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Exotic deer diminish post-fire resilience of native shrub communities on Santa Catalina Island, southern California

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Abstract Browsing by exotic mule deer on Santa Catalina Island (SCI) off the coast of southern California may diminish the post-fire resilience of native shrublands. To assess this, deer exclosures were established following a wildfire to monitor post-fire recovery of three dominant, native shrub species (*Heteromeles arbutifolia*, *Rhus integrifolia*, and *Rhamnus pirifolia*). Post-fire resprout growth, mortality, and tissue water status as well as pre- and post-fire shrub density and cover were measured inside and outside of deer exclosures. We found that deer browsing significantly limited post-fire resprout growth and led to increased mortality of resprouting *H. arbutifolia* shrubs (88 % mortality outside compared to 11 % inside exclosures). Post-fire resprouts maintained favorable water status during the study despite drought conditions, indicating that water stress was not a proximate cause of resprout mortality. Deer browsing resulted in a >93 % reduction in canopy coverage of dominant shrub species. The dramatic reduction of native shrubs at this site may create opportunities for displacement by exotic species, resulting in eventual vegetation-type conversion. The observed link between intense browsing and post-fire shrub mortality provides much needed information concerning the environmental impact of exotic deer on SCI and illustrates the interaction between exotic herbivores and fire on an island system.

Keywords Chaparral · Mediterranean-type ecosystem · Exotic herbivores · Deer browsing · Post-fire resprouts · Shrub mortality · Vegetation-type conversion · Water potential · Xylem cavitation · Turgor loss point

Introduction

Exotic mammalian herbivores have been implicated as drivers of environmental change and extinction of native and endemic species on islands (Carlquist 1974; Coblentz 1978; Vitousek 1988; Atkinson 1989; Potvin et al. 2003; Côté et al. 2004). A key challenge to understanding the consequences of exotic herbivores on islands is uncovering the potential interactions between herbivores and other forms of disturbance.

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For example, communities that periodically experience top-kill by crown fire may be particularly susceptible to browsing by mammalian herbivores because the vegetation that is above the browse line at maturity is temporarily brought within reach of the herbivores during the regeneration phase (Quinn 1986).

Stand replacing crown fires are a recurrent disturbance in the shrublands of the Mediterranean-type climate (MTC) regions of California, the Mediterranean Basin, Southwestern Australia, and the Cape Region of South Africa (Mooney and Dunn 1970). In California, following a fire, the dominant species of chaparral shrubs rapidly recapture their pre-fire dominance without significant local extinction or invasion of pioneer species in a process termed auto-succession (Hanes 1971). Chaparral communities persist through vigorous resprouting and fire-stimulated seed germination and seedling recruitment (Keeley and Keeley 1981; Keeley et al. 2012).

Although chaparral communities typically display resilience to periodic wildfire, the auto-succession process may fail under certain conditions. For example, when chaparral burns in short fire-return intervals, the vegetation can type-convert from a closed canopy shrubland to an open canopy savanna dominated by monotypic vigorous resprouters, disturbance dependent sage scrub species, and exotic grasses and forbs (Zedler et al. 1983; Stylinski and Allen 1999; Jacobsen et al. 2004). In addition, browsing by mammalian herbivores can be an important factor affecting post-fire vegetation recovery in chaparral communities, especially for species that recruit from seed following fire (Mills 1983, 1986; Quinn 1986; Tyler 1995).

Chaparral communities on the California Channel Islands may be particularly susceptible to the effects of post-fire herbivory because of their isolated history. Santa Catalina Island (SCI), located along the coast of southern California, has no evidence that it was ever connected to the mainland or had any large native herbivores in its ~300,000 year history (Schoenherr et al. 1999). In the last two centuries, introduced herbivores to SCI include cattle (*Bos taurus*), sheep (*Ovis aries*), goats (*Capra hircus*), pigs (*Sus scrofa*), American Bison (*Bison bison*), and mule deer (*Odocoileus hemionus*). Cattle operations largely ceased in the mid-1900s, sheep were removed in the 1920s, and goats and pigs were removed in 2002 and 2005, respectively (Catalina Island Conservancy Staff, *personal communication*). The bison, which are grazers, have a population that is managed at about 150–200 animals. At present, the only large exotic browser that remains on the island is the mule deer.

Little is known about the ecological impacts of introduced deer on SCI. Although exotic herbivores have been linked to vegetation change and environmental degradation on SCI, previous studies were conducted prior to the removal of goats and pigs and thus were confounded by herbivore interactions and did not examine the solitary effects of exotic deer (Coblentz 1980; Minnich 1982; Brumbaugh and Leishman 1982). In addition, these previous studies did not address the significance of interactions between exotic deer and post-fire recovery of native shrubs.

This study was undertaken to address a critical knowledge gap regarding the impact of exotic mule deer on post-fire recovery of native, dominant chaparral shrubs on SCI. We hypothesized that browsing of post-fire resprouts by introduced mule deer would increase shrub mortality and contribute to vegetation-type conversion (defined as a shift in the dominant vegetation type) of chaparral on SCI. To investigate this possibility, we measured growth, mortality, and water status of post-fire resprouting shrubs inside and outside of deer exclosures following a wildfire. In addition, we measured the effect of deer browsing on shrub density and canopy coverage.

Materials and methods

Study site and treatments

SCI lies 22 miles (35 km) off the coast of southern California and shares the recurrent crown fires and MTC that typify the California mainland (Schoenherr et al. 1999). The historic fire regime in southern California has been described as a late summer—fall regime with fire return intervals of 30–100 years (Keeley 1999; Keeley and Fotheringham 2001). However, the island regime may be characterized by longer intervals between fires due to the rarity of lightening ignitions (Carroll et al. 1993).

On July 16, 2006, a lightning strike ignited a fire that burned 445 ha of SCI. In December 2006, three deer exclosures (approximately 10 × 40 m) were established within an Island Chaparral/Coastal Sage

Scrub community by the Catalina Island Conservancy. Exclosures were constructed shortly following the emergence of post-fire resprouts. The exclosures restricted access by large animals only (deer and bison), whereas small terrestrial animals and birds were not restricted. Since bison are grazers and do not regularly browse woody vegetation, this experimental design allowed us to isolate the impacts of deer browsing on post-fire shrub recovery. The site is approximately 285 m in elevation and located on the east, channel-facing, side of the island (N 33°24′50″, W 118°26′20″).

We chose to focus our study on one of the dominant, native shrubs, *Heteromeles arbutifolia* (Lindley) Roemer (Rosaceae), as an indicator of shrub recovery. We chose *H. arbutifolia* because it was the most abundant and conspicuous resprouting shrub inside the exclosures and provided the best opportunity to compare recovery between treatments. We also conducted a less extensive survey of the other common shrubs at the site that included *Rhus integrifolia* (Nutt.) Brewer & S. Watson (Anacardiaceae) and *Rhamnus pirifolia* E. Greene (Rhamnaceae). The three species studied are obligate post-fire resprouters, which do not produce a soil stored seed bank that survives fire and instead rely on fire-free periods for seedling recruitment. Therefore, survival of the post-fire resprouts is necessary for population recovery. Chaparral species that survive fire by post-fire seed recruitment (i.e., post-fire seeders) were not present at this site.

On June 5, 2007, burned and resprouting individuals of *H. arbutifolia* were tagged. These included all resprouts inside exclosures (non-browsed treatment; $n = 26$), resprouts outside exclosures (browsed treatment; $n = 76$), and unburned shrubs located nearby at the margin of the burn (unburned treatment; $n = 26$). All resprouting *H. arbutifolia* outside of exclosures showed evidence of deer browsing, which justified identification of this treatment as the "browsed treatment."

In addition to the occurrence of one of the largest fires on Catalina Island in recorded history, 2006–2007 was also one of the driest years on record. From August 2006 to August 2007, Catalina Island received only 130.3 mm of rain compared to an 80-year average of 323 mm. The second year of the study, 2007–2008, was an above average rainfall year totaling 383.3 mm. Rainfall totals and averages were calculated from weather station records from the Catalina airport (approx. 2.4 km from the site) provided by the Western Regional Climate Center (www.wrcc.dri.edu).

Growth and mortality

Deer impacts on the growth of resprouts were assessed by measuring the height of the tallest shoot on each individual. Measurements of height were made eight times from June 2007 to October 2008 (monthly during first dry season and approximately every 2 months thereafter). Mortality was measured in tandem with resprout height by counting the number of dead individuals in each sample population and dividing by the initial population size.

Water relations

Plant water status was monitored to determine the role of water deficits on resprout growth and survival. Pre-dawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potentials were measured to assess plant water status. Pre-dawn leaf water potentials are a function of the soil water potential in contact with plant roots and provided an estimate of daily maximum water availability. Midday water potentials are a function of rates of evapotranspiration and hydraulic conductance of plants and soil and provided an estimate of the daily maximum water deficit. Measurements were made on branchlets or leaves in the field immediately following harvest ($n = 12$) using a pressure chamber (Model 1000, Plant Moisture Stress Instrument Co., Albany, OR). Water status was measured concurrently with measurements of growth and mortality.

To determine the sensitivity of stem xylem to drought conditions, resistance to water stress-induced cavitation was estimated using a centrifuge technique (Alder et al. 1997) on non-browsed and unburned plant treatments (browsed stems were too short to measure). In brief, stems approximately 5–6 mm in diameter were harvested on July 2, 2007. The samples were bagged and transported to a laboratory where they were refrigerated until the next morning. Stems were cut to 140-mm long and flushed for 60 min at 100 kPa to remove emboli with an ultra-filtered (0.1 µm pore exclusion filter) solution of deionized and degassed water brought to a pH of 2.0 using HCl. Following flushing, hydraulic conductivity (K_h) of stem xylem was measured using a tubing apparatus under a low-pressure head (about 4 kPa), which gave the maximum K_h (K_{hmax}) with xylem emboli removed. Stems were then spun in a centrifuge to generate negative xylem pressure potentials and repeatedly measured to determine loss of K_h. Percentage loss of K_h (PLC) was calculated as:

$$\mathrm{PLC} = (1 - K_h/K_{h\,\max}) \times 100$$

Vulnerability curves were constructed by plotting decreasing values of xylem pressure versus PLC (Online Resource 1—Fig. 5). For each treatment, vulnerability curves were used to estimate the pressure potential value at 50 % loss in conductivity (Ψ_{50}; $n = 6$), and were used in conjunction with pre-dawn water potentials measured during the drought to estimate the loss in conductivity due to water stress ($\mathrm{PLC}_{\mathrm{drought}}$; $n = 6$). Pre-dawn water potential was used because it is a better estimate of stem xylem pressure potential than the midday water potentials measured on transpiring leaves. Because hydraulic conductivity measurements could not be made on browsed stems, the vulnerability curve from non-browsed resprouts was used to calculate $\mathrm{PLC}_{\mathrm{drought}}$ for browsed resprouts.

To assess the sensitivity of leaf tissue to drought conditions, we used a pressure–volume curve technique (Tyree and Hammel 1972) to determine the bulk tissue water relations for all treatments ($n = 6$). Branches were collected December 15, 2007, transported to a laboratory, and re-hydrated for 2 h. Following rehydration, water potential and mass were measured repeatedly while leaves dehydrated on a bench top. Water potential was measured with a pressure chamber and mass with a four point precision balance (Model CP124s, Sartorius Mechatronics, Goettingen, Germany). Following these measurements, leaf samples were dried to constant weight to obtain dried leaf mass (g). A pressure–volume curve was constructed by plotting the inverse water potential ($1/\Psi_w$) versus the relative water content (RWC). The curve was then used to calculate the turgor loss point (TLP), osmotic potential at saturation, bulk modulus of elasticity, and capacitance (Koide et al. 1989). Pre-dawn and midday water potentials were analyzed in reference to the calculated TLP to determine the degree to which plants were able to maintain positive turgor during the field experiment.

Stand structure

To evaluate the potential for vegetation-type conversion, stand structure of the site was sampled in June 2008, 2 years after fire, using a point-quarter sampling technique (Cox 1985). Surveys were conducted by randomly selecting points along a pre-determined compass direction (i.e., transect). Three transects were used outside of exclosures among browsed resprouts ($n = 12$ points) and three inside exclosures among non-browsed resprouts ($n = 5$ points). At each point, the closest living plant was measured in each of four quadrants defined by the cardinal directions. Measured parameters included: distance to each plant, basal diameter, crown diameter, and crown height. Calculated values included: relative density, stand density, and canopy coverage (Cox 1985). A second survey was conducted simultaneously that sampled the closest individual (living or dead) in each quadrat and allowed us to estimate pre-fire density. The relatively small area inside exclosures limited the number of points that could be used without including plants beyond the perimeter of exclosures. However, this small sampling effort included a high proportion of the enclosed area.

Statistical analyses

Resprout mortality was analyzed using a logistic ANOVA (a glm with binomial errors) with treatment, time, and treatment * time as fixed factors. Resprout height and water potential were analyzed using two-way repeated-measures ANOVAs with treatment, time, and treatment * time as fixed factors, and individual nested in treatment as a random factor. Cavitation resistance (P_{50}), % loss of conductivity ($\mathrm{PLC}_{\mathrm{drought}}$), and pressure–volume data were analyzed using one-way ANOVAs with treatment as a fixed factor. A two-way ANOVA was used to analyze stand density with treatment, species, and treatment * species as fixed factors. Two sample t tests were used to compare canopy coverage between browsed and non-browsed areas. Data were transformed to meet the assumptions of parametric statistical tests and additional pairwise comparisons with Bonferroni adjusted P values were used where appropriate (Rice 1989). All statistics were conducted in R 2.14.0 (R Foundation for Statistical Computing 2011).

Results

Growth and mortality

Deer browsing greatly reduced the growth of resprouting shrubs (Figs. 1, 2B). There was a significant interaction between treatment and time ($F_{1,84} = 11.45$, $P < 0.01$); however, browsed resprouts remained significantly shorter than non-browsed resprouts throughout the experiment ($P < 0.001$). Height of browsed resprouts appeared to increase during the second summer of the study (Fig. 2B); however, >80 % of browsed resprouts were dead by this point, leaving only those protected by rocks or branches available for measurement.

Mortality of browsed resprouts was significantly greater than non-browsed resprouts throughout the experiment ($F_{1,712} = 115.3$, $P < 0.001$). Browsed resprout mortality continued to increase for the duration of the study, while no new mortality was recorded for non-browsed resprouts after the first summer (Figs. 1, 2A). By the end of the experiment, mortality of browsed resprouts was 88 % compared to 11 % for non-browsed resprouts. The unburned treatment had zero mortality.

Water relations

Pre-dawn water potential (Ψ_{pd}) was within a favorable range ($\Psi_{pd} > -1$ MPa) for both browsed and non-browsed resprouts, indicating they had access to ample soil water throughout the study (Fig. 3A). In contrast, unburned shrubs experienced seasonal fluctuation in Ψ_{pd} characterized by sharp declines during dry summer months (Fig. 3A), which led to a significant interaction between treatment and time ($F_{2,178} = 3.33$, $P = 0.04$). In general, resprouting and unburned shrubs were significantly different during dry summer months ($P < 0.001$), whereas browsed and non-browsed resprouts were not different ($P > 0.05$).

Midday water potentials (Ψ_{md}) were significantly different among treatments ($F_{2,37} = 95.62$, $P < 0.001$) and varied seasonally ($F_{1,178} = 12.09$, $P < 0.001$). Throughout the study, browsed resprouts had the highest Ψ_{md} (most hydrated), unburned shrubs had the lowest Ψ_{md} (least hydrated), and non-browsed resprouts were intermediate (Fig. 3B). Both non-browsed and unburned treatments lost turgor at midday during the driest months, indicating a greater level of water stress compared to the browsed treatment, which maintained positive turgor pressure throughout the experiment (Fig. 3B).

Water relations of bulk leaf tissues did not vary among treatments, indicating that leaf tissue was similarly resistant to water stress (Table 1). In contrast, water relations of stem xylem differed among treatments (Table 1), where non-browsed resprouts had reduced cavitation resistance (less negative Ψ_{50}) compared to unburned shrubs ($F_{1,10} = 11.57$,

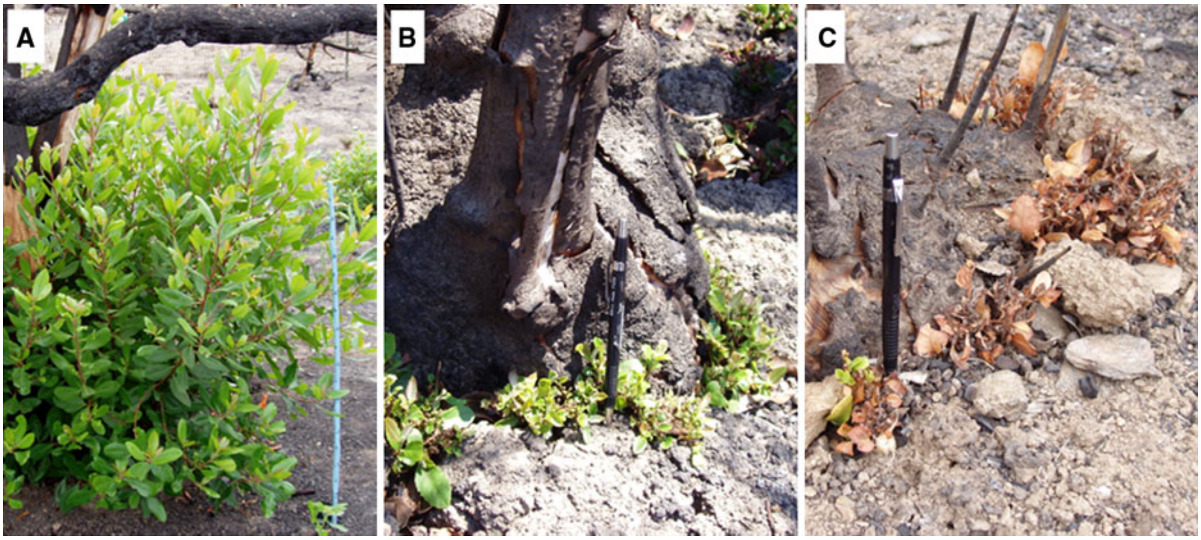

Fig. 1 Photos of resprouting *H. arbutifolia* taken 1 year after fire, showing a non-browsed resprout inside a deer exclosure (**A**), a browsed resprout outside exclosures (**B**), and a browsed resprout with dieback outside exclosures (**C**). To reference plant size a 1 m stick (*blue*; **A**) or a 0.14 m mechanical pencil (**B**, **C**) is shown in each panel. Photos by Stephen D. Davis

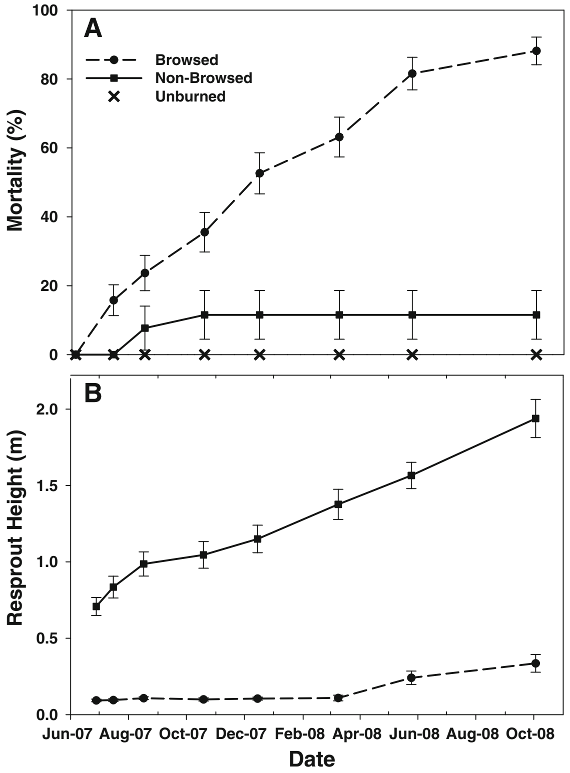

Fig. 2 Mortality (**A**) and height (**B**) for browsed ($n = 76$) and non-browsed ($n = 26$) resprouts and unburned shrubs ($n = 26$) of *H. arbutifolia*. Values are means ± 1 SE

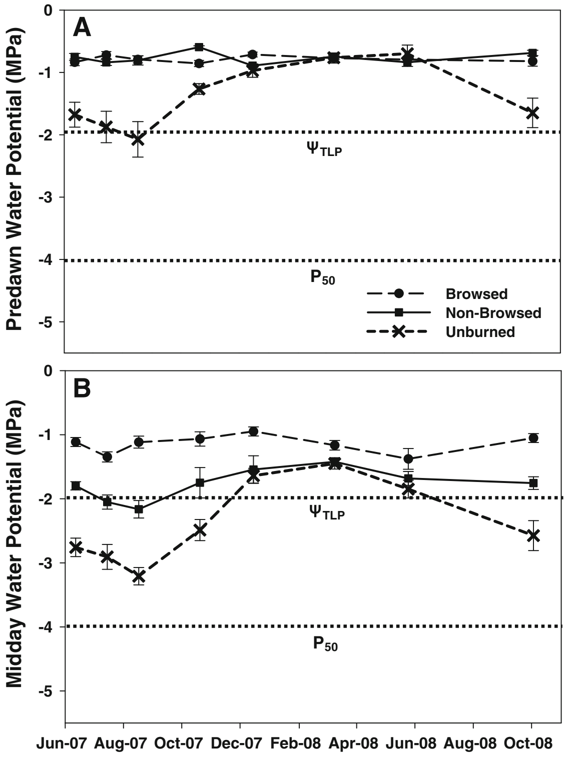

Fig. 3 Pre-dawn (**A**) and midday water potentials (**B**) for browsed resprouts, non-browsed resprouts, and unburned shrubs ($n = 12$) of *H. arbutifolia*. Upper dotted line indicates the water potential at the turgor loss point (TLP) for resprout leaf tissue. Lower dotted line indicates the water potential at which resprouting stems lose 50 % of hydraulic conductivity (P_{50}). Values are means ± 1 SE

$P < 0.01$; Table 1; Online Resource 1—Fig. 5). The $\text{PLC}_{\text{drought}}$ was low (≤10 %) for all treatments (Table 1). Furthermore, $\text{PLC}_{\text{drought}}$ was greater for unburned plants than resprouts ($F_{2,26} = 33.88$, $P < 0.001$; Table 1), but not different between browsed and non-browsed resprouts ($P = 0.99$). It should be noted that any comparisons between browsed and non-browsed resprouts in $\text{PLC}_{\text{drought}}$ would only reflect differences in pre-dawn water potentials during the drought as the same vulnerability curve was used to estimate $\text{PLC}_{\text{drought}}$ for both treatments (see "Materials and methods" section).

Stand structure

Stand density was significantly affected by treatment, but this response was species specific ($F_{4,393} = 25.79$, $P < 0.001$; Fig. 4A). *Heteromeles arbutifolia* density was significantly lower in burned areas subjected to deer browsing compared to burned areas protected from deer ($P < 0.001$) and to pre-fire density ($P < 0.001$). Density of *R. integrifolia* and *R. pirifolia* did not differ among pre-fire, browsed, and non-browsed areas ($P > 0.05$). Canopy coverage was significantly lower in the browsed stand compared to the non-browsed stand for all three species (Fig. 4B; $t_{(65)} = 4.275$, $P < 0.001$ for *H. arbutifolia*; $t_{(65)} = 3.305$, $P = 0.002$ for *R. integrifolia*; and $t_{(65)} = 3.806$, $P < 0.001$ for *R. pirifolia*). At the community level, total canopy coverage of the browsed stand was >93 % lower than the non-browsed stand.

Comparison with mainland studies

In order to better understand the magnitude of the effects of deer browsing on post-fire resprout growth and survival that we recorded, a comparison of our results with those of previous studies from the mainland was included (Online Resource 2). In

Table 1 The stem xylem cavitation resistance (Ψ_{50}), percentage loss in stem hydraulic conductivity during drought ($PLC_{drought}$), leaf water potential at the turgor loss point (Ψ_{TLP}), the relative water content at the turgor loss point (RWC_{TLP}), the osmotic potential for saturated tissue (Ψ_S), the apoplastic relative water content, the bulk modulus of elasticity near saturation (ε), and the tissue capacitance (C) of resprouting (browsed and non-browsed) and unburned *H. arbutifolia* shrubs

Treatment	Stem water relations		Leaf water relations					
	Ψ_{50} (MPa)	$PLC_{drought}$ (%)	Ψ_{TLP} (MPa)	RWC_{TLP} (g/g)	Ψ_S (MPa)	Apoplastic water (g/g)	ε (MPa^{-1})	C ($\Delta RWC/\Delta MPa$)
Browsed	n/a[a]	0.4 A	−2.1 A	0.94 A	−1.7 A	0.71 A	6.5 A	0.032 A
		(0.40)	(0.15)	(0.01)	(0.07)	(0.02)	(0.10)	(0.001)
Non-browsed	−4.0 A	0.5 A	−1.7 A	0.95 A	−1.5 A	0.76 A	5.0 A	0.033 A
	(0.39)	(0.36)	(0.18)	(0.01)	(0.12)	(0.02)	(0.63)	(0.001)
Unburned	−5.6 B	10.5 B	−2.3 A	0.94 A	−1.9 A	0.74 A	5.6 A	0.029 A
	(0.26)	(0.31)	(0.21)	(0.01)	(0.17)	(0.03)	(0.82)	(0.001)
ANOVA results	df = 1, 10	df = 2, 26	df = 2, 15	df = 2, 15	df = 2, 15	df = 2, 15	df = 2, 15	df = 2, 15
	F = 11.57	F = 33.88	F = 2.564	F = 1.311	F = 1.99	F = 0.97	F = 0.74	F = 2.92
	$P < 0.01$	$P < 0.001$	$P = 0.11$	$P = 0.299$	$P = 0.171$	$P = 0.400$	$P = 0.495$	$P = 0.085$

Data points represent means with 1 SE indicated in parentheses. Different letters indicate significant differences between treatments (post-hoc comparisons, $P < 0.05$)

[a] Plants were too small to sample

addition, a mainland study we conducted in parallel with our island study is included (Online Resource 3) and provides an important comparison because it took place during the same intense drought period. Comparison of our results with previous and concurrent mainland studies reveals that *H. arbutifolia* shrubs on SCI experienced higher levels of browsing intensity and mortality.

Discussion

Causes of resprout mortality

Our results suggest that deer browsing is associated with increased mortality of *H. arbutifolia* resprouts (88 % mortality of browsed resprouts compared to 11 % of non-browsed resprouts). It is unlikely that water stress caused by low precipitation in the first post-fire year directly interacted with deer browsing to exacerbate mortality in *H. arbutifolia*. Seasonal water status was more favorable in browsed resprouts than either non-browsed resprouts or unburned adults. Even at midday during the peak of the drought, when water potentials were most negative, browsed resprouts did not lose turgor. Thus, positive turgor was persistently available for cell expansion and shoot elongation and therefore could not account for the reduced height or increased mortality in browsed resprouts. However, the drought conditions during the first post-fire year may have had an indirect effect on resprout mortality by increasing deer browsing intensity. It is likely that browsing preference toward post-fire resprouts was enhanced during the drought because it offered more hydrated juvenile tissues than unburned shrubs that experienced greater water stress.

The well-hydrated status of resprouting shrubs despite drought conditions may be related to the high root-to-shoot ratio that is characteristic of top-killed shrubs (Clemente et al. 2005). Higher root-to-shoot ratios would improve water availability and tissue water status for both browsed and non-browsed resprouts relative to unburned shrubs. Furthermore, the reduced canopy of browsed resprouts would reduce water use and further increase root-to-shoot ratio in favor of improved water status relative to the non-browsed treatment. In addition, the general reduction of the shrub canopy by deer (>93 % reduction) may have led to shifts in community level water-use patterns that increased soil water availability.

The high intensity browsing we recorded may be capable of driving mortality of resprouting shrubs via depletion of stored reserves. The lignotubers of plants like *H. arbutifolia* are storage organs that house carbohydrates, nutrients, and adventitious buds (James

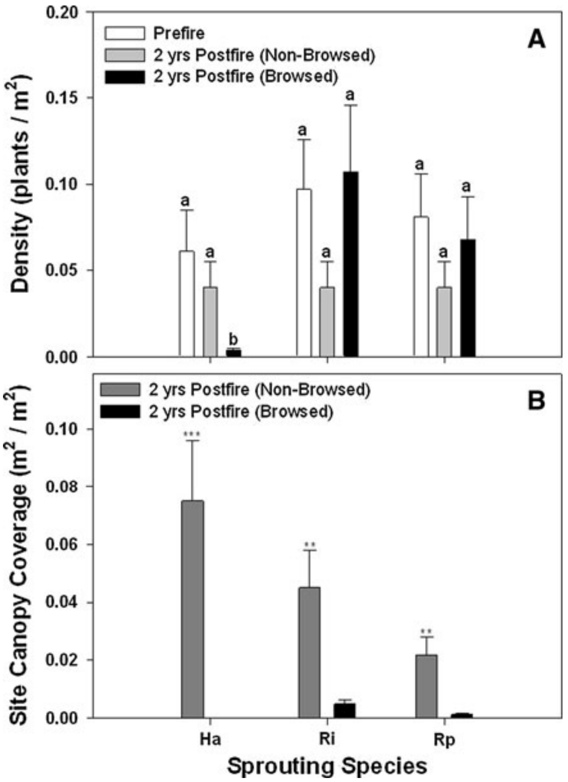

Fig. 4 Density of shrubs across the site as estimated pre-fire (*open bars*) and 2 years post-fire in non-browsed (*gray bars*) and browsed (*black bars*) stands for the three dominant sprouting species at the site, *Heteromeles arbutifolia* (Ha), *Rhus integrifolia* (Ri), and *Rhamnus pirifolia* (Rp) (**A**). *Different letters* above bars indicate significant differences in density (**A**). Canopy coverage of all species was significantly lower in the browsed stand compared to the non-browsed stand (**B**). Mean value and standard error bars were plotted for browsed Ha (**B**) but are too small for detection within the scale of the graph. In panel **B**, ***$P < 0.001$ and **$P < 0.01$

1984; Desouza et al. 1986; Clemente et al. 2005, Enright et al. 2011). These stored resources are mobilized post-disturbance to facilitate resprouting, and plant survival then depends on the capacity of newly expanded canopies to acquire carbon resources through photosynthesis (Moreira et al. 2012). Short-fire intervals and/or repeated clipping (or browsing) of resprouts can prevent acquisition of new resources resulting in reduced resprouting vigor and increased plant mortality (Canadell and López-Soria 1998; Paula and Ojeda 2006; Enright et al. 2011). In our study, resprouting *H. arbutifolia* shrubs were continuously browsed to a degree that likely limited their ability to capture new carbon through photosynthesis. Thus, carbon limitation may have been a factor contributing to browsed resprout mortality in this study.

Consequences of shrub mortality

The population of unprotected *H. arbutifolia* has been effectively extirpated from the burn area. The exclosures are protecting roughly 25 % of the sampled population, yet the portion of the population that was unprotected and lost may not recover. Among chaparral shrubs, obligate resprouters like *H. arbutifolia* typically require closed canopy, mature chaparral stands for seedling recruitment (Patric and Hanes 1964; Zedler 1981; Keeley 1991). Since the dominance of the chaparral shrubs in the unprotected area is diminished, creating a more open canopy, there may be few sites suitable for seedling recruitment. Moreover, if the deer are capable of killing large resprouts, they may also cause mortality of small, sensitive seedlings (e.g., Mills 1983; Quinn 1986; Tyler 1995). The long-term viability of this population is unclear at present and a better understanding of the recruitment potential of SCI shrubs, particularly in the presence of deer, is needed.

At the community level, the three dominant shrub species that we measured showed greatly reduced canopies in the browsed area (>93 % reduction) compared to plants protected by exclosures. However, *R. integrifolia* and *R. pirifolia* did not exhibit the same levels of mortality that we observed in *H. arbutifolia*. Thus, the response to exotic deer browsing is differential and will likely influence shrub community structure. In addition, changes in shrub cover have created opportunities for expansion of less palatable sage scrub species (e.g., *Artemisia californica*, *Baccharis pilularis*, and *Opuntia litoralis*) and non-native grasses and forbs (e.g., *Avena fatua*, *Bromus* spp., *Lolium multiflorum*, and *Hordeum* spp.) already present at this site. Over time it is possible that the island chaparral in recently burned areas may undergo vegetation-type conversion to a sage scrub and alien-dominated landscape, similar to what has been observed in mainland chaparral following short fire-return intervals (Zedler et al. 1983; Stylinski and Allen 1999; Jacobsen et al. 2004).

Sensitivity of island chaparral to deer browsing

In mainland southern California chaparral communities, there is evidence that mammalian herbivores can impact post-fire vegetation dynamics through browsing (Biswell 1952; Davis 1967; Mills 1983, 1986; Quinn 1986; Thomas and Davis 1989; Moreno and Oechel 1991, 1993). However, the levels of browsing intensity and mortality recorded in our study exceed the values reported by previous mainland studies concerning post-fire recovery of resprouting shrubs. Moreover, comparison of the results from SCI and our concurrent mainland study reveals that *H. arbutifolia* shrubs on SCI experienced increased browsing intensity and mortality compared to the mainland site, despite experiencing less severe water deficit. These findings suggest that the effects of deer browsing on post-fire vegetation recovery may be more pronounced on SCI than chaparral communities on the southern California mainland.

The extreme levels of deer browsing we observed may be related to the historical absence of native browsers on SCI. In the absence of deer, plants may evolve lower concentrations of chemical and morphological defenses (Côté et al. 2004; Takada et al. 2001), including plants on islands (e.g., Vourc'h et al. 2001). On a nearby California Island, Santa Cruz Island (~114 km northwest of SCI), shrubs were found to have reduced defenses and increased herbivore preference relative to conspecific mainland populations, which the authors attribute to the historical absence of native herbivores on the island (Bowen and Van Vuren 1997). Further examination is required to test the hypothesis that shrubs on SCI lack the morphological and chemical defenses of their mainland relatives.

High browsing intensity on SCI may also be related to altered deer behavior due to the lack of a natural predator on the island. Surveys of the deer population on SCI suggest it is not likely that SCI deer densities greatly exceed mainland densities, although they are more abundant in island chaparral communities than other island habitats (Garcelon 1988; Stapp and Gutilla 2006). Instead, the absence of a natural predator for the introduced deer may alter their behavior, as predicted by the enemy-release hypothesis (Brown et al. 1999), and this might increase local browsing intensity beyond the level experienced in areas where predators are present (Ripple and Beschta 2003; Potvin et al. 2003; Côté et al. 2004). It should be noted that although the deer lack a "natural" predator on the island, they are exposed to annual sport hunting and the effects of this on deer behavior are less well understood.

Another factor that may be related to deer browsing intensity on SCI is that island chaparral is characterized by lower diversity and more open canopy structure than comparable mainland habitats (Schoenherr et al. 1999). At our study site, seedlings of shrubs that rely on post-fire seed recruitment (obligate seeders) were absent. The reduced diversity of woody shrub species at this site may have increased browsing intensity on post-fire resprouts beyond what would have been recorded if palatable seedlings were also present. Furthermore, the lower initial density of shrubs may have resulted in a breakdown of the "phenological defense" created when synchronized flushes of new growth in the post-fire environment satiate herbivores (Quinn 1986; Moreno and Oechel 1991), resulting in greater browsing pressure on individual shrubs.

A related factor is fire size, where smaller fires are likely to create increased browsing intensity by increasing access to and decreasing the availability of preferred forage relative to larger burns (Quinn 1986). However, small fire size is not a likely explanation for the patterns observed in our study because many mainland studies citing lower browsing intensity were conducted following fires much smaller than the fire we studied (Online Resources 2 and 3).

As described above, the island chaparral community and exotic deer population on SCI may have several key features that are not frequently encountered on the mainland. It is not likely that any one of these island attributes explain the patterns we observed, but rather they may work in concert to increase browsing pressure on post-fire resprouts to levels not typically observed on the mainland.

Conclusion

We found that resprouting individuals of *H. arbutifolia* that were browsed by deer experienced reduced growth and increased mortality, whereas those protected from deer generally displayed vigorous, successful resprouting. Intense deer browsing, not water stress, is the most likely proximate cause of resprout mortality. Common resprouting shrubs other than *H. arbutifolia* were also impacted by deer browsing, resulting in a >93 % reduction in total shrub cover in areas unprotected from deer. Several unique features of the island environment may explain the unusually high levels of browsing. From this study, it is clear that the deer pose an acute threat to post-fire regeneration of the native chaparral communities on SCI and that the interaction between deer browsing and fire may lead to vegetation-type conversion.

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