Title

Do a threatened native amphibian and its invasive congener differ in response to human alteration of the landscape?

Journal

Biological Invasions, 12(1)

ISSN

1573-1464

Authors

D’Amore, Antonia
Hemingway, Valentine
Wasson, Kerstin

Publication Date

2010

DOI

10.1007/s10530-009-9438-z

Peer reviewed

Biol Invasions (2010) 12:145–154
DOI 10.1007/s10530-009-9438-z

ORIGINAL PAPER

Do a threatened native amphibian and its invasive congener differ in response to human alteration of the landscape?

Antonia D'Amore · Valentine Hemingway · Kerstin Wasson

Received: 28 June 2008 / Accepted: 20 January 2009 / Published online: 6 February 2009

Abstract Anthropogenic changes to habitat are a global phenomenon and the impact of these changes may act in tandem to cause loss of biodiversity. One major global change is the introduction of invasive species. In order to determine whether other human impacts might correlate with populations of invaders, we examined the habitat correlates of distribution, persistence and reproduction of a global invader, the American bullfrog (*Rana catesbeiana*). We then compared these correlates with those of a threatened, native congener, the California red-legged frog (*Rana draytonii*). We found striking differences between the two species in response to habitat fragmentation and degradation. Our work suggests that human alteration of habitat, in particular the hydrology of freshwater sites and through building roads, favors this invasive species across the landscape.

Keywords Invasive species · *Rana draytonii* · *Rana catesbeiana* · Anthropogenic change

---

A. D'Amore (✉) · K. Wasson
Elkhorn Slough National Estuarine Research Reserve,
Watsonville, CA 95076, USA
e-mail: nina@elkhornslough.org;
damore@biology.ucsc.edu

V. Hemingway · K. Wasson
Ecology and Evolutionary Biology, University of
California, Santa Cruz, CA 95064, USA

Introduction

Human alterations of the environment such as pollution (Edinger et al. 1998), climate change (Thomas et al. 2004), habitat destruction (Brooks et al. 2002) and fragmentation are known to have direct negative effects on biodiversity. Exemplifying this, extent of human impact is the best predictor of the distribution of extinct or threatened taxa globally (Davies et al. 2006), though this pattern may be confounded by richer datasets on biodiversity and distribution existing in sites with greater human influence. While each individual threat may be potentially destructive, emerging research suggests that multiple human impacts can have synergistic effects that outweigh the additive impact of threats (Opdam and Wascher 2004).

One far reaching human impact is the introduction of non-native species and this threat affects virtually all ecosystems (Vitousek et al. 1997). Invasive species introduction is hypothesized to be a leading cause of animal extinctions world-wide (Clavero and Garcia-Berthou 2005) and as with other anthropogenic threats, may become especially problematic when combined with other human alterations of the environment. For example, impacts to habitat may favor invasive competitors or predators over native species (Byers 2002), and habitat modification may work in synergy with invaders to contribute to native species decline (Didham et al. 2007).

Part of the success of invaders in human-modified landscapes may arise because they possess a suite of characteristics that are inherently favored by anthropogenic changes to the landscape and atmosphere, such as increased disturbance and increasing atmospheric nitrogen deposition (Dukes and Mooney 1999). Invaders may also simply be tied to human presence; species that are likely to be introduced far from their native range are often ones with a long history of association with humans and with multiple releases or introductions (Kolar and Lodge 2001). In addition, invasive species are also more likely to be habitat generalists than species that do not become established in new ranges, and this may preadapt them to human changes which fall within their tolerance range (Marvier et al. 2004).

In cases when an invader co-occurs with a native congeneric species, researchers have a unique opportunity to study what factors contribute to increases in invasive distribution across the landscape (Meiners 2005) and whether effects of the invader work in conjunction with other human impacts (Didham et al. 2007). We examined the habitat characteristics correlated with the presence and success of populations of a globally detrimental freshwater invader, the American bullfrog (*Rana catesbeiana*), and its federally threatened native congener, the California red-legged frog (*Rana draytonii*) throughout the same watershed in order to understand how they differ with respect to their response to and success in the face of habitat modification and degradation.

Methods

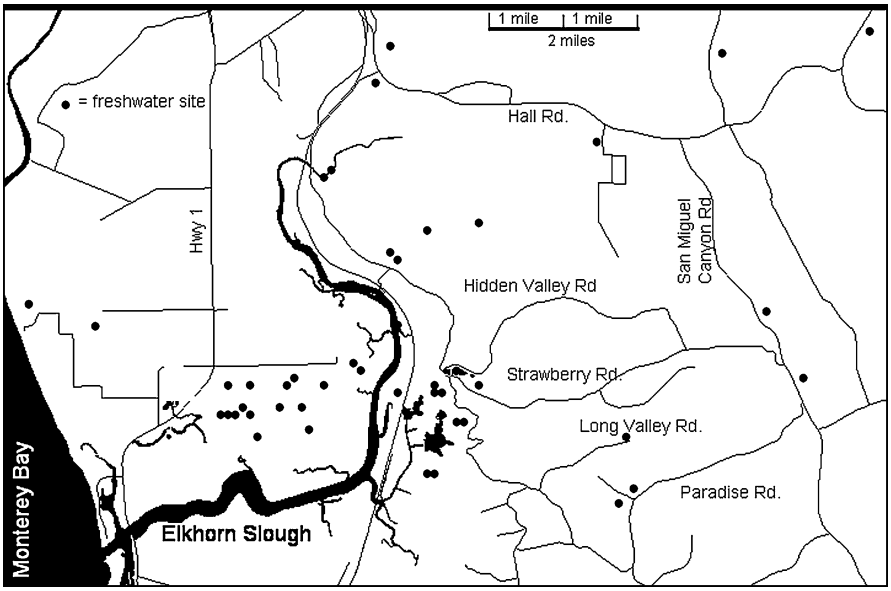
Study system

In order to quantify habitat characteristics associated with presence of both invasive American bullfrogs (hereafter bullfrogs) and native California red-legged frogs (hereafter red-legged frogs), we surveyed freshwater habitats in the western half of the Elkhorn Slough watershed in northern Monterey County, California, USA (Fig. 1). Using topographic maps, local knowledge and extensive field searches, we located a total of 42 different freshwater sites representing over 80% of freshwater sites detected by GIS analysis of the western watershed. Surveys of 38 of the sites were conducted from 2004 to 2006; the four additional sites were surveyed only in some years because of varying landowner permission.

Determining native and invader distribution and reproduction

To assess adult distribution, we conducted nighttime eyeshine surveys by surveying within the pond around the entire perimeter, a minimum of two nights a year. All frogs spotted by eyeshine were approached and identified. To determine whether breeding attempts were made each year, we

Fig 1 Map of the western Elkhorn Slough watershed, with *black dots* representing study sites



conducted one nighttime listening survey (20 min length) in each site during the appropriate breeding period: January to early March for red-legged frogs and during May–June to assess bullfrog reproduction.

To sample for the presence of reproductive stages, we seined and dip-netted each site for amphibian larvae 1–3 times per year per site in the early summer, as well as using night-time surveys in the late summer to look for young-of-the-year in ponds where larval ranid frogs had been detected. Each dip-netting effort consisted of $\sim$10 dip-nets at each 25 m interval around the pond. If no larvae were detected by dipnetting on two separate surveys, we subsequently spent $\sim$30 min seining the site. If larvae of a species were still not detected, we scored reproduction as absent from this site. We also noted all fish species encountered during our dip-netting or seining.

Native versus invader habitat correlates

In order to compare the habitat correlates of red-legged distribution versus bullfrog distribution, we collected data on a suite of habitat characteristics, most of which can be heavily altered by humans: hydroperiod, whether a site was naturally occurring or man-made, characteristics of freshwater vegetation, surrounding land-use and water quality. We used a binary classification for hydroperiod, determined by whether sites remained wet through August (when native amphibians in the watershed are likely to have completed metamorphosis). Our study sites either dried down well before August or remained wet all year, so this dichotomous classification was appropriate. We spoke with landowners and accessed historical maps to determine whether the site was manmade. In February, we estimated percent cover of the pond surface area of four categories of aquatic vegetation: floating, submerged, shoreline and emergent. ‘Floating’ encompassed all plants growing on the surface of the water with detached roots (e.g., *Lemna* spp., *Azolla* spp.). ‘Submerged’ included all plants growing completely below the surface of the water (e.g., *Potamogeton* spp.). For ‘shoreline’ we estimated the percent cover of the terrestrial habitat in a 1 m swath around the site perimeter (e.g., *Scirpus* spp.). ‘Emergent’ described plants with roots in the ground that extended through and over the surface of the water (e.g., *Hydrocotyle* spp.).

We evaluated water quality at each site in February and May from 2004 to 2006 in daytime surveys. To measure water temperature, salinity, dissolved oxygen, turbidity and pH, we used a Yellow Springs Instruments 6,600 sonde in situ at about 0.5 m depth, away from surface vegetation and about 1 m from shore. To assess nutrient concentrations, we collected a water sample from each site in an opaque bottle at the same spot that the sonde readings were taken. Nutrient analysis was performed only in May 2006 and in February and May in other years. We stored samples on ice and analyzed nitrate, nitrite, phosphate and ammonia concentrations using standard reactions to create pigments and analyze absorbance levels with a spectrophotometer.

We measured the aerial extent (estimated as length times width of the pond) of each freshwater site and categorized each site as shallow (greatest water depth < 1 m), medium (water depth between 1 and 2 m) or deep (water depth > 2 m).

Measuring landscape characteristics and human alterations

To evaluate landscape features, we used Geographic Information System (GIS) analyses. We used ArcMap 9.1 to overlay a land-use/land-cover layer for the watershed available from the Elkhorn Slough National Estuarine Research Reserve (http://www.elkhornslough.org/GIS/GIS.html) onto a 10 m digital elevation model obtained from the United States Geological Survey. To assess site connectivity, we used a number of different measurements, including the distance to the nearest freshwater wetland, the number of freshwater wetlands within a 500 m radius of each site and the distance of each pond to the nearest patch of three different land-use or habitat types: actively cultivated fields, paved roads and riparian corridors.

We calculated the area of habitat that was comprised of agricultural land and riparian land within a 1 km radius of each site, a method previously used for evaluating landscape-level effects on amphibian distribution (Pellet et al. 2004; Rubbo and Kiesecker 2005). We also estimated the relative amount of agricultural run-off each site receives by calculating the area of the sub-watershed upstream from the pour point, or outlet, of each pond that comes from agricultural sources.

Statistical analyses

To assess persistence of each species we sorted the data to determine the number of years that they were detected at each site. We then used these databases to assess which variables affected the distribution of each life history stage of each species, using both univariate and multivariate tests ($\alpha = P \leq .05$, marginal significance denoted by $P > .05$ and <.75).

Univariate tests

Given little variation between within-year samples, we averaged continuous variables across multiple surveys within years in order to obtain one value for each year. We then used ANOVA to test for differences in continuous environmental variables (e.g., pH, dissolved oxygen, temperature, distance to roads, percent drainage from agricultural lands) between sites with and without each life history stage of each species, using year as a replicate for each site. We used Chi-square tests to evaluate whether the detection of each life history stage varied with the nominal environmental variables.

Multivariate tests

We used the software package PRIMER (Plymouth Routines in Multivariate Ecological Research) version 6 to perform all of our multivariate tests (K.R. Clarke and R.N. Gorley, PRIMER version 6: User Manual/Tutorial, PRIMER-E, Plymouth). We chose this package primarily because many of its tests, such as ANOSIM (Analysis of Similarities) were designed to test for spatial and temporal differences in multi-species distribution, are robust to autocorrelation (Chapman and Underwood 1999) and do not assume multivariate normality (Clarke 1993). More traditional tests, such as MANOVA, have assumptions that are not likely to be met by this kind of dataset (Clark and Warwick 1994).

We performed ANOSIM analyses on the environmental data, first normalizing the data by subtracting the mean value for a variable from each entry and then dividing by the standard deviation of that entry from the mean (McCune and Grace 2002). ANOSIM tests for differences between predefined community samples (such as sites with red-legged frogs detected) and uses randomization techniques on a resemblance matrix to distinguish between the different communities (Clarke and Warwick 1994). We used an Euclidean distance similarity matrix on the environmental data to create a resemblance matrix between all variables. We then used the distribution data for each species to look for differences in continuous environmental characteristics at sites with and without each species detected, or with the species detected in different numbers of years.

We visualized significant environmental differences between sites detected by ANOSIM using non-metric multi-dimensional scaling or nMDS, an ordination technique. We then used a SIMPER (Similarity Percentages) test to query which environmental variables played the largest role in explaining any significant differences detected by ANOSIM (Clarke 1993). SIMPER uses resemblance between each sample group to calculate the percentage that each variable contributes to the dissimilarity (Clarke and Warwick 1994).

Results

Of all of the multivariate and univariate tests we performed, we report here only the results of tests that were significant. For a summary of all tests, please see Table 1.

Distribution

California red-legged frogs: We found adult frogs at 16–23 sites per year, for a total of 25 different sites over all 3 years. Sites with adults detected had marginally significantly fewer roads within 500 m [ANOVA ($df = 1{,}37$) $F = 4.066$, $P = .051$]. Sites with adults detected had significantly more agriculture in a 1 km buffer around the site than sites that did not contain the species [ANOVA ($df = 1{,}37$) $F = 6.905$, $P = .025$].

Bullfrogs: Adult frogs were found in 15–16 sites per year, for a total of 16 different sites over all 3 years. Permanent freshwater sites were significantly more likely to contain adults than ephemeral sites (Chi-square = 7.726, $df = 1$ $P = 0.005$) (Table 2c). Sites where adults were detected had significantly more agriculture in a 1 km buffer around the site than sites that did not have adult animals [ANOVA ($df = 1{,}37$) $F = 5.437$, $P = .012$].

Table 1 Summary of significant pair-wise analyses, ANOSIM and SIMPER tests for California red-legged frogs (CRLF) and American bullfrogs (BF)

ANOSIM	Distribution		Persistence		Reproduction	
	CRLF	BF	CRLF	BF	CRLF	BF
	NS	NS	*S*	NS	*S*	NS
Pond attributes						
Water quality						
DO						
pH					ANOVA (+)	
Temp					ANOVA (+)	
Salinity			SIMPER (−)			
Nitrate						
Ammonia			SIMPER (−)			
Phosphate			SIMPER (−)			
Size						
Hydroperiod		Chi-square (+)	SIMPER (−)			
Manmade					SIMPER (+)	
Vegetation						
Submerged						
Emergent						
Floating						
Shoreline						
Landscape attributes						
Connectivity						
Number of ponds within 500 m					Chi-square (+) SIMPER (+)	
Distance to nearest road			ANOVA (−)			
Number of roads within 500 m	ANOVA (−)					
Agriculture						
Proximity to agriculture					SIMPER (−)	
% Cultivated in 1 km buffer	ANOVA (+)	ANOVA (+)			SIMPER (+)	

(+), Positive relationship; (−), negative relationship; NS, the ANOSIM was not significant; *S*, the ANOSIM was significant

Persistence among years

California red-legged frogs: An ANOSIM detected a significant difference between sites where adult frogs were found in 0, 1, 2 or all 3 years of the study (Global $R = 0.214$, $P = .002$) (Fig. 2a). A SIMPER found a positive association between adults and longer hydroperiod, lower phosphate levels, lower ammonia levels and lower salinity. These environmental characteristics contributed the most (>4%) to this significant difference. An ANOVA found that the distance to the nearest road was significantly different for sites where the adult frogs were found in 0, 1, 2, or 3 years [ANOVA ($df = 3$, 37) $F = 3.036$, $P = .042$], with increased road proximity related to decreasing occupancy by the species.

Bullfrogs: The distribution of bullfrogs did not vary among years; they were detected in the same sites each of the 3 years.

Reproduction

California red-legged frogs: We found that fewer than half the occupied sites had successful breeding by this species, as defined in the methods. We found that larvae were more likely to occur in sites that had another freshwater site within 500 m (Chi-square $= 4.202$, $df = 1$ $P = 0.04$), and that ponds containing

Table 2 Charts depicting Chi-squared analyses of the relationship between California red-legged frog (CRLF) and American bullfrog (BF) life stages and the hydroperiod of the freshwater site in which they were found

	Dry before August	Wet through August	Total
(a) Pearson Chi-square = 4.934, *df* = 1 *P* = 0.026			
CRLF tadpoles absent	14	14	28
CRLF tadpoles present	1	9	10
Total	15	23	38
(b) Pearson Chi-square = 10.097, *df* = 1 *P* = 0.001			
CRLF YOY absent	15	12	27
CRLF YOY present	0	11	11
Total	15	23	38
(c) Pearson Chi-square = 7.726, *df* = 1 *P* = 0.005			
Adult BF absent	13	10	23
Adult BF present	1	14	15
Total	15	24	38
(d) Pearson Chi-square = 7.726, *df* = 1 *P* = 0.005			
Juvenile BF absent	13	10	23
Juvenile BF present	1	14	15
Total	14	24	38
(e) Pearson Chi-square = 7.726, *df* = 1 *P* = 0.005			
BF tadpole absent	13	10	23
BF tadpole present	1	14	15
Total	14	24	38

larvae had a greater number of other freshwater sites within 500 m than sites without larvae [ANOVA ($df = 1,37$) $F = 11.157$, $P = .001$]. All reproductive stages were found more frequently in ponds that were wet through August (Chi-square = 4.934, $df = 1$ $P = 0.026$) (Table 2a, b). Ponds with successful breeding (young-of-the-year seen) in all years surveyed were significantly warmer [ANOVA ($df = 1,84$) $F = 3.965$, $P = .05$] and had higher magnitude pH than ponds without successful breeding detected [ANOVA ($df = 1,84$) $F = 7.850$, $P = .006$].

An ANOSIM found significant differences in environmental characteristics between sites with and without breeding detected (Global $R = 0.168$, $P = .002$) (Fig. 2b). Subsequent SIMPER analysis found that $\sim$20% of the dissimilarity in breeding versus non-breeding sites was determined by landscape factors: the number of roads within 500 m of the site (negative correlation with roads), proximity to agriculture (negative correlation with agriculture), whether or not the site was man-made (positive correlation with man-made sites), the area within a 1 km buffer that was cultivated (positive correlation with cultivation) and number of freshwater sites within 500 m of the site (positive correlation with other freshwater sites).

Bullfrogs: We found that reproduction (larval production and metamorphosis) was found significantly more frequently in ponds that were wet through August (Chi-square = 7.726, $df = 1$ $P = 0.005$) (Table 2d, e). Bullfrogs bred successfully in every pond they occupied in every year, unless directly controlled.

Discussion

Our investigation revealed striking differences between how a globally important invasive species and its threatened native congener differ in response to human alterations of the landscape. The invader appears to be favored over the native in sites with hydrological alteration, landscape-level habitat fragmentation and degradation of habitat. These results confirm hypotheses by Byers (2002) and Dukes and Mooney (1999) that suggest the prevalence or success of invaders may increase in human-altered landscapes.

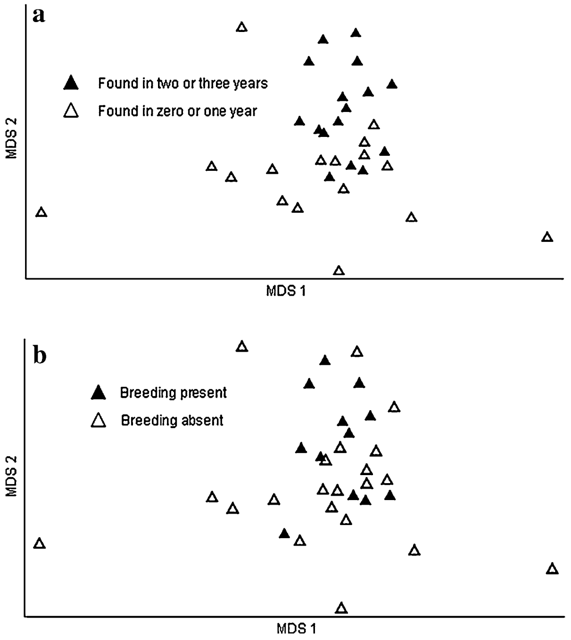


Fig 2 **a** Non-metric multi-dimensional scaling (nMDS) plot depicting the dissimilarity in environmental characteristics between sites containing California red-legged frog presence in multiple years and those containing them in one or less years. **b** nMDS plot depicting the dissimilarity in environmental characteristics between plots where California red-legged frog reproduction was found and where reproduction was not found

Alteration of hydrology—changing selection regime

Human alteration of habitat may directly affect selection regimes, by changing the abiotic or biotic composition of an ecosystem that native species have adapted to (Byers 2002). The evolutionary advantage that a native species may maintain through evolving in a given landscape can be removed when selection regimes are altered, giving invasive species an opportunity to invade and become dominant competitors (Byers 2002). For example, a large scale review of landscape-level change and invasive fish species found that non-natives were largely associated with human disturbance (Meador et al. 2003). A assessment of human alterations to freshwater habitat found that agricultural inputs and sedimentation, invasive species and altered hydrology were the primary threats to freshwater species throughout the United States (Richter et al. 1997). Alteration of the hydrology of freshwater habitat has also been identified as a major threat to native anurans in northwestern North America and altered hydroperiod is correlated with establishment of invasive aquatics across this large scale (Adams 1999).

The remaining freshwater sites within the watershed we studied are predominately man-made sites with year-round water. California red-legged frogs require sites that hold water through the end of the summer to complete metamorphosis, while invasive bullfrogs require permanent water for a full year of development as larvae (Stebbins 1966). This is a case where the invasive species has a narrower tolerance than the native species in question. In a landscape with freshwater sites that predominately persist through the summer and then dry, the native amphibian would be at an advantage. In this highly modified system however, there is little representation of this class of habitat due to human alterations. Sites either dry down too early for breeding of either ranid species or are maintained artificially wet throughout the year, relegating both species of ranid frogs into permanent sites for breeding.

This low variation in water availability means that both species rely on the same habitat for breeding, even though their biological needs in terms of hydroperiod could allow for niche differentiation. Indeed, if we had found California red-legged frogs and bullfrogs in very different types of ponds, it might be due to this native species actively avoiding bullfrogs. As California red-legged frogs are found in a subset of ponds containing bullfrogs, the less human-impacted ones, it seems very unlikely that differences in pond use are due to interspecific interactions. Permanent sites are more likely to contain invasive fish species, many of which the bullfrog can readily coexist with (Adams et al. 2003). Unfortunately, invasive fish species may be highly detrimental to native frogs (Hayes and Jennings 1986). Our findings suggest that human alteration of pond hydrology has large impact on species composition and invader distribution.

Habitat fragmentation at the landscape scale

Human land-use activities cause fragmentation of natural landscapes, resulting in negative effects on native biodiversity (Debinski and Holt 2000). For instance roads, can have widespread effects on animal communities, both directly via road-kill and indirectly through reduced dispersal and behavioral avoidance (Forman and Alexander 1998). Agriculture can fragment large stretches of the landscape and it can change species composition within fragments (Hobbs 2001). Invasive species in particular may be adapted to fragmentation because they tend to be species with long-distance dispersal and who have evolved with human-fragmented landscapes in their home range (Trakhtenbrot et al. 2005).

Our multivariate tests found landscape characteristics such as the number of roads and the isolation of the site to be important negative correlates of red-legged frog reproduction but not for bullfrogs. This suggests that unobstructed movement between sites is vital to some aspect of successful reproduction of the native species, whether it is formation of breeding choruses, avoiding predators, maintaining genetic diversity and/or that native amphibian larvae are more sensitive to agricultural contaminants or roads. Recent work has suggested that site isolation primarily becomes a concern in degraded habitats and indicates low-quality surrounding habitat rather than an effect of the spatial distribution of ponds (Marsh and Trenham 2001). Bullfrog populations may not be impacted by habitat fragmentation in similar ways due to higher fecundity (and therefore a larger pool of dispersing young frogs; Stebbins 1966).

Degradation of habitat quality at the site level

Human alterations globally include dramatic increases in contaminants in the environment (Wania and Mackay 1996). These increased contaminant levels have direct negative effects on biodiversity, but may also have indirect effects on natives by favoring an invasive species. For example, low level herbicide exposure interferes with native toad (*Bufo bufo*) species recognition of non-native crayfish cues (Mandrillon and Saglio 2007). Another indirect pathway favoring the invader results if it is more pollution tolerant than natives. This might be the case if the invader is more generalist and tolerates a wide range of conditions, a common attribute of invasive species (Marvier et al. 2004).

Despite presence of both species being correlated with increased agricultural in the upland, our multivariate analyses found that phosphate levels, ammonia levels and salinity levels were all negatively correlated with persistence of California red-legged adults but not bullfrogs. While a mixed agricultural landscape (ponds within 1 km of cultivated fields) may provide adult ranid frogs with a network of ponds allowing for the possibility of successful dispersal between sites, direct proximity to agricultural fields may impact water quality and larval stages predominately. This may explain why California red-legged frog breeding was negatively affected by increasing proximity to agriculture. Successful breeding of California red-legged frogs, defined by presence of metamorph frogs, was correlated with increased water temperatures and pH. Thus, even if adults are able to occupy a site, water quality may limit their reproductive success. The global distribution of invasive bullfrogs may relate directly to their ability to tolerate and succeed in a wide range of conditions, including highly compromised water quality.

Conclusions

Human alterations can thus have indirect negative effects on native biodiversity by favoring invasive species, as well as well-documented direct effects. Recent studies of California red-legged frog distribution found an association between declines of the frog and landscape-level factors such as upwind agricultural land-use, extent of urbanization and elevation (Davidson 2004). Others have implicated introduced predators (Hayes and Jennings 1988; Lawler et al. 1999; Doubledee et al. 2003) as within-site determinants of declines. In this system, anthropogenic modification of hydroperiod, fragmentation at the landscape scale and degradation of breeding habitat act in tandem to determine where native and invasive species are found, persist, and successfully reproduce.

Acknowledgments We would like to thank E. Kirby, M. McNicholas, D. Steely and many other volunteers for their help in conducting field work. Water quality laboratory analyses were performed by J. Haskins. E. Van Dyke was instrumental for GIS analyses. We are grateful to A. Ritter and P. Raimondi for assistance with statistical analyses and to T. Comendant, D. Doak, N. Scott, P. Raimondi and anonymous reviewers for thoughtful input on the writing process. Funding was provided by grants to the Elkhorn Slough Foundation on behalf of the Elkhorn Slough National Estuarine Research Reserve from the National Oceanic and Atmospheric Administration's Estuarine Reserve Division and to V. Hemingway through California State University Monterey Bay's Earth Science and Systems Policy Internship and the National Science Foundation's

Graduate Research Fellowship. The cost of materials was covered by grants to A. D'Amore from the STEPS Institute, UC Santa Cruz. This work complies with all laws in the country in which it was performed.

References

Adams MJ (1999) Correlated factors in amphibian decline: exotic species and habitat change in western Washington. J Wildl Manage 63:1162–1171. doi:10.2307/3802834

Adams MJ, Pearl CA, Bury BR (2003) Indirect facilitation of an anuran invasion by non-native fishes. Ecol Lett 6:343–351. doi:10.1046/j.1461-0248.2003.00435.x

Brooks TM, Mittermeier RA, Mittermeier CG et al (2002) Habitat loss and extinction in the hotspots of biodiversity. Conserv Biol 16:909–923. doi:10.1046/j.1523-1739.2002.00530.x

Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97:449–458. doi:10.1034/j.1600-0706.2002.970316.x

Chapman MG, Underwood AJ (1999) Ecological patterns in multivariate assemblages: information and interpretation of negative values in ANOSIM tests. Mar Ecol Prog Ser 180:257–265. doi:10.3354/meps180257

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Warwick RM (1994) Similarity-based testing for community pattern: the two-way layout with no replication. Mar Biol 118:167–176. doi:10.1007/BF00699231

Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110. doi:10.1016/j.tree.2005.01.003

Davidson C (2004) Declining downwind: amphibian population declines in California and historical pesticide use. Ecol Appl 14:1892–1902. doi:10.1890/03-5224

Davies RG, Orme CDL, Olson V et al (2006) Human impacts and the global distribution of extinction risk. Proc Biol Sci 273:2127. doi:10.1098/rspb.2006.3551

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14:342–355. doi:10.1046/j.1523-1739.2000.98081.x

Didham RK, Tylianakis JM, Gemmell NJ et al (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489. doi:10.1016/j.tree.2007.07.001

Doubledee RA, Muller EB, Nisbet RM (2003) Bullfrogs, disturbance regimes, and the persistence of California red-legged frogs. J Wildl Manage 67:424–438

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends Ecol Evol 14:135. doi:10.1016/S0169-5347(98)01554-7

Edinger EN, Jompa J, Limmon GV et al (1998) Reef degradation and coral biodiversity in Indonesia: Effects of land-based pollution, destructive fishing practices and changes over time. Mar Pollut Bull 36:617. doi:10.1016/S0025-326X(98)00047-2

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29:207–231. doi:10.1146/annurev.ecolsys.29.1.207

Hayes MP, Jennings MR (1986) Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? J Herpetol 20:490–509. doi:10.2307/1564246

Hayes MP, Jennings MR (1988) Habitat correlates of distribution of the California red-legged frog (*Rana aurora draytonii*) and the foothill yellow-legged frog (*Rana boylii*): implications for management. In: Proceedings of the symposium on the management of amphibians, reptiles, and small mammals in North America. USDA Forest Service General Technical Report RM-166

Hobbs RJ (2001) Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. Conserv Biol 15:1522–1528. doi:10.1046/j.1523-1739.2001.01092.x

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199. doi:10.1016/S0169-5347(01)02101-2

Lawler SP, Dritz D, Strange T, Holyoak M (1999) Effects of introduced mosquitofish and bullfrogs on the threatened Calfornia red-legged frog. Conserv Biol 13:613–622 doi:10.1046/j.1523–1739.1999.98075.x

Mandrillon A-L, Saglio P (2007) Herbicide exposure affects the chemical recognition of a non native predator in common toad tadpoles (*Bufo bufo*). Chemoecology 17:31. doi:10.1007/s00049-006-0354-8

Marsh DM, Trenham PC (2001) Metapopulation dynamics and amphibian conservation. Conserv Biol 15:40–49. doi:10.1046/j.1523-1739.2001.00129.x

Marvier M, Kareiva P, Neubert MG (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Anal 24:869–878. doi:10.1111/j.0272-4332.2004.00485.x

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon

Meador MR, Brown LR, Short T (2003) Relations between introduced fish and environmental conditions at large geographic scales. Ecol Indic 3:81. doi:10.1016/S1470-160X(03)00013-X

Meiners SJ (2005) Seed and seedling ecology of *Acer saccharum* and *Acer platanoides*: a contrast between native and exotic congeners. Northeast Nat 12:23–32. doi:10.1656/1092-6194(2005)012[0023:SASEOA]2.0.CO;2

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol Conserv 117:285. doi:10.1016/j.biocon.2003.12.008

Pellet J, Guisan A, Perrin N (2004) A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. Conserv Biol 18:1599–1606. doi:10.1111/j.1523-1739.2004.0421a.x

Richter BD, Braun DP, Mendelson MA et al (1997) Threats to imperiled freshwater fauna. Conserv Biol 11:1081–1093. doi:10.1046/j.1523-1739.1997.96236.x

Rubbo MJ, Kiesecker JM (2005) Amphibian breeding distribution in an urbanized landscape. Conserv Biol 19:504–511. doi:10.1111/j.1523-1739.2005.000101.x

Stebbins RC (1966) A field guide to western reptiles and amphibians; field marks of all species in western North America. Houghton Mifflin, Boston

Thomas CD, Cameron A, Green RE et al (2004) Extinction risk from climate change. Nature 427:145. doi:10.1038/nature02121

Trakhtenbrot A, Nathan R, Perry G et al (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181. doi:10.1111/j.1366-9516.2005.00156.x

Vitousek PM, D'Antonio CM, Loope LL et al (1997) Introduced species: a significant component of human-caused global change. N Z J Ecol 21:1–16

Wania F, Mackay D (1996) Tracking the distribution of persistent organic pollutants. Environ Sci Technol 30:390–396