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Dispersal Limitation Does Not Control High Elevational Distribution of Alien Plant Species in the Southern Sierra Nevada, California

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ABSTRACT: Patterns of elevational distribution of alien plant species in the southern Sierra Nevada of California were used to test the hypothesis that alien plant species invading high elevations around the world are typically climate generalists capable of growing across a wide elevational range. The Sierra Nevada has been heavily impacted for more than a century and a half, first by heavy grazing up into high elevation meadows, followed by major logging, and finally, by impacts associated with recreational use. The comparative elevational patterns of distribution and growth form were compared for native and alien plant species in the four families (Asteraceae, Brassicaceae, Fabaceae, and Poaceae) that contribute the majority of naturalized aliens in the study area. The distribution of realized climatic niche breadth, as measured by elevational range of occurrence, was virtually identical for alien and native species, with both groups showing a roughly Gaussian distribution peaking with species whose range covers a span of 1500–1999 m. In contrast to alien species, which only rarely occurred at higher elevations, native species showed a distribution of upper elevation limits peaking at 3000–3499 m, an elevation that corresponds to the zone of upper montane and subalpine forests. Consistent with a hypothesis of abiotic limitations, only a few alien species have been ecologically successful invaders at subalpine and alpine elevations above 2500 m. The low diversity of aliens able to become established in these habitats is unlikely due to dispersal limitations, given the long history of heavy grazing pressure at high elevations across this region. Instead, this low diversity is hypothesized to be a function of life history traits and multiple abiotic stresses that include extremes of cold air and soil temperature, heavy snowfall, short growing seasons, and low resource availability. These findings have significant implications for resource managers.

Index terms: alpine, dispersal, invasives, niche breadth, propagules

INTRODUCTION

As the field of invasion ecology has developed, it has organized itself around the primary topics of invasiveness of species, invasibility of communities, and invasive impacts on ecosystems (Alpert et al. 2000). The second of these topics, invasibility, has come under increasing attention for mountain ecosystems where numbers of invasive alien plant species are relatively low and the ecological dominance of such species is often small. In recent years, there has been particular focus on high mountain habitats that have long been considered to be relatively resistant to invasion by alien species (Pauchard et al. 2009; Tomasetto et al. 2013). Several drivers have been suggested to explain this pattern of relatively low ecological success of alien species at high elevations. Depending on the driver, this low level of invasion may be only a transitory stage with potentially higher levels of invasion in the future (Alexander et al. 2009; Pauchard et al. 2009; McDougall et al. 2011). Since much of the protected lands in parks and reserves is at higher elevation, this possibility has profound implications for conservation, particularly in the Sierra Nevada where there are extensive areas of subalpine and alpine habitat with a diverse native flora (Rundel 2011).

Limited propagule dispersal has been widely cited as an important constraint on range increases of alien plant species into new areas, including at high elevations (Wilson et al. 2009; Warren et al. 2013). A number of authors have observed that the great majority of alien plant species in mountain areas are taxa characteristic of adjoining coastal and foothill areas, indicating a lowland pathway of introduction (Becker et al. 2005; Haider et al. 2010; McDougall et al. 2011). This is not surprising since the majority of introductions of alien plant species occur in lowlands in association with human activities. The dynamics of this invasion process into higher elevations appear to have changed over recent history and invasion may be tied to residence time of invasive plant species at lower altitudes (Pyšek et al. 2011).

It is certainly true that the establishment of alien plant species is pronounced in areas of active or past human disturbance, including land use changes due to urbanization, agriculture, and livestock grazing, and that such sites are widespread in lowland areas (Alpert et al. 2000). However, this pattern has also been observed in high mountain systems as well where roadsides and open riparian habitats are particularly subject to invasion (McDougall et al. 2005; Kane et al. 2006; Marini et al. 2009; Aikio et al. 2012).

Recently, Alexander et al. (2010) have suggested that mountain gradients exhibit directional ecological filtering of lowland alien plant species, a process that causes a progressive loss of alien plant species richness with increasing elevation. They hypothesized that most alien plant species invading high elevations around the world are climate-generalists capable of growing across a wide elevational range, with their presence at higher elevations largely limited by dispersal rather than ecophysiological tolerances. They contrast this pattern of filtering with montane native plant species that they argue have narrow ecological ranges in climatic tolerance relative to nonnative invasives. They further suggest that invasion resistance is not conferred by extreme conditions at higher elevations, but instead determined by pathways of introduction of nonnative plant species. If this conclusion is true, it has important management implications since major portions of the world's conservation areas occur at higher elevations and future global changes may include intensification of invasions into such regions.

Alternatively, abiotic stress conditions may be a factor that strongly limits the invasibility of high elevation regions. Alien plant species adapted to lowland conditions may not be able to tolerate the extremes of temperature, short growing seasons, and low resource availability typically present at high elevations (Alpert et al. 2000), particularly in the extreme conditions of subalpine and alpine environments where native plant species often exhibit specific adaptations to these conditions (Billings 1974). On many landscapes there is a shift from open nonforested habitats to closed canopy forests in montane elevations, and these are typically less favorable habitats for mostly high-light requiring invasive species (Rejmánek 1989; Martin et al. 2009). Under conditions of decreasing growing season and increasing shade, herbaceous species are expected to switch from annual to perennial life forms.

Limits to niche and range dimensions have been broadly described as important factors in the distribution of alien species, with the widespread assumption that such species will be constrained by the inability

of their populations to expand beyond the abiotic limits of their fundamental niche. While niche shifts of alien plant species into new habitats have been hypothesized as potentially significant (Alexander et al. 2009), there are few quantitative demonstrations that such niche shifts have taken place (Broennimann et al. 2007).

A biogeographic test of the contrasting hypotheses of directional ecological filtering through limited dispersal vs. life history and ecophysiological limitations to the establishment of alien plant species along elevational gradients can be made by examining patterns of species occurrence in mountain areas where a history of major anthropogenic disturbance has potentially led to the removal of many dispersal limitations for alien plant species. The southern Sierra Nevada of California provides such a landscape, with a steep elevational gradient and more than a century of significant anthropogenic impacts along this gradient.

Elevations in the southern Sierra Nevada extend from about 100 m in the Central Valley at the base of the mountains to 4421 m at the summit of Mount Whitney in Sequoia National Park, the highest point in the continental United States. There are 27 native plant species that occur at or above 4200 m, and three of these reach to an elevation of 4400 m (Rundel 2011).

Although extensive areas enjoy protected status today, there have been 150 years of intense human impact ranging from sheep grazing and logging in the 19th century to tourism pressures that continue today (Vankat 1970). A substantial portion of this region is protected by Sequoia and Kings Canyon National Parks, covering 350,400 ha. Most alien plant species present today in these parks are known to have been well established in the Central Valley by the late 1800s, at the time when heavy grazing and logging activities provided ready pathways for the dispersal of propagules from low to high elevations (Bossard et al. 2000). The history of anthropogenic impacts is important in this region and expanded on in the Discussion.

Data on alien plant species occurrence in

these parks and the elevational and geographical distribution of these species in California provide a measure of realized niche space for alien species and con-familial native species, suggesting three hypotheses for testing. The first of these, consistent with (Alexander et al. 2009), is that alien plant species as climate-generalist invaders should have relatively broad niche dimensions, as measured by elevational range of occurrence, compared to native plant species that have had more opportunity for local adaptation to temperature and precipitation along the full elevational gradient. The second hypothesis is that increased environmental stress associated with montane and subalpine habitats will sharply restrict the upper elevational limits of alien plant species such that these will decline in relative species richness more rapidly with elevation compared to the native flora, which would be expected to have evolved adaptations to abiotic stress conditions. Finally, we hypothesize that the life form distribution will have a strong influence on potential distributions of alien plant species, with annuals more proportionally successful at low foothill elevations and herbaceous perennials at higher elevations.

METHODS

Floristic Data

The vascular plant flora of Sequoia and Kings Canyon National Parks has been well studied for more than a century. Frequent field studies by park staff and other scientists regularly survey both lower and upper elevational areas of the parks, allowing recordings of alien plant species as they become established, with attention increased for alien plant species in recent decades. The vascular plant checklist contains 1545 taxa in 108 families, with 188 of these taxa (12%) being aliens (Akin et al. 2005). This database is based on records in all of the major California herbaria as well as 11,199 vascular plant vouchers collected within the parks, with 7409 specimen records from Sequoia National Park, 3735 from Kings Canyon National Park, and 55 collected along the boundary between the two parks. Nearly half of these vouchers

(5506 or 49%) are in the park herbarium, with the remaining 5693 vouchers in regional and national herbaria.

Data from the most recent edition of the Jepson Manual (Baldwin et al. 2012) were used to determine the lower and upper elevation limits of selected native and alien species in California. Although new observations on species occurrences are constantly being made, the Jepson Manual is a highly reliable source as treatments are thoroughly checked against distribution databases prior to publication. The data on species in this reference are specimen-based and, thus, provide the most reliable and broadest available record of the elevational distribution of California species. The great majority of alien plant species were early introductions to California and have been part of the state's flora since at least the early 19th century.

We calculated the lower and upper elevational boundaries of occurrence in California as a measure of the realized niche breadth to abiotic conditions for the alien species present in the parks. Although data are available to carry out an analysis for all 188 species of aliens present in the park flora, these taxa are from 30 families and, thus, their full inclusion would potentially bias the data because of the multiple evolutionary lineages involved in comparing all native versus all alien plant species. The four families analyzed here allowed for phylogenetic coherency in the analyses. Phylogenetic coherency refers to studies utilizing a specific family or clade to minimize issues of canalized traits that are not selective in modern taxa. Without this correction in the data analysis, bias could easily be introduced by comparing the phylogenetic diversity of the full native flora with that of the alien species. The four families analyzed (Asteraceae, Brassicaceae, Fabaceae, and Poaceae) collectively contribute the great majority of alien plant species, and these were compared with the flora of native species in the same families.

A chi-squared test was used to determine whether there was a significant difference between the expected frequencies and the observed frequencies of native

and alien species by elevation zones and categories of plant life form. Differences were considered to be highly significant if $P < 0.01$.

Community Gradient

Vegetation zonation in the southern Sierra Nevada has been studied in considerable detail, with a mix of temperature and moisture availability as the controlling factors in community occurrence (Stephenson 1998; Fites-Kaufman et al. 2007). Lower elevation foothills up to about 1500–2000-m elevation on the west slope of the southern Sierra Nevada are dominated by a mosaic of deciduous oak woodlands, chamise or mixed chaparral, and mixed evergreen woodlands. Open deciduous woodlands have an herbaceous understory dominated by alien annual grasses and forbs and are a major source of alien propagules for other communities. The alien annual grasses include *Avena barbata* Link and *A. fatua* L., *Bromus diandrus* Roth., and *B. hordeaceus* L., (plus five other *Bromus* species), *Hordeum marinum* Hudson and *H. murinum* L., *Lolium multiflorum* Lam., and *Vulpia myuros* (L.) C. Gmelin. Alien annual forbs are also present but in lower abundance and biomass. The most abundant of these are *Centaurea melitensis* L., *Cerastium glomeratum* Thuill., four species of *Erodium*, *Silene gallica* L., *Geranium molle* L., and two species of *Torilis*. Many of the alien annuals have a history of increased abundance with grazing (Keeley et al. 2003). The widespread occurrence of alien plant species throughout the foothill elevational range and the open conditions of woodland habitats suggests that there are few abiotic limiting factors for these species over this elevational range.

Mature stands of chamise chaparral in the foothill zone are a special case, as they are relatively free of alien plant species because of environmental factors of shade tolerance rather than dispersal limitations. Only a few herbaceous natives or aliens are able to grow in the low light conditions under dense chaparral canopies, although a number of alien annual grasses readily invade postburn sites. These include *Aira caryophyllea* L., *Bromus madritensis* L., *B. hordeaceus* L., and *Vulpia myuros*

(L.) C. Gmelin.

The diversity and abundance of alien plant species drop sharply in the montane and higher elevation zones of Sequoia and Kings Canyon. Mixed conifer and upper montane forests are largely free of alien plant species. However, high-intensity fires create gaps that decrease tree canopy coverage and increase light levels and nutrients that allow for the establishment of an ephemeral successional flora of both natives and aliens (Keeley et al. 2003). Subalpine and alpine ecosystems along the gradient have very few alien plant species, although several of these are widespread and may form local ecological dominants, such as *Taraxicum officinale* Wigg.

Climate Gradients

Climatic gradients in the southern Sierra Nevada are relatively well understood and these allow a means to correlate environmental conditions with major vegetation zones. Mean annual temperature declines steeply with elevation from 17 °C at 520-m to 12 °C at 1400-m elevation at the upper limits of chaparral and woodland communities. Seasonal drought more than cold temperatures is thought to be the major limiting factors for species survival in the foothill zone. At higher elevations, however, short growing seasons and low winter temperatures become increasingly important as limiting factors. Mean annual temperatures drop to about 8 °C at 2000-m elevation in mixed conifer forest, and finally to about 1 °C at 3400-m near upper treeline. This is equivalent to 0.6 °C 100 m⁻¹ over the entire gradient. Mean minimum monthly temperatures below freezing occur over six months of the year in mixed conifer forests at about 2000-m elevation, but winter lows are moderate compared to continental mountain ranges. At treeline, the mean minimum temperature is below freezing for ten months of the year and can commonly reach temperatures of -15 °C, or lower.

In contrast to temperature, gradients in mean annual precipitation and water availability in the southern Sierra Nevada are more complex, varying from about 670 mm at 520-m elevation to 1050 mm at 1400-

m elevation, and peaking at about 1400 mm at 2000-m elevation before declining slightly with increasing elevation beyond 2000-m. However, the fraction of annual precipitation that falls as snow increases greatly with elevation from only 20 to 25% at the upper limits of chaparral and woodland communities to 95% at treeline (Stephenson 1998). Compared to lower elevations, the deeper snow pack and cold winter temperatures at higher elevations mean that snowmelt is slowed until late spring or early summer. Thus, the length and magnitude of the summer drought period experienced by plants decreases sharply as elevation increases because of both higher precipitation and cooler temperatures with lower evaporative demand at higher elevations (Stephenson 1998; Urban et al. 2000).

RESULTS

The four plant families analyzed included 397 native species and 111 alien species, representing, respectively, 26% of the native flora and 59% of the alien flora of Sequoia and Kings Canyon National Parks. Broken down by family, these were

the Poaceae (106 native and 58 alien species), Asteraceae (172 native and 23 alien species), Fabaceae (59 native and 18 alien species), and Brassicaceae (60 native and 12 alien species).

All of the alien plant species from our four selected families had an elevational range in California that began at or near sea level. In contrast, fewer than half of the native species in these same families had a lower elevational limit below 500 m (Figure 1). Native species showed a secondary peak of lower distribution limit in the 1000–1499 m elevational belt, but also include high elevation specialists that do not occur below 2500 m, or that are even found in subalpine habitats above 3000 m.

Contrary to the expectation of our first hypothesis that alien species are climate-generalists and should show broader ranges of elevational occurrence than native species, this was not the case. The distribution of realized climatic niche breadth, as measured by elevational range of occurrence, was virtually identical for alien and native species, with both groups showing a roughly Gaussian distribution

peaking with species occurring over a span of 1500–1999 m from lower to upper limits of occurrence (Figure 2). There were proportionally more native species having elevation distributions extending over 3000 m, but their numbers were small and not significant. Among aliens, only 2% had elevational ranges of less than 500 m, and, although not shown, it should be noted that all of these were restricted to low elevations. Although only 5% of native species had such narrow elevational ranges, most of these were high elevation specialists.

The pattern of upper elevation limit of occurrence for native and alien species, as predicted by our second hypothesis, differed significantly (Figure 3, $P < 0.0001$). The upper elevation limit of alien species peaked in the elevation range of 1500–1999 m, which corresponds to the upper boundaries of chaparral and woodland communities as well as the elevations with maximum road and tourist access. It then declined with increasing elevation, supporting the hypothesis of low alien abundance at high elevation but not resolving the causal factors responsible for

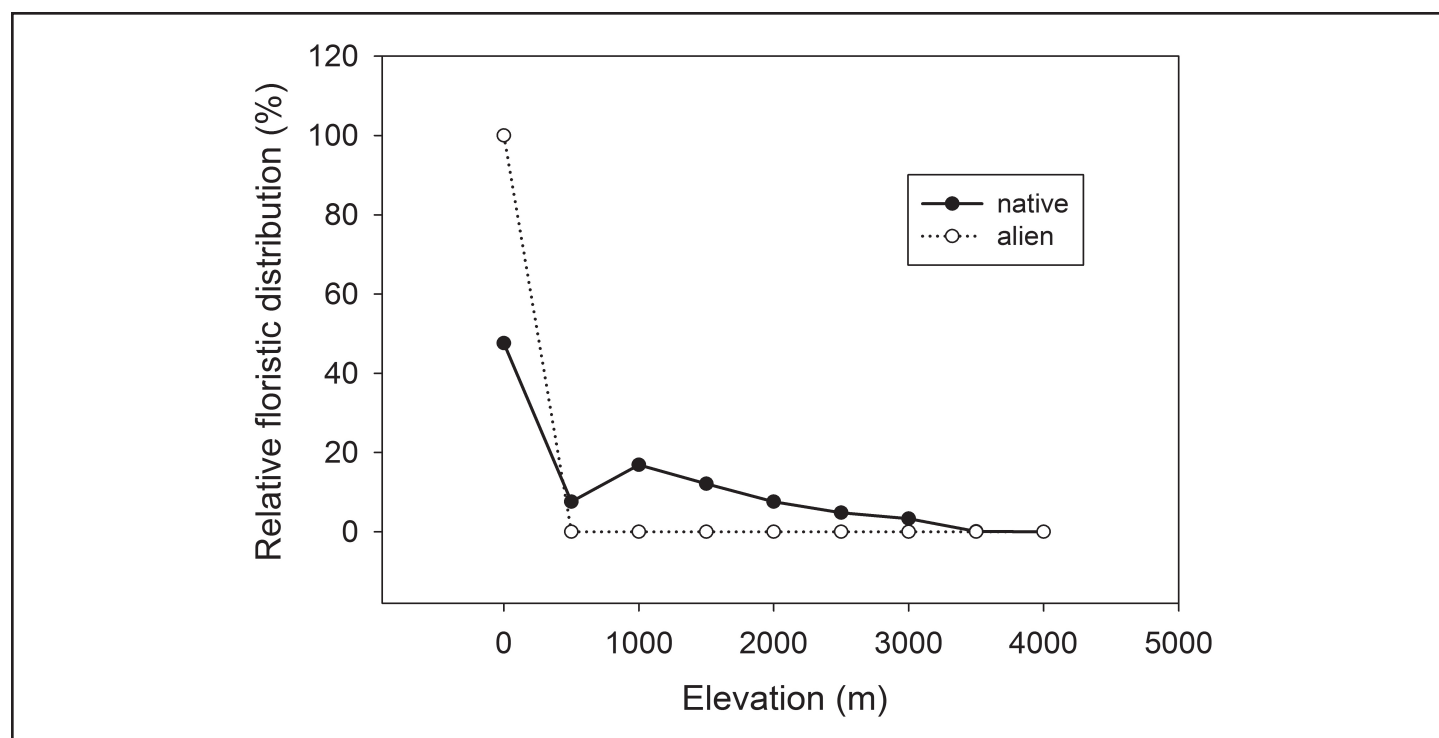


Figure 1. Relative floristic distribution of native and alien species plotted by their lower elevation limit of occurrence in California. These data include all members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae present in Sequoia and Kings Canyon National Parks, California.

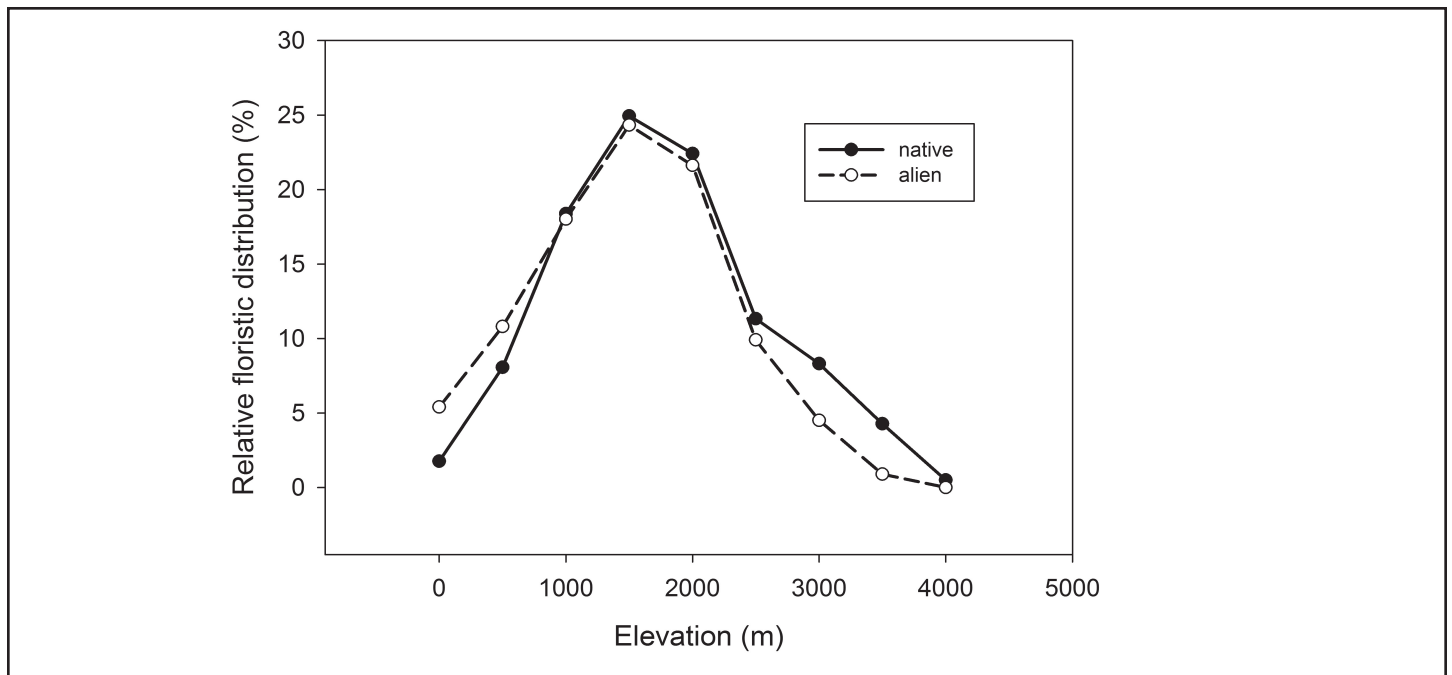


Figure 2. Relative floristic distribution of native and alien species plotted by their total amplitude of elevational occurrence from low to high in California. These data include all members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae present in Sequoia and Kings Canyon National Parks, California.

this decline. Nevertheless, more than 20% of the species had their elevation limit at 2000–2499 m, which corresponds to lower montane conifer forests.

In contrast to the aliens, native species showed a distribution of upper elevation limits peaking at elevations of 3000–3499 m (Figure 3), which corresponds to the zone of upper montane and subalpine forests. Moreover, more than 25% of the species had upper elevational limits that reached to greater than 3500 m, the lower limit of alpine habitats. Five alien species occurred above 3000 m elevation. These were *Taraxicum officinale* (Asteraceae), *Descurainia sophia* (L.) Webb (Brassicaceae), and three grasses – *Bromus madritensis* subsp. *rubens* (L.) Hussnot, *Bromus tectorum* L., and *Poa pratensis* L. All of these species have very broad elevational ranges, and with the exception of *Taraxicum*, have been reported from sea level to high elevations. *Taraxicum* is not reported at elevations below 450 m in California.

The relative distribution of life forms

among native and alien species in these four families was significantly different (Figure 4; $P < 0.0001$). Consistent with our third hypothesis, annuals comprised 58% of the alien species but only 19% of native species (Figure 4). This pattern can be seen most strongly in the Asteraceae where 70% of the alien species were annuals compared to only 19% of native species, and in the Poaceae where annuals comprised 53% of aliens compared to only 7% of natives. In these families, herbaceous perennials made up the remaining 33% of aliens and 71% of natives. Biennials comprised 9.2% of alien species and 5.0% of native species. Only a small number of subshrub or shrub species were present in either group.

The patterns of elevational distribution of native and alien plant species arranged by life form show strong differentiation. Herbaceous perennial native species have a peak in diversity at elevation belts around 2000 and 2500 m, while the peak for this group is at 1000 m and below for aliens (Table 1). Annual plant species drop off quickly in diversity around 2000 m in both groups. The only two alien shrub species included are largely restricted to

elevations below 1000 m, while there are native shrubs well adapted to growth up to near 4000 m.

DISCUSSION

Our results supported two of our three hypotheses. Alien plant species have a significantly lower upper elevation limit of occurrence than native species in the same family, and the alien flora of these families differs in the life form distribution with a significantly greater proportion of annual species. However, our data did not support the hypothesis that aliens as generalists exhibit a broader range of elevational distribution than native species.

The results reported here for Sequoia and Kings Canyon National Parks parallel patterns of alien plant species distribution in other parts of the Sierra Nevada. Studies in Yosemite National Park, a park with a flora quite similar to that of the parks we studied, have found that habitat traits of lower elevation, lower slope position, and more open community architecture are significantly correlated with higher alien plant species occurrence. Of particular interest is the observation that there is a

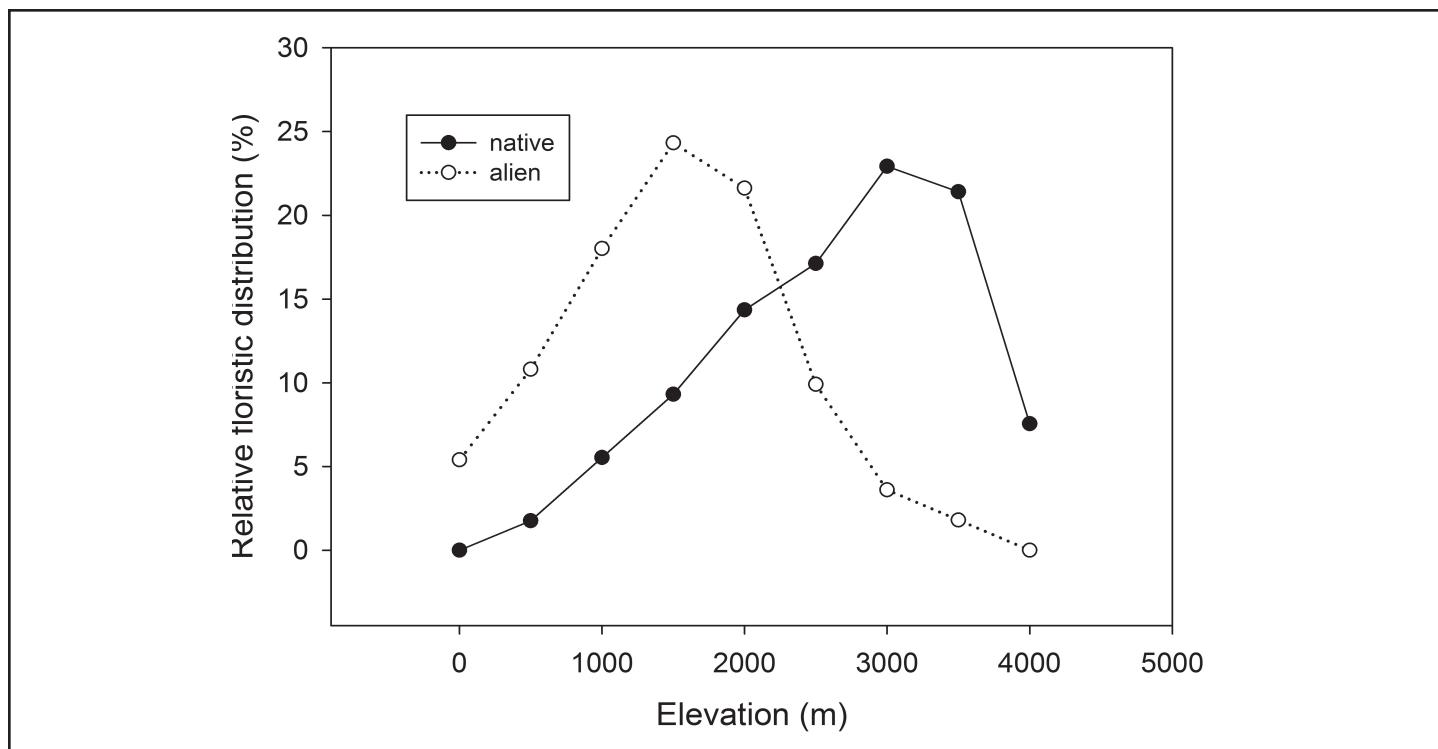


Figure 3. Relative floristic distribution of native and alien species plotted by their upper elevation limit of occurrence in California. These data include all members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae present in Sequoia and Kings Canyon National Parks, California.

strong negative relationship between elevation and alien species richness in those sites with human-mediated disturbances (Gerlach et al. 2003; Underwood et al. 2004). Wet meadows and riparian habitats are typically those most subject to alien invasion, with little indication of dispersal limitation (Kane et al. 2006). Studies in the Rocky Mountains have reported similar results (Stohlgren et al. 2002).

Although the suggestion has been made that higher elevation sites may not have had sufficient time for adequate propagule dispersal (Rejmánek 1989; Mensing and Byrne 1998; Lonsdale 1999; D'Antonio et al. 2001; Alexander and Edwards 2010), the history of human impact on ecosystems of the southern Sierra Nevada over the past 150 years strongly indicates that propagule availability is unlikely to be the major controlling factor for range expansions of existing alien plant species to higher elevations. The great majority of alien plant species in the foothill flora of the mountains have been present in the Central Valley and surrounding foothills since at least the mid-1800s (Bossard et

al. 2000), and have been provided with many opportunities for propagule dispersal to higher elevations (Keeley et al. 2003). There are indications that at least some alien plant species in California became established before the Spanish mission era, possibly from Native American trade with Mexico (Mensing and Byrne 1998).

A major vector of alien plant spread would have been the marked seasonal changes in livestock pasturage of both sheep and cattle. Sheep were introduced into California with the early Spanish missions, and their numbers increased dramatically with the gold rush and associated market for meat to feed the miners. More than half a million sheep were brought to California from New Mexico in the eight years from 1852 to 1860. As the mining boom declined, attention was turned from mutton production to wool production and sheep herding continued. Cattle are thought to have grazed Sierran mountain meadows as early as 1861, and in 1864 there were 4000 head reported in the Big Meadow area of the Sequoia National Forest (King 1902). While cattle numbers subsequently

declined, sheep populations peaked in the 1870s with about 6.4 million head, making California the leading state in mutton and wool production.

The heavy summer grazing of high Sierran meadows began when the record precipitation of 1861–62 was followed by major droughts in 1862–63 and 1863–64 and forced herders to seek higher elevation meadows. This led to the annual practice of summer grazing in the mountains, with associated overstocking and overgrazing of high mountain meadows. All of the major montane and subalpine meadows in the Sierra Nevada were heavily grazed each summer by flocks in search of pasture, with significant overstocking (Ratliff 1985), and the abundance of sheep is reflected in John Muir's reference to them as "hoofed locusts."

There are many graphic accounts describing the damage caused by sheep herding in this era (Vankat 1970; Odion et al. 1988; Dilsaver and Tweed 1990; McKelvey and Johnston 1992; Kinney 1996). One early account from the southern Sierra Nevada in

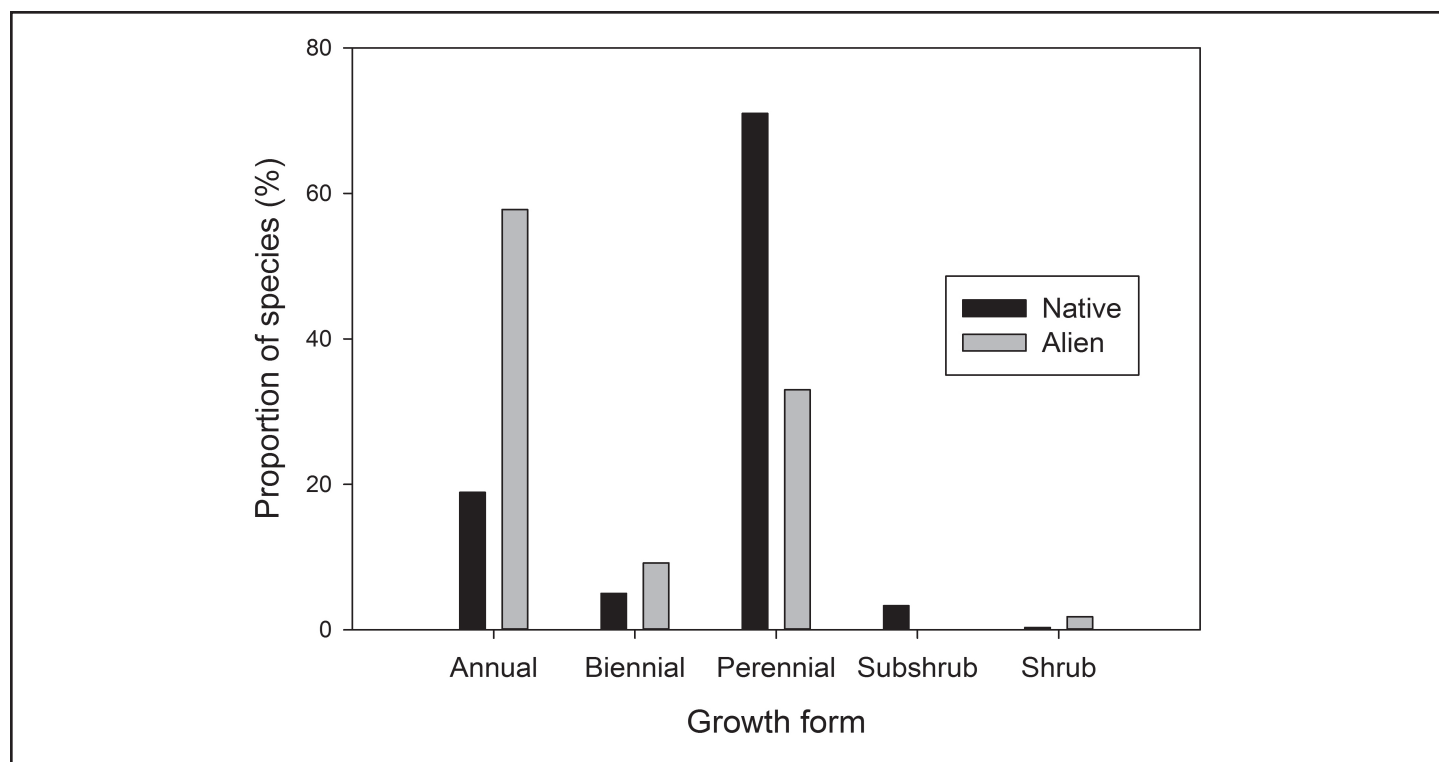


Figure 4. Relative distribution of plant growth forms among native and alien members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae present in Sequoia and Kings Canyon National Parks, California.

1885 reads as follows: “*Mountain meadows are abundant but the sheep-herder and his flocks have more largely worked their ruin in the Whitney region than anywhere else in the Sierra that I have visited. Each of these meadows is yearly cropped several times by various flocks of sheep, and the result is that, even where there was a genuine mountain meadow, there are now only shreds and patches. The sod and the verdure are gone – eaten and trodden out; the gravel is now in the ascendant*” (Vankat and Major 1978).

Early efforts by the National Parks and Forest Reserves to regulate grazing were generally ineffective until about 1900. Grazing permits were not required in National Forest lands until 1905, and cattle grazing remains an important activity today on both USFS and BLM lands adjacent to the parks. While damage to montane and subalpine meadows in the southern Sierra Nevada has been much reduced in recent decades, there remain significant management issues of meadow restoration in Sequoia and Kings Canyon (Sumner 1941; Sharsmith 1959; Bennett 1965; Vankat

1970; Ratliff 1985).

Logging occurred only at lower montane elevations in the southern Sierra Nevada until about 1900, at which time it became increasingly widespread at higher elevations on national forest lands. Overall logging levels increased gradually through much of the 20th century, with 1990 levels near the historical peak amount of cutting. A major change occurred in the 1970s, however, with selective logging giving way to extensive clear cuts that continued for nearly two decades. Today, virtually all stands of mixed conifer forest in the Sierra Nevada have been at least selectively logged, and outside of a few protected areas, there are no stands that can be described as entirely natural or pristine (Laudenslayer and Darr 1990; McKelvey and Johnston 1992). Logged sites provide suitable entry sites for invasive plant species as do sites impacted by other management practices such as the widespread application of herbicides after crown fires in montane forests (McGinnis et al. 2010).

Given this history of major landscape disturbance, patterns of alien plant distribution along the elevational gradient in the southern Sierra Nevada provide multiple indications that environmental limiting conditions control alien species distributions more than dispersal. For example, the foothill zone exhibits mosaics of alien species dominance in the groundcover of open oak woodlands while aliens are largely absent from adjacent shaded stands of chaparral. Postfire chaparral stands where light is not limiting are readily invaded by alien species through propagules of alien species from adjacent vegetation, indicating that dispersal limitations are not significant (Keeley et al. 2003). A similar pattern is seen in montane forests. Cold winter temperatures, winter snow accumulation, and deep litter layers are stresses for many species but perhaps more important is light availability as a limiting resource in shaded forest understory environments (Martin et al. 2009). Although dispersal does not appear to be limiting to establishment of aliens in open areas after fire, few alien species in this habitat have persistent seed banks and, thus, the time since fire is

Table 1. Relative distribution of native species (A) and alien species (B) by elevational zone for each major plant life form. Values shown are percent of total number of species within each life form at the indicated elevation belt.

Native species					
Elevation (m)	Annuals	Biennials	Herbaceous perennials	Subshrubs	Shrubs
0	85	42	31	50	50
500	69	75	39	58	50
1000	73	75	56	75	75
1500	63	88	73	75	75
2000	37	88	80	75	68
2500	20	88	87	75	75
3000	8	88	62	58	68
3500	6	75	41	42	25
4000	1	25	15	33	12
4500	0	0	2	0	0
Total species	84	8	284	12	8
Alien Species					
Elevation (m)	Annuals	Biennials	Herbaceous perennials	Subshrubs	Shrubs
0	100	60	97	0	100
500	73	30	100	0	100
1000	57	30	94	0	100
1500	46	20	78	0	0
2000	27	10	50	0	0
2500	11	0	22	0	0
3000	5	0	8	0	0
3500	2	0	6	0	0
4000	0	0	0	0	0
4500	0	0	0	0	0
Total species	63	10	36	0	2

an important determinant of colonization success (McGinnis et al. 2010).

Consistent with the hypothesis of abiotic limitations, only a few alien species have been ecologically successful invaders at subalpine and alpine elevations above 2500 m. The low diversity of aliens able to become established successfully in these habitats is unlikely due to dispersal limitations given the history of major grazing pressure at high elevations across this region. Instead, this low diversity is

hypothesized to be a function of multiple abiotic stresses that include extremes of cold air and soil temperature, heavy snowfall, short growing seasons, and low resource availability. These conditions have led to the evolution of a native flora with specialized traits of ecophysiological and phenological adaptation to subalpine and alpine abiotic conditions (Billings 1974; Korner 2003). If this is true, it would have important ramifications for future conditions since global warming should reduce this barrier of stressful conditions

at high elevations and open up new sites for invasion by alien plants.

There are six alien species known to have become established at high elevation conditions above 3000-m elevation in Sequoia and Kings Canyon National Parks. Previous studies have described two of these as broadly distributed and ecologically successful. The most widely established is *Poa pratensis* (Kentucky blue grass), which has widely invaded and even dominated subalpine wet to moist meadows, where it shows no indication of dispersal limitation (Ratcliff 1985; Gerlach et al. 2003). Seeds of this perennial grass are spread in the feces of grazing animals, and once established build up persistent soil seed pools (Ratcliff 1985). *Taraxicum officinale* (dandelion), a perennial with wind dispersed seeds, is present in a widespread manner along trails up to elevations of 3000 m or more, but is not an aggressive invader of nondisturbed communities (Gerlach et al. 2003). *Taraxicum* is also well known as a successful invader of high elevation habitats in other mountain areas, including the Andes of central Chile (Muñoz and Cavieres 2008). The other species of alien plants reaching these elevations are all annuals and relatively limited in occurrence and abundance.

Plant communities at subalpine and alpine elevations show an increased dominance of herbaceous perennials in their floras (Rundel 2011). Thus, it is not surprising that the two most successful alien plant invaders at these elevations are also herbaceous perennials. The short growing season and summer drought associated with high elevations in the Sierra Nevada makes this a difficult habitat for native and alien plant species alike. If new alien plant invasions occur in the future, they would be expected to occur with herbaceous perennials adapted to such environments in other parts of the world.

CONCLUSIONS

Our data do not support the hypothesis that most alien plant species in mountains are climate-generalists whose elevational range is determined by directional ecologi-

cal filtering along elevational gradients, with dispersal limitations as the controlling factor (Alexander and Edwards 2010). Alien plant species distribution along such gradients is much more complex in causality, with life history traits and abiotic stress as primary limiting factors influencing alien plant species occurrence at high elevations. This influence can be seen in the sharp drop in upper elevational limits of occurrence for alien plant species beginning near the lower boundary of the montane forest communities, where abiotic stress of extreme conditions becomes important (Figure 3). In contrast, native species show this sharp drop in upper elevational limits near treeline where alpine environmental conditions produce extreme abiotic stress.

The distribution of life forms among alien species, a trait that is often ignored, has major implications for the abiotic limits of alien plants at high elevations, and particularly in subalpine and alpine communities. For example, the short growing season and cool growing season temperatures at high elevations strongly limits the ability of annual species to survive (Billings 1974; Körner 2003). Annuals are generally rare in the typical circumboreal arctic-alpine floras of the Northern Hemisphere, although the Sierra Nevada and adjacent White Mountains, with their mediterranean-climate conditions, support larger diversities of alpine annuals (Billings 1974; Spira 1987; Rundel et al. 2008; Rundel 2011). The dominance of annual life histories among the regional pool of alien plant species provides a strong abiotic limitation to the establishment of annual aliens at high elevations that is independent of dispersal.

The spread of invasive plant species in California generally, and in the Sierra Nevada more specifically, remains potentially dynamic. We cannot rule out the possibility that alien plant species may increase their realized niches and expand their elevational ranges of occurrence in the future. From our data, however, we suggest that past disturbance and continuing human activity along roads and trails long ago reduced dispersal limitations for alien species present along the elevational gradient of the southern Sierra Nevada. Under current

conditions, the upper elevational limits of alien species appear to be controlled more by life history traits and abiotic stress than by dispersal.

Certainly, however, there is concern that alien species establishment at high elevations may increase in the future under conditions of global change (D'Antonio and Kark 2002; Pauchard et al. 2009; McDougall et al. 2011) or with the introduction of new alien species adapted to high elevations in their home ranges. Projected reductions in winter snowpack and increases in forest disturbance are likely to increase the risk of invasion from lower elevations (Stevens and Latimer 2015). Establishing careful monitoring programs that look for, and identify, new invasions of alien plant species in mountain parks might be informative for resource managers concerned with increased invasibility at higher elevations.

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