

# Habitat restoration affects immature stages of a wetland butterfly through indirect effects on predation

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**Abstract.** Habitat loss worldwide has led to the widespread use of restoration practices for the recovery of imperiled species. However, recovery success may be hampered by focusing on plant communities, rather than the complex suite of direct and indirect interactions among trophic levels that occur in natural systems. Through a factorial field experiment, we tested the effects of wetland restoration on egg and juvenile survival of a locally rare butterfly, *Satyrodes appalachia*, via tree removal and damming. Tree removal more than tripled *S. appalachia* host plant abundance, but neither restoration action directly affected *S. appalachia* egg and juvenile survival. Instead, we found strong indirect effects of habitat manipulation on *S. appalachia* egg and juvenile survival that were mediated through predation. The interaction of tree removal and damming significantly decreased predation of *S. appalachia* eggs relative to each treatment alone. Damming alone had a significant positive indirect effect on the survival of *S. appalachia* juveniles, likely because increases in standing water reduced predator access. Our results emphasize the need for experiments that evaluate the demographic responses of imperiled species to habitat restoration prior to management action and quantify potential indirect effects mediated through higher trophic levels.

**Key words:** *Appalachian Brown*; butterfly; indirect effects; *Neonympha mitchellii francisci*; predation; restoration; *Satyrodes appalachia*; *St. Francis' satyr*.

## INTRODUCTION

Habitat destruction and degradation are critical threats to biodiversity (Wilcove et al. 1998). To ameliorate reductions in habitat quantity or quality, land managers are often tasked with creating or restoring habitat. However, the widespread use of restoration to increase viable habitat for imperiled species has resulted in few successes (Zedler et al. 2003, Holl and Hayes 2006, Suding 2011), and in some cases has resulted in the creation of habitat that reduces rather than restores biodiversity (Breininger and Carter 2003, Robertson et al. 2013). This failure may be in part because the “success” of restoration is often assessed using general indicators of habitat quality, such as plant community composition (Cortina et al. 2006, Suding 2011), rather than detailed demographic responses of imperiled species. Changes to habitat that benefit a rare species may also benefit or impede competitors and consumers (DeCesare et al. 2010), which may result in strong indirect effects that oppose any direct effects of habitat modification. Here, we take an experimental approach to understand the direct and indirect effects of

restoration on the survival of immature stages of a locally rare butterfly species.

Complex interactions between abiotic conditions, resources, and natural enemies have not been well studied within the context of restoration, despite a long history of research showing that both bottom-up and top-down forces influence populations (Hairston et al. 1960, Price et al. 1980, Hunter and Price 1992, Power 1992, Polis and Strong 1996, Hunter 2001). Gotthard (2000) demonstrated in a laboratory experiment that increased light led to increased growth rates in *Pararge aegeria* (Speckled Wood butterfly) larvae, which in turn resulted in predation rates that were 30% higher than for slow growing larvae. Importantly, the results of Gotthard (2000) suggest that manipulations of the environment via restoration may have strong direct and indirect effects in natural systems. Further, restoration actions are often complex and include manipulation of many habitat features simultaneously, such as increases in light, water, and nutrients, or the removal of unwanted species (Suding 2011). Restoration actions may have non-additive effects on the demographic response of the target species, and interactive effects may vary across life stages. An understanding of the complex interactions between habitat manipulation, bottom-up and top-down forces, and demography may be critical for the successful recovery of rare and imperiled species.

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The direct (bottom-up) and indirect (top-down) effects of habitat restoration are also likely to vary in strength and direction over space (Gripenberg and Roslin 2007) and time (Power 1992) with important consequences for restoration actions. For example, the impact of top-down forces may increase as primary productivity increases (Hunter et al. 1997, Forkner and Hunter 2000), such that if habitat restoration improves productivity, predation effects may become more important. Alternatively, increases in primary productivity may relax predation pressure on herbivores because of density-dependent interference among predators (Abrams 1993). Restoration experiments provide a unique opportunity to test fundamental ecological questions about how changes in plant communities affect the top-down regulation of herbivore populations.

Adding further complication, top-down and bottom-up impacts of restoration may vary among the life stages of a target species (Price et al. 1980). Predation effects appear to intensify as herbivorous insects develop from eggs to larvae, with predation being the largest source of mortality for late-instar, leaf-eating caterpillars (Kristensen 1994, Cornell and Hawkins 1995, Hawkins et al. 1997, Cornell et al. 1998). Eggs and early-instar caterpillars, on the other hand, are more vulnerable to desiccation and low plant quality than are later immature stages (Cornell and Hawkins 1995). For species with non-overlapping generations, such as many Lepidoptera, survival in each life stage is equally important to population growth (Caswell 2001). This means that the negative top-down or bottom-up effects of restoration on early stage survival must be accompanied by proportionate improvements in later life cycle events in order for restoration to have an overall neutral or, ideally, beneficial effect on population growth.

One way to better understand how multiple restoration activities interact with top-down forces in their effects on target species is to perform a factorial experiment (Hunter 2001). We conducted such an experiment to assess the direct and indirect effects of restoration on *Satyroides appalachia* Chermock, the Appalachian brown butterfly. Specifically, in large-scale field plots, we crossed tree removal and wetland damming (two restoration treatments aimed at enhancing the abundance, and perhaps quality, of the butterfly's larval host plants, *Carex* spp.) with a predator exclusion treatment, and measured survival of the butterfly's eggs and juvenile stages (larvae and pupae). We hypothesized that tree removal would increase host plant abundance and lead to increased egg abundance, but also influence predation intensity, resulting in indirect negative effects of restoration on egg and juvenile survival. We hypothesized that damming treatments would increase standing water, reduce ground predator access to eggs and juveniles, and result in weak indirect positive effects increasing survival.

## METHODS

### *Study site and species*

Research was conducted at Fort Bragg, North Carolina, USA, a 65 000-ha military installation dominated by longleaf pine forest punctuated with headwater streams. In this system, headwater streams tend toward closed canopy riparian forest via successional processes. Herbaceous, sedge-dominated wetlands are created by disturbances such as beaver colonization or fire (Bartel et al. 2010), and are an ephemeral but important habitat for many wetland-dependent species. Human-caused destruction of habitat (e.g., agriculture, roads, development), the local extirpation of beavers, and the suppression of fire in riparian corridors has reduced the amount of herbaceous, sedge-dominated wetlands found on and around Ft. Bragg and has led to a significant decline of wetland butterflies (Kuefler et al. 2008).

*Satyroides appalachia* is a locally rare, bivoltine butterfly at our study site that overwinters as third- or fourth-instar larvae. The host plants of *S. appalachia* are thought to be primarily sedge (e.g., *Carex*) species (Kuefler et al. 2008). We chose *S. appalachia* as a study organism because it may serve as a surrogate for other rare wetland-dependent butterflies, such as the federally endangered *Neonympha mitchellii francisci* (St. Francis' satyr; Hudgens et al. 2012) for which ethical concerns preclude most experimental manipulation.

### *Experimental design*

In May of 2011 we established four blocks of four 30 × 30 m experimental plots in watersheds that harbored populations of *S. appalachia*. In each block, plots were randomly assigned to one of four treatments in a factorial design: (1) manual removal of most trees; (2) installation of temporary dams; (3) both tree removal and installation of dams; and (4) no manipulation. Tree removal was intended to increase light availability within wetlands to encourage herbaceous plant growth. We intentionally left ~10% of the trees standing in order to mimic the canopy structure found in beaver-created wetlands in our area. Damming was intended to increase soil moisture and the amount of standing water, a key requirement for sedges. In dammed plots, we installed 0.5 m high and 1 m wide water-filled coffer dams (Aquadam, Scotia, California, USA) across the width of the downstream edge of the plot, which inundated ~10 m of the downstream portion of the plot and increased soil moisture throughout the plot. These restoration treatments were chosen in consultation with land managers to insure our experiment informed potential actions for habitat restoration. Following application of the treatments, one dammed plot was colonized by beavers and therefore excluded from the experiment, making one of the blocks incomplete.

Before initiating the restoration treatments, we established 27 uniformly distributed 1.5 × 1.5 m

permanent sub-plots within each plot to estimate the response of the plant community to restoration. In April of 2011, prior to restoration, and again in April of 2012, we estimated percent cover of all major vegetation types (e.g., forbs, grasses, shrubs) and percent cover of common sedge species that were thought to be potential host plants of *S. appalachia*.

#### *Egg survival*

To estimate the direct and indirect (predation-mediated) effects of restoration treatments on *S. appalachia* egg survival, we placed greenhouse-raised, potted *Carex mitchelliana* plants with a known number of eggs into our established experimental restoration plots and counted the number of eggs that remained after 48 hours. We first caged wild-caught *S. appalachia* females on potted sedge plants in a greenhouse at Ft. Bragg, and then counted the number of eggs laid. The number of eggs on each plant at time of deployment varied from 3 to 24 (mean = 11).

Each restoration plot received one pair of potted sedges, one of which was randomly assigned to a predator exclusion treatment in which plants were enclosed in a cage constructed from a 20-L paint strainer of fine mesh fabric (Trimaco, Morrisville, North Carolina, USA) supported by bent wire. A 15-cm band of sticky resin (Tanglefoot Company, Grand Rapids, Michigan, USA) was applied to pots to exclude crawling predators. The second plant in each pair was accessible to all predators. Paired plants were placed in the center of each restoration plot on dry ground within 5 m of each other. All of the restoration treatments within a block received plants simultaneously; however, because the number of females that could be captured for egg laying at any one time was limited, the timing of deployment differed among blocks. All plants were removed from the field after 48 hours and the number of eggs remaining was recorded. This experiment was conducted during both *S. appalachia* flight periods (15 May–15 June and 7 July–7 August).

#### *Juvenile survival*

To estimate survival over the larval and pupal stages, we deployed a known number of larvae into experimental arenas created in each plot and counted the number of butterflies that emerged. We constructed larval arenas by removing the ends of a standard 208-L polyethylene food grade drum and cutting the remainder into thirds, resulting in an approximately 57 × 35 cm ring. At six randomly chosen locations in each plot, rings were buried approximately 10 cm into the ground surrounding naturally occurring, mature *C. mitchelliana*. In one block with low sedge abundance, field cages were placed around greenhouse raised and transplanted *C. mitchelliana* plants. We randomly assigned each arena to a predator-free or predator-accessible treatment. Predator-free arenas were enclosed with tulle netting that was secured to the outside of the rings using nylon straps and

tied at the top of a vertical support structure to hold the fabric off the plants. All potential predators, mainly spiders and ants, were manually removed from predator-free arenas prior to the addition of larvae. We removed on average 4 spiders and 1 ant from each arena. We reared larvae from eggs laid by wild caught *S. appalachia* on potted *C. mitchelliana* plants in the greenhouse. Five larvae varying in age from first to third instars (most commonly second instars) were placed into each arena in a block on the same day. Arenas accessible to predators remained open during larval development. After six weeks, all arenas were checked approximately every other day for the presence of pupae. Once pupae were observed, arenas were enclosed with tulle netting to facilitate capture of emerging adults. Arenas were checked daily for newly emerged adults until no butterflies were found for five consecutive days. Our experiment estimates joint larval and pupal (i.e., “juvenile”) survival.

#### *Statistical analysis*

To assess changes in the plant community resulting from restoration treatments, we performed a Before After Control Impact (BACI) linear mixed effects analysis using the lmer function in the lme4 package (Bates et al. 2013) and the ANOVA function in the car package (Fox and Weisberg 2011) in the statistical platform R 3.0.2 (R Development Core Team 2013). Our model contained fixed effects of tree removal, damming, and year, all interaction terms, and a random effect of plot. We used a Type II Wald chi-square test to evaluate the effect of restoration on: (1) percent cover of *Carex mitchelliana* (the most likely host plant species in our plots); (2) percent cover of all sedges; and (3) percent cover of all understory vegetation.

We assessed whether restoration treatment had direct and indirect effects on egg and juvenile survival using generalized linear mixed models (GLMMs) with the function glmer from the lme4 package. The numbers of eggs or juveniles that survived to the end of the experiment were treated as binomial responses. In all analyses, tree removal, damming, predation treatment, and their interactions, as well as flight period for egg survival, were treated as fixed effects; block and plot were treated as crossed random effects. We used Wald Z tests to assess the statistical significance of the fixed effects.

To assess direct effects, we tested for effects of restoration treatments and their interaction on survival using only the predator-free treatments. For egg survival, we began with a model that included the three-way interaction between tree removal, damming, and flight period (plus all lower-order terms) to test whether the main and interactive effects of the restoration treatments differed between flight periods. Because this three-way interaction was not significant ( $P = 0.14$ ), we fit a model with all two-way interactions between tree removal, damming, and flight period. We

used the same model (without flight period) to assess the direct effect of restoration treatments on juvenile survival. To assess the net effect of restoration treatments (i.e., direct and indirect effects combined), we used the same models as for direct effects, but only used data from the predator-accessible treatment.

Indirect effects of restoration mediated through predation were investigated by comparing the survival in predator-free and predator-accessible treatments as a function of restoration treatment. An effect of restoration treatment on predation intensity would be indicated by a significant tree removal  $\times$  predation treatment, damming  $\times$  predation treatment, or tree removal  $\times$  damming  $\times$  predation treatment interaction. For egg survival, the four-way interaction between tree removal, damming, predation treatment, and flight period was not significant ( $P = 0.57$ ); therefore we dropped the four-way interaction from the model but included all three-way interactions. For juvenile survival, the three-way interaction between the tree removal, damming, and predation treatments was not significant ( $P = 0.76$ ), so we fit a model with all two-way interactions. To estimate the mortality of eggs and juveniles due to predation, we calculated a mortality response ratio by dividing the survival rate in the predator accessible treatment by the survival rate in the predator-free treatment and subtracting this value from 1.

## RESULTS

### *Effects of restoration on vegetation*

The removal of trees had strong, positive effects on understory vegetation (Appendix: Table A1, Fig. A1). Total understory vegetation cover increased significantly from  $33.87\% \pm 7.60\%$  (mean  $\pm$  SE) in 2011 to  $56.66\% \pm 7.84\%$  in 2012 in plots that had trees removed ( $P < 0.001$ ). Cover of *C. mitchelliana* increased significantly from  $3.19\% \pm 1.34\%$  in 2011 to  $7.36\% \pm 3.2\%$  in 2012 after trees were removed ( $P = 0.02$ ). Tree removal also significantly increased the percent cover of all sedge species combined from  $6.54\% \pm 4.19\%$  to  $22.41\% \pm 5.52\%$  ( $P < 0.001$ ). Damming and the interaction between tree removal and damming did not significantly affect *C. mitchelliana* cover ( $P = 0.77$ ;  $P = 0.98$ ) nor total sedge cover ( $P = 0.37$ ;  $P = 0.52$ ), but there was a significant negative effect of damming treatment on total understory vegetation cover ( $P < 0.001$ ; Appendix: Fig. A1). The interaction between tree removal and damming treatments for total cover was not significant ( $P = 0.08$ ).

### *Direct effect of restoration on egg and juvenile survival*

Restoration treatment (i.e., changing light and water availability) had mixed direct effects on the survival of eggs and juveniles (Appendix: Fig. A1, Table A2). There was a significant negative effect of tree removal on eggs ( $P = 0.05$ ) but not on juveniles ( $P = 0.12$ ). The effect of damming was not significant for either eggs or juveniles ( $P = 0.94$  and  $P = 0.41$ , respectively). The interaction between tree removal and damming was significantly

positive for eggs ( $P = 0.05$ ) but not juveniles ( $P = 0.68$ ). When protected from predation, the survival of eggs differed significantly between flight periods (Appendix: Table A2) for unknown reasons, and varied across the restoration treatments from 78% to 94% during the first flight period and from 47% to 58% during the second flight period (Fig. 1A; Appendix: Table A3). Juvenile survival in predator free enclosures ranged from 35% to 59% across the restoration treatments (Fig. 1A).

### *Indirect effects of restoration on egg and juvenile survival mediated through predation*

The restoration treatments differed in their effects on the intensity of predation (Appendix: Table A2). Across all restoration treatment combinations, predator exclusion had a significant positive effect on egg survival ( $P < 0.001$ ). Although egg predation appeared to be more intense in plots with only tree removal or damming relative to controls (Fig. 1B), the tree removal  $\times$  predator treatment and damming  $\times$  predator treatment interactions were not significant ( $P = 0.23$  and  $0.92$ , respectively). However, the interaction of tree removal and damming significantly decreased the predation of eggs relative to what would be expected from the additive effects of tree removal and damming alone (Fig. 1B; tree removal  $\times$  damming  $\times$  predation treatment interaction:  $P < 0.001$ ). Across all restoration treatments, predator exclusion had a significant, positive effect on juvenile survival ( $P < 0.01$ ). Damming significantly decreased predation of juveniles (Fig. 1B, damming  $\times$  predation treatment interaction,  $P = 0.02$ ), but there was no significant effect of tree removal (tree removal  $\times$  predation treatment interaction,  $P = 0.26$ ).

### *Net effects of restoration on egg and juvenile survival*

The net effect of restoration is the combination of direct effects (i.e., bottom-up and abiotic environmental effects) and indirect effects (predation). When exposed to predation, egg survival in the different restoration treatments varied from 32% to 74% during the first flight period and from 12% to 56% in the second flight period (Fig. 1C; Appendix: Table A3). There was no significant effect of tree removal ( $P = 0.36$ ), damming ( $P = 0.68$ ), or their interaction ( $P = 0.38$ ) on the survival of eggs exposed to predators (Appendix: Table A2). Survival of juveniles that were exposed to predation ranged from 7% to 37% (Fig. 1C, Appendix: Table A3). There was a significant negative effect of tree removal on juvenile survival ( $P = 0.04$ ), but no significant effect of damming ( $P = 0.25$ ) or the interaction between tree removal and damming ( $P = 0.80$ ; Appendix: Table A2).

## DISCUSSION

Restoration of wetland habitat via the removal of trees and damming had strong direct effects on the plant community. Tree removal resulted in a three-fold increase in the percent cover of all sedges and a more than two-fold increase in the percent cover of *Carex mitchelliana*,

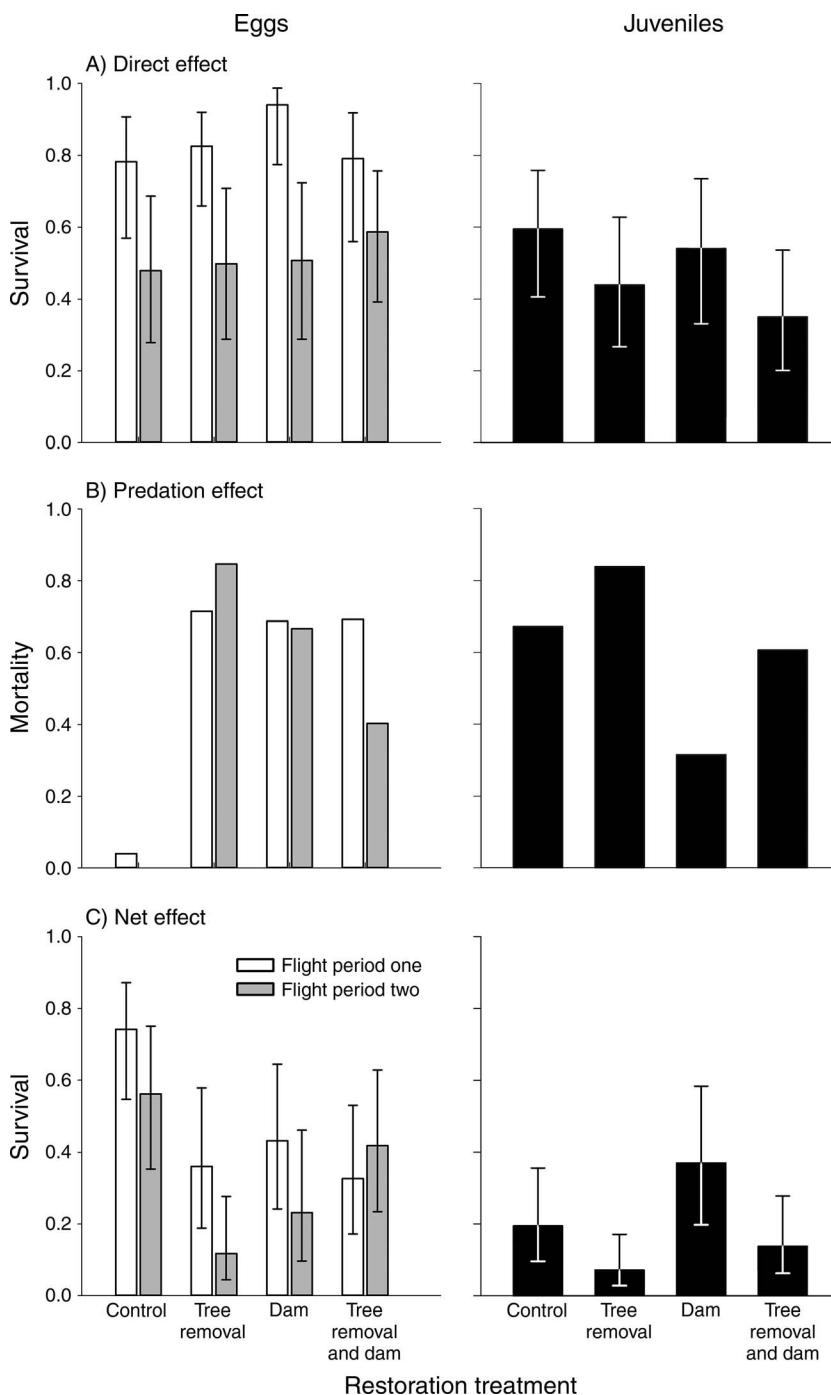


FIG. 1. Proportional survival of *Satyrodes appalachia* eggs and juveniles (A) when protected from predation or (C) accessible to predators in different restoration treatment types. Open bars represent eggs from flight period one (15 May–15 June) and gray bars represent eggs from flight period two (7 July–7 August). (B) The response ratio of eggs and juveniles estimates mortality due to predation in different restoration treatments. Error bars show upper and lower 95% confidence limits.

an important host plant for wetland butterflies (Keufler et al. 2008, Bartel et al. 2010). The change in sedge cover is likely due to increases in light availability. However, changes in the abiotic environment (e.g., water and light availability) and vegetation in our experiment had weak

or no effects on the survival rates of *Satyrodes appalachia* eggs and juveniles (Fig. 1A). The presence of specific host plant species may affect the number of juveniles if greater host plant cover leads to more opportunities for adult butterflies to oviposit, a possibility we did not assess in

our study. However, our results suggest that bottom-up processes are not important drivers of egg or juvenile survival in this system.

Despite the lack of strong direct effects, restoration treatments had strong predator-mediated indirect effects on the survival of *S. appalachia* eggs and juveniles. When *S. appalachia* eggs were exposed to predation, survival in the three types of restored plots was about one third of the survival in control plots (Fig. 1C). This suggests that our manipulation of tree cover and standing water substantially increased predation of butterfly eggs. Interestingly, we found that predation of eggs in plots with both tree removal and damming was less than would be expected if the effects of tree removal and damming were additive (Fig. 1B). While we do not know the mechanism behind this interaction, it reduces the strong negative indirect effect of both tree removal and damming on egg survival when applied alone. In contrast, when *S. appalachia* juveniles were exposed to predation, survival rates differed among types of restoration. Survival of juveniles in dammed plots was two times higher than in control or tree removal and dammed plots, and five times higher than in tree removal plots (Fig. 1C). The differences in predation among restoration treatment types (Fig. 1B) are likely driven by changes in access to juveniles by ground predators. Dams increased the amount of standing water within our plots, and this likely reduced the ability of ground predators, such as ants and some spiders, to gain access to juveniles.

Our experiment measured the total impact of predation by all guilds of predators on immature stages of *S. appalachia*. Restoration treatments could have altered the local abundance, diversity, spatial distribution, or foraging efficiency of predators. Now that we have documented strong effects of restoration on predator impact, future studies will seek to identify specific guilds or species that attack *S. appalachia* and directly measure their responses to habitat modification. In addition, our experimental methods may have influenced the rates of predation we observed. The use of arenas to restrict larval movement may have also prolonged predator foraging. Further, use of potted sedges to measure egg predation rates required careful placement on stable, dry ground, where the increase in standing water in dam treatments may have also concentrated ground predators. Thus, while our methods may have caused us to overestimate predation intensity, the strong effects we observed are unlikely to be purely experimental artifacts.

While the work presented here demonstrates the effects of restoration treatments on immature stages of *S. appalachia*, it does not assess these effects on the adult stage of *S. appalachia*. Positive responses of adult vital rates to restoration, such as increased recruitment due to higher oviposition rates where host plants are more abundant or higher adult survivorship due to lower adult predation, could ameliorate the strong negative effects we document in this study. Nevertheless, for

species such as *S. appalachia* in which the annual population growth rate is simply the product of the separate vital rates, all demographic rates contribute equally to the population growth rate (i.e., they have equal elasticities; Caswell 2001). This means improvements in adult vital rates would have to be proportionate to the reductions in immature survival that we document here for them to be fully compensatory. Future studies will integrate the complete suite of demographic responses to restoration in order to better inform long-term population growth predictions.

Our factorial experimental design provides important insight into how increases in specific resources (e.g., light or water availability) interact with bottom-up and top-down processes to shape communities of plants, herbivores, and predators. We found that tree removal treatments increased light availability and tripled potential host plant cover, a key resource for *S. appalachia*. However, tree removal also led to the highest rates of predation for both eggs and juveniles. In contrast, the addition of dams increased standing water and decreased predation of juveniles, but did not increase the abundance of host plants. Most importantly, we found that no single restoration treatment both increased host plant abundance and had a positive effect on egg or juvenile survival. Instead, because of the conflicting effects of restoration on different life stages, restoration effects on all life stages (including adults) must be integrated into the overall effect on population growth before the optimal management approach can be determined.

We also found that increases in light availability from the removal of trees resulted in a significant increase in total herbaceous plant and shrub cover. The increase in vegetation appears to have led to strong, negative top-down effects on *S. appalachia*; a result consistent with the predictions of classic food web theory (Abrams 1993). This complex relationship between positive direct effects on vegetation and negative indirect effects of some, but not all, restoration treatments on egg and juvenile survival underscores the need for a better link between fundamental food web theory and the restoration of habitat for species specific recovery.

Our results also have important implications for management of other wetland species. The distribution of *S. appalachia* in our study system overlaps with the entire known range of the federally endangered *Neonympha mitchellii francisci* (St. Francis' satyr), one of the rarest butterflies in North America. *S. appalachia* is a potential surrogate for *N. m. francisci* because it demonstrates similar habitat preferences and movement patterns at a landscape scale and is closely related phylogenetically (Hudgens et al. 2012). A major motivation for our work on *S. appalachia* is to inform management actions for recovery of *N. m. francisci* populations across its historic range. Future studies should determine whether habitat restoration for *S. appalachia* imposes similar indirect effects on *N. m. francisci*.

In summary, we found strong, indirect effects of habitat restoration on *S. appalachia*, that were mediated through predation of eggs and juveniles. Importantly, these indirect effects appeared to outweigh any potential direct benefit of the restoration of plant communities. Our findings emphasize the need for detailed, demographic measures of species recovery in restoration programs because of the complex, multi-trophic effects of habitat manipulation.

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## LITERATURE CITED

- Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. *American Naturalist* 141:351–371.
- Bartel, R. A., N. M. Haddad, and J. P. Wright. 2010. Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. *Oikos* 119:883–890.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. lme4: linear mixed-effects models using Eigen and S4. R package version 1.0-4. <http://CRAN.R-project.org/package=lme4>
- Breiner, D. R., and G. M. Carter. 2003. Territory quality transitions and source-sink dynamics in a Florida Scrub-Jay population. *Ecological Applications* 13:516–529.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Cornell, H. V., and B. A. Hawkins. 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *American Naturalist* 145:563–593.
- Cornell, H. V., B. A. Hawkins, and M. E. Hochberg. 1998. Towards an empirically-based theory of herbivore demography. *Ecological Entomology* 23:340–349.
- Cortina, J., F. T. Maestre, R. Vallejo, M. J. Baeza, A. Valdecantos, and M. Pérez-Devesa. 2006. Ecosystem structure, function, and restoration success: are they related? *Journal for Nature Conservation* 14:152–160.
- DeCesare, N., M. Hebblewhite, H. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81:1588–1600.
- Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Second edition. Sage, Thousand Oaks, California, USA.
- Gotthard, K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. *Journal of Animal Ecology* 69:896–902.
- Gripenberg, S., and T. Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos* 116:181–188.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hawkins, B. A., H. V. Cornell, and M. E. Hochberg. 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* 78:2145–2152.
- Holl, K. D., and G. F. Hayes. 2006. Challenges to introducing and managing disturbance regimes for *Holocarpa macradenia*, an endangered annual grassland forb. *Conservation Biology* 20:1121–1131.
- Hudgens, B. R., W. F. Morris, N. M. Haddad, W. R. Fields, J. W. Wilson, D. Kuefler, and T. Jobe. 2012. How complex do models need to be to predict dispersal of threatened species through matrix habitats? *Ecological Applications* 22:1701–1710.
- Hunter, M. D. 2001. Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic and Applied Ecology* 2:295–309.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:723–732.
- Hunter, M. D., G. C. Varley, and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences USA* 94:9176–9181.
- Kristensen, C. 1994. Investigations on the natural mortality of eggs and larvae of the large white *Pieris brassicae* (L.) (Lep., Pieridae). *Journal of Applied Entomology* 117:92–98.
- Kuefler, D., N. M. Haddad, S. Hall, B. Hudgens, B. Bartel, and E. Hoffman. 2008. Distribution, population structure and habitat use of the endangered Saint Francis Satyr butterfly, *Neonympha mitchellii francisci*. *American Midland Naturalist* 159:298–320.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* 73:733–746.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPherson, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11:41–65.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.R-project.org](http://www.R-project.org)
- Robertson, B. A., J. S. Rehage, and A. Sih. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution* 28:552–560.
- Suding, K. N. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics* 42:465–487.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–615.
- Zedler, J., H. Morzaria-Luna, and K. Ward. 2003. The challenge of restoring vegetation on tidal, hypersaline substrates. *Plant and Soil* 253:259–273.

## SUPPLEMENTAL MATERIAL

## Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-2403.1.sm>