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Removing forest canopy cover restores a reptile assemblage

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Abstract. Humans are rapidly altering natural systems, leading to changes in the distribution and abundance of species. However, so many changes are occurring simultaneously (e.g., climate change, habitat fragmentation) that it is difficult to determine the cause of population fluctuations from correlational studies. We used a manipulative field experiment to determine whether forest canopy cover directly influences reptile assemblages on rock outcrops in southeastern Australia. Our experimental design consisted of three types of rock outcrops: (1) shady sites in which overgrown vegetation was manually removed ($n = 25$); (2) overgrown controls ($n = 30$); and (3) sun-exposed controls ($n = 20$). Following canopy removal, we monitored reptile responses over 30 months. Canopy removal increased reptile species richness, the proportion of shelter sites used by reptiles, and relative abundances of five species that prefer sun-exposed habitats. Our manipulation also decreased the abundances of two shade-tolerant species. Canopy cover thus directly influences this reptile assemblage, with the effects of canopy removal being dependent on each species' habitat preferences (i.e., selection or avoidance of sun-exposed habitat). Our study suggests that increases in canopy cover can cause declines of open-habitat specialists, as previously suggested by correlative studies from a wide range of taxa. Given that reptile colonization of manipulated outcrops occurred rapidly, artificially opening the canopy in ecologically informed ways could help to conserve imperiled species with patchy distributions and low vagility that are threatened by vegetation overgrowth. One such species is Australia's most endangered snake, the broad-headed snake (*Hoplocephalus bungaroides*).

Key words: abundance; broad-headed snake; field experiment; fire suppression; habitat quality; habitat use; Hoplocephalus bungaroides; *rock outcrop; southeastern Australia; species richness; vegetation overgrowth.*

Introduction

Humans are modifying natural systems in multiple complex ways, and these modifications often coincide with observed changes in the distribution and abundance of species (Caughley and Gunn 1996). The simultaneous, and often synergistic, nature of these modifications (e.g., climate change, pollution, habitat fragmentation, altered disturbance regimes) makes it difficult to discern which factors actually influence animal populations. Ecological studies often correlate population trends or habitat use with environmental variables (Gardner et al. 2007, Mac Nally and Horrocks 2007), but this approach does not differentiate correlation from causation. Understanding the cause of a decline can increase the likelihood that conservation or management techniques will be successful because these efforts can target the drivers of the decline (Caughley and Gunn 1996). Conversely, not understanding the cause can lead to time and resources being spent on conservation projects with poor outcomes (Green 1995, Caughley and Gunn 1996). To make direct links between population trends and environmental variables, we need field experiments that manipulate a single habitat variable so that we can rule out plausible alternative hypotheses. If a causal relationship is found, insight will be gained as to how that variable affects ecological interactions in the study system, thus providing information on how population declines can be ameliorated or reversed. Alternatively, if a causal relationship is not found, this information can be used to refine hypotheses or experiments (Caughley and Gunn 1996).

Forest canopy cover is an important component of many ecosystems because it provides structural complexity and influences microhabitat conditions by controlling sunlight penetration, thereby influencing the microclimate on the forest floor (Chen et al. 1999, Hunter 1999). Open habitats with little canopy cover provide relatively warm microenvironments at ground level, but such sites often are patchy and rare in forests. Nonetheless, sun-exposed habitats support a wide range of endemic and rare species that are often absent from nearby forested areas, and these specialists contribute substantially to local biodiversity (Hunter 1999). Thus, any change in the availability of open habitats could directly influence faunal assemblages. For example, increases in forest cover have been linked to decreased

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abundances of open habitat specialists, e.g., invertebrates (Anderson et al. 2006, Blaum et al. 2009), amphibians (Skelly et al. 1999), birds (Kaphengst and Ward 2008, Sirami et al. 2009), mammals (Blaum et al. 2007), and reptiles (Ballinger and Watts 1995, Jäggi and Baur 1999). However, the distribution of forest cover is influenced by a myriad array of processes (both natural and anthropogenic), and alternative influences could also explain the correlations between habitat openness and faunal composition. For example, vegetation cover is directly influenced by soil type, soil depth, drainage, and vulnerability or exposure to fire (e.g., Clarke 2002, Sankaran et al. 2005), and these factors (instead of canopy cover per se) may influence the distribution of fauna. We can distinguish between these alternative hypotheses by experimentally manipulating canopy cover; if canopy cover negatively influences abundance, then removing cover should result in colonization by fauna. Thus, experimentally testing whether canopy cover plays a causal role in faunal distributions can provide a critical underpinning for conservation and management plans.

Open habitats within forests are important for ectotherms because they provide access to direct sunlight and temperature mosaics used for behavioral thermoregulation (Vitt et al. 1996, Greenberg 2001). In rocky habitats, reptiles often thermoregulate inside crevices formed by overlying rocks located in sun-exposed locations (Huey et al. 1989, Kearney and Predavec 2000). These microhabitats provide access to the warmest temperatures available (Webb and Shine 1998*a*), but are limited by the openness of the forest canopy (Pringle et al. 2003). For example, Australia's most endangered snake (the broad-headed snake, *Hoplocephalus bungaroides*) is nocturnal and thermoregulates beneath rocks in sun-exposed areas throughout much of the year (April–September; Webb and Shine 1998*a*). However, open sites are patchily distributed and have declined dramatically over the past seven decades due to woody vegetation encroachment (Pringle et al. 2003, 2009). If canopy cover directly influences the use of these shelters by reptiles, any increase in canopy cover could reduce abundances. We manually removed forest canopy cover overgrowing a series of rock outcrops and monitored the responses of reptiles to understand whether canopy cover influences: (1) reptile species richness, (2) the percentage of rocks used by reptiles, and (3) abundances of individual species. We simultaneously monitored reptiles in overgrown and sun-exposed control sites to establish correlative patterns of assemblage structure, and we compared these patterns to the responses of reptiles to our manipulations. Our prediction was that if canopy cover directly influences assemblage structure, and reptiles respond rapidly to decreases in canopy cover, the assemblages of manipulated outcrops should resemble those of sun-exposed outcrops. Finally, if we can demonstrate this causal link, then manually removing canopy cover could offer a way to restore overgrown habitat.

Methods

Study area and experimental design

We manipulated canopy cover along Monkey Gum plateau, an elevated sandstone ridgeline in southeastern New South Wales, Australia (35° S, 150° E). The plateau and surrounding valleys are dominated by closed-canopy eucalypt forest, except for bare rock outcrops located near cliff edges (Fig. 1). At our site, sun-exposed bare rock habitat has declined by 24% over the past 65 years due to vegetation encroachment (Pringle et al. 2009). In April 2007 we selectively removed trees shading 25 overgrown rock outcrops (Fig. 1), and quantified the resultant changes in canopy cover, solar radiation transmitted through the canopy, and thermal regimes beneath rocks. These variables were compared to 30 overgrown outcrops ("shady," the initial state) and 20 sun-exposed outcrops ("sunny," the desired state). Manipulated outcrops ("treatments") initially resembled the shady outcrops in terms of canopy cover, incident radiation, direct sunlight exposure, and rock temperatures; canopy removal successfully changed these characteristics so that they were more similar to open, sunny outcrops in these respects (Table 1; see Pike 2010). Outcrops were $\sim$107 m^2 in size, and were separated from neighboring sites by an average distance of 80 m. Within each outcrop, all rocks large enough to shelter a juvenile lizard were given a unique number.

Sampling and statistical analysis

We sampled for reptiles at monthly intervals from May 2007 to October 2009 ($n = 30$ months, spanning three autumn-winter-spring periods and two summers). During sampling, we searched each outcrop for active reptiles and turned all loose rocks to find sheltering reptiles. For each capture, we recorded the rock number and gave each individual a unique mark: toe clips for lizards and PIT (Passive Integrated Transponder) tags for snakes. Analyses in the present study are based on a single capture record (the initial capture) for each individual, to avoid pseudoreplication. We used these capture data to calculate: (1) the number of species observed in each rock outcrop (species richness), (2) the percentage of rocks within each outcrop used by reptiles, and (3) the total number of individuals marked per outcrop for each of the common species. We compared species richness and rock usage among outcrop types using analysis of covariance (ANCOVA) with rock density (rocks/m^2) as the covariate (to control for differences in shelter availability and outcrop size; Table 1) and either species richness or the number of rocks recorded to house reptiles as the dependent variables. Alpha was set at 0.05.

To explore the effects of our habitat manipulation on the seven most common reptile species, we first examined correlative patterns of abundance between

FIG. 1. Removing canopy cover from an overgrown rock outcrop along Monkey Gum plateau in southeastern New South Wales, Australia. This is the last tree to be removed from this treatment site, and it is in the process of falling down. Fallen trees were later removed from the exposed bare rock. Photo credit: D. A. Pike.

preexisting (unmanipulated) sunny and shady outcrops. This comparison allowed us to identify which species were most abundant in sun-exposed sites, and hence would be predicted to increase in numbers following canopy clearing. For each species, we calculated the total number of individuals marked in each outcrop, and divided this by the number of rocks in that outcrop (to control for shelter availability). We then used a randomization procedure to pair the 20 sunny outcrops with 20 randomly selected shady outcrops and calculate the mean difference in abundance between these pairs. This randomization procedure was repeated 100 times, and we used the resultant grand means and 95% confidence intervals to quantify patterns of habitat use for each species. For example, a species that was more abundant in sun-exposed outcrops than shady outcrops would have positive scores for this contrast measure (abundance in sunny minus shady sites), whereas shade-

TABLE 1. Characteristics of control outcrops (unmanipulated shady or sunny) and treatment outcrops (following canopy removal) along Monkey Gum plateau in southeastern New South Wales, Australia.

Characteristic	Outcrop type		
	Shady	Sunny	Treatment
Number of replicates	30	20	25
Mean canopy openness (%)	44.2 ± 1.2	71.2 ± 2.2	65.8 ± 2.1
Mean transmitted solar radiation (mols/m^2/d)	19.7 ± 0.4	28.5 ± 0.6	26.6 ± 0.5
Mean rock temperature over 24 h (°C)	19.5 ± 0.1	21.3 ± 0.2	21.3 ± 0.1
Mean afternoon rock temperature (°C)	24.3 ± 0.3	27.3 ± 0.4	27.8 ± 0.5
Total number of rocks	346	266	348
Mean number of rocks per outcrop	11.5 ± 0.7	13.3 ± 1.7	13.9 ± 1.1

Notes: Temperatures are mean values beneath rocks during the spring following canopy manipulation (October–November 2007; $n = 34$–55 rocks per outcrop type). Means are presented ±SE.

TABLE 2. The percentage of rocks used by each reptile species (mean ± SE), by outcrop type, in the Monkey Gum study area, NSW, Australia.

Species	Common name	Activity	Rocks used (%)		
			Shady	Sunny	Treatment
Lizards					
Acritoscincus platynotum	red-throated skink	diurnal	10.4 ± 1.5	6.6 ± 1.5	6.8 ± 1.0
Amphibolurus muricatus	jacky dragon	diurnal	0.4 ± 0.3	0.5 ± 0.5	0.5 ± 0.3
Cryptoblepharus pulcher	wall skink	diurnal	3.1 ± 0.8	20.7 ± 3.0	11.8 ± 2.4
Ctenotus taeniolatus	copper-tailed skink	diurnal	2.6 ± 1.2	5.4 ± 2.1	12.0 ± 2.7
Egernia cunninghami	Cunningham's skink	diurnal	0.2 ± 0.2	5.0 ± 2.6	0
Eulamprus quoyii	eastern water skink	diurnal	1.5 ± 0.7	2.2 ± 1.2	0.4 ± 0.4
Lampropholis delicata	delicate skink	diurnal	6.4 ± 1.2	4.0 ± 1.2	2.7 ± 0.9
Lampropholis guichenoti	garden skink	diurnal	1.9 ± 0.8	1.6 ± 1.0	0.9 ± 0.5
Oedura lesueurii	velvet gecko	nocturnal	10.4 ± 2.0	26.4 ± 3.2	15.7 ± 3.0
Varanus varius	lace monitor	diurnal	0	0	+
Snakes					
Hoplocephalus bungaroides	broad-headed snake	nocturnal	0.9 ± 0.5	4.6 ± 1.6	1.4 ± 0.8
Morelia spilota	diamond python	diurnal	0	+	0
Pseudonaja textilis	brown snake	diurnal	0	0	+
Rhinoplocephalus nigrescens	small-eyed snake	nocturnal	3.9 ± 1.2	4.6 ± 1.5	5.6 ± 1.4

Note: Species found active (as opposed to beneath rocks) are indicated by a "+."

tolerant species would have negative scores. A species with no distinct preference would have a contrast score overlapping zero (Quinn and Keough 2002). To quantify the effect of our manipulations on species abundances, we repeated this procedure using differences in relative abundance between the treatment (manipulated) and shady (unmanipulated, baseline) outcrops. If canopy cover has a causal effect on reptile abundance, then our experimental canopy clearing should change reptile distributions in the same directions as seen in comparisons between naturally sunny and naturally shady outcrops. Conversely, if canopy cover does not have an effect, the abundances in the manipulated outcrops should match those of the shady outcrops due to their initial similarity.

Results

All 75 rock outcrops were used by reptiles, comprising 14 species in total (range 1–8 species per outcrop; Table 2). Mean species richness differed among outcrops (ANCOVA; $F_{2,71} = 5.28$, $P = 0.007$); sunny and treatment outcrops contained similar numbers of species (Tukey's honestly significant difference posthoc test: $P = 0.63$), whereas shady outcrops contained relatively few species ($P < 0.008$ and $P < 0.05$, respectively; Fig. 2a). The percentage of available rocks used by reptiles also differed among outcrops (ANCOVA; $F_{2,71} = 8.81$, $P < 0.001$); reptiles used more rocks in sunny and treatment outcrops ($P = 0.46$) than in shady outcrops ($P < 0.001$ and $P = 0.01$, respectively; Fig. 2b).

During our study, we captured 776 individuals of the seven most common reptile species. Comparisons between sunny and shady outcrops revealed nonrandom habitat use, with five species showing increased abundances in sun-exposed outcrops and the other two species showing decreased abundances in sun-exposed outcrops (Fig. 3a). Reptile abundances changed significantly in the manipulated outcrops relative to shady outcrops (Fig. 3b), and in the same directions as predicted from the patterns seen in unmanipulated outcrops (Fig. 3). The shifts induced by canopy clearing were statistically significant (confidence limits not overlapping zero) for six of the seven species (Fig. 3b). The sole exception (the broad-headed snake) showed a slight, but nonsignificant, increase in relative abundance in the predicted direction (Fig. 3b).

Discussion

Woody vegetation encroachment is a global management problem brought about by the large-scale suppression of natural disturbance regimes and/or herbivore removal (Bond et al. 2005, Nowacki and Abrams 2008). Active management can be effective at reducing woody vegetation density by increasing habitat heterogeneity, patchiness, and microhabitat diversity, while decreasing habitat uniformity. However, many common forms of management (e.g., prescribed fire) cannot be applied in all instances. In our study, manually removing canopy cover from overgrown rock outcrops rapidly increased species richness (Fig. 2a), rock use (Fig. 2b), and abundances of both nocturnal and diurnal reptiles that prefer sun-exposed habitat, while decreasing the abundances of shade-tolerant species (Fig. 3). Canopy cover therefore plays a direct, causal role in determining the distribution and abundance of reptiles in this assemblage. Consequently, sun-exposed rock habitats are important for maintaining reptile species richness and abundance, and increases in canopy cover (e.g., following long-term fire suppression and/or removal of herbivores; Nowacki and Abrams 2008, Pringle et al. 2009) could negatively influence assemblage structure, including abundances of the endangered broad-headed snake and its main prey, the velvet gecko.

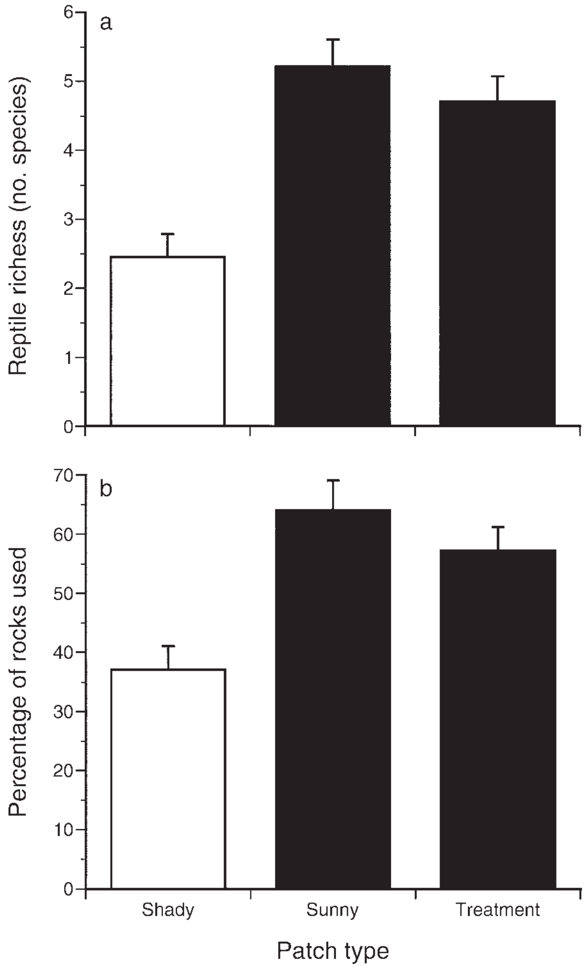

FIG. 2. (a) Reptile species richness and (b) percentage of rocks used by reptiles in the three types of outcrop (data given as mean + SE). Sunny and treatment outcrops had higher species richness and percentages of rocks used than shady outcrops.

Although six of the focal species responded significantly to reductions in canopy cover, broad-headed snakes showed a positive, but not significant, response to our manipulation. This was probably due to their rarity (e.g., treatment: $n = 5$ individuals in four outcrops, shady: $n = 3$ in three outcrops). This scarcity, combined with their slow life history (Webb and Shine 1998*b*), suggests that responses of broad-headed snakes to decreases in canopy cover will occur over timescales longer than our current study. Importantly, the availability of velvet geckos, which influences the abundance of broad-headed snakes (Shine et al. 1998), increased significantly (Fig. 3b). Thus, canopy removal not only restored habitat quality for this endangered snake in terms of abiotic conditions (Table 1; see Pike 2010), but also increased prey availability. All of the broad-headed snakes from shady outcrops were captured in late September, a time when rocks are becoming too hot for reptiles (Webb and Shine 1998*a*, Kearney 2002). This seasonal pattern suggests that shady rock outcrops may be important at some times of the year, and that heterogeneity in canopy cover not only helps to maintain individual members of this assemblage (e.g., Fig. 3), but also allows reptiles to continue using rock outcrops during months when temperatures under sun-exposed sites exceed lethal levels.

Our results do not support the common assertion that canopy removal negatively influences biodiversity and habitat quality (e.g., selective or salvage logging;

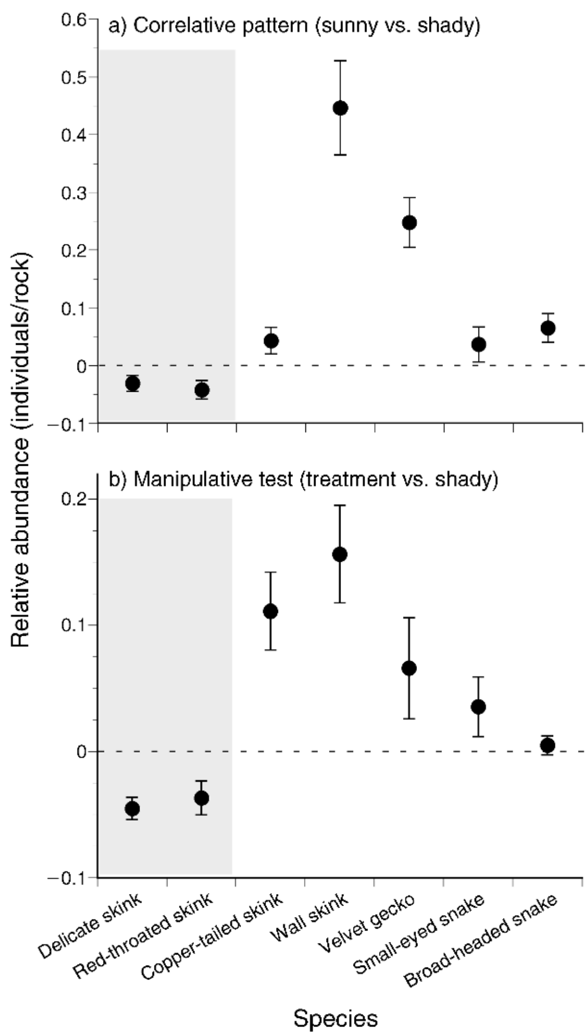

FIG. 3. Abundances of the seven most common reptile species (expressed as the number of individuals marked per rock), used (a) to generate correlative predictors of habitat use for each species by comparing abundances in sunny outcrops relative to shady outcrops, and (b) to test our experimental manipulation by comparing treatment (manipulated) outcrops to shady outcrops (the baseline condition). Shown are means and 95% confidence intervals; intervals falling below zero (dashed horizontal line) indicate a preference for shady habitat, those above zero indicate a preference for (a) sunny or (b) manipulated outcrops, and those overlapping zero show no significant habitat association.

Thiollay 1992, Vitt et al. 1998, Lindenmayer et al. 2008). For example, canopy removal is often associated with deforestation, which can modify habitats in ways that do not occur in nature. Such modified habitats often have harsh microclimates (Vitt et al. 1998, Greenberg 2001, Lindenmayer et al. 2008, Todd and Andrews 2008), which often reduce biodiversity (but see Greenberg 2001, Todd and Andrews 2008). In contrast to economically driven canopy removal, our fine-scale management of canopy cover was different both in scale and intent to typical deforestation activities; and thus, was carefully designed to mimic both the vegetation structure and abiotic conditions found within naturally occurring open rocky areas (Table 1). Consequently, our manipulation increased microhabitat temperatures in biologically meaningful ways (Table 1), and temperature is an important proximal cue used by reptiles to select shelter sites (Huey et al. 1989, Webb et al. 2004). Manipulated outcrops contained both adults and juveniles of the most common species, suggesting that increased abundances were due to both immigration from surrounding habitats and reproduction within these outcrops. The influence of habitat structure on abundances was strong, but whether canopy reduction also influences fitness-related traits (e.g., growth, survival, reproduction) is currently unknown.

Open habitat in our system is limited and has become increasingly rare (Pringle et al. 2003, 2009); thus, canopy removal could serve to reduce contemporary vegetation overgrowth while immediately benefitting most members of this assemblage. Therefore, artificially creating open habitat patches can be used as a conservation strategy, especially because this approach has little impact on nontarget areas (e.g., our manipulations increased open habitat in the landscape by 2% and only decreased forest cover by <0.1%; Pike 2010). Although manual vegetation removal is somewhat analogous to other common forms of habitat management, alternatives such as prescribe fire can have negative effects on biodiversity (e.g., Russell et al. 1999) or can be ineffective (e.g., where vegetation is too thick to carry fire, or in highly fragmented areas; Nowacki and Abrams 2008). In contrast, our manipulations probably benefitted other taxa (i.e., many other taxa depend upon sun-exposed sites and there are no shade specialists under threat in this system), and are very effective in areas with thick vegetation or habitat fragments. In sum, we demonstrate the importance of canopy removal in maintaining open-habitat patches in the landscape, which can help to maintain populations of imperiled species that have patchy distributions, low vagility, and are threatened by vegetation overgrowth.

Forest canopy structure plays an important role in many systems, and canopy gaps often support diverse taxa not found within the forest itself (Hunter 1999). Consequently, vegetation overgrowth has been implicated in the decline of a wide range of animal taxa (e.g., Ballinger and Watts 1995, Anderson et al. 2006, Sirami et al. 2009), and our field experiment provides empirical support for these observations. We also show that manually removing canopy cover can serve as an effective conservation and habitat management strategy. For habitat manipulation to be useful in conservation, it should (1) manipulate variables that directly influence the distribution and/or abundance of species, (2) elicit responses by those species over short timescales, and (3) be sufficient in scale to benefit those species (Shoemaker et al. 2009). Our field experiment met all of these criteria, demonstrating that canopy cover is easy to manipulate in biologically meaningful ways, and results in an immediate change in abiotic conditions (Pike 2010), followed by faunal responses (this study). Recent reports of large-scale vegetation thickening (e.g., Anderson et al. 2006, Nowacki and Abrams 2008, Donohue et al. 2009, Pringle et al. 2009), combined with the difficulty of applying fire in fragmented or overgrown habitats, strongly suggest that alternative forms of habitat management are necessary. Manually removing trees is one effective approach.

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