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Time since disturbance affects colonization dynamics in a metapopulation

Jessie Mutz 🆔 | Nora Underwood | Brian D. Inouye

Department of Biological Science, Florida State University, Tallahassee, FL, USA

Correspondence
Jessie Mutz
Email: jmutz@bio.fsu.edu

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Abstract

1. Disturbances are widespread in nature and can have substantial population-level consequences. Most empirical studies on the effects of disturbance track population recovery within habitat patches, but have an incomplete representation of the recolonization process. In addition, recent metapopulation models represent post-disturbance colonization with a recovery state or time-lag for disturbed ("focal") patches, thus assuming that recolonization rates are uniform.

2. However, the availability of colonists in neighbouring "source" patches can vary, especially in frequently disturbed landscapes such as fire-managed forests that have a mosaic of patches that differ in successional state and undergo frequent local extinctions. To determine how time since disturbance in both focal and neighbouring source patches might affect metapopulations, we studied the effects of time since fire (TSF) on abundances of a specialist palmetto beetle within and between fire management units in Apalachicola National Forest, Florida.

3. We measured beetle abundances at three distances from the shared edge of paired units, with units ranging from 0 to 64 months since fire and the difference in time since burning for a focal-source pair ranging from 3 to 58 months.

4. Soon after fire, beetle abundances within management units were highest near the unit edge, but this pattern changed with increasing TSF. Between paired units, the more recently disturbed ("focal") unit's beetle abundance was positively related to source unit abundance, but the shape of this relationship differed based on focal unit TSF and the units' difference in time since burning.

5. Results suggest that both focal and source habitat history can influence recolonization of recently disturbed patches and that these effects may persist over years. Thus, when predicting metapopulation dynamics, variation in habitat characteristics should be considered not only for patches receiving colonists but for patches supplying colonists as well.

KEYWORDS

fire management, *Hemisphaerota cyanea*, insect herbivores, recolonization, time since fire

1 | INTRODUCTION

Disturbance is an important source of heterogeneity in ecological communities and can have substantial direct and indirect effects on the dynamics and distributions of populations (Pickett & White, 1985; Sousa, 1984). Population recovery from disturbance will depend on the ability of individuals to survive disturbance events, of survivors to contribute to population growth, and of colonists to establish.

Understanding the extent to which each of these factors limits the recovery rate and influences the spatial distributions of populations following disturbance can aid in the design of management regimes and, more broadly, contribute to our understanding of population dynamics for species subject to frequent disturbances. Ecological studies on population-level effects of disturbance have historically focused on how species may be adapted to tolerate disturbance (Schowalter, 1985; Simon & Pennington, 2012) or the rate at which disturbed areas once again become suitable for habitation by the species of interest (Abrahamson, 1984; Wood & del Moral, 1987) and are typically carried out at the scale of a single habitat patch. By comparison, the role of colonist availability—which requires a more regional perspective—has received relatively little attention, particularly in animals (but see Pavlacky et al., 2012; Watson et al., 2012).

In many terrestrial systems, fire is a common type of disturbance that affects local populations directly by prompting emigration and causing significant mortality or even local extinction (Bond & Keeley, 2005; Sousa, 1984). Populations may also experience indirect effects of fire mediated through other species with which they interact, e.g. resource, competitor, or prey species. The process of recovery within burned habitats, which will depend on the extent of in situ survival, the within-population growth rate, and recolonization from unburned refugia (Banks et al., 2011; Panzer, 2003) can be relatively slow for populations that have been locally eradicated or have low mobility (Swengel, 2001). For example, although many insect species survive fires of moderate intensity as eggs or other resting forms buried in the soil (e.g. Brennan, Moir, & Wittkuhn, 2011), other species may be locally extirpated and depend solely on colonists from external source populations to re-establish (Swengel, 2001). For organisms that cannot easily survive in situ, the demographic consequences of disturbance, and of fire in particular, could persist over several generations.

In addition to effects on total abundance, population recovery through within- or between-patch recolonization can also lead to distinctive spatial patterns. For example, immigration from adjacent habitat patches can create a gradient of abundance from edge to interior of disturbed patches as colonists move inward, as observed for grasshoppers in the regularly burned Florida scrub (Knight & Holt, 2005). A similar pattern may emerge in already-populated patches if residents hesitate to disperse, particularly in fragmented landscapes. Such patterns can in turn generate spatial structure in the intensity of species interactions, e.g. herbivory (Hahn & Orrock, 2015a). Insect herbivores are a ubiquitous class of consumers in fire-dependent natural systems, vary in their level of specialization and mobility, and have complex life cycles, making them an ideal system for investigating the spatial and temporal intricacies of post-disturbance recolonization. And, while there exists a considerable literature on the population-level consequences of fire on insects (e.g. Buffington, 1967; Cancelado & Yonke, 1970; Evans, 1984; Vogel, Koford, & Debinski, 2010), few studies have characterized effects of disturbance beyond a single habitat patch.

Disturbance events often occur over large spatial scales, affecting one or several local populations or habitat patches, while others may be less or not at all affected. Studies generally describe population recovery following disturbance within a single area or at a single scale (Fay, 2003; Stein, Price, Abrahamson, & Sacchi, 1992; Vogel et al., 2010; but see Kim & Holt, 2012), but the process of recolonization—which will be particularly important in the case of local extinction—is expected to play out across many habitat patches and multiple scales. Thus, in order to understand population-level responses, it is necessary to consider recolonization patterns at multiple scales: not only within recently disturbed areas but also at the landscape level.

Several recent metapopulation models provide a multi-patch perspective on disturbance dynamics. This current theory suggests that metapopulation persistence and long-term patch occupancy depend on the rate of patch recovery (i.e. how quickly after disturbance a patch can be colonized) and disturbance frequency (Ellner & Fussmann, 2003; Johnson, 2000), and that these main effects may be modified by a species' colonization ability (Amarasekare & Possingham, 2001) and the spatial extent of disturbance (Wilcox, Cairns, & Possingham, 2006). While these models focus primarily on factors affecting suitability of disturbed patches, many empirical studies suggest that the characteristics of nearby source habitats should also affect recolonization rates through differences in the abundance or behaviour of potential colonists, or some aspect of patch quality (e.g. Fletcher, Ries, Battin, & Chalfoun, 2007; Hahn & Orrock, 2015b,c; Haynes & Cronin, 2003). Yet, we lack evidence for which characteristics of source patches have a substantial, predictable effect on recolonization rates and how differences may scale up to affect dynamics at a metapopulation level, particularly in systems where local extinction arises from extrinsic factors such as disturbance rather than demographic factors. Our study addresses the first of these knowledge gaps—how differences among source habitats affect recolonization—in a fire-managed forest with variation in the time since disturbance of individual habitat patches.

We tested how disturbance in focal and neighbouring patches affects the abundance and distribution of a monophagous tortoise beetle (*Hemisphaerota cyanea* (Say)) in a longleaf pine forest at two spatial scales—within and between fire management units—using time since fire (TSF) as a measure of each unit's recovery state. Specifically, we asked:

1. *Within units*, does post-fire recolonization result in a gradient of beetle abundance from the edge of the unit to its interior, and how long does this gradient persist?
2. *Between units*, how do the burn histories of focal and neighbouring units affect beetle abundance in focal units? In particular, can variation in the burn histories of neighbouring source units help to explain variation in colonization rates?

2 | MATERIALS AND METHODS

2.1 | Study system

Apalachicola National Forest (hereafter ANF) comprises over 230,000 ha of flatwood and sandhill habitat in northwest Florida. This region was historically a fire-adapted longleaf pine and wiregrass ecosystem, but after generations of logging and fire suppression, many areas are now dominated by slash or loblolly pine with a saw

palmetto understorey. Current fire management prescribes controlled burns of c. 90 out of over 200 fire management units (hereafter "burn units"), or roughly one-third of the forest area, annually (U.S. Forest Service 1999). Burns are performed throughout the year. The result is a landscape-level mosaic of burn units that vary in the amount of time since last burned (TSF), which we consider a proxy for the state of recovery after disturbance.

Saw palmetto (*Serenoa repens* (Bartram) (Arecaceae)) is a dominant understorey shrub in ANF and the host plant of a native phytophagous tortoise beetle, *Hemisphaerota cyanea* (Say) (Coleoptera: Chrysomelidae). The palmetto beetle completes its entire life cycle on palmetto, including oviposition, feeding during larval and adult stages, and pupation (Woodruff, 1965) (Appendix S1). During prescribed burns, populations of *H. cyanea* sharply decline and may even go locally extinct. In addition, the above-ground biomass of palmetto is severely depleted, rendering the plants unsuitable as hosts (Appendix S1). Recovery of *H. cyanea* populations within burned units, therefore, depends on the regrowth of palmetto into suitable beetle habitat (*S. repens* resprout from below-ground rhizomes and typically attain knee-height with newly expanded leaves by c. 4 months after fire) and recolonization from nearby populations. The discrete spatial heterogeneity in tortoise beetle extinction and palmetto regrowth generated by fire management provides a unique opportunity for investigating the immediate and residual spatial effects of disturbance on a natural metapopulation.

2.2 | Tortoise beetle surveys

We approached the study of recolonization at two scales: within- and between-burn units, which we consider as separate habitat patches potentially occupied by beetle subpopulations. To investigate the effects of TSF on *within-unit* patterns of tortoise beetle abundance, we conducted 5- to 6-min timed count surveys for beetles at three distances from the unit edge (10, 50 and 100 m) along two transects in each of 31 units (one unit was surveyed along two edges—1 N-S and 1 E-W, >1 km apart—for a total of 32 "edge" observations per survey) (Figure 1). We classified individuals by life stage (egg, small larva [1st–2nd instar], large larva [3rd–4th instar], adult) and estimated mean palmetto height and total percent cover within a 5-m radius of the observer at each survey site.

To investigate *between-unit* effects on beetle abundance, we grouped the same units into focal-source burn unit pairs (*n* = 16) that varied in both the focal unit's TSF and the difference in TSF between the units (Appendix S2), with survey transects placed perpendicularly to their shared edge. We defined source burn units as the one in each pair that had gone longer since fire (i.e. greater TSF) and used difference in TSF rather that source unit TSF as a potential predictor to avoid inflating estimates for focal units with high TSF (the difference in the range of "difference in TSF" values between high and low TSF focal units was only slight; see Appendix S2). With this design, we were able to capture the existing variability in TSF with units ranging from 0 to

FIGURE 1   Map of Apalachicola National Forest burn units. Used with permission of U.S. Forest Service, Apalachicola and Wakulla Ranger Districts (see Appendix S2 for GIS data disclaimer)

64 months since fire and pairs ranging from 3 to 58 months difference in TSF. We surveyed over a 5- to 6-day period every 4 weeks during May, June, and July 2015.

2.3 | Analyses

We used model selection on separate sets of generalized linear mixed models (GLMMs) to test for within- and between-unit effects of TSF on beetle abundance, assuming Poisson error distributions for count data. For all analyses, we first used AICs to compare random effects structures among potential models and tested for overdispersion using the ratio of a model's residual deviance to its residual *df*; as this ratio was never >2, we retained Poisson error distributions. Then, working stepwise from the full model of relevant covariates and interactions, we eliminated non-significant fixed effects until arriving at a best-fit model.

First, we explored differences in how TSF affected within-unit beetle distributions among life stages by using counts of either adults, immature stages (i.e. eggs and larvae), or all stages combined as the response (*n* = 573 observations), unit TSF, log (distance from unit edge), palmetto height and cover as predictors, and transect nested within burn unit and month of survey as random effects. Palmetto height and cover were both included because we had no a priori expectation for how or which of these would affect beetle abundance and their values were not strongly correlated (ρ = .15).

For between-unit analyses, we grouped all life stages (including eggs, see Appendix S2) at each focal unit sampling site as the response (*n* = 279 observations). Focal unit TSF, difference in TSF between source and focal units, source unit beetle abundance (summed along each transect), palmetto height and cover, and relevant interactions were used as predictors; after testing several random effects structures, we included distance from road nested within burn unit and month of survey as random effects (see Appendix S2 for the full models used in the model selection procedure). Analyses were performed with the lme4 (for GLMM analyses) and MuMIn (to calculate marginal R^2 values) packages in R 3.3.1 (R Core Team, 2016).

3 | RESULTS

3.1 | General patterns of beetle abundance

We counted an average of 780 beetles across all burn units during each monthly survey. The proportion of individuals in each life stage varied by month (Figure 2): in May, the regional population was dominated by larvae (54% of beetles counted) and relatively few adults were observed (3% of beetles counted), while adults made up a much greater proportion of the total beetles counted in both June and July (24% and 28% of totals, respectively). Counts of eggs were high across all surveys, especially June and July; this may be due at least in part to repeated sampling of inviable eggs still present from earlier surveys in addition to newly laid eggs. At the local scale, burn units with greater TSF generally hosted larger populations of beetles (GLMM, *p* < .001, Figure 3).
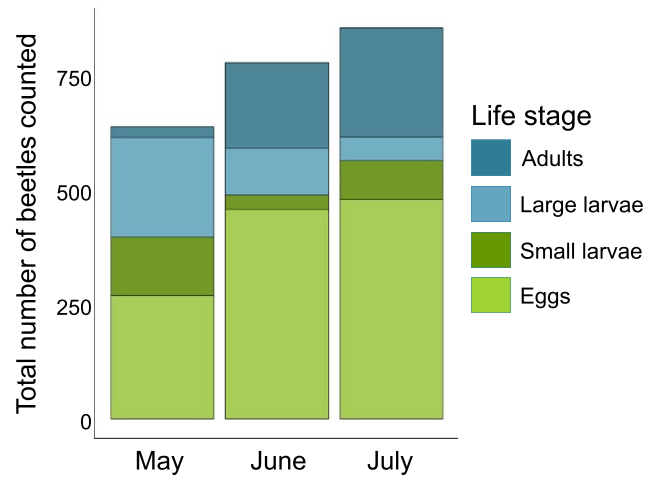

FIGURE 2 Total number of beetles counted during each monthly survey, grouped by life stage [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Within-unit effects of TSF

Within-unit effects of TSF differed between adults and immature stages. Adult abundances were affected by TSF only, with no difference in abundance based on distance from the edge of the burn unit (Figure 3a, Table S1). Effects of TSF on the abundance of eggs and larvae were more complex: units with the lowest TSF (<10 months) tended to have higher beetle abundance near the edge (i.e. at 10 m from the edge) than in the unit's interior (i.e. at 50 m and 100 m), whereas units with the greatest TSF (>50 months) tended to have more beetles at interior sites (i.e. 50 m and 100 m from the edge) than edge sites (i.e. at 10 m) (Figure 3b, Table S1). This interaction between TSF and distance from unit edge was also apparent for total beetle abundances (all life stages pooled, Table 1). Palmetto height at the survey location was also a significant predictor of beetle abundance (Table 1). However, the proportion of variation explained by fixed effects in the best-fit model was low, only c. 20% (marginal R^2 = .21).

3.3 | Between-unit effects of TSF

In general, focal unit beetle abundance increased with increasing focal unit TSF (*p* < .001; Table 1) and source unit abundance (*p* < .001; Table 1), but the main and interactive effects of focal unit TSF, source unit abundance, and the difference in TSF between paired units are best understood in the context of their three-way interaction (Figure 4; Table 1). Visualizing the interaction by separating pairs that have low (i.e. <25 months) versus high (i.e. ≥25 months) difference in TSF is informative: the positive effect of source unit beetle abundance on focal unit beetle abundance increases as focal unit TSF increases for unit pairs with a low difference in TSF (compare steepness of focal unit TSF × focal unit beetle abundance slopes at source unit abundance = 0, 15 and 30, highlighted in Figure 4a), but this is not the case for pairs with high difference in TSF (i.e. there is a large, positive initial effect of high source unit abundance, but this effect stays relatively weak with increasing focal unit TSF; see highlighted paths in

TABLE 1 Results of generalized linear mixed model (GLMM) analyses for within- and between-unit effects of time since fire (TSF). Best-fit GLMM results for within- and between-unit effects of TSF on focal unit beetle abundance for full dataset (all months included). Palmetto cover was dropped in the best-fit models. *p*-values <.05 are indicated in bold

	Estimate (*SE*)	*p*
Within-unit effects		
(Intercept)	0.489 (0.27)	.071
Unit TSF	0.0152 (0.008)	.0545
log (distance from unit edge)	−0.103 (0.04)	**.0052**
Palmetto height	0.384 (0.11)	**<.001**
Palmetto cover	—	—
Unit TSF × log (distance from unit edge)	0.004 (0.001)	**<.001**
Between-unit effects		
(Intercept)	−2.052 (0.64)	**.001**
Focal unit TSF	0.175 (0.05)	**<.001**
Diff. in TSF (source unit TSF − focal unit TSF)	0.0276 (0.02)	.222
Beetle abundance in source unit	0.0661 (0.011)	**<.001**
Palmetto height	0.386 (0.20)	**.048**
Palmetto cover	—	—
Focal TSF × diff. in TSF	−0.00157 (0.002)	.341
Focal TSF × beetle abundance in source unit	−0.00453 (0.001)	**<.001**
Diff. in TSF × beetle abundance in source unit	−0.00116 (0.0003)	**.0017**
Focal TSF × diff. in TSF × beetle abundance in source unit	0.000109 (0.00)	**<.001**

Figure 4b). These relationships suggest that the combined effects of a focal unit's recovery state and the beetle abundance in its neighbouring "source" unit on focal beetle abundance vary based on the disturbance history of the source. Overall, the best-fit model explained c. 40% of the variance in between-unit abundances (marginal R^2 = .39) and again retained palmetto height as a predictor.

4 | DISCUSSION

Our landscape-level survey revealed persistent effects of disturbance on the distribution and abundance of an herbivorous beetle at two spatial scales. Within burn units, small-scale patterns of distribution suggest that the effects of burning can persist for months or even years and therefore span several generations of our focal species, a multivoltine tortoise beetle. At the regional scale, differences in beetle abundance among patches suggest effects of both focal patch suitability (e.g. palmetto regrowth) and colonist availability on the rate of recolonization. While many empirical and theoretical studies have focused on the role of patch suitability in post-disturbance population recovery, our results are novel in their emphasis on the importance

of between-patch processes: in particular, we found that colonist availability is affected by both a source unit's disturbance history and population size, which together help to explain variation in the recolonization rates of recently burned units.

One of our findings was the presence of a gradient in palmetto beetle abundance at a relatively small scale: along sampling transects from 10 to 100 m. *Hemisphaerota cyanea* is generally patchily distributed among palmetto plants (N. Underwood and B. Inouye, unpublished data), so detecting an effect of TSF on small-scale spatial structure attests to the consistency of this effect across burn units even though actual differences in abundance between distances were small. The direction of the gradient for immature stages only as well as all stages combined—higher abundances near the edge than in the interior for recently disturbed units—suggests that beetle populations spread gradually to the interior of units during recolonization from external source units and sites closer to the edge. Similarly, the persistence of edge-skewed beetle distributions until about 35 months TSF suggests that recolonization is relatively slow compared to the rate of palmetto regrowth. Differences of only a few beetles between edge and interior for recently burned units may be important when population sizes are already small (e.g. for mate finding), but likely do not change the beetles' effect on other species; this is in contrast to some other studies of insect recolonization which demonstrate changes to interspecific interaction strength (e.g. herbivory) associated with large differences in insect abundance through space (e.g. Knight & Holt, 2005). Interestingly, instead of observing a more even within-unit distribution for burn units with greater TSF, we find that the gradient reverses (i.e. greater abundances are found in the unit's interior). This pattern is more consistent with the effects of roads or abrupt edges on populations residing in forest fragments ("edge effects"; Murcia, 1995; Ries, Fletcher, Battin, & Sisk, 2004). Since our transects originated along forest access roads, edge effects such as increased predation along the forest edge (Andrén, 1995; Andrén & Angelstam, 1988) or differences in palmetto abundance, structure or quality for oviposition could play a role in beetle distribution after initial post-fire recovery. In contrast with immature stages, adult beetle abundances did not differ based on sampling location within units (no effect of distance from unit edge; Figure 2a); this could be biologically attributable to mobile adults displaying bias in oviposition location or statistically attributable to lack of power due to low adult counts.

At the between-unit scale, we found effects of TSF on the total abundance of beetles in each burn unit. Ecologists have long recognized the necessity of suitable resources and abiotic conditions for immigrant survival following disturbance (Pickett & White, 1985; Sousa, 1984; Wood & del Moral, 1987). For insect herbivores responding to fire, patch suitability can be mediated through changes in vegetative structure (Bock & Bock, 1991; Evans, 1984; Kerstyn & Stiling, 1999; Swengel, 2001; Vieira, Andrade, & Price, 1996), plant quality (Stein et al., 1992; Swengel, 2001), and plant- or neighbourhood-level traits associated with host plant finding (Strong, Lawton, & Southwood, 1984; Swengel, 2001). Because *H. cyanea* is a palmetto specialist, we expect its recolonization to depend strongly on the rate of palmetto regrowth, which is among the fastest of Florida scrub species (Maguire

& Menges, 2011). We measured two aspects of palmetto regrowth in this study: height and percent cover. Palmetto height was usually retained as a predictor of beetle abundance, while percent cover was not (Table 1). Although we did not measure aspects of palmetto quality, foliar concentrations of nitrogen (N) and phosphorous (P) (which are often limiting for herbivorous insects) have been previously shown to increase in *S. repens* after fire, with the greatest concentrations measured at about 1 year after burning (Schafer & Mack, 2010, 2014). In additional, leaves that emerge after a burn are likely less tough than more mature leaves (Vieira et al., 1996). Thus, changes to leaf toughness, foliar nutrients, and other aspects of plant quality may contribute to patch suitability beyond the more visible effect of palmetto abundance. We used a burn unit's TSF as a composite measure of all of these effects and a more explicit representation of the time-lag associated with patch recovery. As expected, TSF was a significant main effect in our models (Table 1).

Compared with patch suitability, the role of colonist availability in the post-disturbance recolonization of animals has received little empirical attention. Colonist availability should be especially important in systems such as ours, where local populations are often extirpated following disturbance events and rely on immigration to re-establish. This study focused on two habitat-level characteristics of neighbouring patches—source unit burn history (i.e. difference in TSF between paired units) and beetle abundance—both of which modified the individual effect of patch suitability on the recolonization of focal burn units. The positive effect of source unit abundance is expected, since it represents the number of beetle individuals that may potentially emigrate and ultimately recolonize focal units. In contrast, the role of difference in TSF is less clear. Our data show that the initial benefit for a focal unit of having a high-abundance source is much greater when source units have gone longer since a burn (e.g. see the difference in intercepts at source unit abundance = 30 between Figure 4a and b). Given equal source population sizes, these differences in colonist availability suggest variation in the emigration rate, or proportion of individuals that leave a habitat patch, based on the unit's disturbance history. In our system, emigration rate is likely influenced by a population's demography or individuals' behavioural response to habitat quality. For example, adults are highly mobile compared with immatures, so even source populations with high abundance may not contribute many colonists if primarily made up of eggs and larvae. Because adult abundance is positively correlated with TSF (Table 1, Figure 3), the stage structure of source populations based on their disturbance history (the higher abundance of adults in source units with greater TSF) likely contributes to colonist availability by altering emigration rates. The increase in colonist influx as both focal and source units recover (see highlighted focal unit TSF × focal beetle abundance slopes in Figure 4a) further attests to the probable importance of the adult stage in influencing patterns of recolonization in focal units. While total beetle abundance in focal units does appear to be more strongly related to the number of adults in source units than to all life stages combined (Figure 5), we were unable to assess the effect of adults or stage structure directly because of the relatively small proportion of total counts made up by adults.
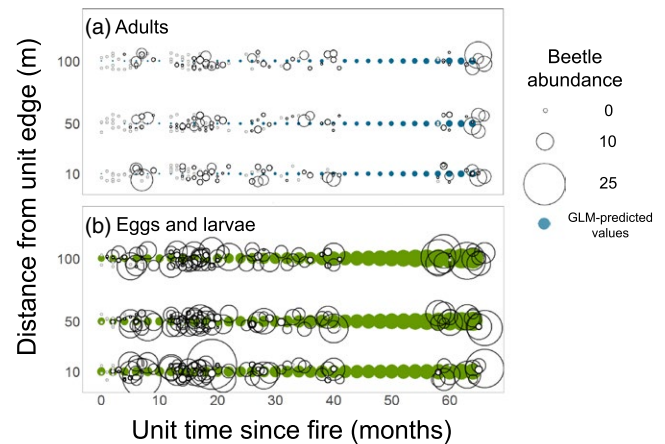

FIGURE 3 Effects of time since fire (TSF) and distance from unit edge on the abundance of (a) adult and (b) egg and larval *Hemisphaerota cyanea* at each sampling site. Adult abundances are affected by TSF but do not differ based on the within-unit location of the sampling site (GLMM, adult total ~ TSF, *p* < .001). Beetles in the egg and larval stages show a slight gradient in abundance, which reverses with time (GLMM, TSF × log (distance from unit edge), *p* < .001): in units burned more recently, more beetles were observed at 10 m from the edge and therefore closest to neighbouring units; units with greater TSF showed the opposite pattern, with more beetles found in the interior at 50 or 100 m. Point size is scaled to beetle abundance and jittered vertically to reduce overlap, with open grey points indicating zero counts. Solid points show GLM-predicted values. GLMM, generalized linear mixed model [Colour figure can be viewed at wileyonlinelibrary.com]

Time since fire is rigorously catalogued by the U.S. Forest Service and does not rely on time-consuming population surveys, making it a particularly convenient metric for prediction (even though TSF did not fully account for variation in recolonization). Other types of disturbance or land use can produce similar effects to those we observed, although the relevance of specific metrics (e.g. frequency of fire [Glitzenstein, Platt, & Streng, 1995] vs. TSF) will likely depend on the ecology of the study organism. For example, recent empirical work suggests that the effect of colonists can be mediated through behavioural, rather than exclusively numerical, effects (Hahn & Orrock, 2015b). Specifically, increased herbivory in patches with agricultural and fire suppression land use histories in Hahn & Orrock (2015b) did not correlate with increased herbivore abundance, but was instead attributed to differences in foraging behaviour based on disturbance-mediated changes to the plant community. Therefore, in addition to exploring the influence of other habitat-level characteristics, such as landscape successional state (Watson et al., 2012) or structure (Pavlacky et al., 2012), future studies should investigate the role of both organismal (e.g. individual behaviour) and population-level traits (e.g. demographic structure), perhaps using path analysis to assess their relative contributions to observed patterns of recolonization.

Current metapopulation models of disturbance-driven extinction and colonization tend to incorporate patch recovery rates (i.e. the length of time after disturbance before a patch is suitable for colonization), but dismiss any potential effects of variation in colonist
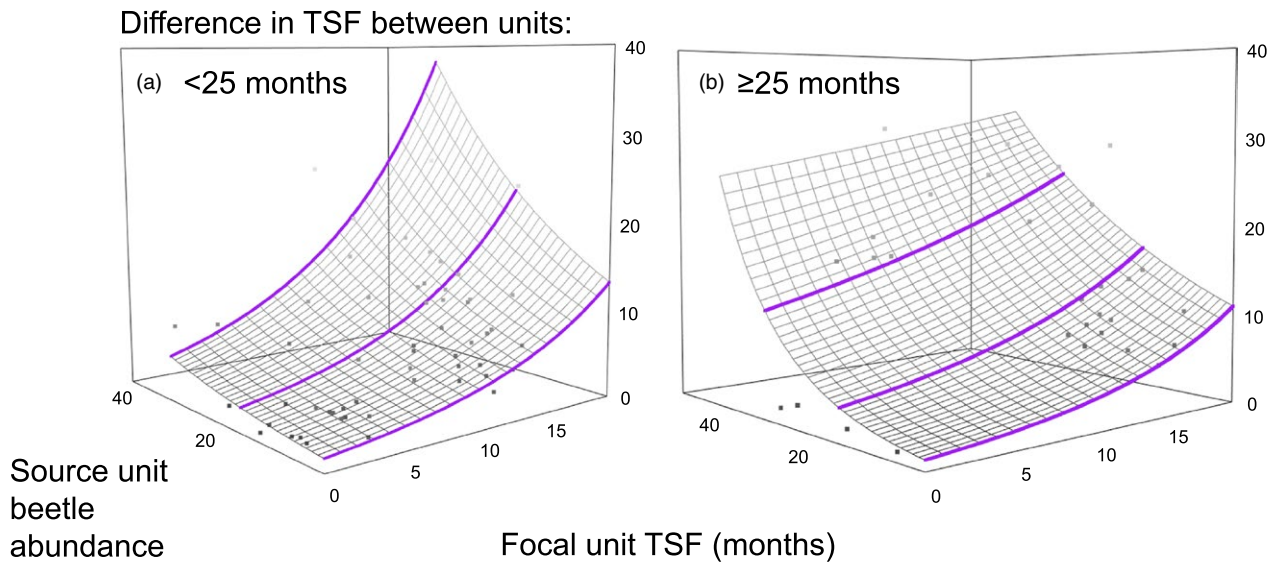
FIGURE 4 Beetle abundance in a focal burn unit is affected by that unit's fire history and the beetle abundance in a neighbouring "source" unit, with the shape of this relationship differing based on the fire history of the source unit (best-fit surface; GLMM, focal TSF × diff. in TSF × source unit beetle abundance, $p < .001$). For visual clarity, unit pairs have been separated into those with (a) low or <25 months and (b) high or ≥25 months difference in TSF. Points indicate focal unit beetle abundance summed by transect and shading of points varies with location along the vertical axis, from dark (low values of beetle abundance) to light (high values of beetle abundance). Solid lines represent the relationship between focal unit TSF and focal unit beetle abundance when source unit beetle abundance is held constant at 0, 15 or 30 individuals. TSF, time since fire; GLMM, generalized linear mixed model [Colour figure can be viewed at wileyonlinelibrary.com]
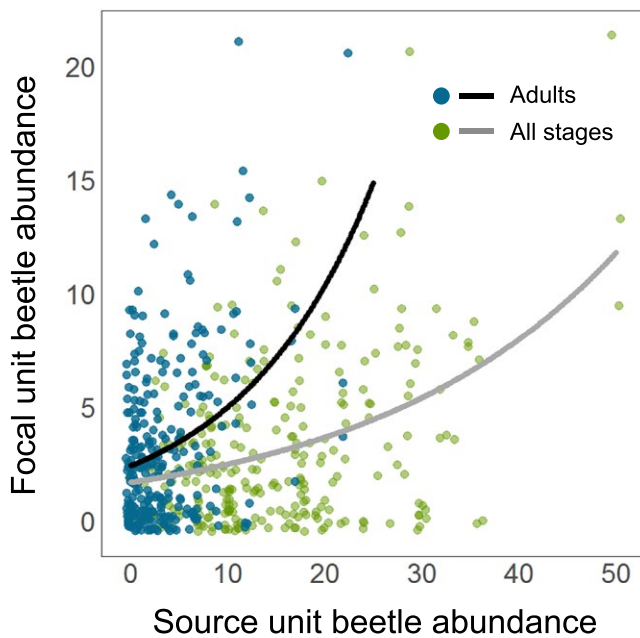
FIGURE 5 The numbers of adults and total *Hemisphaerota cyanea* in a source unit (summed by transect) are positively related to the total beetle abundance at each sampling site in its paired focal unit. Data points are jittered to reduce overlap; solid lines represent GLM-predicted values [Colour figure can be viewed at wileyonlinelibrary.com]

availability. By empirically identifying local patch- or population-level traits that are predictive of colonization rate, we can more easily model the role of variable colonist availability in metapopulation dynamics. A general assumption of metapopulation models is homogeneous,

instantaneous within-patch population dynamics and equal, fixed colonization and extinction rates for all patches (Hanski, 1998, 1999; Levins, 1969), but modelling the effect of differential colonist availability would require variation in colonization rates through space or time. One way to include variation in colonization rates is by tracking individual patch densities and calculating a fraction of residents for local or global dispersal at each time step; however, this would be mathematically cumbersome. A simpler approach is to use empirically predictive characteristics of patches to assign patch-specific extinction and colonization rates. In the Incidence Function Model (Hanski, Moilanen, Pakkala, & Kuussaari, 1996), for example, an individual patch's size and connectivity are used to determine its extinction and colonization rates, respectively. Although empirical support for these assumed relationships is mixed (Eber, Roland, & Brandl, 1996; Fleishman, Ray, Sjögren-gulve, Boggs, & Murphy, 2002; Robles & Ciudad, 2012), accounting for variation among patches with this method often improves model predictions over unstructured models (Hanski et al., 1996).

Our data suggest that natural populations, especially those subject to disturbance, are likely to violate basic metapopulation assumptions by exhibiting variation in patch-specific colonization rates through time. Even in the Incidence Function Model, rates are determined by a patch's own traits, which are considered fixed. Disturbance or successional dynamics, on the other hand, would necessitate that patch characteristics can change through time (e.g. TSF) or depend on spatial context (e.g. neighbouring patch's TSF or abundance). We argue that traits of neighbouring patches, which are spatially explicit and temporally dynamic, are important for predicting variation in colonization rates among patches in a natural metapopulation of tortoise beetles. However, fitting a model with this level of detail would be prohibitively

complex and overly specific for generating general theoretical predictions about disturbance-driven metapopulation dynamics. Instead, we suggest that future work in metapopulation theory should focus on investigating the general effects of spatial and temporal variation in colonization rates on long-term metapopulation outcomes and identifying which aspects of biological realism are particularly important to these outcomes (especially in disturbance-driven systems), using both analytical and spatially explicit simulation models.

AUTHOR CONTRIBUTIONS

J.M., N.U. and B.D.I. designed the study. J.M. led and N.U. and B.D.I. contributed to data collection, data analysis and manuscript preparation.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.60326 (Mutz, Underwood, & Inouye, 2017).

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