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# Fire as Friend and Foe of Amphibians: a Reply

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The intermediate disturbance hypothesis (Connell 1978) provides a conceptual model for understanding how prescribed burns restore and maintain biological diversity in fire-adapted ecological communities. It is a rich theory (Roxburgh et al. 2004) that explains how the magnitude and frequency of disturbance, and time since disturbance, affect species richness, evenness, and abundance. In our paper (Schurbon & Fauth 2003), we tested whether diversity of a nontarget taxon—amphibians—was highest in temporary ponds with an intermediate time since last burn. We concluded that in the Francis Marion National Forest (FMNF), South Carolina (U.S.A.), amphibian species richness increased linearly with time since last burn over the 0- to 12-year interval we sampled, and we recommended burning every 3–5 years to maintain both the desired plant assemblages and amphibian diversity. Critiques of our paper by Means et al. (2004 [this issue]) and Robertson and Ostertag (2004 [this issue]) provide testable alternative hypotheses to explain the pattern of amphibian diversity we attributed to time since fire (Schurbon 2000; Schurbon & Fauth 2003). Here, we (1) test several of their hypotheses, (2) demonstrate through autecological analyses why longer fire-return intervals increase amphibian species richness, and (3) explain why conservation biologists and restoration ecologists might choose different fire regimes.

To make our response complete, we provide information that was not communicated in previous publications (Schurbon 2000; Schurbon & Fauth 2003) and that probably should have been. Past burns were conducted on our study sites from late November to May, which is the prescribed-burn season in the FMNF. Four burns occurred during our study on the following dates: 30 November 1999, 26 February, 10 March, and 12 April 2000. During this interval, amphibian migrations occurred on 15 December 1999 and 6 and 26 January for ambystomatid

salamanders; 2 March 2000 for *Pseudacris crucifer*; 20 March 2000 for *Rana virgatipes* and *Pseudacris nigrita*; and 26 April 2000 for *Bufo terrestris*. We conducted anuran calling censuses from 1 hour after sunset to between 2400 and 0200 hours. Ponds within spatiotemporal blocks (Schurbon 2000) were visited in random sequence, so, contrary to the claim of Means et al., estimates of species richness were not biased. Ponds burned more recently were on a shorter fire-return cycle, so these two measures of disturbance were positively correlated. Thus, contrary to the argument of Means et al., it is appropriate to make recommendations about fire-return intervals based on our data.

We carefully crafted the sampling design and analyses to avoid problems such as pseudoreplication (Hurlbert 1984). In contrast to Robertson and Ostertag, we avoided response variables such as the Shannon-Weiner diversity index because it confounds species richness and evenness (Hurlbert 1971). We used counts of the minimum number of amphibians because they are conservative. Simple algebra on the linear equation provided by Means et al. demonstrates that this is true because detection probabilities cannot exceed 1. It is also self-evident that the probability of detecting an amphibian caught in a trap or at the bottom of a pitfall does not vary among burn types. Logical application of simple rules—for example, amphibians can increase in snout-vent length over time but do not shrink; tadpoles can metamorphose into juveniles but not the reverse—made it easy to avoid recounting individuals even among sampling events.

To ensure that we did not miss migrating amphibians, we opened pitfall traps even during marginal conditions for amphibian activity (Fig. 3 in Schurbon 2000). Thus, on 184 of 240 sampling days (77%) no amphibians were caught in pitfalls. Of the five species that Means et al. note were missing from our species list, *Ambystoma tigrinum* has not been reported in the FMNF in over 13 years (Schurbon & Fauth 2003) and *Eurycea quadridigitata* was an uncommon species. During sampling conducted from 1991–2003, we did not find *E. quadridigitata* in any

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of the 88 ponds we sampled (Fauth 1999; Eason & Fauth 2001; J.E.F. unpublished data). *Ambystoma cingulatum*, *Hyla gratiosa*, and *Rana capito* also were uncommon. During 1991–2003 we found these three species in natural ponds within 6 of 81 (7.4%) forest compartments, none of which were selected (at random) for inclusion in our study (Schurbon & Fauth 2003). Mean species richness in our study ( $8.5 \pm 0.76$ , mean and SE; Schurbon & Fauth 2003) did not differ significantly from that of 1-year studies conducted in 1996–1997 ( $9.6 \pm 0.64$ ,  $n = 21$  ponds; Fauth 1999; Eason & Fauth 2001), 2000–2001 ( $8.1 \pm 0.84$ ,  $n = 12$ ; J.E.F. unpublished data) and 2002–2003 ( $9.8 \pm 0.69$  species,  $n = 18$ ; J.E.F. unpublished data), which included at least twice as many trapping sessions and calling censuses. In summary, we sampled all ponds in our study with equal intensity and comprehensively enough to accurately reflect amphibian assemblages in the FMNF (Fauth 1999; Eason & Fauth 2001).

Means et al. and Robertson and Ostertag suggest several testable hypotheses. Both groups suggest that variation among burn categories in terrestrial vegetation, hydroperiod, or burn season might explain observed patterns of amphibian abundance and diversity. We tested these hypotheses by locating ponds on U.S. Forest Service stand maps and recording from them the forest type immediately surrounding each pond. Stands included three pine-dominated forest types, one hardwood-pine mixture, and two hardwood-dominated forest types (Fig. 1). We scored each pond as within either a pine or a non-pine stand; we considered the hardwood-pine mixed stand to be a non-pine stand. We recorded three hydroperiod parameters: maximum pond depth in meters ( $0.65 \pm 0.078$ ), days with water ( $300 \pm 12.8$ ), and number of times a pond dried completely ( $1.9 \pm 0.27$ ). We also recorded burn season as winter (November–February,  $n = 4$ ) or spring (March–May,  $n = 8$ ). Records were unavailable for the 12-year category, so we excluded those ponds from analysis.

The  $G$  tests of independence (Sokal & Rohlf 1995) showed that terrestrial vegetation was independent of burn category ( $G = 3.82$ ,  $p = 0.43$ ,  $df = 4$ ), and, when added to regression models (Schurbon & Fauth 2003), the dummy variable for terrestrial vegetation did not explain significant variation in amphibian species richness, evenness, or total abundance (all  $F < 0.46$ ,  $p > 0.53$ ). Similarly, none of the hydroperiod parameters varied significantly among burn categories (one-way analysis of variance [ANOVA], all  $F_{4,10} < 0.57$ ,  $p > 0.68$ ) or explained significant variation in amphibian species richness, evenness, or total abundance in regression models (all  $F < 4.2$ ,  $p > 0.11$ ). Burn season was also independent of time since burn ( $G = 3.8$ ,  $p = 0.28$ ,  $df = 4$ ). The effect of time since burn remained virtually unaltered and was always statistically significant in all models. Therefore, variation in terrestrial vegetation, hydroperiod, and burn season are not viable hypotheses for the diversity and abundance patterns we reported (Schurbon & Fauth 2003). This is

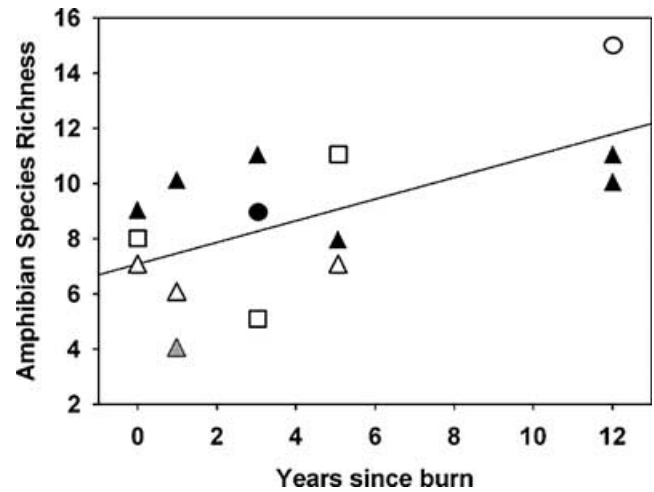


Figure 1. Amphibian species richness as a function of years since burn and forest type of the surrounding upland, as defined by U.S. Forest Service stand types. Triangles denote pine stands composed of >70% of the dominant species by basal area: open triangles, longleaf pine (*Pinus palustris*); closed triangles, loblolly pine (*P. taeda*); shaded triangle, pond pine (*P. serotina*). The open square denotes a hardwood-pine type composed of 51–69% of the codominant species by basal area, bottomland hardwood-yellow pine. Circles denote hardwood types composed of >70% of the dominant species by basal area: open circle, sweet gum–Nuttall oak–willow (*Liquidambar styraciflua*–*Quercus nuttallii*–*Salix* sp.); closed circle, brush species, which includes titi (*Cyrilla racemiflora*). Regression equation: species richness =  $7.1 + 0.4$  years since burn;  $F_{1,13} = 8.1$ ,  $p < 0.02$ ,  $R^2 = 0.38$ . Data are from Schurbon and Fauth (2003).

not surprising, because the models we reported fit the data well and left little variation unexplained ( $1 - R^2 = 1.5$ – $14.3\%$ ). The only realistic way for a parameter to remove time since fire as a significant predictor of amphibian diversity and abundance would be if it were strongly correlated with time since last burn (e.g., fire-return interval).

Means et al. and Robertson and Ostertag infer from our data that species richness increased with time since burn because nonspecialist amphibian species were added to the assemblage. We tested this hypothesis in three ways. First, we removed each species from the data set, recalculated species richness, and determined the correlation with years since the previous burn. This jackknifing approach determined the influence of each species on the overall pattern. Second, we used logistic regression to test whether the presence and absence of each species depended on years since burn. This is an autecological approach that can identify species that are fire dependent and fire sensitive. Third, we used linear regression or

**Table 1.** Influence of individual amphibian species on the correlation between species richness and time since fire.<sup>a</sup>

Species	r'	% D
<i>Rana clamitans</i> , <i>Hyla squirella</i>	0.62	0-1
<i>R. sphenoccephala</i> , <i>Bufo terrestris</i> , <i>Ambystoma talpoideum</i>	0.61-0.63	2
<i>Plethodon variolatus</i> , <i>Pseudacris nigrita</i>	0.62-0.63	3
<i>Ambystoma maculatum</i>	0.61	4
<i>Acris gryllus</i> , <i>H. femoralis</i> , <i>Ambystoma opacum</i> , <i>Pseudacris</i> <i>ocularis</i> , <i>Scaphiopus holbrookii</i>	0.60-0.65	5
<i>Amphiuma means</i> , <i>R. catesbeiana</i>	0.60-0.64	6
<i>B. quercicus</i> , <i>Pseudacris ornata</i> , <i>Siren intermedia</i> , <i>Gastrophryne</i> <i>carolinensis</i>	0.64-0.65	7-9
<i>Ambystoma mabeei</i>	0.58	11
<i>Notophthalmus viridescens</i> <i>louisianensis</i>	0.57	16
<i>H. cinerea</i> , <i>H. chrysoyelis</i>	0.55	19-20
<i>Pseudacris crucifer</i>	0.510 <sup>b</sup>	41

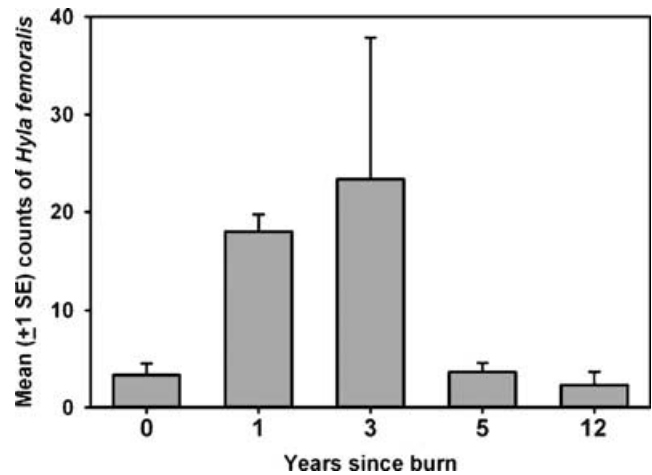
<sup>a</sup>Table entries are correlations ( $r'$ ) with each species removed and percent difference (%D) from the full model with all species included ( $r = 0.62$ ).

<sup>b</sup>Correlation not statistically significant at  $\alpha = 0.05$ ; critical value of  $r = 0.514$ ,  $v = 13$ .

one-way analysis of variance to test the hypothesis that the abundance of each species was independent of years since burn. These analyses can reveal numerical responses of individual species to fire regime.

*Pseudacris crucifer* was the only species that, once removed from the model, made the correlation between amphibian species richness and fire nonsignificant (Table 1). The model was sensitive to the removal of other species, including four that were significantly more likely to be found in ponds that had not been burned in 4-8 years: *Pseudacris crucifer*, *Notophthalmus viridescens louisianensis*, *Hyla cinerea*, and *H. chrysoyelis*. Thus, Means et al. and Robertson and Ostertag deduced the correct mechanism underlying the significant increase in amphibian diversity with time since burn in the FMNF: addition of new species in longer burn intervals. However, we disagree with their assertion that *Pseudacris crucifer*, members of the *H. chrysoyelis*-*Hyla versicolor* species complex, and subspecies of *Notophthalmus viridescens* are not characteristic of (longleaf) pine ecosystems. All three are dominant components of amphibian assemblages in the sandhills of North and South Carolina (Resetarits & Fauth 1998), the FMNF, pine barrens in upstate New York and New Jersey (e.g., Morin 1995), and elsewhere.

The abundance of *H. femoralis* was significantly higher in ponds within the intermediate burn categories than in the two extremes (Fig. 2), suggesting that it is a fire-dependent species. On average, burning during the study increased its minimum abundance 60%, from 8.7 to 14 in-



**Figure 2.** Mean ( $\pm 1$  SE) counts of pine woods treefrog (*Hyla femoralis*) as a function of time since burn in the study by Schurbon and Fauth (2003). Differences among means were statistically significant: Welch analysis of variance,  $F_{4,4.8} = 11.70$ ,  $p < 0.011$ .

dividuals per pond. No other amphibian species had significant linear or nonlinear responses to time since burn. In a recent study within the FMNF, however, counts of *Acris gryllus* and *Ambystoma talpoideum* were significantly lower and counts of *Hyla chrysoyelis* were significantly higher in ponds within burned stands than in those within unburned stands (J.E.F., unpublished data). *Ambystoma talpoideum* is a keystone predator (Fauth 1999) and the most common salamander in the FMNF. Our results suggest that the shortest burn intervals (1-2 years) advocated by Means et al. would adversely affect its abundance.

However, we see no fundamental conflict between the fire regimes advocated by us and the two groups of respondents. Both are ecologically valid. Prescribed burning regimes should vary based on restoration or conservation management goals. If the primary goal is to restore longleaf pines, ecologists should favor frequent fire-return intervals. Means et al. take this view and suggest that, for amphibians, if you burn it they will come, and if they do not come then they must not belong in the community. We weighted all amphibian species equally because they all are components of the native ecosystem. The FMNF system includes a mixture of fire-dependent coastal-plain endemics, such as *Ambystoma cingulatum* and *Rana capito*, and fire-sensitive northern and upland species, such as *N. v. louisianensis*, *Pseudacris crucifer*, and *H. chrysoyelis*. To maintain diversity within a fire-dominated matrix, conservation biologists should favor a longer fire-return interval of 3-5 years (Schurbon & Fauth 2003; also see Mushinsky 1985, 1986). Neither recommendation deviates far from historic fire intervals of 2-4 years (Frost 1995) or neglects the importance of frequent

fires, which are vital to proper ecosystem function and structure (Brennan et al. 1998; Chapin et al. 2000).

Because of limited resources, forest managers often struggle to implement prescribed burning regimes that meet restoration goals. An understanding of how different fire regimes affect both target and nontarget taxa is needed to allocate resources and to design management strategies that maximize the conservation value of North American forests. It should be obvious that homogeneous burning regimes and single-species management are not sustainable means of managing fire-dependent ecological communities. Current fire management in the FMNF exemplifies how variable burns can maintain and restore diverse native plant and animal species even after a catastrophic disturbance such as Hurricane Hugo (Streng et al. 1993; Conner et al. 2001; Schurbon & Fauth 2003, this paper). Quantifying the responses of individual amphibian species to fire regimes, such as we have done here, allows forest managers to more effectively manage this oft-forgotten taxon. We support Pilliod et al. (2003) in their call for population-level research to better determine how prescribed burning affects amphibians, a topic on which there remains a surprising dearth of information. Careful scrutiny of the ideas exchanged in this set of papers (Schurbon & Fauth 2003, this paper; Means et al. 2004; Robertson & Ostertag 2004) will suggest fertile avenues for future research.

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