

The University of Maine DigitalCommons@UMaine

Publications

Senator George J. Mitchell Center for Sustainability
Solutions

2012

The role of forest harvesting and subsequent vegetative regrowth

Viorel D. Popsedu
University of Maine

David A. Patrick
Paul Smith's College

Malcolm L. Hunter Jr.
University of Maine, mhunter@maine.edu

Aram J K Calhoun
University of Maine, Calhoun@maine.edu

Follow this and additional works at: https://digitalcommons.library.umaine.edu/mitchellcenter_pubs

 Part of the [Forest Management Commons](#), [Terrestrial and Aquatic Ecology Commons](#), and the [Zoology Commons](#)

Repository Citation

Popsedu, Viorel D.; Patrick, David A.; Hunter Jr., Malcolm L.; and Calhoun, Aram J K, "The role of forest harvesting and subsequent vegetative regrowth" (2012). *Publications*. 22.
https://digitalcommons.library.umaine.edu/mitchellcenter_pubs/22

This Article is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Publications by an authorized administrator of DigitalCommons@UMaine. For more information, please contact um.library.technical.services@maine.edu.

**The role of forest harvesting and subsequent vegetative regrowth in determining
patterns of amphibian habitat use**

Viorel D. Popescu ^{a,*}, David A. Patrick ^b, Malcolm L. Hunter Jr. ^a, Aram J.K. Calhoun ^a

^a University of Maine, Department of Wildlife Ecology, 5755 Nutting Hall, Orono, ME 04469, USA

^b Paul Smith's College, School of Natural Resources, Routes 86 & 30 Paul Smith's, NY 12970, USA

Abstract

Introduction

Methods

Results

Discussion

Acknowledgements

References

Figures

Abstract

Conservation of forest-dependent amphibians is dependent on finding a balance between timber management and species' habitat requirements. To examine the effect of short-term vegetative regrowth post-harvesting on amphibian habitat use, we studied the response of eight species (four forest specialists and four habitat generalists) to four forestry treatments (partial harvest, clearcut with coarse woody debris [CWD] removed, clearcut with CWD retained, and uncut control) over a 6-year period, using replicated experimental treatments in Maine, USA. Forest amphibians showed a strong negative response to clearcutting through the duration of the study, regardless of the presence of CWD, but only during the post-breeding season (i.e., summer). The spring breeding migrations of wood frogs and spotted salamanders to experimental pools were not affected by the forestry treatments. The use of partial cut treatments by forest amphibians differed between animals emerging from experimental pools (i.e., juvenile wood frogs and spotted salamanders), and animals originating from outside the experimental arrays (i.e., adults of all forest species, juvenile wood frogs and spotted salamanders). Animals emerging from our experimental pools showed no difference in the use of control and partial cut treatments, while all the other animals preferred control plots. In addition, we found a modest increase in the use of clearcuts over the 6 years following harvesting by juvenile wood frogs from experimental pools (from an 8-fold difference between forest and clearcut treatments in the first year post-clearcutting to a 3-fold difference during years 3–5). However, this increase was not significantly associated with vegetation regrowth. Forest specialists declined in abundance in all treatments beginning 2–3 years post-disturbance. Despite high yearly fluctuations in abundance, there was a shift in relative abundance towards habitat generalist species, most notably green frog juveniles. Most habitat generalist species were not affected by clearcutting or vegetative regrowth; however, we observed a lower use of clearcut treatments by green frogs starting 3 years post-harvesting, perhaps due to an increase in habitat resistance to movements associated with vegetative regrowth. These

general patterns of habitat use were overridden at the local scale by site-specific variation in the use of forestry treatments, most evident in emigrating juvenile wood frogs. From a management standpoint, implementing broad silvicultural prescriptions could be a viable strategy in extensively forested landscapes, but local variation in habitat use has to be acknowledged when managers focus on a limited area.

Introduction

Understanding the effects of forestry practices on amphibian populations has been of particular interest to forest managers and conservationists in the past two decades. This attention is a result of the known sensitivity of forest-dependent amphibian species to habitat change (Homan et al., 2004), and a move towards integrating timber management with the conservation of biodiversity (Lindenmayer, 2009; Hunter and Schmiegelow, 2011). In particular, complete canopy removal (i.e., clearcutting) has been shown to have long-term negative effects on amphibian abundance, with some populations reaching pre-disturbance levels two to seven decades post-harvesting (Pouch et al., 1987; Petranka et al., 1993; Ash, 1997; Homyack and Haas, 2009). Hence, our ability to predict responses of amphibian populations to forest harvesting is highly dependent on species-specific life strategies, as well as the temporal and spatial extent of studies.

Quantifying the effects of forestry practices on patterns of occurrence and abundance is particularly challenging for amphibians due to their complex life cycles, where different life-history stages may occur in disjunct habitats and function at different spatial scales (Cushman, 2006). Specifically for pond-breeding amphibians, long-term population persistence is dependent on the conservation of both aquatic and terrestrial environments (Semlitsch, 1998; Gibbons, 2003). The population dynamics of these species are driven by natural and human-induced disturbance manifested in both environments and across all life stages (Sjögren, 1991). The aquatic stages (eggs and larvae) are affected by within-pond factors, such as variable hydroperiod, predation, and larval density-dependence (Vonesh and De la Cruz, 2002; Altwegg, 2003). These factors also affect the terrestrial stage through carryover effects (Chelgren et al., 2006). The patterns of occurrence and abundance in the terrestrial environment are further influenced by habitat quality, predation, and terrestrial density-dependence (Altwegg, 2003; Harper and Semlitsch, 2007). The net result of aquatic and terrestrial factors acting synergistically is high species turnover in amphibian communities (Werner et al., 2007). In addition, species with different life-history traits (e.g., forest specialists

versus habitat generalists, or anurans versus salamanders) are likely to respond differently to forestry practices. As such, in order to understand commonalities and differences among species and to provide general management guidelines for amphibian conservation it is critical to monitor the full amphibian assemblage.

Most researchers who have investigated the timeframe for population recovery post-logging have used short-duration studies that compare spatially-replicated chrono-sequences of stands spanning decades (e.g., Petranka et al., 1993; Ashton et al., 2006; Welsh et al., 2008). While such studies can detect the long-term effects of forestry practices, as well as potential ecological thresholds for population recovery (Huggett, 2005), they offer little insight as to how disturbance affects local populations. Moreover, the natural background fluctuations in abundance typical of amphibian populations (Marsh, 2001) are not well incorporated using short-term studies, and might mask the influence of disturbance and vegetation regrowth (Kroll, 2009). For a better understanding of population responses to forestry practices it is important to monitor the patterns of habitat use using a longitudinal approach, where the same populations are sampled in consecutive years. Such studies, even if conducted across a single or few populations, provide critical information allowing differentiation between natural variation and human-induced disturbance (Berven, 2009). Furthermore, such studies should be able to capture fine-scale responses to vegetative regrowth not evident from coarse-scale studies (e.g., seasonal use, emigration and dispersal movements), and better account for the natural stochasticity of amphibian populations.

In this paper we report on a detailed experimental investigation of the effects of disturbance caused by partial and complete canopy removal and successive vegetation regrowth on habitat use of a 14-species North American amphibian assemblage for a period of 6 years (2004–2009). Although this is a rather short-term study from a forest management standpoint, it is nonetheless useful for understanding changes in population structure and for interpreting short-term behavioral responses to disturbance and vegetative succession. The strongest effects of logging disturbance on amphibian

habitat use is likely to occur within the first 5 years due to harsh microclimatic conditions associated with canopy removal and associated edge effects (Keenan and Kimmins, 1993). Furthermore, in our study area (i.e., the Acadian Forest of northeastern North America) changes in stand structure are rapid following a wide variety of silvicultural disturbances that reduce canopy cover (Saunders and Wagner, 2008). Thus a longitudinal approach replicated across multiple sites will detect seasonal and site-specific variation in habitat use, as well as changes in habitat use associated with vegetative regrowth.

This study allowed us to test a number of specific and highly relevant hypotheses linking the responses of amphibian communities to forest harvesting. Specifically, we hypothesized that the use of clearcuts and partial harvests by forest specialists would be reduced compared to the uncut forest, while habitat generalists would not be affected by the forestry treatments. This difference would result in a shift in species richness and relative abundance from forest specialists to habitat generalists. For forest specialists, which are known to be highly sensitive to water loss (Schmid, 1965; Rittenhouse and Semlitsch, 2009), we also hypothesized that the effects of canopy removal would be most evident during physiologically limiting periods (i.e., summer). We further hypothesized that because of the moist climate and the rapid vegetation regrowth following canopy removal specific to our study area (Saunders and Wagner, 2008), vegetative regrowth over 6 years would have a positive effect on clearcut habitat use by forest specialists.

Methods

Study sites

This research was part of the NSF project “Land-use Effects on Amphibian Populations” (LEAP), a collaborative investigation of amphibian community responses to forestry practices among the University of Maine, University of Missouri – Columbia, and University of Georgia (Semlitsch et al., 2009). This study uses a 6-year dataset; data from years 1–3 were partly published in Patrick et al. (2006) and Patrick et al. (2008a,b).

Our study was conducted on the Penobscot and Dwight B. Demeritt Experimental Forests, Penobscot County, Maine. Four replications of four forestry treatments – partial cut (50% canopy removed), clearcut with coarse woody debris (CWD) retained, clearcut with CWD removed, and control (not harvested) – centered on a breeding pool, were created between November 2003 and April 2004. The pools were constructed using an excavator in naturally occurring forested wetlands to provide wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*) with breeding sites with a suitable hydroperiod to insure recruitment of juveniles. As such, none of the experimental pools dried between April to September during the study period, which is the period between egg-laying by both species and spotted salamander juvenile emergence (wood frog juveniles emerge as early as July). One site was a natural vernal pool where low numbers of wood frogs and spotted salamanders were recorded breeding prior to excavation. The other three had no previous amphibian breeding detected and had a short hydroperiod (1–2 months) prior to enlargement (Patrick et al., 2006). The treatments extended up to 164 m from the pool, a distance assumed to include the life zone of 95% of the local salamander populations (Semlitsch, 1998), and thus each quadrant covered approximately 2.1 ha (Fig. 1). In the clearcuts, all marketable timber was removed, and the remaining standing trees were felled and left on site (in the CWD retained treatment) or removed (in the CWD removed treatment). The volume of coarse woody debris was highest in the CWD-retained treatment ($45.6 \pm 21.6 \text{ m}^3/\text{ha}$ [mean \pm 1 SE]; Patrick et al., 2006). The orientation of treatments with respect to cardinal directions was randomly assigned among sites. However, at all sites the forested treatments (and consequently the clearcut treatments) were opposite of each other (Fig. 1). The pre-treatment vegetation of the experimental forests was mature mixed coniferous and deciduous forest (Patrick et al., 2006). The codominant tree species were balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), northern white-cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), paper birch (*Betula papyrifera*), American beech (*Fagus grandifolia*), and bigtooth aspen (*Populus grandidentata*). Canopy cover amounted to $73.8 \pm 22.7\%$

[mean \pm 1 SE] in control and $53.0 \pm 33.5\%$ in the partial harvest (Patrick et al., 2006). The experimental pools were completely encircled by drift fence (70 cm tall and 30 cm buried in the ground) with pitfall traps located every 5 m on both sides along the fence (at each pool, there were at least three pitfall traps associated with each forestry treatment). The pool fences were located 1–2 m from the pool edge. Upland drift fences (10-m long) were also erected at 16.6, 50, 100, and 150 m (1, 3, 6, and 9 fences, respectively) from the experimental pool in each treatment, in a circular setup that allowed sampling approximately 38% of the circumference at each distance. Four pitfall traps were associated with each upland drift fence: one at each end, and two in the middle, one on each side of the fence (Fig. 1).

Study species

Fourteen species have been documented at our study sites (Patrick et al., 2006). These include two forest amphibians that successfully bred in the experimental pools – wood frog (*L. sylvaticus*) and spotted salamander (*A. maculatum*) – and were the most abundant at our experimental sites. Other forest specialist species, whose population persistence depends on contiguous closed-canopy habitat (Gibbs, 1998a) with sufficient captures to analyze the effects of forestry practices on habitat use included the red-backed salamander (*Plethodon cinereus*), and the eastern red-spotted newt (*Notophthalmus viridescens*). Habitat generalist species (i.e., species that do not show a strong affinity to a particular vegetation type) with sufficient captures were represented by four anurans: green frog (*Lithobates clamitans*), bullfrog (*Lithobates catesbeianus*), northern leopard frog (*Lithobates pipiens*), and pickerel frog (*Lithobates palustris*).

Other amphibians detected at our sites either had very low captures: blue-spotted salamander (*Ambystoma laterale complex*), American toad (*Anaxyrus americanus*), mink frog (*Lithobates septentrionalis*), and four-toed salamander (*Hemidactylium scutatum*), or were not suitable for pitfall trap

sampling: spring peeper (*Pseudacris crucifer*) and gray tree frog (*Hyla versicolor*) (whose adhesive toe pads allowed them to escape from pitfall traps). These species were not included in the analysis.

Amphibian and habitat sampling

We sampled amphibians between 2004 and 2009, during two distinct periods: April–May (breeding season of *L. sylvaticus* and *A. maculatum*) and June – August/September (post-breeding and juvenile emergence and emigration). We captured adult *L. sylvaticus* and *A. maculatum* as they entered the four experimental pools to breed in early spring (13 April–4 May 2005, 2–20 April 2006, 16 April–3 May 2007, 12–30 April 2008, and 8–27 April 2009). During this period, we opened the traps associated with the pool fence located on the outside of the fence, as well as the 16.6 and 50 m fences to capture the entire breeding population. Animals captured at the 16.6 and 50 m fences were released at the experimental pools. We did not attempt to capture breeding adults in 2004, as the experimental pools were stocked with egg masses from surrounding pools during the first year. We closed the traps at the end of the breeding season (May). We re-opened all traps associated with the upland drift fences, as well as the pool fence traps (located on the inside of the pool fence) at each site before the onset of juvenile *L. sylvaticus* emergence (late June–early July). We continued sampling until the fall to encompass the emergence and emigration season of juvenile *L. sylvaticus* and *A. maculatum*. During this sampling window we also captured individuals of all the other members of the amphibian assemblage foraging or migrating through the experimental sites. Logistical and weather constraints led to different sampling periods each year, but we incorporated the yearly trapping effort into our analyses (1 July– 27 October 2004, 24 June–17 September 2005, 30 June–20 August 2006, 1 July–12 September 2007, 30 June–15 September 2008, and 30 June–28 August 2009).

We checked the traps every other day during both the breeding and the non-breeding seasons. We released the animals on the opposite side of the fences so they could continue migrating or dispersing in their presumed direction of movement. Upon capture at the pool fence, juvenile *L.*

sylvaticus emerging from the experimental pools were marked using a combination of Visible Implant Elastomer (VIE, Northwest Marine Technologies, Shaw Island, WA, USA) and toe clip (2004), or a single toe clip (2005–2009). Individuals recaptured at terrestrial fences were remarked using VIE (2005–2006), or Visible Implant Alpha Tags (VIAT, Northwest Marine Technologies) (2007–2009). Juvenile spotted salamanders were marked at the pool fence using VIE indicating the treatments they entered in 2004–2006 (limited or no recruitment occurred during 2007–2009).

We conducted repeated habitat sampling in August 2004, 2005, 2006, and 2008. Sampling was based on 96 9-m² permanent plots equally distributed among treatments and sites. The sampling plots were located approximately 25 m from equally-spaced selected drift fences (three 150-m fences, two 100-m fences, and one 50-m fence in each treatment) in the direction of the pool. Each occasion, we sampled percent vegetation cover in four height classes (0–0.5, 0.5–1, 1–2, and >2 m) and dominant species composition, percent leaf litter cover and leaf litter depth, and percent canopy cover (using a Moosehorn densitometer, Moosehorn Cover-Scopes, Medford OR, USA).

Predicting the effects of canopy removal and vegetative regrowth

We assessed the effects of disturbance created by forestry practices on the spatial and temporal dynamics of the amphibian habitat use generalized linear mixed effects (GLME) models (Pinheiro and Bates, 2000). We analyzed three groups of animals separately: (1) breeding adults *L. sylvaticus* and *A. maculatum* captured as they entered the experimental pools in early spring; (2) juveniles *L. sylvaticus* and *A. maculatum* originating from our experimental pools; and (3) all other amphibians captured in the upland during foraging or migration. The latter category comprised all animals captured during the summer/fall sampling window, including *L. sylvaticus* and *A. maculatum* juveniles originating from pools outside our experimental arrays.

For model fitting and model selection we followed the procedure recommended by Zuur et al. (2009). We started with a full fixed-effects model, fitted various random effects to find the optimal

structure of the random component, and used AIC to compare among the models and select the optimal random structure. Fitted models had different fixed effects and the optimal random structure, and we used AICc and likelihood ratio tests to compare between competing models (Burnham and Anderson, 2002; Royle and Dorazio, 2008).

We tested our ability to predict the use of forestry treatments by amphibians across spatial scales as well as changes in habitat use due to vegetative succession by fitting three models for each event, species, and life stage. The abundance and distribution of amphibians as a response to disturbance was investigated by examining: (1) the overall effect of forestry treatments (treatment only as fixed effect), (2) the between-sites spatial variability (treatment x site interaction as fixed effect), and (3) the between-years variability (treatment x year interaction as a fixed effect). For emigrating *L. sylvaticus* juveniles we also included the interaction term treatment x distance from natal pool (i.e., 16, 50, 100, and 150 m) as fixed effect to assess within-treatment variability in habitat use. The optimal random structure for all models (Zuur et al., 2009) was a nested random intercept (separate intercepts for year and site within year). We used Treatment contrasts using the forested control as the reference treatment to investigate differences among treatments. We used ANOVAs to test for the significance of the fixed-effect interaction terms in models that contained such terms. All analyses were conducted in R version 2.9.2 (R Development Core Team, 2009).

Because the spatial and temporal extent of amphibian sampling varied among years, we used different dependent variables that incorporated the sampling effort for each life stage that we investigated using GLME's. For breeding adults we used the mean number of captures per trap per treatment per year as our dependent variable to account for the slightly different number of traps within each treatment and site. For emigrating juveniles, we assessed the effects of forestry treatments on the emergence of newly metamorphosed *L. sylvaticus* and *A. maculatum* by using the mean number of captures per trap at the pool-encircling fence as the dependent variable. Juvenile recruitment was characterized by high variability in both total number and number of pools producing individuals.

Recruitment failure occurred for both *L. sylvaticus* and *A. maculatum* at several pools throughout the study (*L. sylvaticus*: one pool in 2008, and three pools in 2007 and 2009; *A. maculatum*: one pool in 2005 and 2008, and three pools in 2009 failed to produce juveniles). We then used the raw number of animals recaptured at the upland terrestrial fences as the dependent variable to investigate the effects of forestry treatments on emigration movements. Only five juvenile *A. maculatum* were recaptured during 2007–2009 at all sites, and the 2004–2006 data were too sparse to fit a reliable model. For post-breeding *L. sylvaticus* and *A. maculatum* adults, juvenile *L. sylvaticus* and *A. maculatum* emerging from pools outside the experimental arrays, as well as for the other species composing the amphibian community that used the experimental sites for foraging or migration movements, we used the average number of captures per day as our dependent variable to account for the differences in trapping effort among years. We fitted different mixed effects models for adult and juvenile *L. sylvaticus*, adult and juvenile *A. maculatum*, juvenile *L. clamitans*, juvenile *L. catesbeianus*, and combined (juveniles and adults) *L. pipiens*, *L. palustris*, *P. cinereus*, and *N. viridescens*. For models assuming a Gaussian distribution (all except for the model investigating the effects of treatments on *L. sylvaticus* juveniles emerging from experimental pools, which assumed a Poisson distribution), the response variable was transformed via $[\log(X + 1)]$ or $[\text{sqrt}(X)]$ transformations to achieve normality (assessed using the Shapiro–Wilk test).

We assessed the effect of vegetation regrowth on the use of clearcuts by juvenile *L. sylvaticus* originating from our pools as well as from outside the experimental arrays, as well as adult *L. sylvaticus*, and juvenile *L. clamitans*. These species and life-stages comprised the bulk of all amphibian captures in the years that we conducted habitat sampling: 2004, 2005, 2006, and 2008. We fitted quasibinomial generalized linear models that adjust for data over-dispersion (McCullagh and Nelder, 1989) using the proportion of individuals captured in clearcut treatments per site and year as the dependent variable, and percent vegetation cover 0.5–1 m in height, site, and the interaction of the two as predictor variables. We only used the 0.5–1 m vegetation class because the three vegetation

height classes sampled each year – 0–0.5, 0.5–1, and 1–2 m – were highly correlated (Pearson correlation coefficient >0.8), and the 0.5–1 m class exhibited the greatest temporal variation during the study.

Results

Differential use of forestry treatments by forest specialists and habitat generalists

We captured 26,374 post-breeding adults, as well as juvenile amphibians originating from pools outside our experimental arrays between 2004 and 2009 (Table 1). Of these, 91% (24,015 individuals) were juveniles, and 54% of juveniles (12,884 individuals) were *L. sylvaticus*. The number of species recorded varied between 14 in 2005 and five in 2009 (Table 1).

All forest specialist species (i.e., *L. sylvaticus*, *A. maculatum*, *N. viridescens*, and *P. cinereus*) were affected by the forestry treatments throughout the duration of this study (Tables 2 and 3). The former two species showed decreased abundance in all forestry treatments, most notably in the two clearcut treatments, while the later two responded in a negative manner to the clearcut treatments only (Fig. 2, Table 3). Habitat generalists (i.e., *L. clamitans*, *L. catesbeianus*, *L. pipiens*, and *L. palustris*) were not affected by the forestry treatment, showing only a slight avoidance of one clearcut type or another (Fig. 2, Table 3).

For most species, there were strong yearly and site-specific demographic fluctuations, with juveniles of three forest-dependent species, *L. sylvaticus*, *A. maculatum*, and *P. cinereus* experiencing the greatest variation across the study period (Table 1). Overall, the number of captures for forest specialists declined after the first 2–3 years of the study across all treatments, and the decline was related to time-since-harvest. *P. cinereus* virtually disappeared from the clearcut treatments by the second year post-harvest and only five captures were recorded between 2006 and 2009 in these treatments (Table 1). In contrast, the proportion of juvenile *L. clamitans* using the forested treatments

increased post-harvesting, especially in the uncut control, which accounted for approximately 50% of the total captures in 2009 (Fig. 2).

Seasonal differences in use of forestry treatments by forest specialists

Adult breeding migrations – we captured 1278 adult *A. maculatum* and 1176 adult *L. sylvaticus* entering the experimental pools for breeding during the study. There was variability among sites with respect to the use of treatments during breeding migrations for both species (treatment x site ANOVA; $F_{9,30} = 2.517$, p -value = 0.028 for *L. sylvaticus*, and $F_{9,30} = 2.464$, p -value = 0.030 for *A. maculatum*), but no differences among the forestry treatments (Table 3). There were no differences among years in the use of treatments, suggesting no effects of forest succession on breeding migration (treatment x year ANOVA; p -value >0.5).

Juvenile migrations – we captured 14,066 juvenile *L. sylvaticus* and 1521 juvenile *A. maculatum* emerging from the experimental pools between 2004 and 2009 (Table 4). Newly metamorphosed *L. sylvaticus* did not show a preference for forested or clearcut treatments at the fences encircling the pools, while *A. maculatum* showed a slight preference for the CWD retained treatment (Table 3). However, there were site-specific differences for emerging *L. sylvaticus*, as shown by a significant treatment x site interaction ($F_{9,39} = 3.280$, p -value = 0.005), but the model had a low level of support ($w = 0.01$, Table 2). We found no effect of vegetation regrowth on the choice of forestry treatments for either species upon exiting the natal pools (treatment x year ANOVA, p -values >0.15).

We recaptured 1993 *L. sylvaticus* (14.2% of the total number of *L. sylvaticus* emerging from the experimental pools) and 87 *A. maculatum* (5.8% of the total individuals emerging) in the upland habitat (Table 4). In the upland, the frequency of *L. sylvaticus* recaptures was strongly biased towards the forested treatments (Table 3), and did not vary temporally (treatment x year ANOVA, $F_{9,30} = 0.615$, p -value = 0.774). Across all sites, *L. sylvaticus* showed no difference in use between the control and partial cut, or between the CWD-removed and the CWD-retained treatments (Fig. 3). However,

there was strong site-specific variability in the use of upland forestry treatments (treatment x site ANOVA, $F_{9,30} = 2.517$, p -value = 0.028; Table 2), which was maintained across years (Fig. 4). Along with the strong preference for forested treatments, animals that entered each treatment maintained their direction of movement (model treatment x distance had the lowest level of support, $w = 0$, Table 2). By examining the interaction plot between the mean proportion of recaptures (pooled across sites), treatment, and year (Fig. 3), we found a slight, non-significant trend toward an increasing proportion of *L. sylvaticus* individuals captured in clearcut treatments in later years. During the first year, the difference between the use of forests and clearcuts expressed as proportion of captures was approximately eight-fold (forest: clearcut = 0.89:0.11). This difference decreased to 3.3-fold by the third year (0.77:0.23), and it was maintained during the fifth year post harvesting.

Effects of vegetative regrowth on habitat use

Vegetation regrowth during the study period resulted in rapid changes in vegetation structure and composition, especially in the clearcut treatments. Due to specific regeneration processes of early-successional tree species (root suckers versus stump sprouts), micro-topography, existing dormant seed banks, and retained advance regeneration, and there was high heterogeneity within and between experimental arrays. Overall, there was an increasing trend in percent cover in vegetation strata 1–2 m and >2 m in height (Fig. 5), with the latter covering approximately 23% of the clearcuts 5 years post-disturbance. Low regeneration (up to 1 m) consisted mainly of pioneer species such as *Rubus* spp. (which in some cases formed continuous patches), and gray birch (*Betula populifolia*) and covered >50% of clearcuts in 2008 (Fig. 5). Tall regeneration (which in some cases reached >4 m in 2008) was dominated by bigtooth aspen (*P. grandidentata*) and red maple (*A. rubrum*).

These significant changes in vegetation structure were not associated with higher use of clearcuts over time by either juvenile or adult *L. sylvaticus*. The percent vegetation 0.5–1 m in height was a poor predictor of clearcut habitat use by emigrating juveniles (quasibinomial GLM, $t_{31} = -0.152$,

p -value = 0.88) and post-breeding adults ($t_{31} = -1.002$, p -value = 0.32). Juvenile *L. clamitans* showed a negative response to the increase in vegetative cover 0.5–1 m in height ($t_{31} = -2.889$, p -value = 0.007), which resulted in higher use of forested treatments during the last 4 years of the study (Fig. 2c).

Discussion

The coarse effects of various silvicultural practices on amphibian populations are relatively well understood, with physiological and behavioral mechanisms driving patterns of abundance and distribution for 2–3 years post-harvesting (Patrick et al., 2006; Semlitsch et al., 2009; Todd et al., 2009). Less emphasis has been placed on understanding whether or not these general patterns remain consistent during vegetative regrowth after disturbance. Also, we know little about the variability in habitat use manifested at the local (site) scale. Both of these issues can be addressed in a longitudinal study like this one which covered 6 years.

Effects of forestry treatment on forest specialist and habitat generalist amphibians

In agreement with existing research, strong negative responses to clearcutting (i.e., avoidance, low abundance) were the norm for forest specialist amphibians across all experimental sites for up to 6 years post-disturbance (Fig. 2). Another general pattern was the similar use of clearcuts with and without CWD, suggesting that in our region CWD does not play a role in mitigating the effects of clearcutting for forest amphibians. Understanding the use of partial cuts was complicated because we had two sets of animals: (1) foraging adults and juveniles originating from pools outside the experimental arrays, and (2) juveniles emerging from experimental pools. Animals from the first category used the partial cuts less compared to the uncut controls (Fig. 2a, b, e, i). In contrast, juveniles emerging from the experimental pools used both forested treatments (partial cut and control) in a similar manner, despite site-specific variation (Figs. 3 and 4). One potential explanation for this difference may be that foraging adults and juveniles originating from outside the arrays were better able to assess lower quality habitat and avoid it. Avoidance behavior was found to drive habitat use in

juvenile wood frogs and spotted salamanders (Semlitsch et al., 2008; Todd et al., 2009; Popescu and Hunter, 2011). By comparison, juvenile wood frogs showed randomness upon exiting the experimental pools (Table 3), perhaps because the drift fence interfered with their perception of the surrounding habitat. After clearing the pool fence, they migrated mainly through either of the forested habitats, resulting in similar proportions of animals using either the control or the partial cut treatments (Fig. 3).

These patterns were further complicated by high site-specific variability in habitat use (significant treatment x site interactions for most species, life stages, Table 2). For example, juvenile *L. sylvaticus* emigrating from the experimental pools showed a pattern of use of forested treatments (control plus partial harvests) that varied from site to site, but the site-specific differences were maintained across all study years. At one site juveniles moved preferentially through the partial cut, at another site through the control, while at another site the number of captures was roughly equal between the two forested treatments (Fig. 4). The consistency of these patterns across years clearly demonstrates that broad generalizations on habitat use by forest amphibians are not consistent across spatial scales, and that site-specific variation plays an important role in modifying the general patterns of habitat use by local populations.

Habitat generalist species were less influenced by the forestry treatments or even showed an increase in abundance (Fig. 2). The increased abundance of one generalist species, *L. clamitans*, was an expected outcome of this study. Disturbance creates heterogeneous landscapes that tend to favor generalist species, while negatively affecting specialist species (Lemckert, 1999). Although we expected an increase in abundance of other generalist species (i.e., *L. pipiens* and *L. palustris*) no obvious trends were observed during the study. These species were instead characterized by high yearly fluctuations, but overall lower number of captures (compared to *L. clamitans*) (Table 1).

In contrast, the number of adult and juvenile *L. sylvaticus*, *A. maculatum*, *P. cinereus*, and *N. viridescens* captured in both the forested and clearcut treatments declined during the study period (Table 1), indicating a potential decrease in habitat quality across all silvicultural treatments due to edge effects. All these species are known to avoid abrupt forest edges during emigration movements (Ash, 1997; deMaynadier and Hunter, 1998; Gibbs, 1998b; Rothermel and Semlitch, 2002; Popescu and Hunter, 2011). If we conservatively consider an edge effect depth of 30 m (deMaynadier and Hunter, 1998), then almost half of the forested treatments fall outside what we might consider good quality habitat for forest specialist amphibians. In the absence of control sites with no logging at all we cannot exclude the possibility that the observed declines of forest specialists were driven by other factors, such as short-term extreme climatic events that affected the overall local population. However, the years with lower abundance of juvenile *L. sylvaticus* and *A. maculatum*, 2007–2009, did not have adverse climate conditions (i.e., unusually hot and/or dry) from May–August: 2007 was cooler, but drier than normal; 2008 fluctuated above and below normal for both precipitation levels and temperature but overall was relatively cooler and wetter; while 2009 was both cooler and wetter than normal (www.ncdc.noaa.gov). Temperatures >30 °C, which are considered as potentially lethal for ranid frogs (Rome et al., 1992), were rarely recorded in the clearcuts (Popescu and Hunter, 2011; V.D. Popescu, unpubl. data).

Seasonal and ontogenetic differences in use of forest treatments

The spring migrations of adult *L. sylvaticus* and *A. maculatum* towards breeding pools were not influenced by clearcutting (Table 3), and pool colonization occurred rapidly (within the first year post-logging). This suggests that both species are abundant in the area of study, and that the degree of philopatry might not be as high as in other regions of the species' ranges (Patrick et al., 2008b). During the post-breeding season, all forest specialists (i.e., post-breeding adults and emigrating juveniles) preferred closed-canopy habitats over clearcuts (with uncut control being used more than the partial cut), which corroborates findings of Todd et al. (2009) in a similar experimental setting. In

contrast to their preferential use of closed-canopy habitat during emigration movements, juvenile *L. sylvaticus* and *A. maculatum* exited the natal pools in random directions during the 6 years of the study (Table 3). Given the narrow field of perception of juvenile amphibians and reliance on proximate cues for orientation (Rothermel, 2004; Popescu and Hunter, 2011), we would expect random orientation when environmental cues are not very strong (i.e., our treatments converged towards the pool, masking the transition between the forested and clearcut treatments, and the pool was completely surrounded by drift fence), but non-random habitat use when prominent habitat features, such as sharp forest edges, intercept the movement paths (Gibbs, 1998b).

Effects of short-term vegetative regrowth on habitat use

The deleterious effects of clearcutting are mitigated by vegetative regrowth, with mature, closed-canopy stands providing suitable habitats for population recovery (Herbeck and Larsen, 1999; Welsh et al., 2008). Our findings of decreased abundance of forest amphibians for up to 6 years post-clearcutting are not surprising, and corroborate the majority of the research investigating the relation between timber harvesting and amphibian conservation (reviewed by deMaynadier and Hunter, 1995). However, the effects of clearcutting and early vegetative regrowth on amphibian habitat use, abundance, and vital rates are controversial, and comparisons among studies, regions, and species are complicated by the different spatial and temporal scales, experimental design, landscape context, and disturbance history (Kroll, 2009), as well as interspecific, seasonal, and ontogenetic differences in habitat use. For example, Chazal and Niewiarowski (1998) showed that body condition of newly metamorphosed forest-dwelling mole salamanders (*Ambystoma talpoideum*) in terrestrial enclosures was not affected by recent clearcuts. In contrast, Todd and Rothermel (2006) found that survival and growth rates in juvenile southern toads (*Anaxyrus terrestris*), a generalist species, were reduced in enclosures located in clearcuts compared to mature forests. At the same experimental sites as ours, Patrick et al. (2008a) showed that survival of juvenile *L. sylvaticus* in shaded terrestrial enclosures located in recent clearcuts (mimicking low shade) was higher than in compartments lacking shade.

This is a clear indication that in our landscape short-term vegetation regrowth, which in our case was substantial (Fig. 5), provides suitable microclimate conditions for amphibian use during the warmest part of the year. However, the general preference for closed-canopy habitat by all forest amphibians was maintained throughout the 6 years of study, suggesting that the potential positive effects of vegetative regrowth (notably in the 0.5–1 m stratum) were overridden by other factors (i.e., lack of canopy cover). This is consistent with another study in our landscape in which clearcutting affected the permeability to movements of juvenile *L. sylvaticus* for up to 10–20 years (Popescu and Hunter, 2011). Despite not being strongly associated with time since clearcutting, the subtle increase in clearcut use by emigrating *L. sylvaticus* (Fig. 3) might still be important from a population connectivity standpoint. Clearcuts are not complete barriers to movements of juvenile forest amphibians (Rothermel and Semlitsch, 2002; Rothermel, 2004; Popescu and Hunter, 2011), and any increase in emigration and dispersal success might potentially be translated into increased gene flow and connectivity between populations.

In contrast to forest specialists, vegetative regrowth negatively affected the proportion of juvenile *L. clamitans* using the clearcut treatments. As a habitat generalist, *L. clamitans* is known to use open habitats during upland movements (Birchfield and Deters, 2005), and the potential increase in vegetative cover and associated stem density might have hindered the movements. As such, movements were conversely facilitated in the forested treatments, which lacked abundant understory regeneration (Fig. 5).

Management and conservation implications

While the ultimate goal of studies such as ours is to provide management prescriptions that meet both silvicultural objectives and the conservation of forest amphibians, broad generalizations (e.g., Semlitsch et al., 2009) may not be universally applicable. Prescriptions such as retaining a certain amount of canopy (deMaynadier and Houlahan, 2008), protecting upland habitat in the proximity of

breeding pools (Calhoun and deMaynadier, 2004), or minimizing disturbance by concentrating harvesting to small-size clearcuts (Knapp et al., 2003) are likely to be widely applicable in large forested landscapes (e.g., industrial forests where a range of different-aged stands of various structures and spatial configurations are available at any point in time). However, acknowledging that high variability in habitat use occurs at the local (site) scale, could allow for wider margins of error during the management action implementation process, resulting in more flexible conservation strategies. Ignoring the finer-scale variation as “background noise” may have deleterious consequences when managing particular sites or clusters of sites is the goal. Such cases may include managing or restoring scarce habitat for a particular threatened species (Gibbons, 2003) or for species reintroductions (Germano and Bishop, 2009), or protection of habitat critical to source population persistence (Stevens and Baguette, 2008).

Specifically for vernal pool-breeding amphibians, we found that active avoidance of clearcuts persists for at least 6 years post-logging. This suggests that a forest management strategy for pond-breeding amphibians should combine: (1) the retention of a minimum protective buffer around breeding pools (*sensu* Calhoun et al., 2005) and (2) harvesting operations that are spatially and temporally structured to retain canopy both between highly productive pools and between pool and high-quality terrestrial habitat (Baldwin et al., 2006).

Our study also has implications for designing monitoring programs for amphibian populations following logging disturbance. Populations need to be monitored periodically if the goal of the monitoring program is to identify thresholds at which the populations recover to background levels. For example, because in our region 20 years of natural vegetative regrowth mitigated the effects of clearcutting on habitat use by juvenile *L. sylvaticus* (Popescu and Hunter, 2011), undertaking surveys every 3–4 years post-disturbance would probably suffice to detect changes in habitat use by wood frogs and other forest specialist amphibians. On the other hand, more intensive amphibian monitoring

accompanied by vegetation sampling is required if the goal is to understand the immediate effects of forest harvesting on amphibian abundance and species richness.

Acknowledgments

Research was funded by the National Science Foundation (Research Grant O239915) and a Maine Economic Improvement Fund Doctoral Dissertation Fellowship awarded to V.D.P. We thank Sean Blomquist, Steve Barteaux, Jaqui Bertmann, Steve Campbell, Chelsea Corcoronquadt, Betsy Dionne, Dave Ellis, Kate Gaudet, Scott Helmke, Ashley Hoskins, Laura Leighton, Andrea Long, Alicia Miller, Lindsey Munson, Damon Oscarson, Kara Ray, Steph Smietana, David Veverka, and Brittany Wilson for help in the field. We also thank James Gibbs, Robert Seymour, Joseph Zydlewski, and two anonymous reviewers for thoughtful comments on earlier drafts of this paper. This is Maine Forest and Agricultural Experiment Station Paper # 3254.

References

- Altwegg, R., 2003. Multistage density dependence in an amphibian. *Oecologia* 136, 46–50.
- Ash, A.N., 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the Southern Blue Ridge Mountains. *Conservation Biology* 11, 983–989.
- Ashton, D.T., Marks, S.B., Welsh, H.H., 2006. Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. *Forest Ecology and Management* 221, 183–193.
- Baldwin, R.F., Calhoun, A.J.K., deMaynadier, P.G., 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. *Journal of Herpetology* 40, 442–453.
- Berven, K.A., 2009. Density dependence in the terrestrial stage of wood frogs: evidence from a 21-year population study. *Copeia* 2009, 328–338.
- Birchfield, G.L., Deters, J.E., 2005. Movement paths of displaced northern green frogs (*Rana clamitans melanota*). *Southeastern Naturalist* 4, 63–76.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference, 2nd edition. Springer, Berlin.
- Calhoun, A.J.K., deMaynadier, P.G., 2004. Forestry habitat management guidelines for vernal pool wildlife. Metropolitan Conservation Alliance, Wildlife Conservation Society, Bronx, New York.
- Calhoun, A.J.K., Miller, N.A., Klemens, M.W., 2005. Conserving pool-breeding amphibians in human-dominated landscapes through local implementation of Best Development Practices. *Wetlands Ecology and Management* 13, 291–304.
- Chazal, A.C., Niewiarowski, P.H., 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. *Ecological Applications* 8, 1133–1143.
- Chelgren, N.D., Rosenberg, D.K., Heppell, S.S., Gitelman, A.I., 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. *Ecological Applications* 16, 250–261.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128, 231–240.
- deMaynadier, P.G., Houlahan, J.E., 2008. Conserving vernal pool amphibians in managed forests. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), *Science and Conservation of Vernal Pools in Northeastern North America*. CRC Press, pp. 253–280.
- deMaynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* 3, 230–261.

- deMaynadier, P.G., Hunter, M.L., 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12, 340–352.
- Germano, J.M., Bishop, P.J., 2009. Suitability of amphibians and reptiles for translocation. *Conservation Biology* 23, 7–15.
- Gibbons, J.W., 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. *Wetlands* 23, 630–635.
- Gibbs, J.P., 1998a. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13, 263–268.
- Gibbs, J.P., 1998b. Amphibian movements in response to forest edges, roads, and streambeds in Southern New England. *Journal of Wildlife Management* 62, 584–589.
- Harper, E.B., Semlitsch, R.D., 2007. Density dependence in the terrestrial life history stage of two anurans. *Oecologia* 153, 879–889.
- Herbeck, L.A., Larsen, D.R., 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. *Conservation Biology* 13, 623–632.
- Homan, R.N., Windmiller, B.S., Reed, J.M., 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14, 1547–1553.
- Homyack, J.A., Haas, C.A., 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. *Biological Conservation* 142, 110–121.
- Huggett, A.J., 2005. The concept and utility of ‘ecological thresholds’ in biodiversity conservation. *Biological Conservation* 124, 301–310.
- Hunter, M.L., Schmiegelow, F.K.A., 2011. *Wildlife, forests, and forestry*, 2nd edition. Prentice Hall, Upper Saddle River, New Jersey.
- Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clear-cutting. *Environmental Reviews* 1, 121–144.
- Knapp, S.M., Haas, C.A., Harpole, D.N., Kirkpatrick, R.L., 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. *Conservation Biology* 17, 752–762.
- Kroll, A.J., 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review. *Forest Ecology and Management* 257, 1188–1199.
- Lemckert, F., 1999. Impacts of selective logging on frogs in a forested area of northern New South Wales. *Biological Conservation* 89, 321–328.
- Lindenmayer, D.B., 2009. Forest wildlife management and conservation. *Annals of the New York Academy of Sciences* 1162, 284–310.

- Marsh, D.M., 2001. Fluctuations in amphibian populations: a meta-analysis. *Biological Conservation* 101, 327–335.
- McCullagh, P., Nelder, J.A., 1989. *Generalized linear models*, 2nd edition. Chapman and Hall, London.
- Patrick, D.A., Hunter, M.L., Calhoun, A.J.K., 2006. Effects of experimental forestry treatments on a Maine amphibian community. *Forest Ecology and Management* 234, 323–332.
- Patrick, D.A., Harper, E.B., Hunter, M.L., Calhoun, A.J.K., 2008a. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. *Ecology* 89, 2563–2574.
- Patrick, D.A., Calhoun, A.J.K., Hunter, M.L., 2008b. The importance of understanding spatial population structure when evaluating the effects of silviculture on spotted salamanders (*Ambystoma maculatum*). *Biological Conservation* 141, 807–814.
- Petranka, J.W., Eldridge, M.E., Haley, K.E., 1993. Effects of timber harvesting on Southern Appalachian salamanders. *Conservation Biology* 7, 363–370.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed effects models in S and S-Plus*. Springer-Verlag, New York.
- Popescu, V.D., Hunter, M.L., 2011. Clearcutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecological Applications* 21, 1283–1295.
- Pough, F.H., Smith, E.M., Rhodes, D.H., Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. *Forest Ecology and Management* 20, 1–9.
- R Development Core Team, 2009. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3900051-07-0, <http://www.R-project.org>.
- Rittenhouse, T.A.G., Semlitsch, R.D., 2009. Behavioral response of migrating wood frogs to experimental timber harvest surrounding wetlands. *Canadian Journal of Zoology* 87, 618–625.
- Rome, L.L., Stevens, E.D., John-Alder, H.B., 1992. The influence of temperature and thermal acclimation on physiological function. In: Feder, M.E., Burggren, W.W. (Eds.), *Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago, pp. 183–205.
- Rothermel, B.B., 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications* 14, 1535–1546.
- Rothermel, B.B., Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology* 16, 1324–1332.

- Royle, J.A., Dorazio, R.M., 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego, California.
- Saunders, M., Wagner, R., 2008. Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. *Canadian Journal of Forest Research* 38, 498–517.
- Schmid, W.D., 1965. Some aspects of the water economies of nine species of amphibians. *Ecology* 46, 261–269.
- Semlitsch, R.D., 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12, 1113–1119.
- Semlitsch, R.D., Conner, C.A., Hocking, D.J., Rittenhouse, T.A.G., Harper, E.B., 2008. Effects of timber harvesting on pond-breeding amphibian persistence. Testing the evacuation hypothesis. *Ecological Applications* 18, 283–289.
- Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P., Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter, M.L., Patrick, D.A., Rittenhouse, T.A.G., Rothermel, B.B., 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. *BioScience* 59, 853–862.
- Sjögren, P., 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42, 135–147.
- Stevens, V.M., Baguette, M., 2008. Importance of habitat quality and landscape connectivity for the persistence of endangered natterjack toads. *Conservation Biology* 22, 1194–1204.
- Todd, B.D., Rothermel, B.B., 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). *Biological Conservation* 133, 178–185.
- Todd, B.D., Luhring, T.M., Rothermel, B.B., Gibbons, J.W., 2009. Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. *Journal of Applied Ecology* 46, 554–561.
- Vonesh, J., Delacruz, O., 2002. Complex lifecycles and density dependence. Assessing the contribution of egg mortality to amphibian declines. *Oecologia* 133, 325–333.
- Werner, E.E., Yurewicz, K.L., Skelly, D.K., Relyea, R.A., 2007. Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116, 1713–1725
- Welsh, H.H., Pope, K.L., Wheeler, C.A., 2008. Using multiple metrics to assess the effects of forest succession on population status: a comparative study of two terrestrial salamanders in the US Pacific Northwest. *Biological Conservation* 141, 1149–1160.
- Werner, E.E., Yurewicz, K.L., Skelly, D.K., Relyea, R.A., 2007. Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116, 1713–1725.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Figures

Figure 1

Experimental setup of the forest treatment centered on a breeding pool (drawing not to scale).

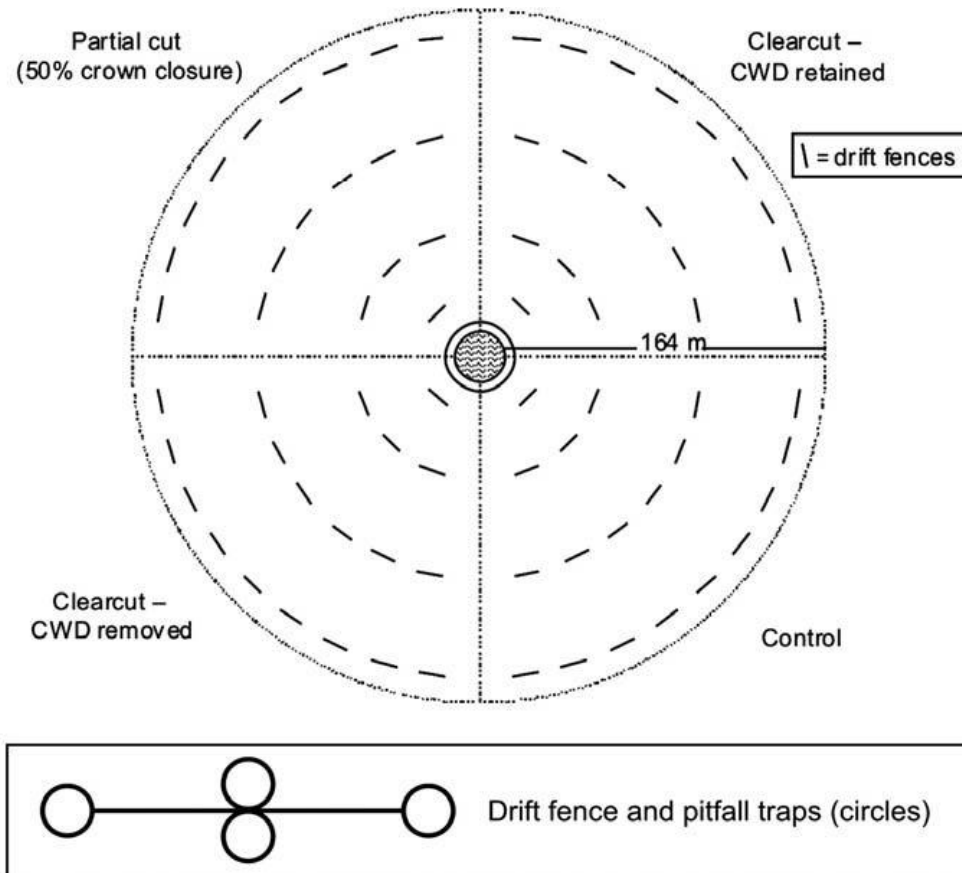


Fig. 1. Experimental setup of the forest treatments centered on a breeding pool (drawing not to scale).

Table 1

Total number of amphibians captured between 2004 and 2009 by forestry treatment (C = control; P = partial cut; Rm = clearcut with CWD removed; Rt = clearcut with CWD retained).

Species	2004				2005				2006				2007				2008				2009				
	C	P	Rm	Rt	C	P	Rm	Rt	C	P	Rm	Rt	C	P	Rm	Rt	C	P	Rm	Rt	C	P	Rm	Rt	
<i>Juveniles</i>																									
<i>Salamanders</i>																									
AMLA	7	1	1	1	11	2	2	6	16	1	3	8	-	-	-	-	2	-	-	-	-	-	-	-	-
AMMA ^b	8	197	105	158	502	239	48	82	230	174	94	90	24	8	2	-	16	7	2	1	27	28	3	2	
HESC	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NOVI	3	20	7	10	29	10	10	3	8	1	5	1	10	4	7	2	11	7	4	-	3	-	-	2	
PLCI	2	15	15	13	12	11	2	2	15	4	2	-	4	-	-	-	2	-	-	-	-	-	-	-	
<i>Anurans</i>																									
BUAM	3	2	2	-	1	-	-	-	-	-	-	-	-	-	-	-	6	2	3	1	-	-	-	-	
HYVE	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
LICA	4	29	30	31	76	66	41	55	23	59	16	22	19	20	6	7	40	37	15	36	-	-	-	-	
LICL	2	146	139	97	371	325	228	236	600	544	245	229	440	413	192	229	732	483	154	219	113	51	20	16	
LIPA	1	12	1	3	4	9	8	3	12	7	15	10	28	13	12	5	3	17	7	4	-	-	-	-	
LIPI	4	43	24	20	45	38	35	24	45	61	15	15	20	11	9	8	6	25	3	12	-	-	-	-	
LISE	-	-	-	-	-	-	-	-	18	4	5	4	-	-	-	-	-	-	-	-	-	-	-	-	
LISY	1	1176	664	547	1155	1017	359	503	1499	1119	512	749	287	161	111	89	440	309	151	129	89	60	26	22	
PSCR	8	1	3	1	4	1	1	-	-	-	-	-	-	-	-	-	9	2	-	1	-	-	-	-	
<i>Adults</i>																									
<i>Salamanders</i>																									
AMLA	5	2	1	5	1	1	-	-	2	1	-	-	2	-	-	2	-	-	1	1	-	-	-	-	
AMMA ^b	1	79	39	59	11	9	1	4	4	2	3	1	3	5	1	3	2	1	1	-	-	-	-		
HESC	-	-	-	-	2	1	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	
NOVI	-	1	1	3	4	6	1	-	2	1	1	2	8	1	5	1	3	2	1	2	2	3	-	1	
PLCI	3	38	31	21	32	21	12	4	15	1	1	-	9	5	1	1	7	4	2	-	-	-	-		
<i>Anurans</i>																									
BUAM	3	1	2	-	-	-	2	1	-	-	-	-	-	-	-	-	4	3	1	-	-	-	-		
HYVE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
LICA	1	4	8	11	14	5	11	4	-	2	-	-	-	-	-	-	-	1	1	1	-	-	-		
LICL	2	42	75	38	58	34	33	28	8	5	4	6	10	7	3	3	4	3	1	1	8	4	2	6	
LIPA	5	1	1	1	1	-	4	2	-	-	1	1	9	2	4	9	4	-	-	-	-	-	-		
LIPI	7	11	4	2	2	3	1	-	-	-	1	2	-	-	-	-	1	3	2	-	-	-	-		
LISE	-	-	-	-	3	3	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-		
LISY	9	87	41	38	277	106	41	42	67	64	15	13	48	17	3	4	36	24	14	10	22	38	4	4	
PSCR	1	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	3	-	-	-	-	-	1	-	

^a Species: AMLA = *Ambystoma laterale* (blue-spotted salamander); AMMA = *A. maculatum* (spotted salamander); BUAM = *Bufo americanus* (American toad); HESC = *Hemidactylium scutatum* (four-toed salamander); HYVE = *Hyla versicolor* (gray treefrog); NOVI = *Notophthalmus viridescens* (red-spotted newt); PLCI = *Plethodon cinereus* (red-backed salamander); PSCR = *Pseudacris crucifer* (spring peeper); LICA = *Lithobates catesbeianus* (bullfrog); LICL = *L. clamitans* (green frog); LIPA = *L. palustris* (pickrel frog); LIPI = *L. pipiens* (northern leopard frog); LISE = *L. septentrionalis* (mink frog); LISY = *L. sylvaticus* (wood frog).

^b In 2004, the bulk of *A. maculatum* adult and juvenile captures (approx. 83%) occurred late in the season (between 15 September and 27 October). For comparison purposes, we are presenting data truncated to 15 September to match the sampling period of the rest of the years.

Table 2

Models investigating the effects of forestry treatment on eight amphibian species during distinct life stages. N = number of parameters estimated, ΔAIC_c = AICc difference between the model with lowest AICc [in bold] and each model; w = AICc weight; -2LL = -2 x model log-likelihood.

Species	Model	N	ΔAIC_c	w	-2LL	Species	Model	N	ΔAIC_c	w	-2LL
Adult breeding migration to experimental pools (April–May)						Juvenile emergence from experimental pools (July)					
LISY	Treatment x site	19	0.00	0.99	52.62	LISY	Treatment x year	27	0.00	0.99	79.56
	Treatment + site	10	9.45	0.01	65.06		Treatment x site	19	9.64	0.01	84.36
	Treatment	7	17.76	0.00	77.14		Treatment + site	10	18.37	0.00	100.00
AMMA	Treatment x year	19	21.14	0.00	73.76	AMMA	Treatment	7	22.89	0.00	108.76
	Treatment x site	19	0.00	1.00	56.38		Treatment	7	0.00	0.41	118.56
	Treatment + site	10	11.47	0.00	70.84		Treatment x year	23	0.61	0.30	106.92
	Treatment	7	23.90	0.00	87.02		Treatment x site	19	1.95	0.15	108.34
	Treatment x year	19	26.83	0.00	83.20		Treatment + site	10	2.19	0.14	116.38
Foraging adults and juveniles originating from outside the experimental arrays (June–September)											
LISY Juv.	Treatment x site	19	0.00	0.86	73.30	LIPA & LIPI _b Juv. and adult	Treatment	10	0.00	0.53	-82.98
	Treatment + site	10	4.02	0.12	88.04		Treatment + site	13	0.23	0.47	-86.98
	Treatment	7	7.42	0.02	96.22		Treatment x site	22	11.62	0.00	-84.18
LISY Adult	Treatment x year	27	19.42	0.00	88.18	AMMA _b Juv.	Treatment x year	30	58.48	0.00	-38.20
	Treatment	7	0.00	1.00	-80.98		Treatment	10	0.00	0.98	12.34
	Treatment + site	10	10.63	0.00	-75.14		Treatment + site	15	7.89	0.02	12.84
	Treatment x site	19	38.45	0.00	-58.06		Treatment x site	20	16.01	0.00	17.54
LICL Juv.	Treatment x year	27	39.56	0.00	-60.48	NOVI _b Juv. and adult	Treatment x year	30	27.95	0.00	26.60
	Treatment x site	19	0.00	0.96	52.22		Treatment + site	13	0.00	1.00	-150.80
	Treatment	7	7.24	0.03	74.96		Treatment	10	12.60	0.00	-133.98
	Treatment + site	10	7.87	0.02	70.82		Treatment x site	22	23.94	0.00	-135.46
LICA _b Juv.	Treatment x year	27	25.25	0.00	73.90	PLCI _b Juv. and adult	Treatment x year	30	79.44	0.00	-80.84
	Treatment	10	0.00	0.82	-78.52		Treatment	10	0.00	0.94	-109.12
	Treatment + site	13	3.01	0.18	-79.74		Treatment + site	13	5.65	0.06	-107.70
	Treatment x site	22	23.64	0.00	-67.68		Treatment x site	22	17.54	0.00	-104.42
	Treatment x year	30	57.48	0.00	-34.74		Treatment x year	30	57.74	0.00	-65.10
Juvenile emigration from experimental pools into upland (July–August)											
LISY	Treatment x site	19	0.00	1.00	376.00						
	Treatment	7	16.34	0.00	413.30						
	Treatment x year	23	17.38	0.00	387.14						
	Treatment + site	10	18.86	0.00	410.28						
	Treatment x Distance	19	41.29	0.00	417.30						

^a Species: AMMA = *A. maculatum* (spotted salamander); NOVI = *Notophthalmus viridescens* (red-spotted newt); PLCI = *Plethodon cinereus* (red-backed salamander); LICA = *Lithobates catesbeianus* (bullfrog); LICL = *L. clamitans* (green frog); LIPA = *L. palustris* (pickerel frog); LIPI = *L. pipiens* (northern leopard frog); LISY = *L. sylvaticus* (wood frog).

^b Model contained a variance function that allowed for modeling heteroscedastic variances specific to each site.

Table 3

Forestry treatment use by amphibians up to 6 years post-harvesting (coefficients \pm SE and p-values [italics below coefficients, with bold emphasis for significance at $\alpha = 0.05$] from the best mixed effects model for each event/species/life stage). For all models, we compared the mean Control value to all the other treatments (the coefficients show a higher (+) or lower (-) use of those particular treatments compared to the Control, and the p-values indicate significant departures from the mean Control value); A = adults; J = juveniles.

Category	Species	Life stage	Forestry treatments				
			Control	Partial cut	CWD removed	CWD retained	
Breeding migration	<i>L. sylvaticus</i>	A	1.44 \pm 0.22	-0.02 \pm 0.20	-0.13 \pm 0.20	0.16 \pm 0.20	
			0.911		0.537	0.444	
	<i>A. maculatum</i>	A	1.82 \pm 0.21	-0.02 \pm 0.23	0.18 \pm 0.23	0.19 \pm 0.23	
			0.917		0.448	0.429	
Juvenile emergence (pond fence)	<i>L. sylvaticus</i>	J	3.67 \pm 0.48	-0.18 \pm 0.22	-0.11 \pm 0.22	-0.12 \pm 0.22	
			0.435		0.610	0.598	
	<i>A. maculatum</i>	J	1.53 \pm 0.24	-0.08 \pm 0.12	-0.09 \pm 0.12	0.34 \pm 0.12	
			0.526		0.478	0.009	
Juvenile upland dispersal	<i>L. sylvaticus</i>	J	3.73 \pm 0.62	0.53 \pm 0.27	-0.91 \pm 0.27	-1.49 \pm 0.27	
			0.0646		0.0023	<0.001	
	<i>A. maculatum</i>	J	-data not analyzed				
Foraging adults and juveniles from outside experimental pools	<i>L. sylvaticus</i>	J	1.52 \pm 0.27	-0.39 \pm 0.13	-0.66 \pm 0.13	-0.63 \pm 0.13	
			0.005		<0.001	<0.001	
			A	0.50 \pm 0.05	-0.09 \pm 0.03	-0.29 \pm 0.03	-0.29 \pm 0.03
				0.007		<0.001	<0.001
		<i>A. maculatum</i>	J	0.55 \pm 0.12	-0.13 \pm 0.05	-0.32 \pm 0.05	-0.31 \pm 0.05
				0.019		<0.001	<0.001
			A	-data not analyzed			
		<i>L. clamitans</i>	J	0.64 \pm 0.18	-0.12 \pm 0.11	-0.23 \pm 0.11	-0.14 \pm 0.11
				0.293		0.047	0.237
	<i>L. catesbeianus</i>	J	0.23 \pm 0.05	-0.02 \pm 0.03	-0.07 \pm 0.03	0.02 \pm 0.03	
			0.544		0.006	0.519	
	<i>L. pipiens and L. palustris</i>	J + A	0.28 \pm 0.05	-0.02 \pm 0.02	-0.02 \pm 0.02	-0.06 \pm 0.02	
			0.369		0.466	0.012	
	<i>P. cinereus</i>	J + A	0.19 \pm 0.04	-0.03 \pm 0.02	-0.07 \pm 0.02	-0.12 \pm 0.02	
			0.219		0.013	<0.001	
	<i>N. viridescens</i>	J + A	0.13 \pm 0.02	-0.03 \pm 0.02	-0.05 \pm 0.02	-0.07 \pm 0.02	
			0.214		0.043	0.003	

Figure 2.

Mean proportions (± 1 SE) of amphibians captured during the summer/fall sampling window in each of the four forestry treatments between 2004 and 2009.

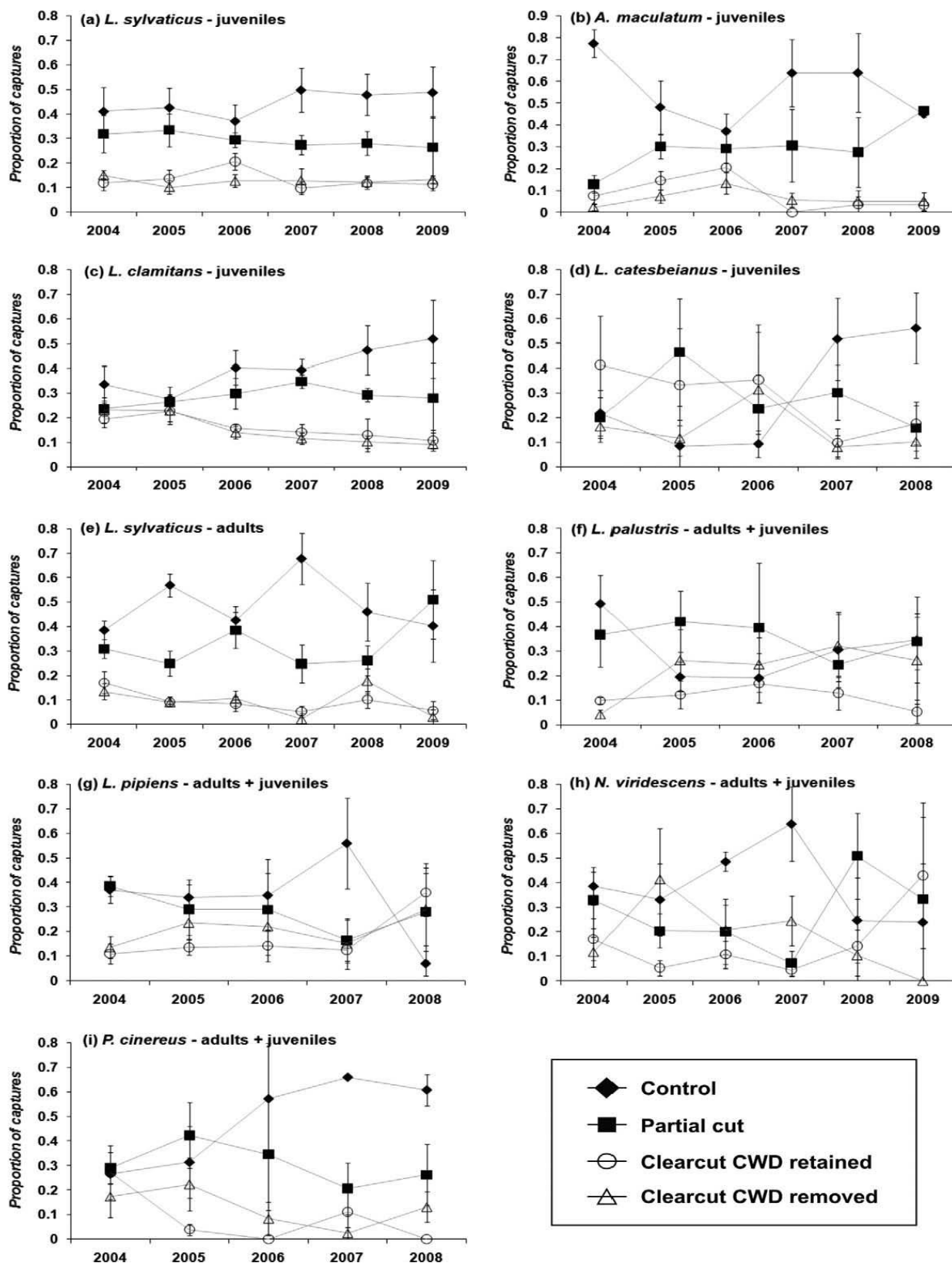


Table 4

Number of newly metamorphosed *L. sylvaticus* and *A. maculatum* emerging from experimental pools and recaptured in the upland habitat (n = number of pools that produced animals).

Year	Total emerged from experimental pools		Total recaptured in upland habitat	
	<i>L. sylvaticus</i>	<i>A. maculatum</i>	<i>L. sylvaticus</i>	<i>A. maculatum</i>
2004	2342 (n = 4)	272 (n =4)	81	32
2005	6085 (n = 4)	589 (n = 3)	1061	35
2006	2083 (n = 4)	319 (n = 4)	410	14
2007	328 (n = 1)	211 (n =4)	41	4
2008	3133 (n = 3)	122 (n = 3)	392	2
2009	95 (n =1)	8 (n =1)	8	0

Figure 3

Use of upland habitat by juvenile wood frogs emerging from the experimental pools expressed as the mean proportion (± 1 SE) of animals captured in each of the four forestry treatments between 2004 and 2008. In 2007 only one site produced juveniles.

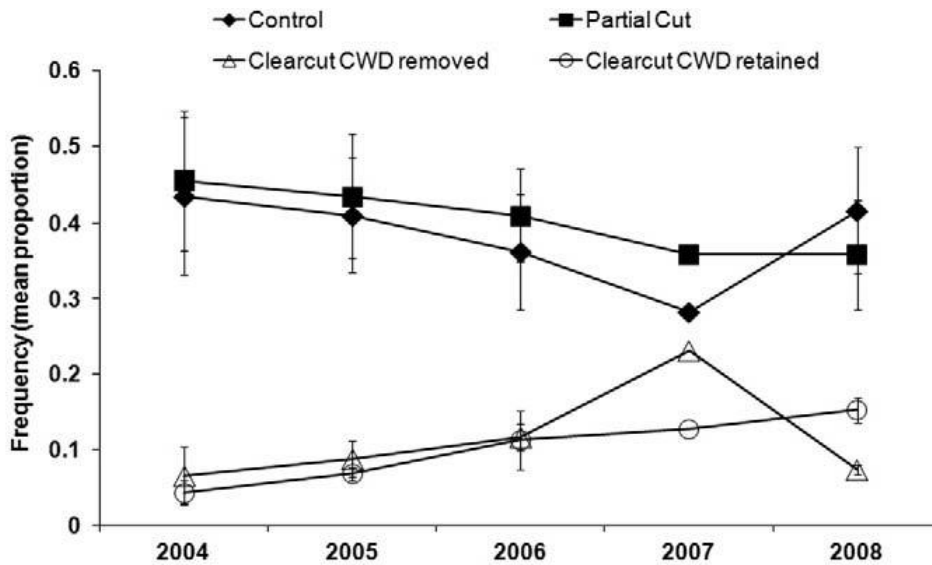


Fig. 3. Use of upland habitat by juvenile wood frogs emerging from the experimental pools expressed as the mean proportion (± 1 SE) of animals captured in each of the four forestry treatments between 2004 and 2008. In 2007 only one site produced juveniles.

Figure 4.

Site-specific difference in the use of the forested treatments by emigrating juvenile *L. sylvaticus* emerging from experimental pools. Site 4 not graphed (only 1 year of data).

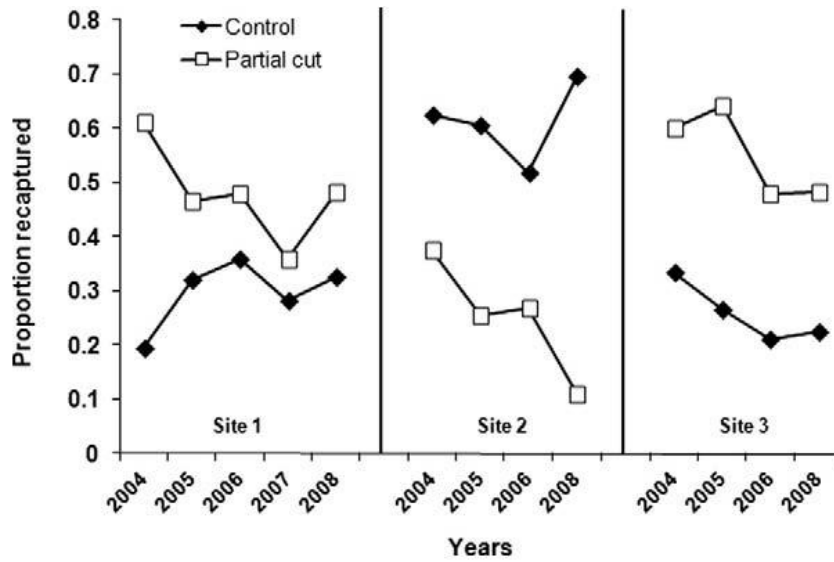


Fig. 4. Site-specific difference in the use of the forested treatments by emigrating juvenile *L. sylvaticus* emerging from experimental pools. Site 4 not graphed (only 1 year of data).

Figure 5

Changes in vegetation cover (by height classes) following forest harvesting.

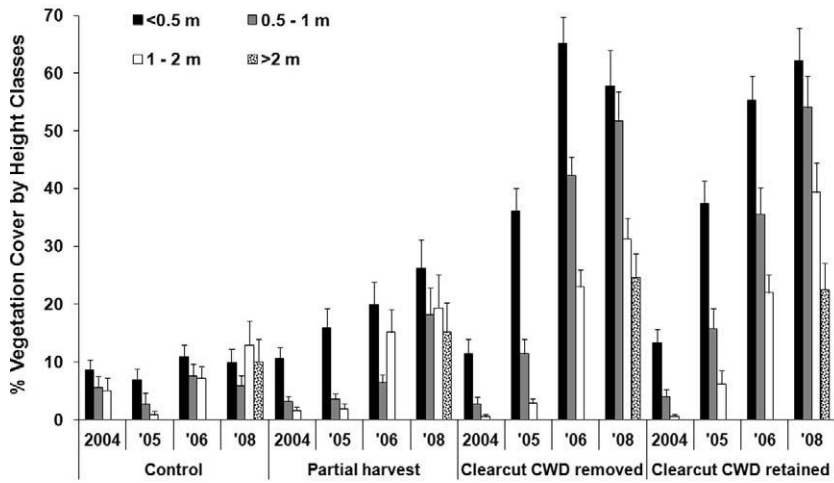


Fig. 5. Changes in vegetation cover (by height classes) following forest harvesting.