous modeling of habitat and species annual dynamics provides a framework for disentangling the processes determining how species will respond to environmental change. Using this framework, we have demonstrated that differences in life histories, species' interactions and the physical environment are important components to consider when the goal is to manage communities in the face of an uncertain future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1442/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.jp34d>