

Joint estimation of habitat dynamics and species interactions: disturbance reduces co-occurrence of non-native predators with an endangered toad

David A. W. Miller^{1*}, Cheryl S. Brehme², James E. Hines¹, James D. Nichols¹ and Robert N. Fisher²

¹US Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Rd, Laurel, MD 20708, USA; and

²US Geological Survey, Western Ecological Research Center, San Diego Field Station, 4165 Spruance Road, Suite 200, San Diego, CA 92101, USA

Summary

1. Ecologists have long been interested in the processes that determine patterns of species occurrence and co-occurrence. Potential short-comings of many existing empirical approaches that address these questions include a reliance on patterns of occurrence at a single time point, failure to account properly for imperfect detection and treating the environment as a static variable.
2. We fit detection and non-detection data collected from repeat visits using a dynamic site occupancy model that simultaneously accounts for the temporal dynamics of a focal prey species, its predators and its habitat. Our objective was to determine how disturbance and species interactions affect the co-occurrence probabilities of an endangered toad and recently introduced non-native predators in stream breeding habitats. For this, we determined statistical support for alternative processes that could affect co-occurrence frequency in the system.
3. We collected occurrence data at stream segments in two watersheds where streams were largely ephemeral and one watershed dominated by perennial streams. Co-occurrence probabilities of toads with non-native predators were related to disturbance frequency, with low co-occurrence in the ephemeral watershed and high co-occurrence in the perennial watershed. This occurred because once predators were established at a site, they were rarely lost from the site except in cases when the site dried out. Once dry sites became suitable again, toads colonized them much more rapidly than predators, creating a period of predator-free space.
4. We attribute the dynamics to a storage effect, where toads persisting outside the stream environment during periods of drought rapidly colonized sites when they become suitable again. Our results support that even in highly connected stream networks, temporal disturbance can structure frequencies with which breeding amphibians encounter non-native predators.
5. Dynamic multi-state occupancy models are a powerful tool for rigorously examining hypotheses about inter-species and species–habitat interactions. In contrast to previous methods that infer dynamic processes based on static patterns in occupancy, the approach we took allows the dynamic processes that determine species–species and species–habitat interactions to be directly estimated.

Key-words: arroyo toad (*Anaxyrus californicus*), disturbance, invasive species, Markov chain, occupancy, predator–prey interactions, state-space model

Introduction

The introduction of non-native predators has been implicated as one of the important causes of global amphibian declines (Fisher & Shaffer 1996; Beebee & Griffiths 2005). Amphibians are especially susceptible to predation during

breeding and larval development. In native systems, they have evolved a wide range of adaptations that reduce predation during this stage. For example many species select temporary wetlands for breeding and larval development that go completely dry during the summer and thus are largely absent of predatory fish (Wilbur 1987; Skelly 1996; Snodgrass *et al.* 2000). These pools are not reliable as breeding habitat, sometimes drying before aquatic larvae can

*Correspondence author. E-mail: davidmiller@usgs.gov

metamorphose, but presumably the risk is outweighed by the reduced risk of fish predation. Less is known about whether the disturbance caused by predictable drying of breeding habitat reduces exposure to predators in well-connected stream breeding habitat, and similarly, whether disturbance can reduce exposure to non-native predators.

The arroyo toad (*Anaxyrus californicus*; hereafter toad) occurs in watersheds dominated either by perennial streams that consistently contain water or by ephemeral streams that experience regular disturbance as a result of drying (Jennings & Hayes 1994). Dependent on rainfall, ephemeral streams are suitable for breeding in some years and completely dry and unsuitable in others. Recent introduction of multiple non-native predators within the toad's range has resulted in a novel predator community composed of bullfrogs (*Rana catesbiana*), crayfish (*Procambarus clarkii*) and predatory fish that threatens the persistence of the toad in its native habitat (U.S. Fish and Wildlife Service 1999). Both perennial and ephemeral systems contain toads and their non-native aquatic predator populations and because stream sites are well connected, any patch in the system has a reasonable chance of being colonized after drying. However, non-native predators appear to occur less frequently in ephemeral systems, which we have hypothesized was a consequence of more frequent disturbance.

Disturbance can permit species coexistence by reducing competitive exclusion (Connell 1978; Huston 1979; Caswell & Cohen 1991) and limiting the effects of predation (e.g. Walde 1986; Hein & Gillooly 2011). In the case of predator–prey interactions, disturbance can act to reduce co-occurrence of predators with prey, increasing the probability that prey occur in enemy-free space (Jeffries & Lawton 1984; Wilbur 1987). This will occur if the prey species can colonize sites more quickly than predators after both are removed by a disturbance event. The asymmetric response during the recovery period creates a predator-free window that can be exploited.

It is common to infer community interactions from observations of static patterns of species occurrence and co-occurrence (e.g. Diamond 1975; Gotelli 2000; MacKenzie, Bailey & Nichols 2004). However, disturbance is a stochastic process, and its effect on community interactions depends on both the dynamics of the interacting species and the dynamics of the habitat itself. Therefore, interpretation of results from static approaches may be misleading. A useful alternative to static approaches is to directly estimate the site transition probabilities that determine species occupancy using Markov chain models (MacKenzie *et al.* 2006; Ruiz-Gutiérrez, Zipkin & Dhont 2010). Markov chain applications to estimate community interactions have typically specified that only a single species, or community type, can occur at one time in a given site (e.g. Waggoner & Stephens 1970; Tanner, Hughes & Connell 1994; Wootton 2001; Hill, Witman & Caswell 2004; Jiménez-Franco & Martínez 2011). The approach we propose for community modelling is an extension of static approaches for systems with two or more species (MacKenzie, Bailey & Nichols 2004) and of joint

habitat-occupancy dynamic inference models (Martin *et al.* 2010; MacKenzie *et al.* 2011). We allow for more than one species to occur within a spatial unit or area, and simultaneously incorporate the temporal dynamics of the habitat in which species occur. We also account for imperfect detection, which is particularly important when species interactions are of interest and the probability of detection differs with the presence of other species (MacKenzie, Bailey & Nichols 2004; Bailey *et al.* 2009). Our objective was to estimate the direct effect of habitat disturbance as a result of drying on co-occurrence of the endangered arroyo toad with non-native predators. At the same time, we account for other factors that could affect co-occurrence, including habitat-specific dynamics and direct predator–prey interactions.

Materials and methods

STUDY SYSTEM AND DATA COLLECTION

The arroyo southwestern toad, an endemic to the coastal plains and mountains from central California to northwestern Baja California, is federally listed as endangered (Jennings & Hayes 1994). Annual reproduction occurs between March and July and is dependent on availability of shallow, still or low-flow pools in which breeding, egg laying and larval development occur. Females produce a single clutch of eggs each year. Following fertilization, tadpoles emerge at 12–20 days and persist in breeding pools for 65–85 days.

The introduction of multiple non-native aquatic predators has contributed to the decline of this species (U.S. Fish and Wildlife Service 1999, Sweet & Sullivan 2005). Many fish species non-native to southern California freshwater systems, such as catfish (*Ameiurus* sp.), bass (*Micropterus* sp.), carp (*Cyprinus* sp.), sunfish (*Lepomis* sp.) and mosquitofish (*Gambusia affinis*), are known to prey upon amphibian eggs, larvae or adults (Grubb 1972; Drost & Fellers 1996; Adams 2000). Similarly, crayfish are opportunistic omnivores known to eat amphibian eggs and tadpoles (Fernandez & Rosen 1996; Gamradt, Kats & Anzalone 1997; Saenz *et al.* 2003), whereas bullfrogs prey upon juvenile and adult toads in the wild (Moyle 1973; Jennings & Hayes 1994). Many of these non-natives have been linked to local amphibian extirpations and declines (Fisher & Shaffer 1996; Kats & Ferrer 2003; Beebe & Griffiths 2005; Riley *et al.* 2005).

We monitored toads and predators in the San Margarita, San Mateo and San Onofre watersheds on Marine Corps Base Camp Pendleton in south-western California. The majority of variation in hydrology occurs among rather than within watersheds. Therefore, we divided watersheds by whether they were dominated by perennial and ephemeral streams to account for differences in temporal variation in hydrology. Water level on the perennial San Margarita River is consistent among years so that even in drought years most habitat is available for breeding. The San Mateo and San Onofre watersheds are comprised of second- and third-order ephemeral streams. In drought years, large portions of the streams remain dry all year.

Within watersheds, potential stream habitat was divided into 60 linear 1.5-km segments. Each 1.5-km segment was then subdivided into six linear 250-m survey sites for a total of 360 sites. We surveyed one randomly chosen site within each segment annually and the remaining sites on a 5-year rotating basis. Thus, 60 permanent and 60 rotating sites were surveyed each year from 2003 to 2009. We attempted to visit each site 2–4 times per breeding season. We considered habitat suitable if it contained water and unsuitable if it was dry

at the beginning of the toad breeding season (determined at the first site visit). At each visit, we recorded whether toad eggs or tadpoles were detected and whether at least one of a list of focal predator species were detected. Focal predators were bullfrogs, large predatory fish (sunfish, catfish, bass and carp) and crayfish.

MULTI-STATE OCCUPANCY MODEL

During each year, a site belonged to one of five discrete states: (1) unsuitable; (2) suitable, toads and predators not present; (3) suitable, toads present, predators not present; (4) suitable, toads not present and predators present; (5) suitable, toads and predators present (Fig. 1). The proportion of sites in each of the states in year t was given by state vector $\psi_t = [\psi_1 \psi_2 \psi_3 \psi_4 \psi_5]$.

We modelled changes in the states of sites as a discrete Markov process (Mackenzie *et al.* 2009; Miller 2012), where the state of a site in year $t + 1$ was solely a function of the state in year t . Thus, in each year, a site either remains in its current state or transitions to any of the four other states at probabilities conditional on the starting state. To estimate these state transitions, we begin by treating habitat, toads and predators separately and combine transition probabilities for each to calculate transition among the five global states.

We use γ to denote gains to a site (colonization for toads and predators, transition from unsuitable to suitable for habitat). Similarly, we use ϵ to denote losses from a site (extinction for toads and predators, transitions from suitable to unsuitable for habitat). Rather than treating each separately, we allow toad and predator dynamics to be conditional on each other's state and the habitat state. However, we assumed that habitat transitions were independent of other state variables. Table 1 contains a complete list of the parameters and their definitions.

Transitions among the five potential states were a function of the combined dynamics of habitat, toads and predators. For example the probability of transitioning from state 4 to state 3 is the product of the probabilities that habitat stays suitable, toads colonize the site and predators become extinct from the site so that $\phi^{[4,3]} = (1 - \epsilon^H) \times \gamma^{T,P} \times \epsilon^{P,S}$. Table 2 defines similar probabilities for all combinations of transitions among the five states. We also allow detection to be conditional on whether or not both toads and predators were present at a site (Tables 1 and 3). We estimated parameters using the maximum likelihood estimator for multi-state occupancy models derived by Mackenzie *et al.* (2009). The estimator requires defining and estimating a transition matrix (Table 2), conditional detection probabilities (Table 3) and probabilities sites are initially in each state. An example of the code we used to fit the model in R (v. 2.12; R Development Core Team. 2010) and datasets necessary to fit a model are provided in Appendix S2 (Supporting information).

HYPOTHESES AND PREDICTIONS

Disturbance can affect community interactions by decoupling occurrence of two species after a disturbed patch becomes suitable again (Caswell & Cohen 1991; Roxburgh, Shea & Wilson 2004). In the case of predator-prey interactions, this will occur if the prey species colonizes newly available patches more quickly than predators after a disturbance event (e.g. Wilbur 1987). This creates a predator-free period that can be exploited by prey species. In our case, we expected that toads, being adapted to irregular habitat availability and not dependent on stream habitat during the non-breeding season, would recover more quickly after a site transitioned from unsuitable to suitable (i.e. $\gamma^{T,u} > \gamma^{P,u}$). In addition to species differences in colonization of an unsuitable habitat, co-occurrence will also be affected by

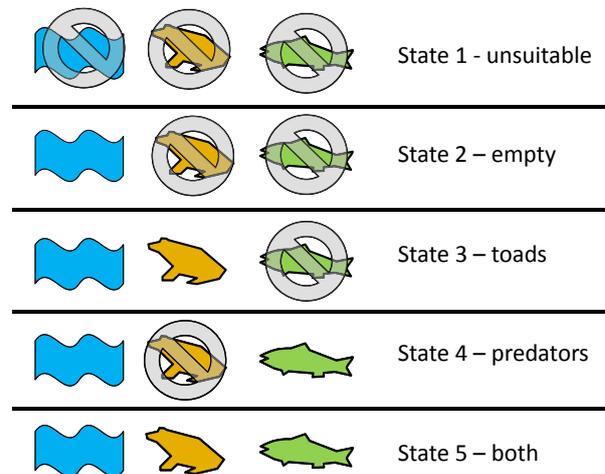


Fig. 1. Possible states in our multi-state occupancy models for the dynamics of toads, predators and habitat.

disturbance frequency, the degree to which other extinction and colonization parameters differ between toads and predators and the degree to which extinction and colonization of toads and predators are conditional on habitat and the presence of the other species. Each of these may be seen to work with disturbance directly or independently outside of the disturbance regime to affect co-occurrence.

We first considered alternative models (Appendix S1, Supporting information) in which detection was allowed to differ between sites in ephemeral and perennial watersheds and to be conditional on co-occurrence. Differences in toad and predator detection between watershed types and depending on whether the other was present could lead to spurious relationships if unaccounted for. In addition, we compared models where detection was constant or differed among years.

We next considered alternative models for transition parameters (Appendix S1), focusing on the following four factors that could affect toad and predator co-occurrence probability.

- 1 *The magnitude and frequency of drying.* Habitat transition dynamics are central to hypothesis that disturbance dynamics generates differences in co-occurrence between ephemeral and perennial systems. Thus, we compared differences between watershed types and considered alternative models where habitat transition probabilities did and did not vary among years.
- 2 *Differences between toads and predators in their transition dynamics.* Differences in extinction and colonization parameters in general, and in colonization post-disturbance specifically, will affect co-occurrence probabilities both by themselves and in combination with habitat dynamics. We estimate these species differences in all models which we considered.
- 3 *Differences in transition probabilities of toads and predators between ephemeral and perennial systems.* If colonization and extinction probabilities of toads and predators are the same for ephemeral and perennial watersheds, differences in state dynamics must be solely a result of differences in habitat transition probabilities. However, attributes of the watersheds other than the habitat suitability metric we measured may influence toad and predator dynamics, indicating that mechanisms other than disturbance are important. Therefore, we considered alternative models in which these transition parameters were the same or differed between ephemeral and perennial systems.
- 4 *The degree to which toad and predator transitions are dependent on whether the other is present.* When disturbance does not occur,

Table 1. List of estimated parameters used in the multi-state occupancy model. In addition, we fixed the colonization probability to be 0 and extinction probability to be 1 for both toads and predators if a site was unsuitable in year $t + 1$

Parameter	Description
$p^{T,s}$	Probability of detecting toads, given that toads but not predators are present
$p^{T,P}$	Probability of detecting toads, given that toads and predators are present
$p^{P,s}$	Probability of detecting predators, given that predators but not toads are present
$p^{P,T}$	Probability of detecting predators given predators and toads are present
$\gamma^{T,u}$	Probability a site is colonized by toads, given that it was unsuitable in the previous year and is now suitable
$\gamma^{T,s}$	Probability a site is colonized by toads, given that it was suitable and predators were not present in the previous year
$\gamma^{T,P}$	Probability a site is colonized by toads, given that it was suitable and predators were present in the previous year
$\varepsilon^{T,s}$	Probability toads no longer occupy a previously occupied site, given that predators were not present in the previous year
$\varepsilon^{T,P}$	Probability toads no longer occupy a previously occupied site, given that predators were present in the previous year
$\gamma^{P,u}$	Probability a site is colonized by predators, given that it was unsuitable in the previous year and is now suitable
$\gamma^{P,s}$	Probability a site is colonized by predators given it was suitable and toads were not present in the previous year
$\gamma^{P,T}$	Probability a site is colonized by predators, given that it was suitable and toads were present in the previous year
$\varepsilon^{P,s}$	Probability predators no longer occupy a previously occupied site, given that toads were not present in the previous year
$\varepsilon^{P,T}$	Probability predators no longer occupy a previously occupied site, given that toads were present in the previous year
γ^H	Probability an unsuitable site becomes suitable
ε^H	Probability a suitable site becomes unsuitable

Table 2. Transition probabilities from time t to time $t + 1$ expressed as a function of extinction and colonization probabilities for habitat suitability, toad occupancy and predator occupancy

Starting state (t)	Ending state ($t + 1$)				
	1	2	3	4	5
1	$(1-\gamma^H)$	$\gamma^H \times (1-\gamma^{T,u}) \times (1-\gamma^{P,u})$	$\gamma^H \times \gamma^{T,u} \times (1-\gamma^{P,u})$	$\gamma^H \times (1-\gamma^{T,u}) \times \gamma^{P,u}$	$\gamma^H \times \gamma^{T,u} \times \gamma^{P,u}$
2	ε^H	$(1-\varepsilon^H) \times (1-\gamma^{T,s}) \times (1-\gamma^{P,s})$	$(1-\varepsilon^H) \times \gamma^{T,s} \times (1-\gamma^{P,s})$	$(1-\varepsilon^H) \times (1-\gamma^{T,s}) \times \gamma^{P,s}$	$(1-\varepsilon^H) \times \gamma^{T,s} \times \gamma^{P,s}$
3	ε^H	$(1-\varepsilon^H) \times \varepsilon^{T,s} \times (1-\gamma^{P,T})$	$(1-\varepsilon^H) \times (1-\varepsilon^{T,s}) \times (1-\gamma^{P,T})$	$(1-\varepsilon^H) \times \varepsilon^{T,s} \times \gamma^{P,T}$	$(1-\varepsilon^H) \times (1-\varepsilon^{T,s}) \times \gamma^{P,T}$
4	ε^H	$(1-\varepsilon^H) \times (1-\gamma^{T,P}) \times \varepsilon^{P,s}$	$(1-\varepsilon^H) \times \gamma^{T,P} \times \varepsilon^{P,s}$	$(1-\varepsilon^H) \times (1-\gamma^{T,P}) \times (1-\varepsilon^{P,s})$	$(1-\varepsilon^H) \times \gamma^{T,P} \times (1-\varepsilon^{P,s})$
5	ε^H	$(1-\varepsilon^H) \times \varepsilon^{T,P} \times \varepsilon^{P,T}$	$(1-\varepsilon^H) \times (1-\varepsilon^{T,P}) \times \varepsilon^{P,T}$	$(1-\varepsilon^H) \times \varepsilon^{T,P} \times (1-\varepsilon^{P,T})$	$(1-\varepsilon^H) \times (1-\varepsilon^{T,P}) \times (1-\varepsilon^{P,T})$

Possible states were 1 – unsuitable, 2 – suitable but no toads and predators, 3 – suitable with only toads, 4 – suitable with only predators and 5 – suitable with both toads and predators.

Table 3. Probability of observing a site being in a state (columns) given the true state (rows)

True State	Observed state				
	1	2	3	4	5
1	1	0	0	0	0
2	0	1	0	0	0
3	0	$(1-p^{T,s})$	$p^{T,s}$	0	0
4	0	$(1-p^{P,s})$	0	$p^{P,s}$	0
5	0	$(1-p^{T,P}) \times (1-p^{P,T})$	$p^{T,P} \times (1-p^{P,T})$	$(1-p^{T,P}) \times p^{P,T}$	$p^{T,P} \times p^{P,T}$

Rows sum to 1. Possible states were 1 – unsuitable, 2 – suitable but no toads and predators, 3 – suitable with only toads, 4 – suitable with only predators and 5 – suitable with both toads and predators.

dependent dynamics have predictable effects on co-occurrence. Co-occurrence will be less likely than expected at random if colonization is lower and extinction higher when the other is present ($\gamma^{T,P} < \gamma^{T,s}$, $\varepsilon^{T,P} > \varepsilon^{T,s}$, $\gamma^{P,T} < \gamma^{P,s}$ and $\varepsilon^{P,T} > \varepsilon^{P,s}$), and more frequent if colonization is higher and extinction lower when the other is present ($\gamma^{T,P} > \gamma^{T,s}$, $\varepsilon^{T,P} < \varepsilon^{T,s}$, $\gamma^{P,T} > \gamma^{P,s}$ and $\varepsilon^{P,T} < \varepsilon^{P,s}$). To capture this possibility, we considered alternative models where dependence did occur (e.g. $\gamma^{T,P} \neq \gamma^{T,s}$) and did not occur (e.g. $\gamma^{T,P} = \gamma^{T,s}$).

MODEL COMPARISONS AND ESTIMATION

We measured support for alternative parameterizations using Akaike Information Criterion (AIC) and used model averaging to incorporate uncertainty in parameter estimates (Burnham & Anderson 2002). We first fit alternative models for detection parameters using the most general model for transition probabilities. Then using the parameterization for the detection model with the lowest AIC, we fit alternative models for transition probabilities. We included 12 mod-

els for detection probabilities and 32 models for transition probabilities (Appendix S1).

Models reflect alternative mechanisms that could affect co-occurrence as discussed in the Hypotheses and Predictions section. In addition, when constructing models, we had to consider sample size limitations for data from the ephemeral watersheds. Although we sampled a large number of sites for multiple years, a large portion of sites were unsuitable in many years, which limited occasions to estimate transition probabilities for toads and predators. To account for this, we limited model complexity for the ephemeral system (i) by constraining some transition probabilities to be the same as the perennial streams, or (ii) by allowing colonization to be conditional on either previous habitat state or presence of the other species, but not both at the same time.

We then calculated the estimated occurrence dynamics for the years of our study and made prospective predictions about the state dynamics. We focused on the predicted state distribution and three derived state variables: proportion of sites occupied by toads ($T = \psi_3 + \psi_5$), proportion of sites occupied by predators ($P = \psi_4 + \psi_5$) and probability that toads co-occur with predators ($C = \psi_5 / [\psi_3 + \psi_5]$). For both watershed types, we calculated the annual state distribution (Ψ_t), the mean distribution over the study period ($\bar{\Psi}$, \bar{P} , and \bar{C}) and the stationary state distribution (Ψ^* , P^* and C^* ; Hill, Witman & Caswell 2004). The stationary state distribution is useful for examining the equilibrium dynamics predicted from Markov models (Caswell & Cohen 1991; Hill, Witman & Caswell 2004; Miller 2012). Finally, we used estimated parameter values for toad and predator transitions to determine how changing habitat transition probabilities would be predicted to affect state variables. We held toad and predator extinction and colonization probabilities at their estimated values and varied habitat transition probabilities (γ^H and ε^H) across the range of possible values (from 0 to 1). For this analysis, we assumed time-constant habitat transitions. Predictions about the stationary state distribution in most cases will be similar for time-constant and time-varying transitions (Miller 2012).

Results

The model for detection probabilities with the lowest AIC was one where detection varied among years, was lower for both toads and predators when they occurred together and did not differ for segments in ephemeral and perennial watersheds. In general, estimated detection probabilities were greater and more variable for toads than they were for predators (Fig. 2).

The model with the lowest AIC for transition dynamics was strongly supported (model weight = 0.70). The model included extinction and colonization probabilities for toads and predators that did not differ between ephemeral and perennial watersheds, but were dependent on the previous state (Table 4). The next ranking model, with much lower support, was one in which colonization and extinction probabilities for toads and predators differed between ephemeral and perennial systems, but only colonization in the perennial streams depended on the previous state. As expected, we found strong differences between watershed types and among years in habitat transition probabilities in all highly ranked models.

Model-averaged parameter estimates are summarized in Table 5. Drying (ε^H) was more variable in ephemeral than perennial sites, and the mean proportion of unsuitable sites was much greater in the ephemeral watershed (Fig. 3). Colonization by toads was highest for sites that were unsuitable in the previous year ($\gamma^{T,u} > \gamma^{T,s}$ or $\gamma^{T,P}$) and was much more frequent than colonization by predators when sites transitioned from unsuitable to suitable ($\gamma^{T,u} > \gamma^{P,u}$). There was weak support for differences in toad and predator extinction and colonization probabilities between watershed types, with the majority of support for models that did not include differences. The largest differences between ephemeral and perennial sites in the model-averaged parameter estimates were for toad extinction probabilities. Large standard errors for these estimates, as a result of a combination of relatively small sample sizes to estimate some parameters and model selection uncertainty, meant that strong conclusions cannot be made about these differences. There was support for state dependence in extinction and colonization probabilities of toads and predators (e.g., $\varepsilon^{T,s} \neq \varepsilon^{T,P}$). In cases where habitat was suitable in the previous year, colonization for each was more frequent, and extinction less frequent, when the other was present. Thus, in the absence of disturbance, co-occurrence would be greater than expected if toads and predators occupied sites independently.

The mean estimated state distribution for the years of the study differed greatly between sites in the perennial ($\bar{\Psi} = [0.06 \ 0.03 \ 0.05 \ 0.09 \ 0.77]$, $\bar{T} = 0.82$, $\bar{P} = 0.86$ and $\bar{C} = 0.94$) and ephemeral watersheds ($\bar{\Psi} = [0.66 \ 0.06 \ 0.22 \ 0.02 \ 0.04]$, $\bar{T} = 0.26$, $\bar{P} = 0.06$ and $\bar{C} = 0.16$). As expected, the mean proportion of unsuitable sites was much greater in ephemeral systems than the perennial. In general, toads in the perennial watershed co-occurred with predators, whereas in the ephemeral watersheds the proportion of sites with predators remained low with little co-occurrence of toads and predators. This occurred because toads colonized sites at a higher probability than predators after drying, but predators, once established, almost always persisted at sites unless the habitat became unsuitable. The proportion of suitable sites occupied by toads was similar between watershed types (0.88 in perennial and 0.76 ephemeral). The proportion of sites in each state was stable among years in the perennial systems, whereas the proportions of suitable sites and sites occupied by toads were highly variable for ephemeral sites (Fig. 3).

The predicted stationary state distributions when habitat transition probabilities were systematically varied were nearly identical for perennial and ephemeral watersheds (Fig. 4). Both toad and predator occupancy (T^* and P^*) were predicted to be highest in undisturbed habitats ($\gamma^H = 1$ and $\varepsilon^H = 0$), whereas co-occurrence with predators (C^*) was lowest when the disturbance probability was high ($\varepsilon^H = 1$). Although increasing γ^H increased the proportion of sites occupied by toads and predators, it had no effect on the probability toads co-occurred with predators. This ratio is instead influenced only by the frequency of drying (ε^H), which effects the mean time since a site was last unsuitable. The longer the site remains suitable, the greater the probability a predator

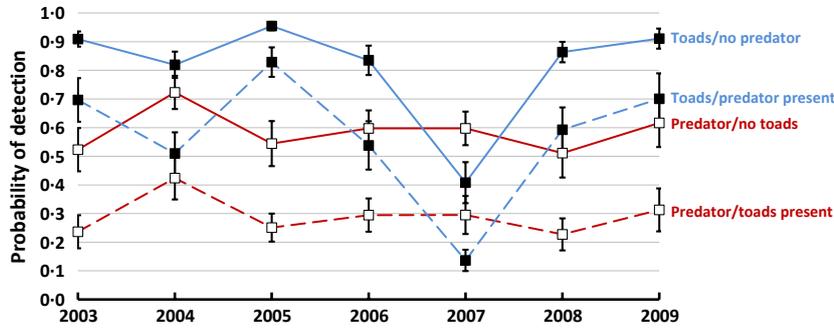


Fig. 2. Estimated detection probabilities for toads (filled boxes) and predators (unfilled boxes). Values are model-averaged estimates based on Akaike Information Criterion (AIC) weights of alternative models (Table 4). Probabilities for both toads and predators were lower when the other was present (dashed line) than when they were not (solid line).

Table 4. Model selection results for transition probabilities of toads, invasive predators and habitat suitability

Perennial Model	Ephemeral Model	Δ AIC	w	K
$\gamma^{T,u} \neq \gamma^{T,s} \neq \gamma^{T,P}, \gamma^{P,u} \neq \gamma^{P,s} \neq \gamma^{P,T}, \epsilon^{T,s} \neq \epsilon^{T,P}, \epsilon^{P,s} \neq \epsilon^{P,T}$	All equal so perennial	0	0.70	54
$\gamma^{T,u} \neq \gamma^{T,s} \neq \gamma^{T,P}, \gamma^{P,u} \neq \gamma^{P,s} \neq \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	3.10	0.15	56
$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	5.01	0.06	52
$\gamma^{T,u} \neq \gamma^{T,s} \neq \gamma^{T,P}, \gamma^{P,u} \neq \gamma^{P,s} \neq \gamma^{P,T}, \epsilon^{T,s} \neq \epsilon^{T,P}, \epsilon^{P,s} \neq \epsilon^{P,T}$	$\gamma^{T,u} \neq \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} \neq \gamma^{P,s} = \gamma^{P,T}, \epsilon^T$ and ϵ^P = perennial	6.04	0.03	58
$\gamma^{T,u} \neq \gamma^{T,s} \neq \gamma^{T,P}, \gamma^{P,u} \neq \gamma^{P,s} \neq \gamma^{P,T}, \epsilon^{T,s} \neq \epsilon^{T,P}, \epsilon^{P,s} \neq \epsilon^{P,T}$	$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	6.56	0.03	58
$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	All equal so perennial	8.69	0.01	50
$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} \neq \epsilon^{T,P}, \epsilon^{P,s} \neq \epsilon^{P,T}$	$\gamma^{T,u} = \gamma^{T,s} = \gamma^{T,P}, \gamma^{P,u} = \gamma^{P,s} = \gamma^{P,T}, \epsilon^{T,s} = \epsilon^{T,P}, \epsilon^{P,s} = \epsilon^{P,T}$	8.98	0.01	54

All models were fit using the best fitting parameterization of detection probabilities where detection of both toads and predators varied among years and was dependent on whether or not the other was present. All top models had the same parameterization of habitat dynamics, with habitat transitions differing between watershed types and among years. The best fitting model with constant habitat transitions among years had Δ AIC = 229.4. All models with Δ AIC < 9 are shown. See Appendix S2 for complete model set. AIC, Akaike Information Criterion.

will occupy the site. As a result, if γ^H was small and ϵ^H large, co-occurrence would be low but the proportion of sites occupied by toads would also be very low. Alternatively, if there was a large value of γ^H and ϵ^H remained similarly large, toads would occur in a little less than half the sites on average. But given the site was occupied, just as in the first example, the probability a predator would also be present would be very low. Similarly, we found that the proportion of sites occupied by toads but no predators (proportion of sites in state 3) was maximized when habitat transitions were most frequent ($\gamma^H = \epsilon^H = 1$). This is because frequent habitat transitions maximize turn-over of sites and thus the frequency of newly suitable habitat where toads tend to occur without predators.

Discussion

Our results support that disturbance and species responses post-disturbance structure differences in co-occurrence of native toads with non-native predators among sites in the stream systems we studied. We found that frequent disturbance, coupled with asymmetric colonization abilities of predators and toads, resulted in infrequent co-occurrence of

toads with non-native predators in the two ephemeral systems. Alternatively, infrequent disturbance, coupled with low extinction probabilities of predators absent disturbance resulted in frequent co-occurrence in the perennial system. Explicitly accounting for previous habitat states and changes in toad and predator presence between years provided insights that would not be possible from a static snapshot of the system.

Our results are consistent with previous work that suggests the stochastic nature of stream environments can affect stream communities by dampening negative interactions (i.e. competition and predation; Townsend 1989; Doubledee, Muller & Nisbet 2003). In our case, high frequency of disturbance in the ephemeral systems decoupled occurrence patterns of toads and predators. This is similar to findings that water permanence is important in determining amphibian community structure in discrete wetlands (Wilbur 1987; Skelly 1996; Snodgrass *et al.* 2000; Baber *et al.* 2004). We have shown that a similar effect can occur even in well-connected stream systems, where species differences in colonization ability were sufficient to have major effects on interaction frequencies of toads with predators.

Table 5. Model-averaged parameter estimates of transitions ($\hat{\beta}$) and standard errors (SE) for state-dependent transition probabilities

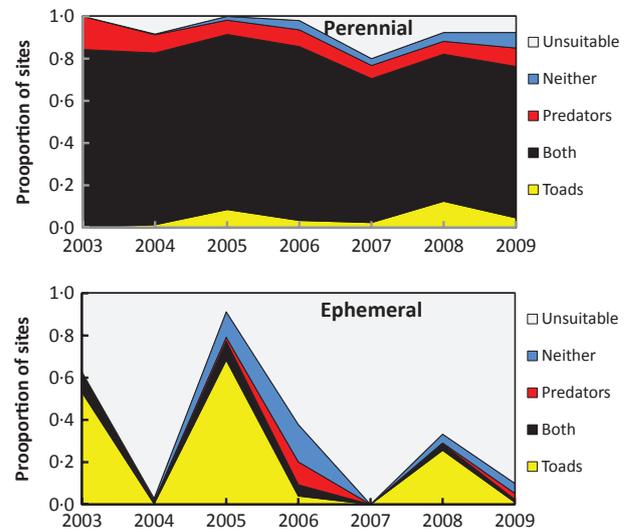
Parameter	Permanent		Ephemeral	
	$\hat{\beta}$	SE	$\hat{\beta}$	SE
$\gamma^{T,u}$	0.89	0.072	0.86	0.045
$\gamma^{T,s}$	0.28	0.396	0.23	0.338
$\gamma^{T,P}$	0.56	0.176	0.64	0.196
$\varepsilon^{T,s}$	0.64	0.302	0.83	0.092
$\varepsilon^{T,P}$	0.03	0.022	0.22	0.298
$\gamma^{P,u}$	0.07	0.062	0.10	0.061
$\gamma^{P,s}$	0.22	0.339	0.06	0.085
$\gamma^{P,T}$	0.40	0.203	0.40	0.178
$\varepsilon^{P,s}$	0.05	0.058	0.03	0.053
$\varepsilon^{P,T}$	0.01	0.023	0.00	^a —
γ^{H}_{2004}	^b —	—	0.00	—
γ^{H}_{2005}	1.00	—	0.91	0.035
γ^{H}_{2006}	—	—	0.00	—
γ^{H}_{2007}	0.00	—	0.00	—
γ^{H}_{2008}	0.62	0.142	0.33	0.057
γ^{H}_{2009}	0.00	—	0.00	—
ε^{H}_{2004}	0.08	0.040	0.95	0.032
ε^{H}_{2005}	0.00	—	0.00	—
ε^{H}_{2006}	0.02	0.019	0.59	0.065
ε^{H}_{2007}	0.18	0.050	1.00	—
ε^{H}_{2008}	0.00	—	—	—
ε^{H}_{2009}	0.00	—	0.70	0.104

^aStandard error could not be estimated either because there was no data to estimate transition or because estimate was near the boundary (0 or 1).

^bNo data to estimate this transition probability because all sites were suitable in the previous year (γ^H) or unsuitable in the previous year (ε^H).

The observed effect of disturbance on co-occurrence appears to be a result of a storage effect (Roxburgh, Shea & Wilson 2004) created by differing dynamics of prey and predator post-disturbance. Adult toads survive outside the stream habitat in the adjacent landscape during non-breeding periods and during drought years, and are sufficiently long-lived to persist until suitable habitat returns (Griffin & Case 2001; Sweet & Sullivan 2005) and are thus stored at the site despite harsh conditions. When conditions became favourable, reproduction is quickly reinitiated. However, their aquatic predators are more dependent on stream habitat, and during drought are likely restricted to wet refugia in the stream network. As a result, colonization by predators is likely dictated by the time it takes to disperse across the stream network (Grant 2011). However, once established, non-native predators in the system appear resilient and persisted in suitable habitat except when drying acted to create a period of habitat unsuitability. This result is consistent with that of Riley *et al.* (2005), who found in southern California that increased watershed urbanization increased water permanence and persistence by invasive aquatic species, having important conservation implications for stream amphibian communities.

Our results were less informative about the direct effects of predators on toads than the ecological factors that determine co-occurrence frequency. In fact, transition probabilities for toads indicate that they are preferentially selecting and


Fig. 3. Estimated proportion of sites in each of the five occupancy states during each year of the study.

remaining at sites occupied by predators. We highly doubt that this is a result of direct benefits of co-occurring with predators. Instead it likely reflects some combination of shared habitat preferences, predator response to toad availability and naïve response of the native toads to a novel set of introduced predators. We observed that detection of toads depended on whether or not predators were present. One explanation for this is that predators are reducing the number of eggs and tadpoles at occupied sites, and thus affecting the probability they are detected. This evidence is circumstantial but consistent with previous findings for predator effects in the system (USFWS 1999). Further work to quantify the direct effect of predator presence on survival of young within seasons is needed.

Disturbance invokes an inverse relationship between the total spatially and temporally available habitat for breeding toads vs. the proportion of breeding habitat that is free of predators. Prior to the introduction of non-native predators, streams in perennial watersheds offered consistent availability of breeding habitat with low predation risk. The introduction of non-natives creates a trade-off where toads minimize the probability of co-occurrence with predators in ephemeral systems but maximize potential sites that are suitable for breeding in perennial systems. The importance of minimizing predators vs. maximizing breeding opportunities will determine the population level outcomes of disturbance on toads. If predation significantly limits recruitment of young when predators are present, then habitat dynamics such as those observed in the ephemeral watersheds are more likely to maximize persistence of the toad, a shift from the pre-invasive condition. Current management to reduce non-native abundances likely reduces predator impacts in the current system and may be important in maintaining persistence of toads in the perennial system.

Observed patterns of species presence and absence from field data reflect both the actual pattern of species occurrence and false absences generated that occur when species

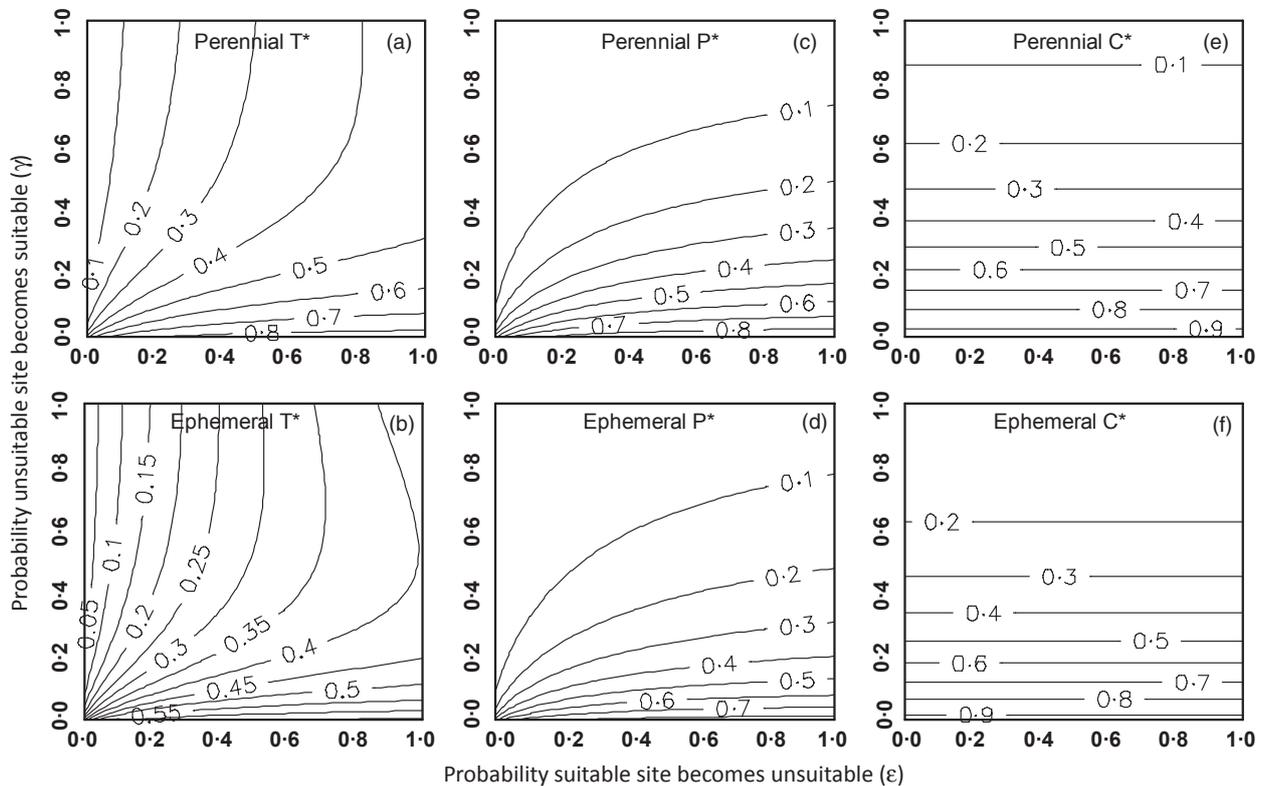


Fig. 4. By keeping all other transition probabilities constant, we determined how changing the annual probability that suitable habitat became unsuitable (ϵ) and unsuitable habitat became suitable (γ) affects co-occurrence of toads and predators for permanent (a,c,e) and ephemeral (b,d,f) systems. Predicted changes were estimated for the equilibrium (i.e. long-term average) proportion of sites occupied by toads (T^* ; a,b), 2) the equilibrium proportion of sites occupied by predators (P^* ; c,d), the equilibrium probability toads co-occurred with predators (C^* ; e,f).

are missed at occupied sites (MacKenzie *et al.* 2006). Not accounting for missed detections will bias estimates of species occurrence (MacKenzie *et al.* 2006) and of co-occurrence and other species interactions (MacKenzie, Bailey & Nichols 2004; Bailey *et al.* 2009). We found that the probability of detecting toads and predators was conditional on whether the other was present. If we had not accounted for this effect, we would underestimate the probability that toads and predators co-occurred and thus the frequency of species interaction. Conclusions regarding colonization and extinction, and influences of other species on these parameters, will also be biased when not accounting for detection. We do not believe this is simply a statistical fine point, as substantial differences have been found in two of the only studies to focus on this issue (our Fig. 2 and Bailey *et al.* 2009). Non-independence of observations are capable of producing substantial biases in inferences about co-occurrence and associated dynamics. It is possible that many historic inferences about competition and predator-prey systems could have been biased by detection effects such as these.

As demonstrated here, dynamic site occupancy models offer a simple and useful framework for studying the temporal dynamics of ecological processes related to community dynamics. They are a concise representation of a process-based model, easily suited to parameterization with empiri-

cal observations, readily adapted to different systems and useful for making a broad set of predictions. The dynamic nature of this approach stands in contrast to traditional approaches that rely on static observations. As a result, these models can be used to directly examine the processes that are responsible for patterns of species occurrence, and tools such as sensitivity analysis can be used to make predictions about the effects of system changes (Hill, Witman & Caswell 2004; Martin *et al.* 2009; Green, Bailey & Nichols 2011; Miller 2012). Similar to static methods, Markov chain models are readily parameterized from field data collected where observations are recorded for discrete sample units, with the additional requirement that data be collected during multiple time periods (Wootton 2001; Hill, Witman & Caswell 2004; Mackenzie *et al.* 2009; Jiménez-Franco & Martínez 2011; MacKenzie *et al.* 2011). The ability to account properly for imperfect detection that occurs when most species presence data are collected will further increase the robustness of inferences about community dynamics in the face of observation error (MacKenzie, Bailey & Nichols 2004; Ruiz-Gutiérrez, Zipkin & Dhont 2010).

Acknowledgements

Monitoring was funded by the Assistant Chief of Staff, Environmental Security, Resources Management Division, Marine Corps Base Camp Pendleton,

California. We thank Sherri Sullivan for project support and review of the draft manuscript. Sara Schuster, Greta VanScoy, Carlton Rochester, Liz Gallagos, Denise Clark, Chris Brown, Tritia Matsuda and Adam Backlin assisted with project support, management and data collection. Evan Grant, Adam Green, Elise Zipkin and two anonymous reviewers provided comments on this manuscript. This is contribution 402 of the US Geological Survey – Amphibian Research and Monitoring Initiative.

References

- Adams, M.J. (2000) Pond permanence and the effects of exotic vertebrates on anurans. *Ecological Applications*, **10**, 559–568.
- Baber, M.J., Fleishman, E., Babbitt, K.I. & Tarr, T.L. (2004) The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. *Oikos*, **17**, 16–27.
- Bailey, L.L., Reid, J.A., Forsman, E.D. & Nichols, J.D. (2009) Modeling co-occurrence of northern spotted and barred owls: accounting for detection probability differences. *Biological Conservation*, **142**, 2983–2989.
- Beebee, T.J.C. & Griffiths, R.A. (2005) The amphibian decline crisis: a watershed for conservation biology? *Biological Conservation*, **125**, 271–285.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd edn. Springer-Science + Business Media, LLC, New York, New York.
- Caswell, H. & Cohen, J.E. (1991) Communities in patchy environments: a model of disturbance, competition & heterogeneity. *Ecological Heterogeneity* (eds J. Kolasa & S.T.A. Pickett), pp. 97–122. Springer, New York, USA.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Diamond, J.M. (1975) Assembly of species communities. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge, MA.
- Doubledee, R.A., Muller, E.B. & Nisbet, R.M. (2003) Bullfrogs, disturbance regimes, and the persistence of California red-legged frogs. *The Journal of Wildlife Management*, **67**, 424–438.
- Drost, C.A. & Fellers, G.M. (1996) Collapse of a Regional Frog Fauna in the Yosemite Area of the California Sierra Nevada, USA. *Conservation Biology*, **10**, 414–425.
- Fernandez, P.J. & Rosen, P.C. (1996) *Effects of the Introduced Crayfish Orconectes virilis on Native Aquatic Herpetofauna in Arizona*. Technical report to the Heritage Program, Arizona Fish and Game Department, Phoenix, Arizona, USA.
- Fisher, R.N. & Shaffer, H.B. (1996) The decline of amphibians in California's great Central Valley. *Conservation Biology*, **10**, 1387–1397.
- Gamradt, S.C., Kats, L.B. & Anzalone, C.B. (1997) Aggression by non-native crayfish deters breeding in California newts. *Conservation Biology*, **11**, 793–796.
- Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.
- Grant, E.H.C. (2011) Structural complexity, movement bias and metapopulation extinction risk in dendritic ecological networks. *Journal of the North American Benthological Society*, **30**, 252–258.
- Green, A.W., Bailey, L.L. & Nichols, J.D. (2011) Exploring sensitivity of a multistate occupancy model to inform management decisions. *Journal of Applied Ecology*, **48**, 1007–1016.
- Griffin, P.C. & Case, T.J. (2001) Terrestrial habitat preferences of adult arroyo southwestern toads. *The Journal of Wildlife Management*, **65**, 633–644.
- Grubb, J.C. (1972) Differential predation by *Gambusia affinis* on the eggs of seven species of anuran amphibians. *American Midland Naturalist*, **88**, 102–108.
- Hein, A.M. & Gillooly, J.F. (2011) Predators, prey, and transient states in the assembly of spatially structured communities. *Ecology*, **92**, 549–555.
- Hill, M.F., Witman, J.D. & Caswell, H. (2004) Markov chain analysis of succession in a rocky subtidal community. *The American Naturalist*, **164**, E46–E61.
- Huston, M. (1979) A general hypothesis of species diversity. *The American Naturalist*, **113**, 81–101.
- Jeffries, M. & Lawton, J. (1984) Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.
- Jennings, M.R. & Hayes, M.P. (1994) *Amphibian and Reptile Species of Special Concern in California*. California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, California.
- Jiménez-Franco, M.V. & Martínez, J.E. (2011) Territorial occupancy dynamics in a forest raptor community. *Oecologia*, **166**, 507–516.
- Kats, L.B. & Ferrer, R.P. (2003) Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity Distributions*, **9**, 99–110.
- MacKenzie, D.I., Bailey, L.L. & Nichols, J.D. (2004) Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, **73**, 546–555.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Hines, J.E. & Bailey, L.L. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, San Diego, California.
- Mackenzie, D.I., Nichols, J.D., Seamans, M.E. & Gutierrez, R.J. (2009) Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology*, **90**, 823–835.
- MacKenzie, D.I., Bailey, L.L., Nichols, J.D. & Hines, J.E. (2011) An integrated model of habitat and species occurrence dynamics. *Methods in Ecology and Evolution*, **2**, 612–622.
- Martin, J., Nichols, J.D., McIntyre, C.L., Ferraz, G. & Hines, J.E. (2009) Perturbation analysis for patch occupancy dynamics. *Ecology*, **90**, 10–16.
- Martin, J., Chamaillé-Jammes, S., Nichols, J.D., Fritz, H., Hines, J.E., Fonnesebeck, C.J., MacKenzie, D.I. & Bailey, L.L. (2010) Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. *Ecological Applications*, **20**, 1173–1182.
- Miller, D.A.W. (2012) General methods for sensitivity analysis of equilibrium dynamics in patch occupancy models. *Ecology*, **93**, 1204–1213.
- Moyle, P.B. (1973) Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. *Copeia*, **1973**, 18–22.
- R Development Core Team. (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Riley, S.P.D., Busteed, G.T., Kats, L.B., Vandergon, T.L., Lee, L.F.S., Dagit, R.G., Kerby, J.L., Fisher, R.N. & Sauvajot, R.M. (2005) Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. *Conservation Biology*, **19**, 1894–1907.
- Roxburgh, S.H., Shea, K. & Wilson, J.B. (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology*, **85**, 359–371.
- Ruiz-Gutiérrez, V., Zipkin, E.F. & Dhont, A.A. (2010) Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. *Journal of Applied Ecology*, **47**, 621–630.
- Saenz, D., Johnson, J.B., Adams, C.K. & Dayton, G.H. (2003) Accelerated hatching of southern leopard frog *Rana sphenoccephala* eggs in response to the presence of a crayfish *Procambarus nigrocinctus* predator. *Copeia*, **2003**, 646–649.
- Skelly, D.K. (1996) Pond drying, predators, and the distribution of *Pseudacris* tadpoles. *Copeia*, **1996**, 599–605.
- Snodgrass, J.W., Komoroski, M.J., Bryan, A.L.J. & Burger, J. (2000) Relationships among isolated wetland size, hydroperiod and amphibian species richness: implications for wetland regulation. *Conservation Biology*, **14**, 414–419.
- Sweet, S.S. & Sullivan, B.K. (2005) *Bufo californicus*. *Amphibian Declines: The Conservation and Status of United States Species* (ed. M. Lannoo), pp. 396–400. University of California Press, Berkeley, California.
- Tanner, J.E., Hughes, T.P. & Connell, J.H. (1994) Species coexistence, keystone species and succession in coral assemblages: a sensitivity analysis. *Ecology*, **75**, 2204–2219.
- Townsend, C.R. (1989) The patch dynamic concept of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36–50.
- U.S. Fish and Wildlife Service (1999) *Arroyo Southwestern Toad Bufo microscaphus californicus Recovery Plan*. U.S. Fish and Wildlife Service, Portland, Oregon.
- Waggoner, P.E. & Stephens, G.R. (1970) Transition probabilities for a forest. *Nature*, **225**, 1160–1161.
- Walde, S.J. (1986) Effect of an abiotic disturbance on a lotic predator-prey interaction. *Oecologia*, **69**, 243–247.
- Wilbur, H.M. (1987) Regulation of structure in complex systems: experimental temporary pond communities. *Ecology*, **68**, 1437–1452.
- Wootton, J.T. (2001) Predictions in complex communities: analysis of empirically derived Markov models. *Ecology*, **82**, 580–598.

Received 30 September 2011; accepted 11 April 2012
Handling Editor: Kim Cuddington

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Candidate model set.

Appendix S2. Code for maximum likelihood estimation in R.

Data S1. Arroyo Toad Data.csv - data set used in analyses.

Data S2. DMp(TSpTNspT).csv - design matrix for detection parameters.

Data S3. DMp(D)e(D)T.csv - design matrix for transition parameters.

Data S4. DMpsi(WNTnN).csv - design matrix for initial occupancy parameters.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.