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Relative abundance of amphibians in forest canopy gaps of natural origin vs. timber harvest origin

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Abstract

Relative abundance of amphibians in forest canopy gaps of natural origin vs. timber harvest origin.— Small-scale canopy gaps created by logging may retain adequate habitat structure to maintain amphibian abundance. We used pitfalls with drift fences to measure relative abundance of amphibians in 44 harvested gaps, 19 natural treefall gaps, and 36 closed-canopy forest plots. Metamorphs had relatively lower capture rates in large harvest gaps for *Ambystoma maculatum*, *Lithobates catesbeianus*, *L. clamitans*, and *L. sylvaticus* but we did not detect statistically significant ($p < 0.1$) differences among gap types for *Lithobates palustris* metamorphs. *L. clamitans* juveniles and *L. sylvaticus* juveniles and adults had relatively lower capture rates in large harvest gaps. For juvenile–adult *A. maculatum*, we caught relatively fewer individuals in all gap types than in closed-canopy areas. Some groups with overall lower capture rates (immature *Plethodon cinereus*, juvenile *L. palustris*) had mixed differences among gap types, and *Notophthalmus viridescens* (efts) and adult *P. cinereus* showed no differences among gap types. One species, *L. clamitans*, was captured more often at gap edges than gap centers. These results suggest that harvest gaps, especially small gaps, provided habitat similar to natural gaps for some, but not all, amphibian species or life-stages.

Key words: Amphibians, Forest management, Canopy gaps, Natural disturbance, Irregular group shelterwood.

Resumen

Abundancia relativa de anfibios en los claros de origen natural del dosel forestal frente a los claros producidos por la explotación forestal.— Los claros a pequeña escala producidos en el dosel forestal por la industria maderera pueden conservar una estructura del hábitat apropiada para mantener la abundancia de anfibios. Utilizamos trampas con vallas de intercepción para medir la abundancia relativa de anfibios en 44 claros en que la madera había sido cortada, 19 claros naturales producidos por la caída de los árboles, y 36 zonas de dosel cerrado. Para *Ambystoma maculatum*, *Lithobates catesbeianus*, *L. clamitans* y *L. sylvaticus* las tasas de captura son relativamente bajas en los claros de tala grandes para los metamorfos, pero no detectamos diferencias estadísticamente significativas ($p < 0,1$) entre los tipos de claros para los metamorfos de *Lithobates palustris*. Los juveniles de *L. clamitans* y los juveniles y adultos de *L. sylvaticus* dieron unas tasas de captura relativamente inferiores en los claros de tala grandes. Para los juveniles–adultos de *A. maculatum*, capturamos relativamente menos individuos en todos los tipos de claros que en las zonas boscosas cerradas. Algunos grupos con tasas de captura general inferiores (inmaduros de *Plethodon cinereus*, juveniles de *L. palustris*), presentaban diferencias mixtas entre los tipos de claros, y *Notophthalmus viridescens* (fase inmadura terrestre) y los adultos de *P. cinereus* no presentaban diferencias entre los distintos tipos de claros. Una especie, *L. clamitans*, fue capturada más a menudo en los bordes de los claros que en sus centros. Estos resultados sugieren que los claros producidos por la industria maderera, y especialmente los más pequeños, proporcionaban un hábitat similar a los claros naturales para algunas, pero no todas, las especies o las fases vitales de los anfibios.

Palabras clave: Anfibios, Gestión forestal, Claros del dosel, Perturbación natural, Clareo sucesivo uniforme de grupos irregulares.

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Introduction

Timber harvests designed to emulate the structural changes that result from natural disturbances may facilitate meeting both biological conservation and timber production goals (Seymour & Hunter, 1999; Perera et al., 2004). This concept assumes that native species have adapted to natural disturbance patterns and therefore will be less adversely affected by human-induced disturbances if they are modeled after natural disturbance regimes. In the forests of northeastern North America, small-scale canopy gaps are a common form of natural disturbance (Lorimer, 1977; Runkle, 1991; Rogers, 1996; Seymour et al., 2002). The Acadian Forest Ecosystem Research Program of the University of Maine, USA implemented a harvesting regime designed to emulate natural canopy gaps in a mixed coniferous-deciduous forest.

Some harvesting methods, notably clearcuts, often negatively affect amphibian populations (Ash, 1997; DeMaynadier & Hunter, 1998; Harpole & Haas, 1999; Chan-McLeod, 2003; Renken et al., 2004; Semlitsch et al., 2009). In a review of 18 independent studies, DeMaynadier & Hunter (1995) found amphibian abundance to be 3.5 times greater in mature forest sites than in clearcut sites. Furthermore, research in an Appalachian hardwood forest showed that terrestrial salamander abundance decreased after group selection, shelterwood, and leave-tree harvests as well as clearcuts (Harpole & Haas, 1999; Knapp et al., 2003; Homyack & Haas, 2009). In contrast, some studies that examined effects of small-scale canopy gap disturbances did not detect differences in relative abundances of red-backed salamanders (*Plethodon cinereus*) (Messere & Ducey, 1998; McKenny et al., 2006) or frogs and salamanders (Greenberg, 2001).

To better understand the ecological effects of harvest origin gaps created to emulate natural disturbance, we investigated forest amphibians in harvest and natural canopy gaps in a mixed forest in central Maine, USA. Specifically, we: 1) compared relative abundance of forest amphibians within harvest-created gaps to determine if location (gap center, edge, north and south aspect) influenced amphibian distributions; and 2) compared relative amphibian abundance among harvest and natural canopy gaps, using adjacent closed-canopy forest as reference plots.

Material and methods

Study area and experimental treatments

We conducted our research at the Penobscot Experimental Forest (PEF) in Penobscot County, Maine, USA. The PEF encompasses 1,540 hectares of predominantly mixed coniferous-deciduous forest. Dominant tree species are *Tsuga canadensis*, *Acer rubrum*, *Pinus strobus*, *Thuja occidentalis*, *Abies balsamea*, *Betula papyrifera*, *Picea rubens*, *Populus tremuloides*, *P. grandidentata*, and *A. saccharum*. We conducted our research within nine, approximately 10-ha, research

areas of mature forest in the PEF. The harvest origin gaps under study are in six research areas that were harvested between 1995 and 1997. Most harvests were completed by manual felling, delimiting, and topping with chainsaws at the stump. We sampled forest amphibians in the nine research areas, where each research area contained a certain type of canopy gap treatment: three research areas had a combined total of 22 large harvest gaps ($1,328 \pm 113 \text{ m}^2$; mean $\pm 1 \text{ SE}$), three had a combined total of 22 small harvest gaps ($674 \pm 65 \text{ m}^2$), and three had a combined total of 19 natural canopy gaps ($249 \pm 28 \text{ m}^2$). Large gaps were created by removing approximately 20% of the canopy within the 10 ha stand, resulting in seven to eight gaps per research area (irregular group shelterwoods with reserves). Small gap harvests removed approximately 10% of the canopy within the stand, creating seven to eight gaps per research area (selection harvests). In the unharvested research areas, natural gaps were defined by any area where at least two tree falls or stem breaks of canopy trees $\geq 25 \text{ cm}$ in diameter created a gap, exposing understory stems to the sky (Runkle, 1991). Basal area of reserve trees (unharvested trees within gaps) was lowest in large harvest gaps ($11 \text{ m}^2/\text{ha}$), and greater in small harvest gaps ($14 \text{ m}^2/\text{ha}$) and natural gaps ($24 \text{ m}^2/\text{ha}$) (Schofield, 2003). We also sampled forest amphibians in 36 closed-canopy plots (four plots per research area) located between the gaps. The basal area of closed-canopy areas averaged $32 \text{ m}^2/\text{ha}$ (Schofield, 2003). These plots were used to test for spatial independence and to control for some of the natural variability among the nine research areas.

Vegetative patterns among harvest gaps, natural gaps, and closed-canopy forest areas were described four years post-harvest by Schofield (2003). Total cover for herbs, shrubs, seedlings, saplings, and ferns was highest (34.9%) in harvest gaps, 25.5% in natural gaps, and 10.6% in closed-canopy plots. In the larger harvest gaps ($1,170\text{--}2,106 \text{ m}^2$), gap centers had greater herbaceous and shrub cover than edges. Natural gaps tended to have more conifer regeneration, lichens, and mosses while harvest gaps had more hardwood regeneration, shrubs, and herbaceous cover. Coarse Woody Debris (CWD) characteristics were compared before and after harvests for each treatment at the stand level (Fraver et al., 2002). Research areas with large harvest gaps had the greatest increase in volume and abundance of small-diameter CWD, with less of an increase in small-gap research areas and the least increase in natural-gap research areas. The proportion of well-decayed CWD to total CWD decreased following harvests because the harvests generated fresh, undecayed CWD.

Amphibian sampling

We sampled amphibians using pitfall traps with drift fences (pitfall arrays) from 10 V–26 VII and 4 IX–23 X in 2002, and 22 IV–25 X in 2003. Traps in all plots were monitored one to two times per week throughout these periods. The temporary closure in 2002 was

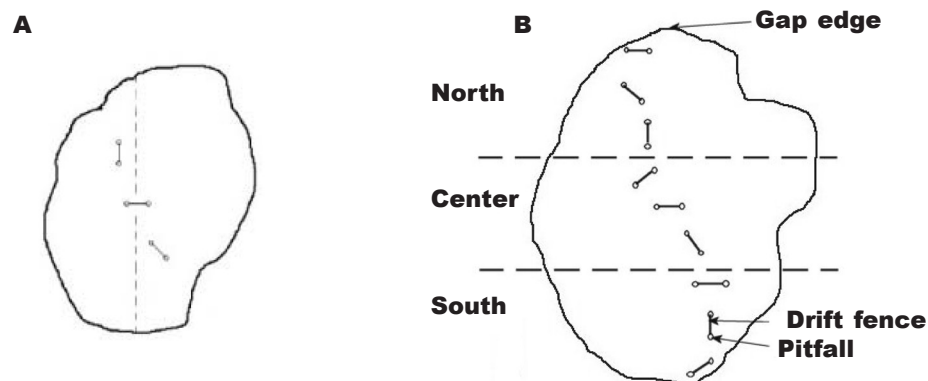


Fig. 1. Diagram of the arrangement of pitfalls with drift fences (arrays) in harvested and natural gaps, where most gaps had 3 arrays (A) and a subset had arrays along the entire north–south transect to test for differences in capture rates within the gap (B).

Fig. 1. Diagrama de la disposición de las trampas de intercepción dotadas de valla de deriva en los claros de tala y naturales; en la mayoría de los claros existían 3 dispositivos (A) y cada subconjunto tenía dispositivos a lo largo de todo su transecto norte–sur, para estudiar las diferencias en las tasas de captura dentro del claro (B).

implemented due to hot and dry conditions in late July and August of 2002. Pitfall traps were constructed from two #10 aluminum cans taped end-to-end (36 cm deep), buried in the ground at each end of a 3-m long by 0.5-m high plastic fence buried into the ground. Moss placed in the bottom of the traps provided shelter to amphibians from dry conditions and predators (Enge, 2001). Plastic funnels in the pitfall traps were used to prevent the escape of amphibians that are able to climb the sides. The diameter of the base of these funnels was 12–14 cm. Sticks (< 1.5 cm diameter) were placed in pitfall traps to facilitate escape of shrews and mice as recommended by Perkins & Hunter (2002).

To study how treatment differences influenced relative amphibian abundance, each canopy gap had three pitfall arrays: 5 m south of the plot center, at center, and 5 m north of the center (fig. 1a). Closed canopy plots also had three arrays. To study how location within a gap was correlated with relative amphibian abundance, a subsample of the gaps (11 large gaps, 12 small gaps, and seven natural gaps) were randomly selected to have pitfall arrays positioned every 5 m along the entire north–south transect of each gap (fig. 1b). All pitfall arrays were randomly oriented in one of the following directions: north–south, northeast–southwest, northwest–southeast, east–west.

Amphibians were captured, measured from snout to anterior end of the vent in length (SVL), and released 6–10 m east or west of the trap. During 2002, we marked amphibians with a visible implant elastomer tag under the skin (Davis & Ovaska, 2001; Bailey, 2004); however, very low recapture rates (< 0.4%) did not warrant repeating this procedure in 2003.

Data analysis

Amphibian abundance was measured by the number of captures per 100 trap nights (TN), with one trap night for every night an individual pitfall was open. Habitat selection of amphibians varies both interspecifically (Stebbins & Cohen, 1995; DeMaynadier & Hunter, 1998) and intraspecifically (i.e. among life stages) (DeMaynadier & Hunter, 1999; Rothermel & Semlitch, 2002). Therefore, we calculated capture rates for each individual species, and for age-classes of spotted salamanders (*Ambystoma maculatum*), red-backed salamanders, bullfrogs (*Lithobates catesbeianus*), green frogs (*L. clamitans*), pickerel frogs (*L. palustris*), and wood frogs (*L. sylvaticus*) (Strojny, 2004). Data from 2002 and 2003 were analyzed independently because of different sampling periods.

Relative abundance within gaps

To test for differences in capture rates between 1) northern and southern areas of the gaps, and 2) edges and center areas of the gaps, we calculated probabilities using BLOSSOM'S (Midcontinent Ecological Science Center, U. S. Geological Survey) multiple response permutation procedures (MRPP) for paired samples, with a probability value < 0.1 considered significant (Cade & Richards, 1999). We analyzed the 11 largest gaps because they represented the most extreme canopy removal conditions with the greatest likelihood of detecting differences in relative amphibian abundance. We only analyzed species that occurred in all 11 gaps. For comparisons between northern and southern areas within a gap, we measured capture rates for the three northern-most and three southern-most pitfall arrays. For comparisons of edges and centers of gaps, we were

concerned that aspect may obfuscate edge effects, so we combined captures for the northern-most and southern-most pitfall arrays to represent edge capture rates. Then we combined captures for the two middle pitfall arrays to derive gap-center capture rates. For each replicate, there was at least 10 m between center and edge pitfall arrays within the gap.

Relative abundance among gap types

In comparing treatment types (large gap, small gap, natural gap), analyses were only conducted on species and age-classes of species that were detected in all nine research areas (table 1). We combined all captures to calculate rates for each plot type (gap or closed-canopy) based on each plot's sampling effort. In order to use individual gaps as the experimental units to compare gap types, we took two measures to guard against confounding factors such as spatial autocorrelation and natural variation among research areas. First we used an analysis of variance (ANOVA) to test for differences in amphibian abundance among the closed-canopy plots for each treatment, using the research areas as the units of replication. A difference would indicate a potential site-related bias on all plots within one or more of the research areas. From this test, juvenile bullfrogs in 2003 were excluded from analyses due to a higher capture rate in closed-canopy plots of the large-gap treatment (F -ratio_{2,6} = 6.01; p = 0.04). Second, to account for natural variation, our response variable was calculated as follows: for each research area, the mean capture rate of the four closed-canopy plots was subtracted from each gap capture rate value (for gaps in that same research area) to derive a "difference value". Therefore, all values reported for gap type are in reference to capture rates of the closed-canopy plots in the same research area, to decrease the likelihood of site-specific effects biasing results. This method is limited in precision because there were only four closed-canopy plots and the method does not account for the variability among them.

We used SYSTAT's (ANOVA) tool to test for treatment effects on ranks of the difference values at the α = 0.1 level. All pairwise comparisons for treatment differences were made using Tukey's multiple comparison procedure. We estimated 90% confidence intervals around the difference value medians of each treatment with a bootstrapping procedure, sampling 5,000 times with replacement (SYSTAT) to compare and contrast treatments. Sign tests were used to determine if capture rates in gaps were significantly (α < 0.1) less than zero. We also compared difference values of harvest gaps (n = 10) that occurred within the size range of natural gaps (n = 19). Because of unequal sample sizes and variation, this test was done with BLOSSOM's MRPP as a nonparametric equivalent of the classical t -test (Cade & Richards, 1999).

Results

Eleven species were caught in 2002, for a total of 2,930 captures in 98,457 TN (2.98 captures per 100 TN)

(table 1). In 2003, we captured 9,069 amphibians representing 12 species over 152,597 TN (5.94 captures per 100 TN).

Relative abundance within gaps

Location within gaps (north vs. south or edge vs. center) had no effect on relative amphibian abundance, except for green frogs (appendix 1). Mean green frog capture rates were higher at gap edges (2.52 captures/100 TN) than in gap centers (1.74 captures/100 TN) (p = 0.02 in 2003; n = 11). Patterns in 2002 were consistent with those of 2003 although we did not analyze wood frogs and red-backed salamanders due to sample limitations. In 2002, mean green frog capture rates were also higher at edges (1.05 captures/100 TN) than gap centers (0.61 captures/100 TN) (p = 0.05; n = 11). Because of the within-gap patterns for green frogs, subsequent analyses of their distributions only used data from the center three pitfall arrays of these 11 large gaps.

Relative abundance among gap types

For the following comparisons, when capture rates in gaps were less than the capture rate means of the associated closed-canopy sites (*i.e.*, difference values were negative) we refer to this as lower abundance within gaps. Conversely, when capture rates in gaps were higher than the associated closed-canopy plot means (*i.e.*, positive difference values), we refer to this as higher abundance.

In 2003, gap type had statistically significant effects on relative abundance in six of seven anuran groups: bullfrog metamorphs, juvenile pickerel frogs, and juvenile and metamorph groups of green frogs and wood frogs (table 2; appendix 2). Three metamorph groups (bullfrogs, green frogs, and wood frogs) showed the lowest relative abundance within large gaps. Bullfrog and green frog metamorph abundances were low in small gaps as well, and relatively high within natural gaps. Abundance values for small and natural gaps were similar for juvenile-adult and metamorph wood frogs, and juveniles of pickerel frogs and green frogs. Of five anuran groups tested in 2002, we detected treatment differences for green frog metamorphs (lowest abundance in the large gap treatment) and wood frog metamorphs (natural gap treatment showed reduced abundance and no change within harvested treatments) (table 3).

Two of five salamander groups showed treatment differences in 2003: spotted salamander metamorphs and immature red-backed salamanders (table 2; appendix 2). For spotted salamander metamorphs, both large and small harvest gaps showed low abundance while natural gaps showed similar abundance to closed-canopy plots. For immature red-backed salamanders, abundance was relatively high in small gaps and relatively low in large gaps, and natural gap treatment values overlapped with both large and small gap treatments. No differences among gap types were

Table 1. Counts of amphibian species and their age-classes captured in the Penobscot Experimental Forest, Maine, in 2002 and 2003: ^a Numbers in parentheses did not occur in all nine research areas and were not included in analyses; ^b Sampling period in 2002: 10 V–26 VII and 4 IX–23 X; ^c Sampling period in 2003: 22 IV–25 X.

Tabla 1. Recuento de las especies de anfibios y de sus clases de edad, capturados en el Bosque Experimental de Penobscot, Maine, en 2002 y 2003: ^a Los números entre paréntesis no se dieron en la totalidad de las nueve áreas de investigación, y no se incluyeron en los análisis; ^b Período de muestreo en el 2002: 10 V–26 VII and 4 IX–23 X; ^c Período de muestreo en el 2003: 22 IV–25 X.

Species	Counts ^a	
	2002 ^b	2003 ^c
Blue-spotted Salamander (<i>Ambystoma laterale</i>)	(21)	(75)
Spotted Salamander (<i>A. maculatum</i>)	712	2,252
Juveniles and adults	381	901
Metamorphs	331	1,350
Eastern Newt (efts only) (<i>Notophthalmus viridescens</i>)	501	1,363
Four-toed Salamander (<i>Hemidactylium scutatum</i>)	(0)	(2)
Eastern Red-backed Salamander (<i>Plethodon cinereus</i>)	163	687
Adults	116	522
Immatures	46	162
American Toad (<i>Anaxyrus americanus</i>)	(1)	(1)
American Bullfrog (<i>Lithobates catesbeianus</i>)	198	554
Adults	(2)	(6)
Juveniles	128	273
Metamorphs	68	273
Green Frog (<i>Lithobates clamitans</i>)	875	2,528
Adults	(0)	(8)
Juveniles	(64)	141
Metamorphs	804	2,359
Pickerel Frog (<i>Lithobates palustris</i>)	144	353
Adults	(4)	(4)
Juveniles	(21)	61
Metamorphs	(116)	281
Northern Leopard Frog (<i>Lithobates pipiens</i>)	(41)	(278)
Mink Frog (<i>Lithobates septentrionalis</i>)	(63)	(66)
Wood Frog (<i>Lithobates sylvaticus</i>)	209	910
Juveniles and adults	102	169
Metamorphs	106	741
Summary		
Total captures	2,930	9,069
Trap nights (tn)	98,457	152,597
Captures/100 tn	2.98	5.94

detected for red eft, adult red-backed salamanders, and juvenile-adult spotted salamanders. Although there were no differences among gap types for juvenile-adult spotted salamanders, all gaps had lower

relative abundance than closed-canopy sites in 2003 (large gaps $p = 0.00$; small gaps $p = 0.00$; natural gaps $p = 0.06$). In 2002, red efts showed lower abundance in large gaps than in small and natural gaps (table 3).

Table 2. 2003 ANOVA results of ranked difference values and Tukey's pairwise comparisons among gap treatments (difference values —reported in captures per 100 trapnights— calculated by subtracting the mean closed-canopy capture rate of a 10-ha research area from the gap capture rate): Lhg. Large harvest gap; Shg. Small harvest gap; Ng. Natural gap; Lg. Large gap; Sg. Small gap; Lg-Sg. Large gap vs. Small gap; Lg-Ng. Large gap vs. Natural gap; Sg-Ng. Small gap vs. Natural gap; I. Immature; J. Juvenile; A. Adult; M. Metamorph; E. Efts.

Tabla 2. Resultados del ANOVA para el 2003 de los valores diferenciales ordenados y la comparación por pares de Tukey entre los tratamientos de los claros (los valores diferenciales —en capturas por cada 100 noches de trapeo— calculados restando la tasa media de captura de un área de investigación de 10 ha de dosel cerrado, de la tasa de captura en el claro): Lhg. Claro de tala grande; Shg. Claro de tala pequeño; Ng. Claro natural; Lg. Claro grande; Sg. Claro pequeño; Lg-Sg. Claro grande frente a claro pequeño; Lg-Ng. Claro grande frente a claro natural; Sg-Ng. Claro pequeño frente a claro natural; I. Inmaduro; J. Juvenil; A. Adulto; M. Metamorfo; E. Individuo inmaduro terrestre.

	Mean (SE) difference values of gap type			<i>p</i>	Pairwise comparisons		
	Lhg (n = 22)	Shg (n = 22)	Ng (n = 19)		Lg-Sg	Lg-Ng	Sg-Ng
Salamanders							
Spotted Salamander							
J & A	-0.25 (0.10)	-0.39 (0.09)	-0.20 (0.08)	0.18			
M	-1.52 (0.54)	-1.96 (0.57)	0.33 (0.54)	0.00	0.95	0.00	0.00
Eastern Newt							
E	-0.19 (0.09)	-0.26 (0.15)	0.20 (0.39)	0.42			
Eastern Red-backed Salamander							
A	0.00 (0.09)	0.00 (0.07)	-0.19 (0.06)	0.10			
I	-0.06 (0.02)	0.03 (0.03)	-0.03 (0.04)	0.08	0.07	0.76	0.337
Anurans							
American Bullfrog							
M	-0.16 (0.03)	-0.07 (0.02)	0.13 (0.06)	0.00	0.00	0.06	0.02
Green Frog							
J	-0.09 (0.02)	0.01 (0.02)	0.03 (0.03)	0.00	0.00	0.01	0.88
M	-0.91 (0.14)	-0.13 (0.07)	0.30 (0.16)	0.00	0.00	0.00	0.05
Pickerel Frog							
J	0.00 (0.02)	0.06 (0.02)	0.01 (0.02)	0.05	0.88	0.05	0.16
M	0.06 (0.06)	0.24 (0.07)	0.59 (0.30)	0.19			
Wood Frog							
J & A	-0.07 (0.02)	0.05 (0.04)	0.06 (0.02)	0.00	0.00	0.00	0.31
M	-0.65 (0.06)	0.10 (0.17)	-0.25 (0.13)	0.00	0.00	0.00	0.58

Immature red-backed salamander results were partially consistent with 2003 results, where large gaps exhibited lower abundance than natural gaps.

When we limited comparisons to harvest gaps that were similar in size (< 512 m²) to natural gaps, we still found low relative abundance within harvest gaps for four groups: bullfrog metamorphs, green frog juveniles and metamorphs, and juvenile-adult wood frogs (Strojny, 2004).

Discussion

Relative abundance within gaps

Overall, there was little evidence that location within a gap (north or south aspect, edges, center) influenced amphibian abundance. Only green frog capture rates (also the species with the highest number captured) were relatively high at the edges of large gaps in

Table 3. 2002 ANOVA results of ranked difference values and Tukey's pairwise comparisons among gap treatments (difference values —reported in captures per 100 trapnights— calculated by subtracting the mean closed-canopy capture rate of a 10-ha research area from the gap capture rate): I. Immature; J. Juvenile; A. Adult; M. Metamorph; E. Efts.

Tabla 3. Resultados del ANOVA para el 2002 de los valores diferenciales ordenados y la comparación por pares de Tukey entre los tratamientos de los claros (los valores diferenciales —en capturas por cada 100 noches de trapeo— calculados restando la tasa media de captura de un área de investigación de 10 ha de dosel cerrado, de la tasa de captura en el claro): I. Inmaduro; J. Juvenil; A. Adulto; M. Metamorfo; E. Individuo inmaduro terrestre.

	Mean (SE) difference values of gap type			<i>p</i>	Pairwise comparisons		
	Lhg (n = 22)	Shg (n = 22)	Ng (n = 19)		Lg-Sg	Lg-Ng	Sg-Ng
Salamanders							
Spotted Salamander							
J & A	-0.38 (0.10)	-0.51 (0.07)	-0.07 (0.06)	0.00	0.06	0.82	0.00
M	0.08 (0.14)	-0.87 (0.27)	0.08 (0.14)	0.00	0.00	0.78	0.01
Eastern Newt							
E	-0.35 (0.06)	-0.18 (0.11)	0.14 (0.10)	0.00	0.00	0.00	0.12
Eastern Red-backed Salamander							
A	-0.05 (0.03)	0.02 (0.04)	-0.01 (0.02)	0.37			
I	-0.04 (0.02)	0.01 (0.01)	0.01 (0.01)	0.08	0.16	0.10	0.95
Anurans							
American Bullfrog							
J	0.04 (0.04)	0.00 (0.03)	0.00 (0.02)	0.80			
M	0.00 (0.02)	-0.01 (0.02)	0.00 (0.02)	0.97			
Green Frog							
M	-0.30 (0.16)	0.57 (0.27)	0.14 (0.15)	0.00	0.00	0.00	0.99
Wood Frog							
J & A	0.00 (0.02)	-0.01 (0.04)	0.00 (0.03)	0.66			
M	0.04 (0.05)	0.04 (0.07)	-0.09 (0.03)	0.00	0.71	0.00	0.04

both 2002 and 2003. In smaller gaps there was no indication of gap aspect or edge effects for any of the species. Location within small gaps also did not affect vegetation patterns (Schofield, 2003).

Relative abundance among gap types

Pairwise comparisons among gap types illustrated how sensitivity to gap size or gap origin varied among species groups. Anurans are more mobile, and therefore thought to be comparatively less physiologically constrained in open habitats than salamanders (Stebbins & Cohen, 1995; DeMaynadier & Hunter, 1998). Nevertheless, in 2003, five of seven anuran groups showed relatively lower abundance for at least one of the harvest gap treatments. Abundances of

bullfrog and green frog metamorphs were lowest in large gaps, moderately low in small gaps, and highest in natural gaps (table 2; appendix 2). Furthermore, when we compared harvest and natural gaps of the same size, we observed lower abundance in gaps of harvested origin (Strojny, 2004), thus indicating both size of gap and gap origin were important. Chan-McLeod (2003) and Patrick et al. (2006) also found anurans, especially smaller individuals, to be limited by conditions created by timber harvesting. For three other anuran groups (green frog juveniles, wood frog juvenile-adults and metamorphs) large gaps exhibited lower abundances—but small-gap and natural-gap treatments were similar (table 2; appendix 2). This suggests that small harvest gaps provided habitat similar to natural gaps even though they were, on

average, larger than natural gaps. Both metamorphs and juveniles of pickerel frogs, a species associated with open habitat (Hunter et al., 1999), showed either no differences among gaps or higher abundance within gaps (table 2, appendix 2).

Juvenile–adult spotted salamanders were the only group with lower abundance in all gap types, and they showed only limited differences among gap types (tables 2, 3). Spotted salamander metamorphs showed lower abundance in both large and small harvest gaps, but not in natural gaps (table 2; appendix 2). These results were consistent with previous research that detected lower capture rates of spotted salamander metamorphs in open–canopy areas such as clear–cuts (DeMaynadier & Hunter, 1998; Renken et al., 2004) and even partially cut stands (Patrick et al., 2006). Gap type effects for our other two salamander species were less definitive or absent.

Red efts showed reduced abundance in large harvest gaps in 2002, but no statistical differences among gap types in 2003—despite much larger sample sizes (tables 2, 3). For adult red–backed salamanders no differences among gap types were detected in 2002 or 2003. Inconsistent treatment effects were detected for immature red–backed salamanders, with relatively higher abundance in small gaps and lower abundance in large and natural gaps in 2003, while abundance in large gaps was lower relative to small and natural gaps in 2002. Although red–backed salamanders have been widely described as sensitive to forest management (Ash, 1997; DeMaynadier & Hunter, 1998; Waldick et al., 1999; Welsh & Droege, 2001; Hicks & Pearson, 2003; Knapp et al., 2003; Homyack & Haas, 2009), they may be relatively insensitive to small–scale harvesting, at least as adults (Messere & Ducey, 1998; McKenny et al., 2006).

The divergence between large and small harvest gaps (observed for metamorphs of bullfrogs, green frogs, wood frogs, and juveniles of green frogs and wood frogs) may be associated with differences in both gap size and residual structure. Per unit area, more reserve trees were left in small gaps (14 m²/ha basal area) than in large gaps (11 m²/ha basal area). Presence of residual structure such as reserve trees (Greenberg, 2001) and CWD (Moseley et al., 2004) may explain the continuation of observed amphibian activity in harvested areas. The strength of the effects in our study may be lower than in similar studies of canopy disturbance and amphibians undertaken in other regions because of the relatively cool, moist conditions found in Maine compared to forests in the southern U.S. (Semlitsch et al., 2009).

Also, when evaluating responses of amphibians to harvesting, time since harvest is important to consider (Knapp et al., 2003; Morneault et al., 2004; Homyack & Haas, 2009). In our gaps, most tree regeneration was under 0.5 m in height with tree abundance decreasing with increasing stem height (Schofield, 2003). The regeneration that had occurred in our harvest gaps 6–8 years post harvest was limited and not as advanced as one would expect to find in a clear–cut where more light is available to stimulate growth.

Management implications

To evaluate harvested and natural gaps, we focused on amphibians that inhabit upland forests, whether for foraging, dispersal, or reproduction. Disturbances that remove a greater proportion of the canopy tend to result in a greater reduction in amphibian abundance than less intense disturbances (Semlitsch et al., 2009). More specifically, research on amphibian response to partial (50%) canopy removal and complete canopy removal in the same region as our study also found variable responses depending on the species and age–class (Patrick et al., 2006). The proportions of juvenile captures for all species in common to the two studies, with the exception of pickerel frogs, were progressively lower from uncut areas to partial canopy removal to complete canopy removal areas (Patrick et al., 2006). With the relatively limited canopy disturbance of our study, we found that harvest gaps, especially small gaps, can provide habitat comparable to natural gaps for some amphibian groups, but not all. It is important to note that the differences we did detect were at a "local" scale, using the gap as the experimental unit. At a landscape scale, the closed–canopy conditions surrounding the canopy gaps likely aid in maintaining species abundance, as found by Renken et al. (2004).

There is a general consensus that long–term forest management needs to incorporate biological and physical diversity into management goals (Franklin et al., 1997; Seymour & Hunter 1999). Since forest biota and processes are closely related to structural elements (Palik et al., 2002), studies such as ours that identify and quantify differences between artificial and natural disturbances can aid foresters in designing harvests that maintain ecological integrity (DeMaynadier & Hunter, 1995; Coates & Burton, 1997; Lindenmayer et al., 2006).

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Appendix 1. Mean relative abundance (captures per 100 trap nights) of amphibians captured in 11 harvest-created gaps^a, 2003, comparing capture rates between a) northern and southern edges of a gap, and b) edges and gap centers: ^a North-south transects of the gaps were between 35–61 m long; ^b Probabilities were calculated using a multiple response permutation procedure, $\alpha = 0.10$.

Apéndice 1. Abundancia relativa media (capturas cada 100 noches de trampeo) de anfibios capturados en 11 claros creados por la industria maderera^a, en el año 2003, comparando las tasas de captura a) de los bordes norte y sur del claro, y b) de los bordes y el centro de los claros: ^a Los transectos norte-sur de los claros estaban entre 35 y 61 m de longitud; ^b Las probabilidades se calcularon utilizando un procedimiento de permutación de respuesta múltiple, $\alpha = 0,10$.

a) Aspect (north vs. south)

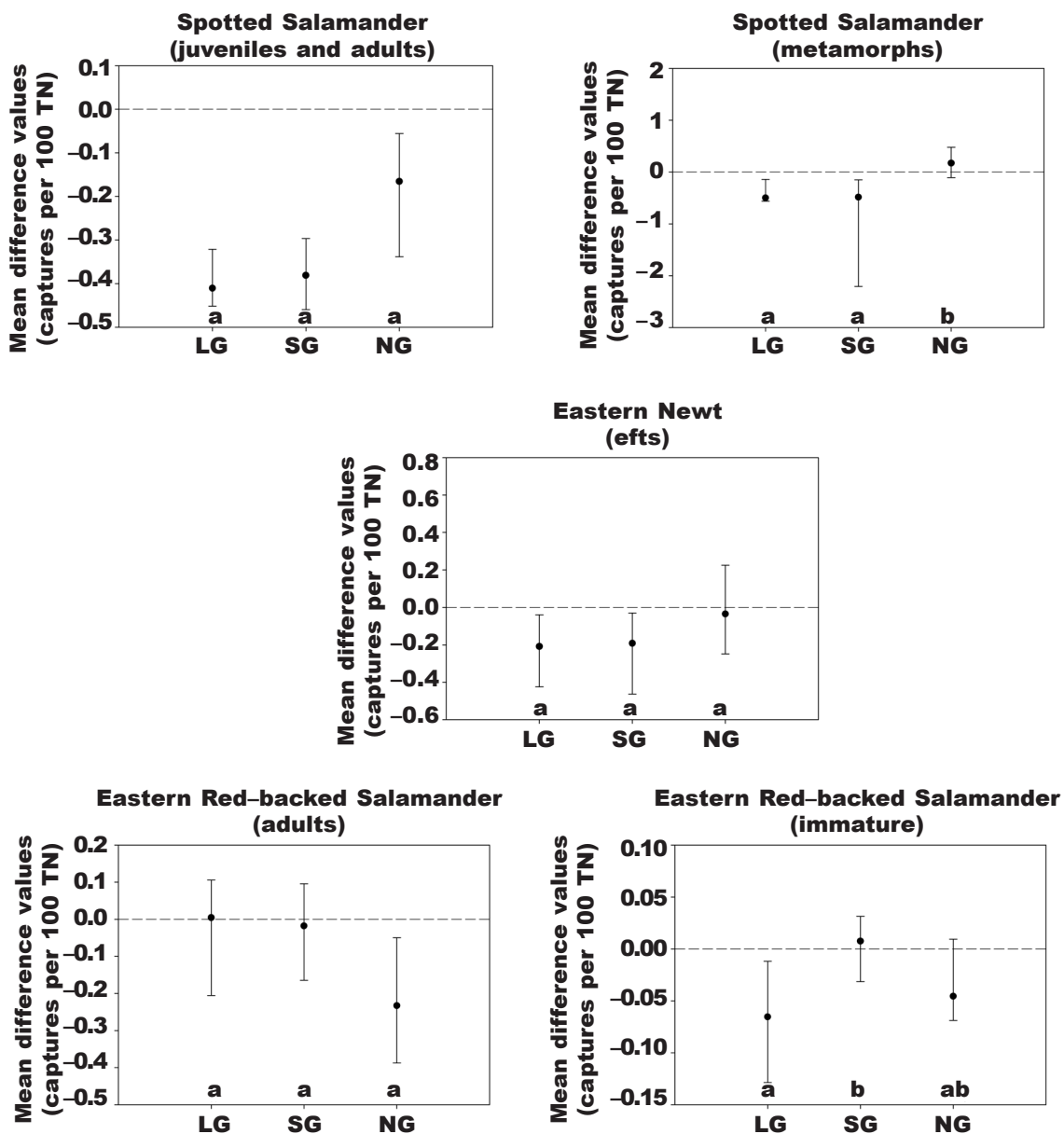
Species (number captured)	Mean (\pm 1 SE)			p^b
	North	South	Difference	
Spotted Salamander (382)	1.97 (0.80)	1.21 (0.41)	0.76 (0.45)	0.13
Juveniles and adults (129)	0.59 (0.19)	0.48 (0.09)	0.11 (0.14)	0.38
Eastern Newt (efts) (183)	0.86 (0.31)	0.66 (0.11)	0.19 (0.28)	0.59
Eastern red-backed salamander (79)	0.30 (0.06)	0.36 (0.09)	-0.06 (0.10)	0.64
Immatures (18)	0.05 (0.02)	0.10 (0.03)	-0.05 (0.03)	0.19
Adults (61)	0.25 (0.06)	0.26 (0.09)	-0.01 (0.09)	0.93
Bullfrog (101)	0.35 (0.10)	0.49 (0.12)	-0.14 (0.10)	0.13
Green Frog (506)	1.90 (0.52)	2.33 (0.57)	-0.43 (0.50)	0.33
Wood Frog (85)	0.32 (0.06)	0.39 (0.10)	-0.07 (0.09)	0.60
Metamorphs (61)	0.47 (0.11)	0.59 (0.18)	-0.11 (0.16)	0.40

b) Edge vs. gap center

Species (number captured)	Mean (\pm 1 SE)			p^b
	Gap edge	Gap center	Difference	
Spotted Salamander (249)	1.43 (0.57)	1.69 (0.86)	-0.27 (0.66)	0.52
Juveniles and adults (81)	0.50 (0.11)	0.52 (0.22)	-0.02 (0.22)	0.80
Eastern Newt (efts) (103)	0.81 (0.31)	0.49 (0.08)	0.32 (0.28)	0.38
Eastern red-backed salamander (49)	0.30 (0.09)	0.32 (0.10)	-0.02 (0.14)	0.70
Adults (35)	0.23 (0.10)	0.22 (0.07)	0.01 (0.13)	0.79
Bullfrog (72)	0.47 (0.11)	0.43 (0.08)	0.04 (0.09)	0.53
Green Frog (336)	2.52 (0.68)	1.74 (0.50)	0.78 (0.31)	0.02
Wood Frogs (57)	0.42 (0.10)	0.29 (0.09)	0.13 (0.11)	0.29
Metamorphs (40)	0.62 (0.19)	0.43 (0.14)	0.19 (0.13)	0.23

Appendix 2. Median difference values with 90% confidence intervals for species/age groups of amphibians captured in the Penobscot Experimental Forest, 2003. Difference values were calculated by subtracting the mean capture rates of closed-canopy plots from gap capture rates for their respective research areas. The x-axis shows treatment type: large harvest gap (n = 22), small harvest gap (n = 22), and natural gap (n = 19). Letter values at the base of each plot show Tukey's pairwise comparison results on the ranked difference values. Shared letters indicate no difference ($\alpha > 0.10$): LG. Large Gap; SG. Small gap; NG. Natural Gap.

Apéndice 2. Valores diferenciales de la mediana con un 90% de intervalos de confianza para los grupos de especie/edad de anfibios capturados en el Bosque Experimental de Penobscot, en el 2003. Los valores diferenciales se calcularon restando las tasas medias de captura de las zonas de dosel cerrado de las tasas de captura de los claros en sus áreas de investigación respectivas. El eje x corresponde al tipo de tratamiento: claro de tala grande (n = 22), claro de tala pequeño (n = 22), y claro natural (n = 19). Las letras en la base de cada registro representan los resultados de la comparación por pares de Tukey de los valores diferenciales ordenados. Las letras compartidas indican que no existía diferencia alguna ($\alpha > 0,10$): LG. Claro grande; SG. Claro pequeño; NG. Claro natural.



Appendix 2. (Cont.)

