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Resprouting and seeding hypotheses: a test of the gap-dependent model using resprouting and obligate seeding subspecies of *Arctostaphylos*

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Abstract Ecological factors favoring either postfire resprouting or postfire obligate seeding in plants have received considerable attention recently. Three ecological models have been proposed to explain patterns of these two life history types. In this study, we test these three models using data from California chaparral. We take an innovative approach to testing these models by not testing community or landscape patterns, but instead, investigating vegetation structure characteristic of four pairs of resprouting and (non-resprouting) obligate seeding subspecies of *Arctostaphylos* (Ericaceae), a dominant and diverse shrub genus in California chaparral. Data were analyzed for percentage bare ground, elevation, annual precipitation, number of fires, and time between fires and were compared independently for each subspecies pair. Results were consistently supportive of the gap-dependent model suggesting that obligate seeders are favored when post-disturbance gaps are large. Results were inconclusive or contrary to expectations for both of the other two models.

Keywords Disturbance · Fire · Regeneration · Reproduction · Resprouters · Seeders

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Introduction

Woody plants in disturbance-prone environments persist through regeneration by resprouting from surviving structures or reproduce from seeds either in situ or that colonize the site. There is little agreement on the selective factors driving the evolution of resprouting and seeding strategies in such environments. Wells (1969) was the first to address this issue when he made the remarkable observation that for the largest woody genera (*Arctostaphylos* and *Ceanothus*) in the highly fire-prone California chaparral, the majority of species totally lacked any capacity for resprouting. He pointed out that these non-resprouting taxa regenerated strictly by postfire seedling recruitment, and he referred to these as obligate seeders. He hypothesized that the obligate

seeding mode had been selected for because it forced the population to turn over 100 % of the individuals every fire-induced generation, and thus it sped up the rate of evolution. However, based on patterns of speciation, this does not appear to be universally true (e.g., Lamont and Wiens 2003). Raven (1973) suggested such obligate seeders were better able to track changes in the environment from generation to generation, an observation of particular interest in an era of rapid climate change.

Alternatively, ecologically oriented models have been proposed that focus on either (1) seedling recruitment, (2) disturbance impacts, or (3) adult competition. These ecological models need not be exclusive of the genetic-based arguments advocated by Wells and others (Keeley et al. 2012) and may be complementary in some aspects. These ecological models consider conditions favoring either resprouting or obligate seeding from a number of spatial scales (e.g., Bond et al. 1988; Lamont and Markey 1995; Ojeda 1998; Clarke et al. 2005; Pausas and Keeley 2014).

The first ecological model, which is referred to as the gap-dependent recruitment model in this paper, focuses on post-disturbance seedling recruitment. Seedling establishment is the most vulnerable life history stage in plants (Grubb 1977; Parker et al. 2008) and represents a potential bottleneck in population dynamics in disturbance-prone or resource-limited vegetation. The gap-dependent model argues that seedling establishment is selected against on sites where high resource availability favors high density of resprouters that rapidly regain most available canopy space after fire or other disturbance (Keeley and Zedler 1978; Keeley 1986; Myerscough et al. 1995; Pausas and Keeley 2014). In contrast, open sites where post-disturbance gaps are large will favor seedling recruitment over resprouting.

The second is often labeled as the disturbance frequency model and contends that resprouters and obligate seeders are distributed along gradients in disturbance frequency (Bellingham and Sparrow 2000; Bond and Midgley 2003). As disturbance frequency and severity increase, the model assumes increasing selection for resprouting over seeding, although the situation reverses at extremely high disturbance frequency. This model is frequently applied to fire-prone environments where a limitation is that it considers resprouting and seeding as continuous functions of fire frequency or fire severity and ignores other components of the fire regime, in particular fuel structure and its control on fuel consumption and trait selection (Keeley et al. 2012). Fire frequency has radically different impacts on resprouting success in shrublands under crown fire regimes compared to forests with surface fire regimes and this problem is not solved by scaling against productivity. At boundaries between such communities, the shift in fire type and fuel structure reinforces the shrubland-forest disjunction (e.g., Odion et al. 2010). Thus, the sharp boundary between a shrubland with a crown fire regime and a forest with a surface fire regime represents a tipping point in which the selective factors for life history characteristics radically change state. This model also has limited applicability to fire-prone systems because different seed storage modes have profound impacts on tolerance to low disturbance frequency; i.e., serotinous species are often poorly adapted to long fire-free periods in contrast to those with soil seed storage (Keeley et al. 2012), although an exception would be the long-lived cypress species associated with chaparral (Zedler 1995).

The third is often referred to as the resource/productivity model (Clarke et al. 2005, 2013) where it is argued that, as resource availability increases, the intensity of competition increases and this favors resprouters, which are presumed to be better competitors. An elaboration of this model has been suggested to be globally applicable in a variety of vegetation types (Clarke et al. 2013). While it is recognized that seedlings eventually have to be recruited to replace adult mortality, the model assumes seedlings of resprouters must also be more competitive (Clarke et al. 2013).

These models have been interpreted to predict landscape distribution patterns for these two life history modes in relation to disturbance patterns and productivity gradients (Clarke et al. 2005). Such large-scale comparisons have produced a plethora of distribution patterns that have contributed to a substantial amount of discussion on driving factors behind resprouting and seeding, although many patterns support more than one model. Here we propose that a potentially useful test of these ecological models would be the distribution patterns of contrasting resprouting and obligate seeding subspecies within the same species. Here we have selected four

subspecies pairs in the genus *Arctostaphylos* (Ericaceae) for a phylogenetically independent contrast of life histories and their associated vegetation structure. We thus tie evolution to ecology and examine key environmental factors that might favor one ecological model over the others. The use of sibling subspecies assumes that the environment has selected for one life history type over the other.

The genus *Arctostaphylos* (Ericaceae) has a number of species that exhibit infraspecific variation in resprouting and obligate seeding. *Arctostaphylos* comprises over 70 species largely concentrated in California and the majority are in highly fire-prone chaparral shrublands (Parker et al. 2012). Both resprouting and (non-resprouting) obligate seeding species rely on persistent soil seed banks in this genus (Keeley 1977) and recruit under similar postfire conditions.

The genus has two major clades with resprouting and obligate seeding species approximately equally distributed within both clades (Boykin et al. 2005; Wahlert et al. 2009). The majority of species are obligate seeding shrubs but a number of *Arctostaphylos* species are noteworthy for the fact that they exhibit intraspecific variation in resprouting capacity (Keeley et al. 2012). We might expect that natural selection parses these intraspecific life history patterns according to one or more of the above models. A fuller description of all *Arctostaphylos* species with resprouting and non-resprouting obligate seeding subspecies is presented in the Supplement, but for this study, we focused on four species having distinct resprouting and obligate seeding subspecies: *A. manzanita, A. mewukka, A. parryana,* and *A. peninsularis.*

We test aspects of the environment that might be favorable or limiting to either seedling establishment or resprouting. If the gap-dependent model is supported, our hypothesis is that, within a single species lineage, obligate seeding has been selected in response to environments conducive to significant gaps for postfire seedling recruitment and thus we predict that such environments will have a greater amount of bareground in the mature community. This relates to reduced shrub density and consequently reduced shrub resprouting competition for recruitment. We also predict the landscapes occupied by these subspecies pairs will not support the disturbance frequency model and thus resprouting subspecies will not be distributed on sites with higher fire frequency. Our third prediction is that the resprouters will not be associated with sites of higher productivity, which would not support the resource productivity model.

Methods

A test of the first hypothesis was to compare the extent of bare ground in mature stands of each subspecies as this should be strongly associated with the size of gaps suitable for seedling establishment after fire. Populations were located from herbarium collections documented in the California Consortium of Herbaria and personal collections. For taxa well represented in collections, we took a random sample of 30 specimens, but most taxa had many fewer collections and in these cases all available specimens, not representing duplicate sites, were selected. Latitude and longitude (WGS84 projections) for each site were entered into Google Earth and sites located. An approximate 0.1-km-diameter circle was estimated around the sample location and the community type was determined and the percentage bare ground (lacking woody cover) estimated to the nearest 5 % by overlaying a grid imprinted on acetate. These data and metadata are available online. Within each species, the estimated bare ground in resprouting and non-resprouting populations was compared statistically with the two sample *t* test.

The hypothesis of disturbance frequency was tested by comparing the fire frequency at each site over the last 100 years. The coordinates used to locate each population were entered into the State of California, CalFire FRAP database (http://frap.cdf.ca.gov/data/fire_data/history/fire_historyfr.html, accessed 13 July 2015) and fire histories extracted for each site in California. For the Baja California populations, we relied on data assembled by Minnich et al. (1993). California sites with multiple samples were compared statistically with a *t* test.

Competition is a notoriously difficult parameter to estimate. Clarke et al. (2005) used various surrogate measures of site productivity. In Mediterranean-climate California, annual precipitation is a reasonably good surrogate measure for site productivity. Using 30-year norms from the PRISM database (http://www.prism.oregonstate.edu/normals/, accessed 15 July 2015), sites with multiple samples of subspecies were compared statistically with a *t* test.

Results

Gap-dependent model

An example of habitat differences for resprouting and obligate seeding subspecies is illustrated for *A. parryana* (Fig. 1). The resprouting taxon (b) generally occurs in dense chaparral, whereas the non-resprouting obligate seeding taxon was in open woodlands and chaparral (b).

Arctostaphylos manzanita. The resprouting *A. manzanita* subsp. *roofii* are localized in widely disjunct chaparral sites ($n = 21$ sites) between latitudes 38.37–40.56 at an average elevation of 1095 m. Populations of the non-resprouting obligate seeder *A. manzanita* subsp. *manzanita* are widespread in northern California ($n = 30$) on both coastal and interior sites in mixtures of chaparral and open oak woodlands. These were distributed between latitudes 37.90 and 41.30 (avg elevation 395 m). The non-resprouting subspecies had a mean bare ground value significantly higher than the resprouting taxon (Fig. 2a).

Arctostaphylos mewukka. The resprouting *A. mewukka* subsp. *mewukka* is widespread throughout the low to moderate elevation sites of the Sierra Nevada ($n = 27$ sites) in foothill chaparral and mixtures of montane chaparral and conifer forest between latitudes 39.62 and 40.03 (avg elevation = 1185 m). The non-resprouting obligate seeder *A. mewukka* subsp. *truei* is localized in northern California ($n = 18$) mixtures of conifer forest and montane chaparral in the northern Sierra Nevada. These were distributed between latitudes 36.19 and 40.01 (ave elevation 705 m). The non-resprouting subspecies had a mean bare ground value significantly higher than the resprouting taxon (Fig. 2b).

Arctostaphylos parryana. The resprouting *A. parryana* subsp. *desertica* (and *A. parryana* subsp. *tumescens*) are more localized in chaparral ($n = 8$) between latitudes 33.15 and 33.45 (avg elevation = 1700 m). The non-resprouting obligate seeder *A. parryana* subsp. *parryana* is widespread ($n = 30$) on more interior southern California sites dominated by pinyon and evergreen oaks interspersed with chaparral. Populations included in this study were between latitudes 34.12 and 35.15 (avg elevation 1525 m). The non-resprouting subspecies had a mean bareground value significantly higher than the resprouting subspecies (Fig. 2c).

Arctostaphylos peninsularis. The resprouting *A. peninsularis* subsp. *peninsularis* occurs disjunct over 100 km southward in the San Pedro Martir range in dense chaparral ($n = 7$), between latitudes 30.51 and 31.02 (ave elevation 1650 m). The non-resprouting obligate seeder *A. peninsularis* subsp. *juarezensis* is restricted to the Sierra Juarez Mtns ($n = 7$) of interior northern Baja California. Populations used here were distributed between latitudes 32.02–32.12 (avg elevation = 1695 m). It is distributed on a rocky landscape associated with chaparral, pinyon pines, and evergreen oak trees. The non-resprouting taxon had bare ground significantly higher than for the resprouting taxon (Fig. 2d).

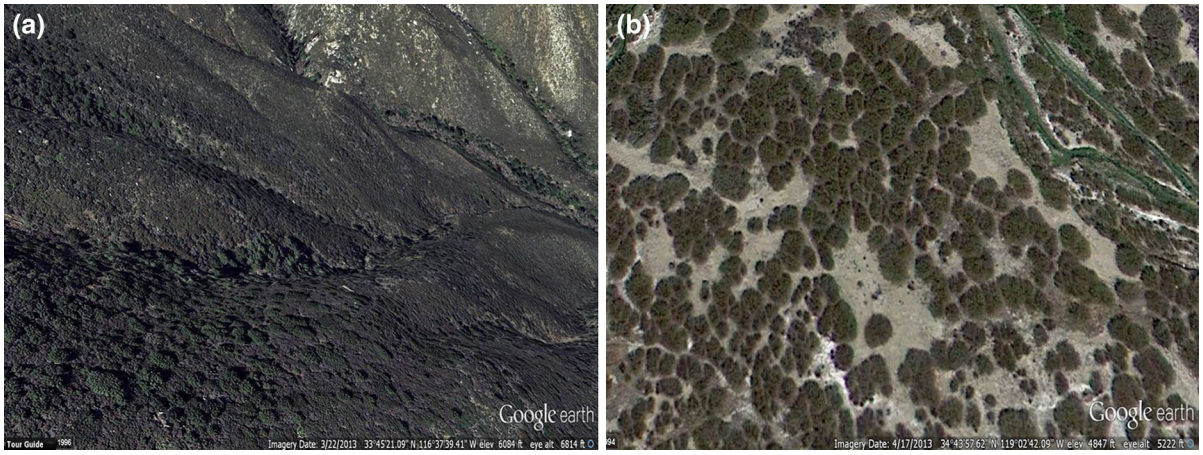

Fig. 1 Example of vegetation structure in a population of a resprouting subspecies (**a**) and an obligate seeding subspecies (**b**) of *Arctostaphylos parryana*

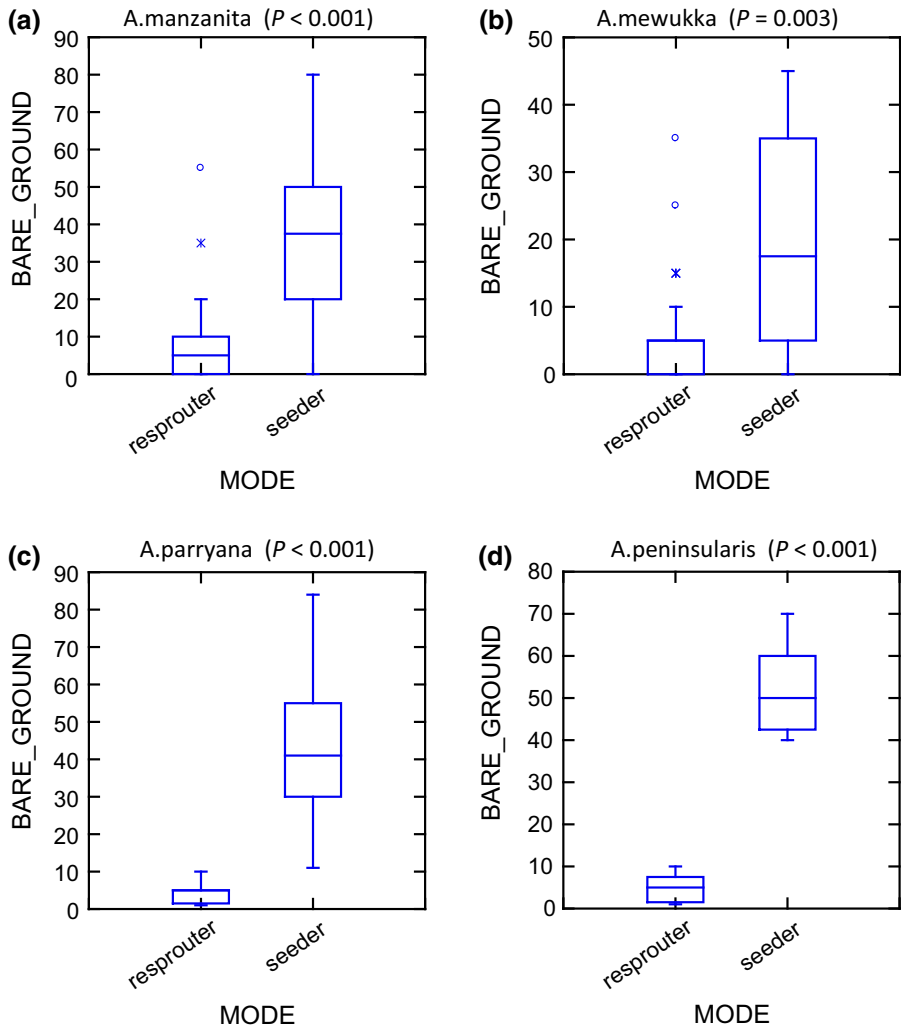

Fig. 2 Bare ground for resprouting and obligate seeding subspecies populations for four species of *Arctostaphylos*

Disturbance model

Neither time between fires nor number of fires as surrogates for disturbance showed any support for the disturbance model. For *A. manzanita*, at the $P < 0.05$ level, there was no significant difference in either disturbance parameter, average number of fires in the last 104 years, or average time between fires (Table 1). Similarly, for *A. mewukka*, the resprouting and seeding subspecies did not differ in either number of fires or average time between fires (Table 1). In the case of *A. parryana*, the seeder subspecies exhibited significantly more fires and shorter intervals between fires than the resprouter taxon (Table 1), contrary to what is predicted by the disturbance model discussed in the introduction. Finally, *A. peninsularis* resprouter and seeder subspecies had nearly identical fire frequencies (Table 1).

Competition/productivity model

The patterns of annual precipitation did not support the competition-resource/productivity model for these four pairs of subspecies. No significant difference in annual precipitation for the resprouter and seeder populations of *A. manzanita* was found (Table 1). For *A. mewukka,* there was a weak difference between subspecies but it was in the opposite direction as

Table 1 Fire history for the last 105 years based on the Cal Fire FRAP fire history database and average annual precipitation based on PRISM data for sites occupied by resprouting and obligate seeding subspecies of *Arctostaphylos* and fire history

		n	Number of fires	Ave time betw fires (years)	Annual ppt (mm)
A. manzanita roofii	Resprouter	30	0.52	79	1064
A. manzanita manzanita	Seeder	21	0.27	91	1181
Significance			$P = 0.121$	$P = 0.091$	$P = 0.268$
A. mewukka mewukka	Resprouter	27	0.70	79	1241
A. mewukka truei	Seeder	18	0.67	78	1512
Significance			$P = 0.905$	$P = 0.899$	$P = 0.013$
A. parryana desertica	Resprouter	8	0.12	104	148
A. parryana parryana	Seeder	30	1.87	56	544
Significance			$P < 0.001$	$P < 0.001$	$P < 0.001$
A. peninsularis peninsularis	resprouter	7	0.53*	–	557** (at 2080 m)
A. peninsularis juarezensis	seeder	7	0.48*	–	566** (at 1580 m)

* Baja California not included in either the FRAP or PRISM databases. These values were extrapolated from the literature; ^ fires per 1000 ha for Sierra Juarez (subspecies *juarezensis*) and Sierra San Pedro Martir (subspecies *peninsularis*) from Minnich et al. 1993

** Data from Hugh Safford, unpublished

predicted by the competition/resource productivity model (Table 1). For *A. parryana*, there was a highly significant difference between subspecies but it was in the opposite direction as predicted by the competition/resource productivity model (Table 1). Finally, *A. peninsularis* resprouter and seeder subspecies had nearly identical annual precipitation (Table 1).

Discussion

For the *Arctostaphylos* subspecies pairs considered here, non-resprouting obligate seeding taxa occupy markedly different habitats from the resprouting subspecies. In general, the obligate seeding taxon is found in decidedly more open communities often interspersed with woodland elements including species of *Quercus* and *Pinus*. The resprouting taxon however is more commonly found in dense chaparral stands having relatively little bare ground. This pattern was consistent across four different species lineages occupying substantially different local climates and soils. We infer that the more open communities occupied by seeders would result in larger gaps for seedling recruitment after fire. These patterns are consistent with predictions from the gap-dependent recruitment model. Similar patterns have been observed in the distribution of these two life history types in Australia (Pausas and Bradstock 2007).

Site characteristics related to the disturbance model and competition-resource/productivity model were not supportive of either of those alternative hypotheses. Number of fires or the between-fire intervals were either not different or in come cases were counter to the expectations of a disturbance model. The disturbance model (Bellingham and Sparrow 2000; Bond and Midgley 2003) seems to be predicated on the assumption that resprouting is somehow the best way to survive disturbance. However, Wells (1969) noted that in woody dicots, resprouting was the norm, regardless of disturbance regime and that the non-resprouting seeding trait was almost uniquely associated with fire-prone California chaparral, and since then this observation has been extended to other Mediterranean-climate ecosystems.

One of the primary limitations to the disturbance model or its combination with the productivity model as described in previous treatments is that it is predicated on the notion that there is a globally relevant model to explain seeding and resprouting (Clarke et al. 2013). However, with respect to fire, this is most assuredly not true because as fire regimes change, the selective value of resprouting changes. As in Wright's (1932) adaptive landscape model, we

might think of a similar metaphor with different fire regimes as representing adaptive peaks in which selection pressures vary from one fire regime to another.

Clarke et al. (2005) examined community composition of resprouters and obligate seeding (non-resprouting) species and found that habitats differed in the proportion of these two fire responses. They concluded that resource/productivity models better explained landscape patterns of resprouting than did disturbance frequency models. The exact mechanism as to how this would translate into a selective advantage for resprouters is not clear and it appears that more productive environments could provide a competitive advantage to resprouters in a variety of ways. Vasey et al. (2014) have found that obligate seeding species tend to dominate coastal chaparral in isolated patches of azonal soils surrounded by forest (Vasey and Parker 2014). Compared to matrix forest habitats, these azonal soils are relatively shallow and/or infertile and thus might promote more gap-dependent recruitment processes than more widespread and dense stands of chaparral found in more interior environments in this coastal region.

These three models probably influence vegetation composition and dominance depending on a complex of environmental influences and history. In this study, we find that obligate seeding appears to be selected when fuel structure is broken up by bare ground and resprouting selected when vegetation is denser. These results principally support the gap dependence model that focuses on providing space for seedling establishment and recruitment. Fire frequency, between-fire intervals, and increased limiting resources (precipitation) demonstrated no consistent pattern; the lack of pattern fails to support either the disturbance frequency or resource/productivity model. Because we tested these models against pairs of subspecies from lineages within *Arctostaphylos*, and because in each case the gap-dependent model was supported, we assume that the overall environments provided selective conditions favoring seeding over resprouting. Recently, the trend has been to focus on what might select for resprouting (e.g., Clarke et al. 2013) rather than conditions selecting for seeding. In our study, both resprouters and obligate seeders require similar conditions for recruitment because both produce persistent soil seed banks with germination stimulated by fire (Keeley 1977). Thus, the consistent predominance of one life history type in each example suggests that natural selection strongly favors seedling establishment and recruitment under particular conditions supported by the gap-dependent model.

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