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Commentary

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Crossing Over the Edge in Modified Landscapes: A Framework for Amphibian Studies Linking Occupancy Patterns With Underlying Mechanisms

Tanya J. Hawley Matlaga[1]

Abstract

The impact of habitat loss and modification on amphibians in the tropics is catastrophic. Ecologists must devote their limited time and resources to research that will allow for the most positive impact on the conservation of species into the future. I suggest a framework to aid in organizing research questions that center on understanding the patterns and underlying mechanisms of how species respond to habitat change. The first step is determining which abiotic and biotic factors have changed in the modified habitat compared with the intact habitat. Then, based on species-specific characteristics that mediate the mechanism, we can identify how vital rates of a given species are impacted and lead to the outcome of either growth or decline at the population level. I apply this framework to previous work to examine how breeding site use and tadpole performance contribute to our understanding of mechanisms that underlie occupancy patterns of species across a modified tropical landscape in the Osa Peninsula, Costa Rica.

Keywords

amphibians, Costa Rica, ecological jackpot, framework, habitat modification, mechanisms

Commentary to: Matlaga, T. J. H. (2018). Mechanisms underlying the occurrence of species in complex modified tropical landscapes: A case study of amphibians in the Osa Peninsula, Costa Rica. *Journal of Tropical Ecology, 34*, 32–40.

Habitat loss and modification are the primary causes of worldwide amphibian population declines and extirpations (Young et al., 2001). In the latest International Union for Conservation (2008) Red List analysis, approximately 60% of the 6,260 amphibians assessed at the time were affected by habitat loss. These numbers demand that we focus more effort on understanding the basic ecology, occupancy patterns, and population dynamics of species in complex modified landscapes. Previous studies recognize that some frog species persist in modified habitats whereas others do not, often resulting in lower species richness and different species composition compared with intact habitats (reviewed by Gardner, Barlow, & Peres, 2007). However, few studies have examined the mechanisms underlying frog occupancy patterns in modified landscapes. My recent study examined how breeding site use and tadpole performance can contribute to an understanding of the mechanisms that underlie occupancy patterns of species across a landscape (Matlaga, 2018). With an understanding of how abiotic conditions influence vital rates of frogs, we can begin to identify the factors that contribute to either population growth or decline in modified landscapes. Then, land managers will be able to concentrate their efforts on the factors that lead to population declines of a species. Here, I propose a framework to assist in studying how amphibians respond to habitat change (Figure 1).

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The landscape that remains after deforestation often consists of forest fragments surrounded by modified matrix habitats, both differing in a suite of abiotic and biotic characteristics compared with the former intact forest (Saunders, Hobbs, & Margules, 1991; Figure 1). These new abiotic environments often have increased solar input, higher air and water temperatures, greater wind speeds, and reduced humidity and soil moisture compared with intact forest (Holl, 1999; Saunders et al., 1991). In addition, dynamics among species may change as competitors; predators and prey populations are impacted by habitat alteration. Therefore, modified and intact habitats offer environments that differ in quality for amphibians. The role of modified, matrix habitats in maintaining regional amphibian biodiversity is not well understood.

Research examining the effects of habitat modification on amphibians has started to shift from a focus on comparing species' occupancy patterns to increased attention given to elucidating the mechanisms underlying these patterns (Figure 1). To understand the mechanisms, we must identify how changes in abiotic conditions in the modified habitats lead to changes in vital rates of particular life stages of species (Funk & Mills, 2003). Because amphibians typically undergo three distinct life stages, egg, tadpole, and juvenile to adult, often in different habitats, it is necessary to study mechanisms acting on each life stage. For instance, adult frogs may use particular breeding sites across a forest-modified habitat continuum (Binckley & Resetarits, 2007; Gascon, 1993; Matlaga, 2018), based on their ability to tolerate abiotic conditions in that habitat or their heat tolerance (Nowakowski et al., 2018). The hatching success of eggs can be lower in pasture compared with forest habitats (Neckel-Oliveira, 2004). Tadpole performance (survival, growth, and development) may also differ in forest compared with modified habitats depending on the species (Hawley, 2010; Matlaga, 2018; Schiesari, 2006; Skelly, Freidenburg, & Kiesecker, 2002; Werner & Glennemeier, 1999). Juveniles may avoid modified habitats when dispersing from ponds (deMaynadier & Hunter, 1999; Rothermel & Semlitsch, 2002) and may have improved performance in forest compared with modified habitats (Todd & Rothermel, 2006). During each life stage, life history and ecological, behavioral, and physiological characteristics contribute to the mechanism and eventual outcome for population growth and persistence in different habitats (Figure 1). Detailed knowledge of mechanisms underlying occupancy patterns may explain why some species persist, whereas others undergo population declines in modified habitats. This framework can be used to visualize and elucidate mechanisms underlying occupancy of species in a given area based on existing research, to identify gaps in our understanding, and to assist land managers in developing conservation plans to reduce population declines in fragmented landscapes.

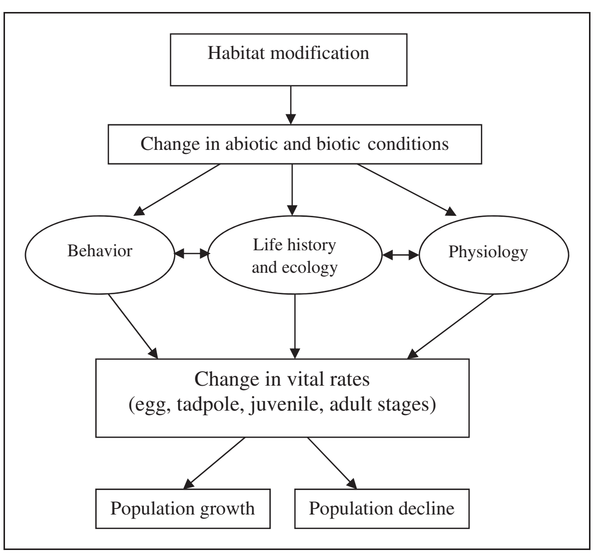

Figure 1. Framework for studying ecological consequences of anthropogenic habitat modification for frog populations. Patterns (in squares) include changes in abiotic and biotic conditions and vital rates of different life stages of species. Mechanisms (mediated by characteristics of species in circles) are the link between patterns and population-level outcomes.

Next, I will describe how the framework assists in understanding how occupancy patterns uncovered by surveys and mechanisms uncovered in experiments lead to population-level outcomes for *Engypstomops pustulosus* and *Dendrobates auratus* within a pasture-forest mosaic in the Osa Peninsula, Costa Rica. In my recent work, I report results from research that aimed to uncover mechanisms which contribute to the occupancy patterns of members of this amphibian community (Matlaga, 2018). I asked whether breeding site use by adults and performance of tadpoles differs among pasture, edge, and forest habitats. I allowed free-ranging adult frogs to use pools along pasture-forest transects and recorded egg and tadpole depositions over 5 months. Then, I determined whether patterns of breeding site use were consistent with tadpole performance among habitats for two species, *E. pustulosus,* a species often associated with modified habitats, and *D. auratus*, a species associated with intact forests. I introduced hatchlings into artificial pools in pasture, edge, and forest and quantified survival, growth, and development through metamorphosis. I quantified air temperature and incident radiation in each habitat and the water temperature in pools to identify how abiotic conditions differ among habitats. In earlier work, I asked whether species richness and composition differ between forest and pasture, and I examined factors that influence occupancy patterns (Hawley, 2008). I used visual encounter and vocalization survey methods to detect frogs in 82 aquatic and terrestrial sites in pasture and forest. The survey results suggest the population-level outcome for *E. pustulosus* and *D. auratus* using detection of adults in a habitat to represent habitat quality. These patterns of occupancy can then be compared with experimental results of the underlying mechanisms to determine the level of support for the mechanistic framework.

The outcome for *E. pustulosus* starts with increased air and water temperatures detected in pasture compared with edge and forest (Figure 2; Matlaga, 2018). *E. pustulosus* has a large clutch size and nocturnal activity period (Savage, 2002) and adults use pools in pasture and the forest edge for breeding activities (Matlaga, 2018). In addition, adults lay eggs in a foam nest, which provides protection from desiccation (Savage, 2002) and tadpoles are known to consume conspecific and heterospecific eggs, which provides additional food sources in ephemeral pasture pools (Hawley, 2009). These behavioral, physiological, and life history and ecology traits mediate the ability of different life stages of *E. pustulosus* to thrive in the pasture abiotic environment. I documented high tadpole performance across the canopy cover gradient, suggesting that *E. pustulosus* has a flexible thermal physiology (Matlaga, 2018). Yet, development was faster and metamorphs were larger in pasture than in forest. Therefore, I suggest that *E. pustulosus* and likely species with similar life histories (*Leptodactylus bolivianus* and *Leptodactylus poecilochilus*) maintain populations in modified habitats because they thrive under the abiotic conditions of open canopy habitats. Modified habitats, such as pastures, represent an ecological jackpot for *E. pustulosus*, permitting improved population growth relative to intact habitats, such as forest. Survey results agree with the experimental outcomes, with adults of *E. pustulosus* detected in pasture, but not in forest, sites (Hawley, 2008).

The outcome for *D. auratus* also begins on the framework with increased air and water temperatures in pasture compared with edge and forest (Figure 3). This species used breeding pools exclusively in forest (Matlaga, 2018) and has small clutch sizes and a small geographic distribution (Savage, 2002). In addition, *D. auratus* has a terrestrial reproductive mode whereby egg development occurs in moist terrestrial areas. I measured decreased tadpole survival and growth in pasture compared with edge and forest, suggesting that the thermal physiology of this species is inflexible (Matlaga, 2018). Overall, my data suggest that *D. auratus,* and

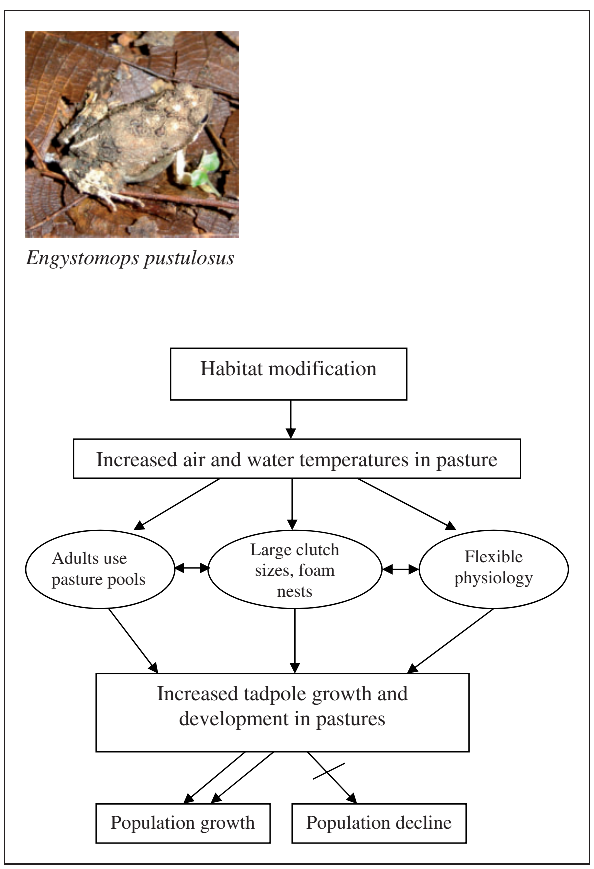

Figure 2. Proposed mechanism leading to population growth in pastures for *Engystomops pustulosus*.

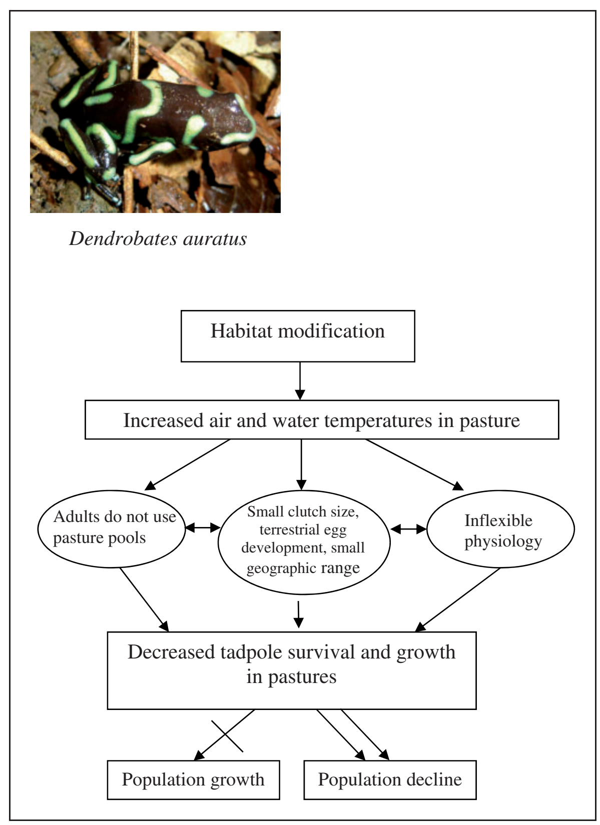

Figure 3. Proposed mechanism leading to restriction to forests for *Dendrobates auratus*.

species with similar life histories (*Phyllobates vittatus* and *Allobates talamancae*) are incapable of surviving in a matrix habitat such as pasture and likely do not venture beyond the forest edge because of behavioral and physiological aversions to the heat. This leads to the restriction of their populations to intact forest and forest fragments. Survey results agree with the experimental outcomes, with *D. auratus* detected only in forest (Hawley, 2008).

These findings have several implications for amphibian conservation in the tropics. The quality of matrix habitats influences the performance and persistence of species. Pastures can support some amphibian species during the egg, tadpole, and adult stages. Therefore, pasture matrix habitats contribute to regional frog diversity, perhaps most effectively when isolated trees and forested corridors along streams are present or near edges with intact forest (Mendenhall et al., 2014). However, for other species, behavioral, life history, or physiological limitations preclude their ability to survive in habitats that are modified. Use of the framework (Figure 1) helps to determine what specific life stages and traits of a species impact their ability to persist. Any single experiment on a particular life stage vastly oversimplifies how a species will respond to habitat conversion; however, the accumulation of multiple experiments and knowledge of the life history of species allows us to piece together a more comprehensive understanding of the occupancy of species in modified landscapes. Conservation managers can use this information to work with policy makers to improve existing land-use regulations and with land owners to educate about the importance of these regulations for maintaining amphibian diversity.

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