

Species Loss In Developed Landscapes: An Experimental Evaluation

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Abstract

Conversion of landscapes for human uses is widely associated with loss of biodiversity. Here we focus on limits to distribution defined by intensity of landscape development. Using a translocation experiment, we ask does degradation of wetland habitat contribute to species loss? Wood frog larvae (*Rana sylvatica* = *Lithobates sylvaticus*), were reared within enclosures in 7 ponds harboring populations of wood frogs and in 5 ponds where they are absent. Survival, growth rate, and development rate were equivalent between ‘present’ and ‘absent’ ponds. While it is clear that landscapes surrounding ‘absent’ ponds had been heavily influenced by human use, we find no evidence that such wetlands provide inferior habitat for wood frog recruitment. Their absence in human altered landscapes may stem from influences outside of pond basins. The results provide a caution to the typically unexamined presumption that relictual habitats in developed landscapes are degraded in their utility for wildlife.

Introduction

Residential development has been a major driver of landscape change in the United States. During the last half of the 20th Century, exurban development affected more than a quarter million ha per year, on average, and ranged as high as 800,000 ha per year [1]. Comparable patterns are emerging in other parts of the globe [e.g., 2]. Because of its widespread nature and the hypothesized influence on ecosystems, conservation biologists have closely studied the creation and influences of developed environments [e.g., 3, 4, 5]. Their efforts have

documented a highly repeatable pattern that transcends geography and taxonomy: the conversion of landscapes for human use has strong negative influences on native biodiversity [6, 7, 8, 9].

Most striking among these influences is the erosion of native biodiversity as homes, transportation networks, and commercial development fill an increasing fraction of the landscape. This effect is most often illustrated as a decline in species richness [8, 10, 11, 12, 13, 14]. But the less frequently estimated corollary is the decay in occupancy experienced by individual species [e.g., 15]. Occupancy studies reveal that, even when fragments of habitat remain, species are often unable to successfully exploit them. It is also clear from a small number of comparative studies that the estimated 'tolerance' of individual species for development differs. Threshold estimates for occupancy - the degree of development for which 50% of sites would be occupied - can vary substantially [15].

The mechanisms behind such widespread losses are a critical concern to conservation scientists [16]. Frequently cited causes include area effects as habitat is lost, isolation among remaining habitats, the influences of invasive species, and degradation of remaining habitat [8]. In spite of the regularity with which these mechanisms are discussed, at least one review [10] has noted that efforts to directly evaluate the roles of particular mechanisms are sparse. As an example, while it is straightforward to demonstrate that landscape conversion leads to increased isolation among remaining habitats [17], the degree to which isolation per se contributes to observed species losses is rarely evaluated. This lack of mechanistic understanding is a critical knowledge gap. As it stands, the broad gauge association between development and biodiversity has led to calls for halting certain forms of development [e.g., 18]. However, there is no sign that such statements have had a material influence on rates of landscape conversion since these have generally accelerated over time [1]. Scientists have had much less to contribute concerning

specific, empirically founded ways in which harms associated with development might be mitigated through alternative design of landscapes. We need to know more about how particular dimensions of development contribute to the loss of native species for this state of affairs to change.

Experimentation has been cited as a particular need in this realm, but the challenges to field experimentation are often exacerbated within human dominated landscapes [10]. Here we take advantage of a system that allows us to adopt an experimental approach to development associated species loss. We focus on a specific hypothesis: that landscape development leads to degradation of habitats in ways that reduce their utility to native species. Our study subject, the wood frog (*Rana sylvatica* = *Lithobates sylvaticus*), offers a typical example of a species that is highly successful in undeveloped landscapes (in fact, it is one of the most widely distributed vertebrate species) but is virtually absent in developed landscapes [12, 15].

Wetlands offer a particularly appropriate system to evaluate the habitat degradation hypothesis. In many contexts, destruction of freshwater wetlands is prohibited, and activities within and near wetland basins are closely regulated [19, 20]. In practice this means that many wetlands survive transition of the landscape from undeveloped to developed. But there are a variety of indications that development affects conditions within wetlands even when they have been saved by protective regulations [21]. Specifically, contamination, changes in vegetation, changes in light and temperature, increased nutrients, altered conductivity and pH, changes in hydroperiod are all documented influences of development [22, 23, 24, 25]. These findings have promoted a more general sense that wetlands in developed landscapes are compromised environments. Responding to this perception, government programs to rehabilitate wetlands in developed landscapes are premised on the need to improve habitat quality to support wildlife

species [e.g., 26]. For many taxa, including amphibians, it is unknown whether wetland habitat quality limits distributions in developed landscapes or whether interventions designed to improve quality increase population abundance or occupancy. As a test of the habitat quality hypothesis, we compared performance of wood frog larvae stocked into ponds within and beyond the species distributional limit defined by development intensity.

Methods

Our study was carried out in 12 freshwater ponds in southern Connecticut, USA. The ponds were located in the towns of Clinton (1), Madison (6), Milford (4) and Orange (1). Some of the Milford/Orange ponds were previously surveyed by James Gibbs during 1993 and 1994 [15]. The ponds, which are generally small in surface area and relatively shallow in maximum depth, were selected to represent two treatments defined by the location of study ponds relative to the distributional boundary of breeding by the wood frog. Present ponds ($n = 7$) were defined as those hosting breeding aggregations of wood frogs. Evidence for breeding was determined by the presence of rafts of wood frog eggs detected during visits timed during the breeding season or by the presence of larvae. Absent ponds ($n = 5$) showed no evidence of wood frog breeding. For the two site types (Present, Absent), we estimated landscape structure using the 2006 National Land Cover Database (NLCD2006) [27]. We estimated the proportion of the landscape within 200 m of the shoreline that was developed. We chose 200 m because it encapsulates typical movement distances for many terrestrial stage wood frogs [28]. We defined development as the fraction of the landscape within three NLCD2006 land cover classes: Developed, Low Intensity; Developed; Medium Intensity; and Developed High Intensity. These three land cover

classes are expected to include 20-49%, 50-79%, and 80-100% impervious surface, respectively. For all 12 study ponds, we compared differences in land cover and other pond attributes between ponds with (Present) and without (Absent) wood frogs.

Following previously developed methods for field experimentation [e.g., 29], in each pond we placed two enclosures in which larvae would be reared. Enclosures were constructed out of a 57 cm diameter cylinder of plastic coated garden fencing (91 cm high) which was placed inside of a sewn bag of fiberglass window screening. Prior to stocking larvae, we collected 10 liters of leaf substrate from the bottom of a given pond and placed it in the enclosure. We collected wood frog eggs from 4 different ponds and allowed them to hatch out in wading pools placed in an outdoor compound on the New Haven, Connecticut campus of Yale University. On 22 April 2013, we stocked 25 wood frog larvae (Gosner Stage 25, [30]) into each of the 24 enclosures. Larvae from different egg masses were assigned to enclosures haphazardly. On 5 June 2013, we took down the experiment when some individuals from each treatment began reaching metamorphosis (Gosner Stage 42). We recovered surviving individuals from each enclosure. Performance estimates included the proportion of individuals surviving (angular transformed), the final body size and progress toward metamorphosis (estimated as Gosner development stage). To estimate response for a pond, performance estimates from the two enclosures were averaged and represented as an individual estimate for each variable.

During the experiment, two of the ponds dried up prematurely. These ponds were excluded from analyses of wood frog responses. In 4 of the ponds, insect predators invaded one of the two replicate enclosures (and predators were recovered when the experiment was taken down). Survivorship was greatly reduced in predator-invaded enclosures. In each pond where predator invasion occurred in an enclosure, we based our performance estimate for the pond on

the noninvaded enclosure. In one additional pond, both enclosures were invaded by predators. This pond was also excluded from analyses of wood frog responses leaving a total of 5 Present ponds and 4 Absent ponds. Data used in the analyses are presented in Table S1.

The research reported here was carried out on private land with landowner permission. Our field research is covered under a permit issued by the Connecticut Department of Energy and Environmental Protection and was approved by the Yale Institutional Animal Care and Use Committee (Protocol #: 2013-10361).

Results

The proportion of the landscape within a 200 m buffer of ponds hosting breeding wood frogs (Present ponds) differed from landscapes around wood frog Absent ponds (t-test: $df = 10$, $t = 3.024$, $P = 0.013$). Landscapes surrounding Present ponds were predominantly forested, averaging just 27% developed. In spite of the prevalence of forest, just one of the Present ponds had no developed land cover within 200 m of the pond shoreline. By contrast, landscapes surrounding Absent ponds averaged 80% developed. Three Absent ponds were 100% developed within 200 m of the pond shoreline. We also assayed attributes of the ponds themselves on at least 5 dates during the experiment in each pond. Pond surface area averaged 821 square meters and depth averaged 34 cm during the experiment. Water temperature averaged 18.2 C, pH averaged 6.5, TDS averaged 256 ppm, conductivity averaged 327 uS/m, and DO averaged 4.3 mg/l. We compared responses from Present versus Absent ponds and found no difference for each variable (t-tests: $P > 0.17$ in all cases).

The performance of wood frogs within Present and Absent ponds was largely indistinguishable (MANOVA: Wilks' Lambda = 0.734; $F_{3,5} = 0.605$; $P = 0.640$). Examination of survival, development and growth of larvae revealed a similar pattern at the level of individual performance variables (ANOVAs: $P > 0.270$ in each case). In general, larvae performed well and survival was high, averaging 69%. Body sizes of larvae collected from enclosures were comparable to sizes of free living larvae collected from the same ponds at the same time; paired t-test: $df = 4$, $t = 0.266$, $P = 0.803$. Individuals from both treatments were recovered from enclosures entering metamorphosis (Gosner Stage 42 and higher, [30]).

Discussion

The loss of biodiversity in landscapes converted for human purposes is a widely documented pattern that has attracted hypotheses based on several different proposed mechanisms, but for which critical evaluations have been relatively rare [10]. One hypothesis is that species loss occurs due to degradation of remaining habitat [8, 31]. Freshwater wetlands offer an excellent opportunity to evaluate the degradation hypothesis since, in the United States and elsewhere, they are often protected from destruction during the conversion of landscapes for uses such as residential development. Despite existing research on the loss of wetland-dependent species [e.g., 12, 14, 15], the role of wetland degradation in these patterns remains poorly known. The lack of mechanistic understanding lies partly in the challenges of experimentation in human modified landscapes. Using an amphibian species with a distribution strongly limited by landscape conversion [12], we undertook a transplant experiment. Specifically, we asked whether conditions within extralimital wetlands contribute to the absence of wood frogs within

developed landscapes. Surprisingly, and in spite of substantial differences in surrounding landscape cover, there is no evidence that the performance of larval wood frogs is compromised by being reared in wetlands located in developed landscapes beyond the edge of their current distribution (as well as the distribution previously documented in 1993/4 for our Milford and Orange ponds [15]). The performance of wood frogs in ponds surrounded by contiguous forest was not generally distinguishable from performance in which the surrounding landscape was entirely developed.

These are remarkable findings: wetlands in heavily developed contexts may provide adequate environments to support larval recruitment of wetland-dependent species. On the one hand it suggests, at least for wood frogs, current wetland protection practices, which are sometimes described as being inadequate [e.g., 20, 21, 25], yield environments with functional attributes that may belie their often times degraded appearance. On the other hand, it can raise questions about the functional benefit of some wetland restoration practices focusing on mitigating basins of wetlands that appear degraded [e.g., 26]. Appearance and upland context may be inadequate to accurately assess functional qualities of small ponds. And there may be reason to conclude that even when degradation extends to influences such as wastewater contamination [e.g., 32, 33], populations may persist in spite of documented effects [34]. These are critical subjects for further research.

One obvious question highlighted by these results is: what limits wood frog distribution? There are multiple possibilities, and the design of this study supports only a limited capacity to assess alternatives. One prominent possibility is a lack of adult habitat. In the terrestrial environment, wood frogs appear to thrive in mature forest [35, 36]. This cover type is limited in extent or entirely missing within 200 m of many of our Absent ponds. The lack of nearby adult

habitat, or a habitat split, has been postulated as a cause for amphibian declines in other contexts [37]. It is a plausible hypothesis in this case of an otherwise widely distributed species as well.

A second, nonexclusive hypothesis is that developed land covers may compromise the ability of wood frogs to reach wetlands [38]. Even in cases where mature forest may be found not too distant from our study ponds, perhaps the intervening covers deter or prevent transit by dispersing wood frogs [39]. There is some evidence from landscape scale experiments [e.g., 40] that wood frogs tend to avoid crossing open landscapes and may be negatively affected by roads [41, 42, 43]. But overall, the use of developed landscapes by amphibians on the move remains relatively poorly understood. Both adult habitat and movement-based hypotheses will be challenging to evaluate in wood frogs and many other species. In addition to correlative assessments of existing landscapes [e.g., 44, 45], there remain opportunities to use planned developments to perform ‘experiments’ [e.g., 46, 47, 48] predicated on proposed best practices that emerge from primarily observational sources but which remain largely untested [e.g., 20]. Such projects will be challenging to carry out, but as the potential payoffs become clearer, the incentives to overcome the obstacles continue to grow.

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Author Contributions

Conceived and designed the study: AS, DKS, LKF. Carried out the experiment: AS, LKF, DKS.

Conducted Analyses: AS, DKS. Wrote the manuscript: DKS, AS, LKF.

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Figure Legends.

Figure 1. Landscape structure within a 200 m buffer surrounding the shorelines of 12 freshwater ponds. Ponds are divided into two site types defined by the presence or absence of the wood frog. Wood frog presence was indicated by eggs or larvae of the species. Landscape structure was measured as the proportion of the landscape under developed land covers (average plus 1 SE). Development was defined as the sum of three land cover classes from the 2006 Land Cover Database: Developed, Low Intensity; Developed, Medium Intensity; and Developed, High Intensity.

Figure 2. Survival, development, and growth of wood frog larvae. Individuals were reared in enclosures placed with ponds within (Present) and beyond (Absent) the development defined distributional limit for wood frogs. Larvae were reared from just after hatching until the most rapidly developing individuals in the experiment were reaching metamorphosis (6 weeks). Survival was estimated as the fraction of individuals recovered at the end of the experiment. Development rate was measured as final Gosner stage. All individuals were at Gosner Stage 25 at the beginning of the experiment. Growth was measured as the final snout vent length. All responses were represented as averages for each pond. Error bars represent 1 SE.



