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RESEARCH ARTICLE

Effects of land use legacies and habitat fragmentation on salamander abundance

Bradley J. Cosentino · Kristen M. Brubaker

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Abstract
Context Landscape modification is an important driver of biodiversity declines, yet we lack insight into how ongoing landscape change and legacies of historical land use together shape biodiversity.
Objectives We examined how a history of agricultural land use and current forest fragmentation influence the abundance of red-backed salamanders (*Plethodon cinereus*). We hypothesized that historical agriculture and fragmentation cause changes in habitat quality and landscape structure that limit abundance.
Methods We measured salamander abundance at 95 forested sites in New York, USA, and we determined whether sites were agricultural fields within the last five decades. We used a structural equation model to estimate relationships between historical agriculture and salamander abundance mediated by changes in forest vegetation, microclimate, and landscape structure.
Results Historical agriculture affected salamander abundance by altering forest vegetation at a local scale and forest cover at a landscape scale. Abundance was lowest at post-agricultural sites with low woody vegetation, leaf litter depth, and canopy cover. Post-agricultural sites had limited forest cover in the surrounding landscape historically, and salamander abundance was positively related to historical forest cover, suggesting that connectivity to source populations affects colonization of regenerating forests. Abundance was also negatively related to current forest fragmentation.
Conclusions Historical land use can have legacy effects on animal abundance on par with effects of ongoing landscape change. We showed that associations between animal abundance and historical land use can be driven by altered site conditions and surrounding habitat area, indicating that restoration efforts should consider local site conditions and landscape context.

Keywords Agriculture · Amphibian · Forest · Historical ecology · Landscape change · *Plethodon cinereus*

Introduction

Landscape change in the form of habitat loss and fragmentation is the leading cause for biodiversity declines worldwide (Wilcove et al. 1998). Population declines occur as a direct consequence of habitat loss

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B. J. Cosentino (✉)
Department of Biology, Hobart and William Smith Colleges, Geneva, NY 14456, USA
e-mail: cosentino@hws.edu

K. M. Brubaker
Environmental Studies Program, Hobart and William Smith Colleges, Geneva, NY 14456, USA

from urbanization, agriculture, and silviculture, and fragmented populations in remaining habitat may decline due to reduced immigration and habitat degradation (Fischer and Lindenmayer 2007). Habitat fragments can also have unique histories of human disturbance, ranging from slight modifications in land use (e.g., thinning treatments in a forest stand) to conversion between land cover categories (e.g., forest regenerating on previously cultivated land; Bürgi et al. 2017). These historical disturbances can have effects on ecosystem structure and function that persist for a century or more (Vellend et al. 2006, Hermy and Verheyen 2007), including changes in soil structure, microtopography (Hightower et al. 2014), and nutrient cycling (Flinn et al. 2005). Despite the importance of land use legacies in ecology (Foster et al. 2003; Fraterrigo 2013), there have been few attempts to understand how historical land use and habitat fragmentation together affect biodiversity (Perring et al. 2016), particularly for animals.

There are multiple pathways by which land use history and habitat fragmentation could affect animal populations (Fig. 1). Legacies of agricultural land use in regenerating forests can take the form of changes in habitat quality at a local scale, especially altered soils and plant communities within an animal's home range (Foster 1992; Foster et al. 1998; Flinn and Vellend 2005). These changes can affect animal recruitment by modifying refuge (e.g., sedimentation effects on stream fishes; Harding et al. 1998) and food availability (e.g., seed abundance for small mammals; Stuhler and Orrock 2016). Modified overstory vegetation in post-agricultural forests also affects structural elements at the forest floor including leaf litter (Compton and Boone 2000) and coarse woody debris (Currie and Nadelhoffer 2002), and changes in the light regime should affect soil temperature and moisture conditions. Forest fragmentation causes similar changes in abiotic and biotic components of habitat quality by exposing forest edges to increased light and wind penetrance (Matlack 1993; Laurance et al. 2002; Tuff et al. 2016) and altering predator-prey interactions (Robinson et al. 1995).

Effects of historical land use and habitat fragmentation on animal abundance can also emerge from dispersal constraints at a landscape scale. Abundance in regenerating habitat may be limited by slow colonization (Cosentino et al. 2014; Szűcs et al. 2014), and a history of fragmentation surrounding a site may further delay colonization and reduce rescue effects via immigration in isolated habitat patches (Sjögren Gulve 1994; Cosentino et al. 2011; Hufbauer et al. 2015). Moreover, the current degree of fragmentation in a landscape may be shaped in part by historical land use decisions. For example, forests with a recent history of agriculture likely had favorable characteristics for production (e.g., slope, drainage; Flinn et al. 2005), making it more likely that regenerating forests are in parts of the landscape fragmented by agricultural fields still in use.

We tested the hypothesis that effects of land use history and habitat fragmentation on animal abundance are driven by changes in local habitat quality and landscape-scale dispersal constraints. We chose eastern red-backed salamanders (*Plethodon cinereus*) in forests of the northeastern United States to test this hypothesis for three reasons. First, there is a recent history of abandonment of agricultural land in the northeastern U.S. that has created a mosaic of forest stands at varying stages of regeneration (Foster 1992; Smith et al. 1993). Second, *P. cinereus* is a lungless salamander that respires cutaneously and relies on high moisture conditions to forage and avoid desiccation (Spotila 1972; Jaeger 1980a), and terrestrial salamander abundance has been shown to respond to temperature and moisture gradients shaped by topography and vegetation (Peterman and Semlitsch 2013). *P. cinereus* should be sensitive to changes in forest vegetation (e.g., canopy cover, leaf litter), refuge availability (e.g., coarse woody debris), and microclimatic conditions associated with legacies of agricultural land use and forest fragmentation (e.g., Pough et al. 1987; Maerz et al. 2009; Otto et al. 2014). Third, *P. cinereus* has limited vagility with typical dispersal distances < 10 m (Liebgold et al. 2011), and dispersal limitation can lead to slow population growth in regenerating forests and population declines in fragmented forests. We estimated abundance of *P. cinereus* across two seasons at 95 locations at the Finger Lakes National Forest in Hector, NY, which has forests in variable stages of regeneration after cultivation but also recent fragmentation due to ongoing agricultural use (DeGloria 1998). We predicted that abundance of *P. cinereus* populations would be lowest in forest stands with a recent history of agriculture and high forest fragmentation due to changes in the quality of forest vegetation structure

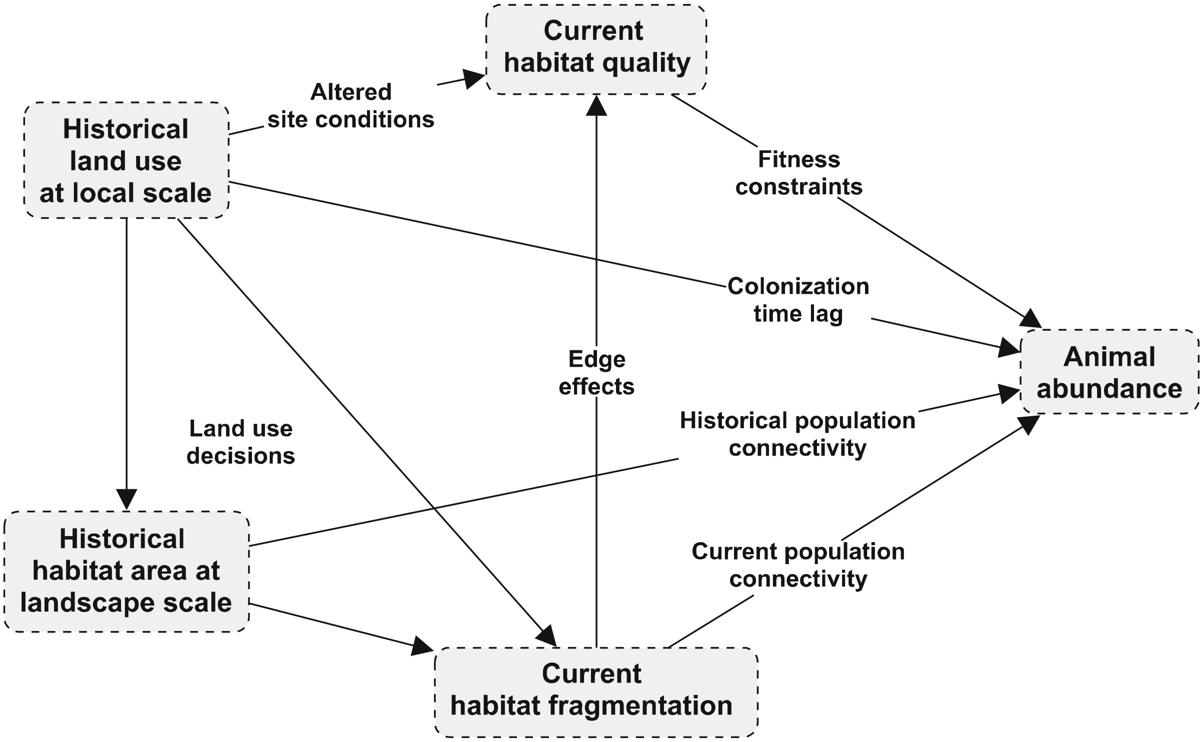


Fig. 1 Structural equation metamodel for the hypothesized effects of historical land use, habitat quality, and habitat fragmentation on animal abundance. Knowledge of historical land use at a site can predict aspects of habitat quality and surrounding landscape structure (i.e., historical and current levels of habitat fragmentation) that affect animal abundance ("indirect effects" of historical land use). Historical land use may directly predict variation in animal abundance if there is a time lag in colonization ("direct effect" of historical land use)

(e.g., low leaf litter, canopy cover and consequently high soil surface temperature) or limited dispersal.

Methods

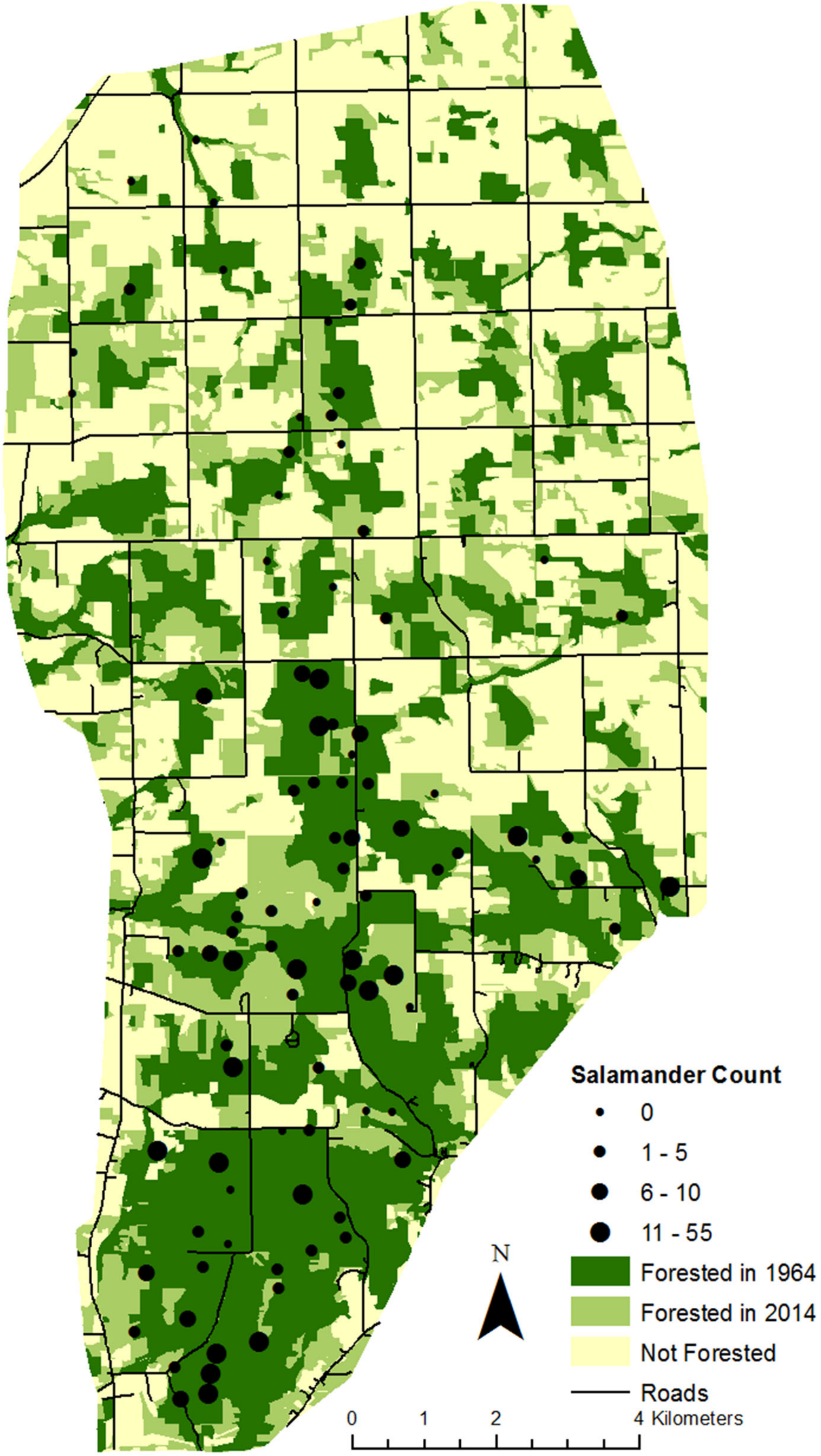
Study area

We conducted our study at the 6521-ha Finger Lakes National Forest (FLNF) in Hector, New York, USA (76°47′29″W, 42°30′55″N). Most of the forest in the study area was completely cleared for agriculture in the late 18th century, and forest stands have been regenerating as land was purchased piecemeal beginning in the late 1930 s (Marks and Gardescu 1992). Historical agriculture was dominated by cultivation of hay and small grains (DeGloria 1998), which is consistent with evidence of a plow layer at most sites inferred from high-resolution elevation data (Lidar; K. Brubaker, unpublished data). Dominant land cover types at FLNF currently consist of forest stands in various stages of succession (54%) intermixed with grasslands managed for cattle grazing and grassland-dependent wildlife (35%). Common tree species at FLNF include *Acer rubrum*, *Acer saccharum*, *Carya ovate*, *Fraxinus americana*, *Quercus rubra*, and *Pinus strobus*. *Plethodon cinereus* and the larger northern slimy salamander (*Plethodon glutinosus*) are the only completely terrestrial salamanders that occur at FLNF, and *P. glutinosus* was rarely encountered during our study. Other salamanders found during our study include *Ambystoma jeffersonianum*, *A. maculatum*, *Desmognathus fuscus*, *D. ochrophaeus*, *Eurycea bislineata*, *Hemidactylium scutatum*, and *Nothophthalmus viridescens*.

Sampling design

We documented abundance of *P. cinereus* at 95 sites in 2013 and 2014 (Fig. 2). We used Geospatial

Fig. 2 Map of 95 study sites at the Finger Lakes National Forest, Hector, New York. Circles represent total counts of *Plethodon cinereus* based on six surveys across 2 years at each site. Land cover shows non-forest and forest habitat that regenerated following agriculture at different times



Modeling Environment (Beyer 2014) to randomly select sites within deciduous, coniferous, and mixed forest habitats at FLNF based on NLCD 2011 land cover data (Homer et al. 2015). Sites were separated by at least 200 m. We established a 10 × 10-m plot at each site to sample salamanders, and sites were sampled three times each between 22 May and 1 August in each year. Sites were marked with rebar and flagging. Surveys at each site were separated by at least four days, and all sites were surveyed during a sampling session before beginning the next repeat survey. Sites were grouped by spatial proximity, and groups of sites were sampled in a random sequence. We measured soil temperature in the center of the plot to a depth of 13 cm before each survey. Sampling involved lifting all natural cover objects (logs, rocks) within the plot and capturing salamanders by hand. We measured mass and snout-vent-length and returned each salamander to its point of capture. Salamanders were not individually marked. Each survey of a 10 × 10-m plot was conducted by one of four observers, and observers were randomly assigned to sites during each sampling session.

Environmental covariates

We measured environmental covariates within the 10 × 10-m plots as indices of habitat quality that could affect salamander abundance. Leaf litter depth was measured by recording the height of uncompressed leaf litter with a ruler pressed to the soil surface (Hocking et al. 2013). Leaf litter depth at each site was calculated as the average of nine randomly-selected locations within the plot. We estimated canopy cover during full leaf out (July in our study area) at the center of each plot using a densiometer. Each tree within the plot was identified to species and measured for diameter at breast height (DBH), and DBH values were used to quantify basal area for each plot. We also measured herbaceous cover in each plot by visually estimating percent cover for the entire plot for each herbaceous species present (0–5, 6–25, 26–50, 51–75, 76–95, 96–100%). We then summed the median cover value for each species to quantify an index of total herbaceous cover per plot.

We quantified soil surface temperature at each site as an index of thermal and moisture conditions experienced by salamanders. Warm temperatures create a desiccating environment at the soil surface due to high evapotranspiration rates resulting in low soil moisture (Murcia 1995; Chen et al. 1999; Laurance 2004). We used Thermochron iButton data loggers (DS1921G-F5#, Maxim Integrated, San Jose, CA) to measure soil surface temperature in each plot. Data loggers were deployed in a 50-ml plastic vial staked to the soil surface underneath leaf litter at the center of each plot. Temperature was recorded hourly between 21 June and 20 July in 2014, and we quantified mean temperature across all hourly records.

Aerial images were used to characterize historical and current land use around each site. We used ArcGIS to digitize agriculture and forest cover in the study area from aerial photos taken in 1964 and 2014 (Fig. 2). Land cover was digitized as forest if trees were present but individual trees could not be distinguished. We classified whether or not each site was "post-agricultural" by determining if the site was an agricultural field in 1964, and we measured the proportion of forest within a 100-m buffer around each plot in 1964. We quantified distance to forest edge based on aerial imagery in 2014 as an index of current forest fragmentation. We considered forest area in 2014 and forest edge-to-area ratio as additional metrics of current forest fragmentation, but most sites had high levels of surrounding forest cover in 2014 (> 95%). Moreover, distance to forest edge was the most direct measure of our hypothesized effect of forest fragmentation on salamander abundance (i.e., edge effects, Fig. 1).

Statistical analysis

We used structural equation modeling (SEM; Grace 2006, Kline 2015) to examine how historical land use, habitat quality, and habitat fragmentation affect animal abundance. SEM is useful for evaluating hypothesized direct and indirect effects in a network of interrelated variables. A direct effect is defined as an effect of one explanatory variable on a response variable (i.e., $X \rightarrow Y$), whereas an indirect effect is defined as an effect of an explanatory variable on a response variable through an intervening variable (i.e., $X \rightarrow Y_1 \rightarrow Y_2$; Kline 2015). We chose SEM over alternative statistical approaches because we were explicitly interested in testing the fit of a model with effects of historical land use and fragmentation via multiple causal pathways. We created a structural equation meta-model to illustrate our hypotheses

(Fig. 1; Grace et al. 2010, 2012). The key components of our model were the hypothesized direct effect of historical land use on abundance (i.e., a time lag in colonization) and the indirect effects mediated by current habitat quality, historical habitat area in the surrounding landscape, and current habitat fragmentation (Fig. 1).

We fit the SEM using the total number of salamanders captured across all surveys at each site as a measure of relative abundance. We also fit a "repeated measures" SEM with the number of captures per survey and included sampling year and covariates measured during surveys that could affect the availability and capture probability of salamanders (Supplementary Fig. 1; O'Donnell and Semlitsch 2015). Inferences about factors that influence abundance were qualitatively the same between the two models, so we present the simpler model with abundance measured as total captures across all surveys. We considered using hierarchical N-mixture models to estimate abundance and detection probability simultaneously (Royle 2004), but these models are unable to estimate a network of direct and indirect effects on abundance. Moreover, our goal was to understand factors that affect relative rather than absolute abundance, and standard regression approaches are adequate for estimating such effects (Barker et al. 2017).

We specified effects of historical land use at local and landscape scales in our SEM. At the local scale, we included an observed variable ("post-agricultural") specifying whether or not a plot was an agricultural field in 1964. At the landscape scale, we included historical forest cover as a latent variable with the estimated proportion of forest cover within 100 m of each site in 1964 as an indicator variable. We specified a direct pathway from post-agricultural status to salamander abundance, which was a latent variable with a single indicator (total number of captures across all surveys). We also specified indirect pathways from post-agricultural status to salamander abundance that were mediated by four latent variables: historical forest cover, forest fragmentation, forest vegetation cover, and soil surface temperature. Forest vegetation was represented by observed herbaceous cover, basal area, leaf litter depth, and canopy cover; forest fragmentation was represented by distance to forest edge in 2014; and soil surface temperature was represented by mean temperature measured from iButtons. We set the loading for distance to forest edge to be –1 because distance to edge is inversely related to fragmentation (Grace et al. 2010). Our model also included total number of cover objects turned at a site across all surveys as an observed measure of cover availability and search effort. We included direct effects of post-agricultural status and forest fragmentation on number of cover objects to account for the possibility of greater density of cover objects at interior forest plots and plots without a history of agriculture. Covariance terms between herbaceous cover and cover objects and between soil surface temperature and cover objects were added to the SEM to improve model fit.

We used the *lavaan* package (Rosseel 2012) in R (R Development Core Team 2017) to fit the SEM. We applied a log transformation to the number of salamanders after adding one to all values (Ives 2015). Herbaceous cover and distance to forest edge were square-root transformed, and we applied a logit transformation to forest cover in 1964 (Warton and Hui 2011). Transformations were used to help meet the assumption of bivariate normality for regression. Observed variables were rescaled so that the variances were similar in magnitude (Rosseel 2012). We used maximum likelihood estimation with robust standard errors to deal with potential deviations from normality in the error distributions (Grace 2006; Kline 2015). We computed standardized and unstandardized regression coefficients to examine the strength of pathways in the model. Model fit was assessed with a χ^2 test (Kline 2015).

Results

Overall, we captured 522 *P. cinereus* individuals across the 95 sites, and we detected at least one individual at 71 of 95 sites (naïve occupancy = 75%). The median number of individuals captured during each survey was 0.92 (range = 0–24), and the median number of captures across the six surveys was 3 (range = 0–55).

Salamander abundance was related to post-agricultural status through multiple indirect pathways (Fig. 3, Supplementary Tables 1, 2). At a local scale, sites with a history of agriculture were characterized by high herbaceous cover and low basal area, canopy cover, and leaf litter depth. Salamander abundance was

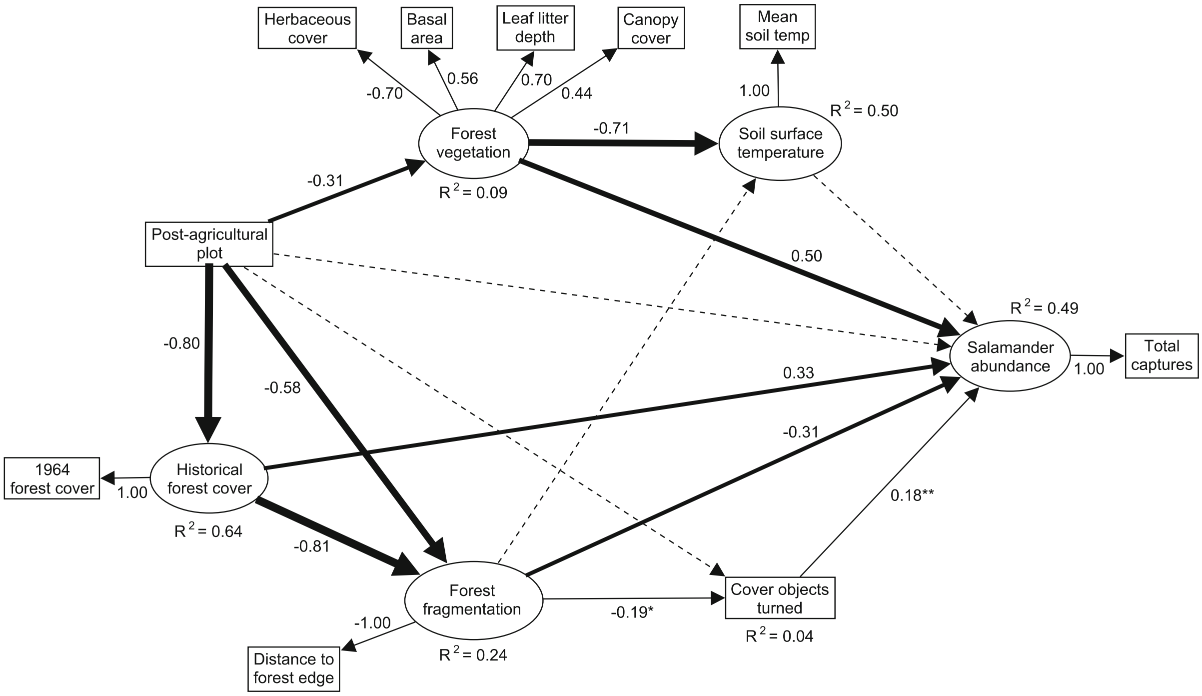


Fig. 3 Structural equation model of the effects of past agricultural land use, habitat quality, and habitat fragmentation on abundance of red-backed salamanders (*Plethodon cinereus*). The model includes latent (ovals) and observed (rectangles) variables. Solid lines represent significant pathways at $P < 0.05$, and dashed lines represent nonsignificant pathways. Standardized coefficients are shown for significant pathways. $*P = 0.056$, $**P = 0.087$

greatest at sites with high woody vegetation cover (i.e., basal area and canopy cover) and leaf litter. Soil surface temperature was lowest at sites with high woody vegetation and leaf litter, but there was no evidence for a direct effect of temperature on salamander abundance.

Salamander abundance was also related to post-agricultural status through pathways operating at a landscape scale. For example, historical forest cover around a site was lowest at sites with a history of agriculture, and salamander abundance had a positive, direct relationship with historical forest cover. Salamander abundance was also linked to historical forest cover indirectly through current forest fragmentation. Salamander abundance was negatively related to current forest fragmentation, and forest fragmentation was greatest at sites with low historical forest cover. Interestingly, we found a direct negative relationship between post-agricultural status and forest fragmentation when controlling for the indirect pathway linking post-agricultural status to forest fragmentation through historical forest cover. This residual relationship offset the tendency for post-agricultural sites to be highly fragmented due to low historical forest cover in the surrounding landscape. Collectively we found that current forest fragmentation was unrelated to post-agricultural status when considering the direct and indirect associations together (total effect of post-agricultural status on fragmentation $= 0.063$, $P = 0.56$).

Highly fragmented sites tended to have fewer cover objects turned than sites with low fragmentation, and abundance was positively related to the number of cover objects turned. There was no evidence for an effect of forest fragmentation on soil surface temperature. There was no relationship between number of cover objects turned and post-agricultural status, and there was no direct relationship between salamander abundance and history of agriculture. Thus, the primary pathways linking salamander abundance to post-agricultural status were through vegetation structure at a local scale and historical forest area at the landscape scale. Collectively our model explained 49% of the variance in salamander abundance, and model fit was good ($\chi^2 = 32.9$, $df = 25$, $P = 0.13$).

Discussion

Our study showed a clear legacy effect of agriculture on the abundance of woodland salamanders that likely operates through multiple mechanisms. The structural equation model suggests that salamander abundance is linked to historical agricultural land use through altered site conditions at a local scale and historical forest cover at a landscape scale. There was no evidence of a direct relationship between salamander abundance and post-agricultural status, suggesting that a history of agricultural land use does not limit salamander abundance by simply delaying colonization. The legacy effect of agriculture on salamander abundance appeared to be driven by reduced habitat quality within post-agricultural forests and limited connectivity of post-agricultural forests to source populations. In addition to land use history, salamander abundance was limited by the current degree of forest fragmentation on the landscape. Previous agricultural land use did not fully explain patterns of forest fragmentation or vegetation structure, indicating there are additional drivers of habitat heterogeneity—potentially including other components of landscape change (e.g., grazing, forest thinning treatments)—that play a role in the system. Overall, our results demonstrate how altered site conditions at a local scale and dispersal constraints at a landscape scale likely drive variation in salamander abundances among sites with varying land use histories and ongoing drivers of landscape change.

Our data suggests historical agriculture affects salamander abundance in part by driving variation in forest vegetation. Forest stands with a recent history of agriculture are dominated by shade-intolerant, fast-growing species (Foster et al. 1998; Thompson et al. 2013). Leaf litter generated by fast-growing species decomposes quickly in young, post-agricultural forests, resulting in low carbon to nitrogen ratios in the soil that take a century or more to recover (Compton and Boone 2000; Hooker and Compton 2003). Decomposition of leaf litter in post-agricultural forests can be driven by non-native earthworms, and low leaf litter depth has been linked to low herbaceous cover (Hale et al. 2006), reduced songbird density (Loss et al. 2012), and reduced terrestrial salamander abundance (Pough et al. 1987; Maerz et al. 2009). Loss of leaf litter negatively affects abundance of terrestrial salamanders by decreasing the abundance of small arthropod prey (Maerz et al. 2009) and potentially by creating warm, dry conditions at the soil surface that increases desiccation risk (Feder 1983). We found the abundance of *P. cinereus* was greatest in forests with high basal area, canopy cover, leaf litter depth, and low herbaceous cover. These forests also had relatively cool microclimatic conditions at the soil surface, but surprisingly there was no direct effect of soil surface temperature on salamander abundance. We think the association between salamander abundance and forest vegetation is most likely due to high abundance of arthropod prey in old forests, but data on arthropod communities are needed to confirm this hypothesis.

In addition to changes in leaf litter, historical agriculture can influence habitat availability by changing micro-site conditions and availability of cover objects. During cultivation, cover objects are often removed as pit and mound topography is smoothed, dead trees and coarse woody debris are removed, and large stones are cleaned out of agricultural areas (Hightower et al. 2014). Cover objects and soil depressions provide refugia for salamanders during warm, dry conditions (Heatwole 1962; Jaeger 1980b). We found that salamander abundance was positively related to number of cover objects turned, which we interpret as an index of cover object availability (both rocks and coarse woody debris). However, we did not find a significant relationship between cover objects turned and history of agriculture at a site. Coarse woody debris, in particular, can be restored relatively quickly to recovering forests, as short-lived early successional species begin dying out of the stand, and competitive exclusion begins thinning the stand (Bormann and Likens 1994).

Our results indicate that historical agriculture affects animal abundance in part by affecting landscape structure, particularly the historical level of forest cover in the surrounding landscape. History of agricultural land use at a site was a good predictor of the extent of historical forest cover in the surrounding landscape, with agricultural land use explaining 64% of the variation in forest cover in 1964 (Fig. 3). Sites with a history of agriculture tended to have low forest cover in the surrounding landscape historically, and these site tended to have low salamander abundance. Historical forest cover surrounding agricultural sites likely played an important role in determining when regenerating forest stands were colonized by salamanders. Dispersal distances within forests for *P. cinereus* are typically < 10 m (Liebgold et al. 2011), and the maximum known dispersal distance is 143 m (Sterrett et al. 2015). Limited dispersal ability alone could lead to slow colonization and subsequent immigration, resulting in a time-lagged response of abundance to historical agriculture (e.g., Cosentino et al. 2014). However, landscape context plays an important role in mediating the timing of colonization (Brudvig and Damschen 2011). *P. cinereus* has been found to cross open fields and colonize artificial forest plots within 1 year, with the primary constraint on colonization being distance from adjacent forest (Marsh et al. 2004). A *post hoc* analysis of our data showed that the probability of salamanders colonizing a post-agricultural site was positively related to adjacent forest cover in 1964 (Fig. 4; logistic regression, $P = 0.045$). We think the positive relationship between salamander abundance and historical forest cover likely represents an effect of proximity to source populations, highlighting the potential importance of landscape context for restoration of animal populations in regenerating forests.

Current landscape structure also played an important role in shaping salamander abundance. In our system, abundance of *P. cinereus* was greatest at sites far from forest edges. We hypothesized that fragmentation effects on *P. cinereus* abundance would be driven in part by abiotic edge effects, primarily warm, dry conditions at forest edges. However, we found no evidence of an association between fragmentation and thermal conditions. Fragmentation affected *P. cinereus* abundance in part due to greater cover object density at interior forests, but the residual direct effect of fragmentation indicates an additional mechanism independent of cover object density. One possibility is that abundance is constrained at sites adjacent to roads due to low soil moisture (Marsh and Beckman 2004), traffic-related mortality (Marsh 2007), or behavioral barriers to movement (Marsh et al. 2005), although only 7 of our 95 sites were near roads (< 35 m; deMaynadier and Hunter 1998). A second possibility is that predators of *P. cinereus* such as shrews and snakes concentrate foraging activity along forest edges (Gibbs 1998). Habitat heterogeneity and edge contrast are particularly attractive to snakes due to greater choice of habitat for thermoregulation, and high use of edge habitat by snakes can lead to increased predation rates (Weatherhead and Blouin-Demers 2004).

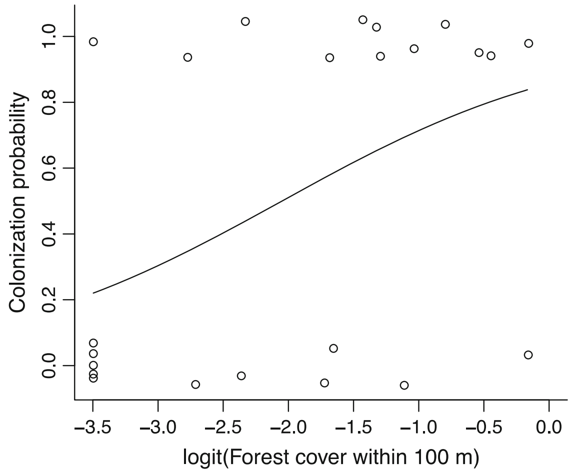


Fig. 4 Relationship of colonization probability by *Plethodon cinereus* at sites that were agricultural fields in 1964 to the proportion of forest cover within 100 m in 1964. Colonization was defined by the presence (1) or absence (0) of salamanders at post-agricultural sites. Proportion of forest cover is shown on the logit scale corresponding to 0–50% forest cover. Jitter display shows overlapping data points

The effects of current forest fragmentation on salamander abundance appeared to be largely independent of agricultural history at a site. Post-agricultural sites tended to have low surrounding forest cover historically, and sites with low surrounding forest cover historically tended to be closer to forest edges today. However, after controlling for this indirect relationship between agricultural history at a site and fragmentation, we found that post-agricultural sites tended to be located at more interior locations than sites without a history of agriculture. We think the latter effect is likely due to patterns of land acquisition. Many post-agricultural sites were located at relatively high elevation, and the degree of forest fragmentation at a large scale (> 100 m) tends to be low at these sites (Supplementary Fig. 2). Low air and soil temperatures and shallow soil depth likely limited yield of small grains and led to early abandonment of farms at high elevation at FLNF (DeGloria 1998), and the U.S. Forest Service may primarily acquire these high-elevation sites over low-elevation sites where conditions are good for agricultural production.

Overall our results suggest that legacy effects can emerge from land use decisions at both the site level and the broader landscape. The spatial variation in habitat conditions created by historical land use may have important implications for understanding ecological processes shaping animal abundance. For example, variation in salamander density driven by historical agriculture could generate spatial variation in density-dependent dispersal. Marsh et al. (2004) found that individuals colonizing artificial forests plots tended to be young, sexually mature individuals that are often competitively inferior with respect to territory acquisition because of their small size (Mathis 1991). Competition for territories is likely greatest in old forest stands where salamander density is high, which could lead to dispersal of competitively weak individuals from old forest stands to young stands where density is lower. There may also be evolutionary consequences of historical land use. In our study area, *P. cinereus* individuals in forests with a recent history of agriculture tend to have lower mobility than individuals in old forests (Cosentino and Droney 2016). Spatial variation in movement behavior could be the outcome of divergent selection pressures in forests with and without a recent history of agriculture (e.g., soil surface temperature, cover object availability). Moreover, our results suggest that the performance of models in spatial ecology (e.g., species distribution models) and population genetics (e.g., landscape genetic models) may benefit from incorporating data on historical land use. Metrics of habitat composition in spatial ecology and evolution are often coarse (e.g., "forest cover"; Cosentino et al. 2014, 2017), and our results show that land use legacies can create significant habitat heterogeneity within continuously distributed habitat.

Our work has important management implications for restoration of large-scale forested habitat and forest-dependent animals such as terrestrial salamanders. Despite changes in site conditions caused by historical agriculture, forests that were originally used for agriculture could be considered for conservation action, particularly if landscape context is taken into account. For example, agricultural land adjacent to core forest habitat should be considered when prioritizing land acquisitions for conservation because proximity to forests likely facilitates rapid colonization of regenerating forests by forests specialists with limited vagility. Our results also suggest that old fields may not require intensive management (e.g., planting of desired species, creation of coarse woody debris) to restore suitable habitat for terrestrial salamanders. Although terrestrial salamanders were in all likelihood extirpated at sites previously used for agriculture, our results suggest passive restoration of forests is often sufficient for recolonization.

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