Apparent competition with an invasive plant hastens the extinction of an endangered lupine

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Abstract. Invasive plants may compete with native plants by increasing the pressure of native consumers, a mechanism known as "apparent competition." Apparent competition can be as strong as or stronger than direct competition, but the role of apparent competition has rarely been examined in biological invasions. We used four years of demographic data and seed-removal experiments to determine if introduced grasses caused elevated levels of seed consumption on native plant species in a coastal dune system in California, USA. We show that the endangered, coastal dune plant *Lupinus tidestromii* experiences high levels of pre-dispersal seed consumption by the native rodent *Peromyscus maniculatus* due to its proximity to the invasive grass, *Ammophila arenaria*. We use stage-structured, stochastic population models to project that two of three study populations will decline toward extinction under ambient levels of consumption. For one of these declining populations, a relatively small decrease in consumption pressure should allow for persistence. We show that apparent competition with an invasive species significantly decreases the population growth rate and persistence of a native species. We expect that apparent competition is an important mechanism in other ecosystems because invasive plants often change habitat structure and plant–consumer interactions. Possible implications of the apparent-competition mechanism include selective extinction of species preferred by seed consumers in the presence of an invasive species and biological homogenization of communities toward non-preferred native plant species.

Key words: Ammophila arenaria; apparent competition; biotic homogenization; coastal dune ecosystems; life-table response experiment; Lupinus tidestromii; *matrix population model; Point Reyes National Seashore, northern California, USA;* Peromyscus maniculatus; *population viability analysis; pre-dispersal seed consumption; stochastic population model.*

INTRODUCTION

Predicting the long-term effects of biological invasions on populations and communities requires an understanding of the mechanisms by which invasive and native species interact. While direct competition between invasive and native species has received significant discussion, indirect interactions such as apparent competition have been overlooked (Levine et al. 2003, Seabloom et al. 2003, White et al. 2006). This is surprising, since, in native ecosystems, indirect effects are often found to be as important, or more important, than direct effects (Strauss 1991, Wootton 1994, Russell et al. 2007).

Apparent competition occurs between plants when one plant species changes the abundance (Holt 1977) or distribution (Holt and Kotler 1987) of consumers, and, in doing so, alters the consumption rate and population dynamics of the other plant species. In plants, apparent competition may involve one species providing refuge for an herbivore or seed predator, which then consumes the other plant species (Connell 1990). While the existence of apparent competition among native plants is well documented (e.g., Connell 1990, Huntly 1991, Chaneton and Bonsall 2000), its importance for invasive plants has received much less attention (Maron and Vilà 2001, White et al. 2006). However, recent evidence suggests that consumer-mediated apparent competition might pose a strong extinction threat to native plant species. Introduced plants can allow large increases in consumer density (Orrock et al. 2008*a*), and consumption (Sessions and Kelly 2002, Orrock et al. 2008*a*). Further, in a review of studies examining consumers' effects on plants, Maron and Crone (2006) demonstrate that pre-dispersal seed consumption can have strong population-level effects on plants.

Invasive species are thought to be the second largest threat to global biodiversity (Wilcove et al. 1998), and yet few studies have conclusively linked the extinction of native plant species to the presence of an invasive plant (Reed et al. 2002, Sax and Gaines 2008). A few notable studies have used population models to demonstrate that invasive plants decrease the population growth rate and increase the extinction risk of native species

(Thomson 2005a, Williams and Crone 2006). However, to date, few population studies explicitly incorporate mechanisms, and none have quantified the effect of apparent competition on population dynamics and viability of native plant species.

The coastal dune grasslands of northern California offer an excellent system in which to examine apparent competition between invasive and native species. The exotic grass *Ammophila arenaria* (European beachgrass) was introduced for dune stabilization in the mid-1800s and has spread along much of the coast (Pickart and Barbour 2007). Densities of the native consumer *Peromyscus maniculatus* are much higher within stands of *A. arenaria* than in native vegetation (Pitts and Barbour 1979), and consumption by *P. maniculatus* occurs at higher rates near *A. arenaria* (Boyd 1988). Further, *P. maniculatus* is known to consume large quantities of seeds of leguminous dune plants (Maron and Simms 1997, 2001). Thus, we can use this system to test if seed consumption of a rare, native plant species is elevated in the presence of an invasive plant species and whether this consumption threatens its population viability.

In our present study we address the effects of apparent competition with the invasive grass *Ammophila arenaria* on the native species *Lupinus tidestromii*. The specific goals of this study were to (1) document the ambient level of seed consumption on *L. tidestromii*; (2) experimentally quantify if proximity to the invasive grass *A. arenaria* mediates consumption; and (3) use stage-structured, stochastic population models to determine if ambient levels of consumption threaten the persistence of *L. tidestromii*.

METHODS

Study system

Native, coastal foredune grasslands are now endangered on the California (USA) coast (Pickart and Barbour 2007). These grasslands have been dramatically reduced in size due to the introduction and proliferation of *Ammophila arenaria* (Wiedemann and Pickart 1996), which spreads at a rapid rate (Buell et al. 1995). Where it has become naturalized, *A. arenaria* alters foredune structure, decreases sand flow in interior dunes (Wiedemann and Pickart 1996), dominates vegetation communities (Barbour et al. 1976), and decreases plant species diversity (Breckon and Barbour 1974) (see Plate 1).

Lupinus tidestromii (Fabaceae) is a perennial herb endemic to coastal northern California. *L. tidestromii* occurs on semi-stable dune systems, many of which have been lost to development and to *A. arenaria* (USFWS 1998). The current range of *L. tidestromii* extends from Monterey County to Sonoma County and includes 14 extant populations in three counties (E. M. Dangremond, E. A. Pardini, and T. M. Knight, *unpublished data*). Owing to its critically low numbers and the aforementioned threats, *L. tidestromii* was listed as a federally endangered species in 1992 (USFWS 1998).

Inflorescences are racemes of whorled, purple flowers with a glabrous, white to yellow banner. Plants flower from April through June and are pollinated by generalist bees, such as *Bombus vosnesenskii* (E. M. Dangremond, E. A. Pardini, and T. M. Knight, *unpublished data*). The fruits are legumes 2–3 cm long and lie prostrate against the sand; each contains 5 to 8 mottled brown and tan seeds (Fig. 1b). Seeds are dispersed via explosive dehiscence in June and July. The seeds have a hard coat and form a persistent soil seed bank (Hickman 1993, USFWS 1998, Coppoletta 2005).

We conducted studies in three populations at Point Reyes National Seashore, Marin County, California, USA, where 9 of the 14 extant populations are located (Fig. 1a). Abbotts Lagoon is the largest extant population of *L. tidestromii*, fluctuating from ~115 000 to 160 000 individuals in a 21-ha area between the years 2001 and 2007. Radio Tower fluctuated between ~100 to 325 individuals in a 0.75-ha area during 2001–2007. North Beach is the smallest population, fluctuating between 15 and 150 individuals in a 0.15-ha area between 2001 and 2007 (Dangremond 2008).

Previous research at Abbotts Lagoon documented that *Peromyscus maniculatus* consume seeds from a variety of sand-dune plants (Boyd 1988) and preferentially consume *Lupinus* species (Pitts and Barbour 1979). To confirm that *P. maniculatus* was the primary seed consumer of *L. tidestromii*, we conducted preliminary studies at our study sites using mammal exclosures to distinguish between mammal and insect predation and track plates to distinguish predator identity based on footprints. We confirmed that mammal predators, and in particular *P. maniculatus,* are responsible for pre-dispersal seed predation (E. M. Dangremond, E. A. Pardini, and T. M. Knight, *unpublished data*).

Ambient consumption rates

We quantified ambient pre-dispersal seed consumption rates on 20–75 reproductive plants at each of three populations (Abbotts Lagoon, Radio Tower, and North Beach) in 2005, 2006, and 2007 (see *Population-level effects of consumption*, below, for more details on plant selection). On each plant we counted the number of fruiting racemes, the number of fruits per unconsumed raceme, and the number of fruiting racemes consumed. We scored as "consumed" racemes with any evidence of consumption (clipped racemes or fruits with large bites) and calculated the proportion of fruiting racemes consumed (c) per population per year.

Effect of A. arenaria on consumption rates

To determine whether proximity to *A. arenaria* influenced consumption rates on *Lupinus* plants, we conducted observations of individuals of endangered *L. tidestromii* occurring at different distances from *A. arenaria* and experiments on fruiting racemes of a surrogate species, *L. chamissonis*, at manipulated variable distances from *A. arenaria*. We followed 102
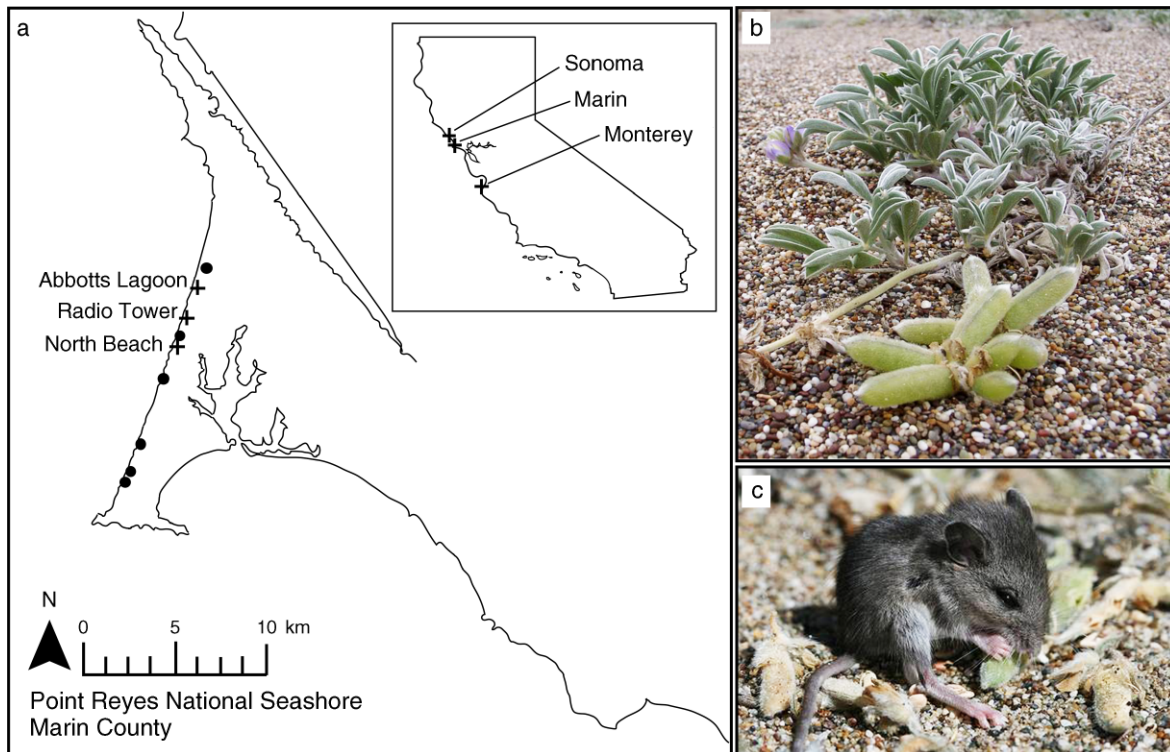
FIG. 1. (a) Map of the geographic distribution of *Lupinus tidestromii*, including nine populations (plus signs and solid circles) at Point Reyes National Seashore in Marin County, California, USA. Demographic matrix modeling was performed for three populations (denoted by plus signs). (b) Fruiting racemes of *L. tidestromii*. (c) *Peromyscus maniculatus* consuming a *L. tidestromii* fruit. Photo credits: (b) T. M. Knight; (c) S. Kroiss.

fruiting individuals of *L. tidestromii* over two seasons in May 2008 and May–June 2009 and documented plants as "consumed" (any racemes consumed) or "not consumed" (all racemes intact). Plants ranged from 1.4 to 143.7 m away from *A. arenaria*. We pooled data over years and used logistic regression to test whether consumption of *L. tidestromii* decreased with increasing distance from *A. arenaria*.

To measure the incidence of fruit consumption, we also experimentally placed fruiting racemes near and far from patches of *A. arenaria* in June 2006. To avoid unnecessary sacrifice of fruits of the endangered species, we used fruiting racemes of the co-occurring, common congener *L. chamissonis*. *Lupinus chamissonis* provides a good surrogate for *L. tidestromii* since low branches of *L. chamissonis* experience levels of fruit predation by *P. maniculatus* similar to those of *L. tidestromii* (T. M. Knight, *unpublished data*). We replicated this experiment at three sites, separated from one another by 500 m: Abbotts Lagoon north, Abbotts Lagoon south and North Beach (Fig. 1a). At each site we laid out five 100-m transects, extending outward from stands of *A. arenaria* into open dunes (similar methodology as Boyd [1988]). We placed one raceme with 3–19 fruits at 10-m intervals on each transect to simulate the range of fruits available on a single *L. tidestromii* plant at that time of year. After four days we scored each raceme for

consumption. We used logistic regression to test whether consumption of *L. chamissonis* decreased with increasing distance from *A. arenaria*.

Population-level effects of consumption

We used stage-structured projection models to explore the effects of seed consumption on population dynamics and viability of *L. tidestromii*. This species is well-described by a stage-structured model that includes seeds in a seed bank that will germinate after one year (seed bank 1) or two years (seed bank 2), seedlings, nonreproductive plants, and reproductive plants (Fig. 2). We modeled population viability at three populations (Abbotts Lagoon, Radio Tower, and North Beach) using demographic data from four years (2005–2008). We tagged plants with metal identification tags at each population in 2005 and monitored survival, growth, and fecundity through 2008 (Fig. 2). We monitored plants along 50 × 1 m transects (Abbotts Lagoon, $n = 100$ individuals, and Radio Tower, $n = 125$ individuals) or over the entire population (North Beach, $n = 67$ individuals) at the three sites. As seedlings germinated after 2005, we included them in the study and monitored them through 2008. The vegetation surrounding all populations was dominated by exotics *A. arenaria* and *Carpobrotus* spp., and native *Baccharis pilularis*.
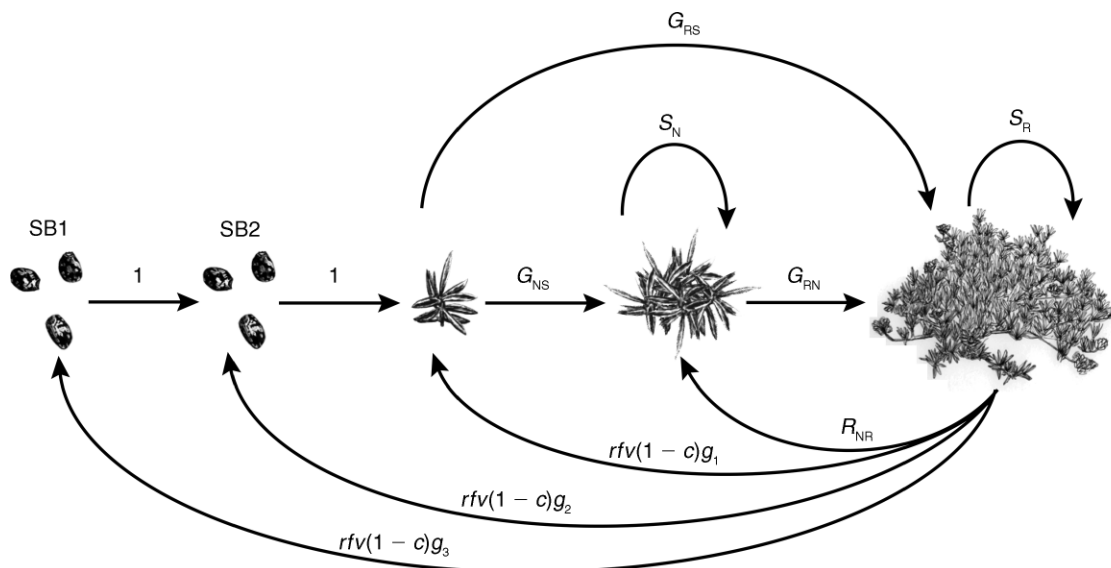
Fig. 2. Life-cycle diagram of *Lupinus tidestromii* illustrating survival (S_N, S_R), growth (G_{NS}, G_{RN}, G_{RS}), and regression (R_{NR}) transitions. The subscripts represent transitions between years. Key to abbreviations: S, seedling; N, nonreproductive plant; R, reproductive plant. A subscript of two letters indicates that a plant changes from one stage to another, so e.g., G_{NS} is mean growth from seedling to nonreproductive plant. Transitions from the reproductive stage to seed bank and seedling stages are a function of fecundity and consumption, where $(1 - c)$ is the proportion of racemes not consumed, r is the number of racemes per plant, f is the average number of fruits per unconsumed raceme for each plant, v is the average number of viable seeds per fruit, and g is the germination (in 2006, g_1; in 2007, g_2; and in 2008, g_3).

All the seeds represent the two seed-bank stages (those that can germinate in one year, SB1, and those that germinate in two years, SB2). However, we use the numeral 1 above the two left-most arrows to show that all the seeds in SB2 (the farthest one on the left) pass into SB1 the next year, and likewise for SB1 to the seedling stage; in other words, the probability that they pass into the next stage is 1. All the other arrows have symbols because they vary from year to year, and those values are presented in Appendix A. (The illustration is by P. Hanly.)

Our model assumes all vital rates are density independent, and we believe that this is a reasonable assumption for two reasons. First, the natural densities of these endangered plant populations are low, and therefore population density likely does not currently limit individual vital rates (e.g., germination) or population growth. Second, in cases where populations are projected to grow, eventually plants will reach densities that saturate seed predators or exhaust available sites for seed germination and establishment, at which point consumption rates and plant population densities will reach an equilibrium level. However, in our case, all natural populations are projected to decline (see *Results*, below), and thus knowing the saturation densities is not relevant for projections. Our model also explores population growth rate in the absence of predation; in that case, understanding how consumers respond to plant density is not relevant. However, we note that in cases for which exponential growth is projected in the absence of predation, such increases in population size would only be possible in the short term. While it might seem intuitive that seed losses will always result in decreased population growth rate in the absence of density-dependent recruitment, the magnitude of this decrease is not clear. A species could have large changes in recruitment and relatively insignificant changes in population growth or extinction risk if the

population dynamics are insensitive to changes in seed vital rates (Maron and Crone 2006).

Three transitions in our model include fecundity and are affected by seed consumption: reproductive stage-to-seed bank 1, reproductive stage-to-seed bank 2, and reproductive stage-to-seedling stage. To estimate total fecundity for each plant in each year we multiplied the number of racemes per plant (r) by the average number of fruits per raceme for each plant (f) by the average number of viable seeds per fruit (v) by germination (Fig. 2). We estimated r and f for each plant in each population and year; we estimated v in 2005 at Abbotts Lagoon by randomly collecting fruits from 15 separate individuals to get an average number of viable seeds per fruit. To incorporate seed consumption into our model we multiplied fecundity by the probability that a raceme was not consumed (1 − proportion of racemes consumed, c, described in *Ambient consumption rates*, above) (Fig. 2).

To quantify seed germination and viability in the seed bank, we planted seeds in seed baskets made from PVC pipe at the Abbotts Lagoon population. This site was chosen since it was the largest site, and the seeds used for this experiment represented <1% of the seeds produced at this site. Harvesting seeds for germination experiments was not possible at the other sites, because seed collections would have removed a large proportion of

the seeds produced; we therefore used the same probability of germination for all three sites.

We installed 10 seed baskets by burying 30-cm-diameter PVC pipes into the ground, leaving a 5-cm rim above the sand. We sifted the sand inside the pipe to exclude any other seeds and then placed 10 *L. tidestromii* seeds in each pipe (100 seeds total). We quantified the proportion of seeds that germinated and survived until May in 2006 (g_1), 2007 (g_2) and 2008 (g_3) (Fig. 2). Our estimates of germination rates are supported by counting the number of seedlings that germinated in our transects at Abbotts Lagoon over four years. For example, in our germination experiment we estimate that g_1 is 0.011. Results from our natural populations show a similar low proportion of seeds recruiting into seedlings (the number of seedlings in 2006 divided by the total number of seeds produced in 2005 = 0.022; the higher number here compared to the germination experiment likely results from some of the 2006 seedlings recruiting out of the seed bank).

We calculated the stochastic population growth rate (λ_s) by simulation. We assumed that the four years of our study represented a range of typical conditions, with each demographic matrix equally likely to occur in the future. For each population, we used $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$ to project population size from time t to $t + 1$, where $\mathbf{A}$ is a demographic matrix and $\mathbf{n}_t$ is a vector that gives the number of individuals in each stage at time t (Caswell 2001). The initial population vector was set to the stable stage distribution of the mean matrix (average across all years) with an initial population size of 1. We project population size over 50 000 successive time intervals, using a matrix drawn at random each time interval to estimate the log λ_s [the arithmetic mean of $\log(\mathbf{n}_{t+1}/\mathbf{n}_t)$ over all pairs of adjacent years] and 95% confidence intervals in log λ_s. Calculations were conducted in a MATLAB (MathWorks 2009) program modified from Morris and Doak (2002). We calculated two estimates of λ_s for each of the populations: one for ambient conditions and one in which we set the proportion of racemes consumed to 0, allowing us to examine projected population growth in the absence of consumption.

To determine the reduction in consumption required for a population projected to decline to switch to a projected increase, we examined the change in λ_s across a gradient of seed consumption. We calculated λ_s for the entire range of possible levels of seed consumption by manipulating the proportion of racemes consumed. We varied the proportion of racemes consumed, c, from 0 (no consumption) to 1 (all racemes consumed) at intervals of 0.1.

Life-table response experiment

Consumption of seeds affects three matrix elements: reproductive stage-to-seed bank 1, reproductive stage-to-seed bank 2, and reproductive stage-to-seedling stage. We used a life-table response experiment (LTRE) to determine the contribution of each of these to the
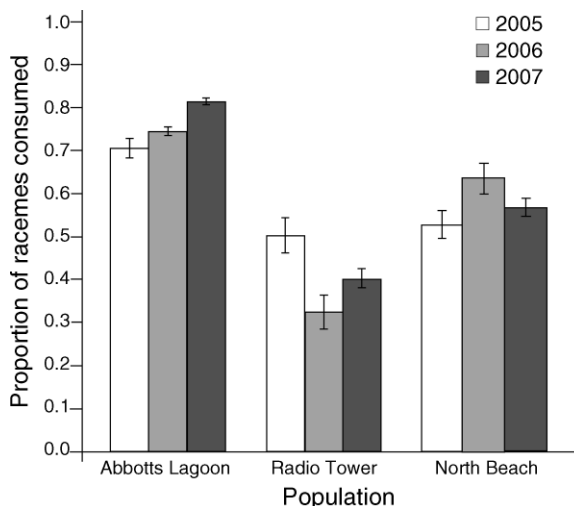

Fig. 3. Ambient consumption rates of *Lupinus tidestromii* for 2005–2007 at Abbotts Lagoon, Radio Tower, and North Beach (Point Reyes National Seashore, California, USA). Data are means ± SE.

difference in λ between the ambient-conditions matrix (A) and the no-consumption matrix (NC) for each population (Caswell 2001). The contribution of each element is determined by the difference between the matrix element for each treatment and the sensitivity (s_{ij}) of λ to changes in that matrix element:

$$\lambda^{NC} - \lambda^{A} \cong \sum_{ij} \left(a_{ij}^{NC} - a_{ij}^{A} \right) s_{ij}.$$

For the LTRE analysis, we considered the mean matrix across all years for each population and consumption type (ambient or no consumption). The sensitivities used for each population were calculated from a matrix that was the mean of A (ambient) and NC (no consumption). Analyses were performed in MAT-LAB (MathWorks 2009).

RESULTS

Ambient consumption rates

Pre-dispersal fruit consumption at the Abbotts Lagoon site ranged from 70% to 82% during 2005–2007. The Radio Tower site had a lower percentage of fruits consumed, ranging from 31% to 42%. Pre-dispersal fruit consumption at North Beach ranged from 52% to 62% (Fig. 3).

Effect of Ammophila arenaria on consumption rates

Observations of fruit consumption on individuals of *Lupinus tidestromii* at Abbotts Lagoon showed that there was a significant effect of consumption decreasing with increasing distance from *A. arenaria* (logistic regression: $n = 102$ fruiting racemes, odds ratio = 0.981 [95% CI 0.967–0.994], $P = 0.006$). Experimental placement of fruiting racemes of *Lupinus chamissonis* also showed that fruit consumption decreased with
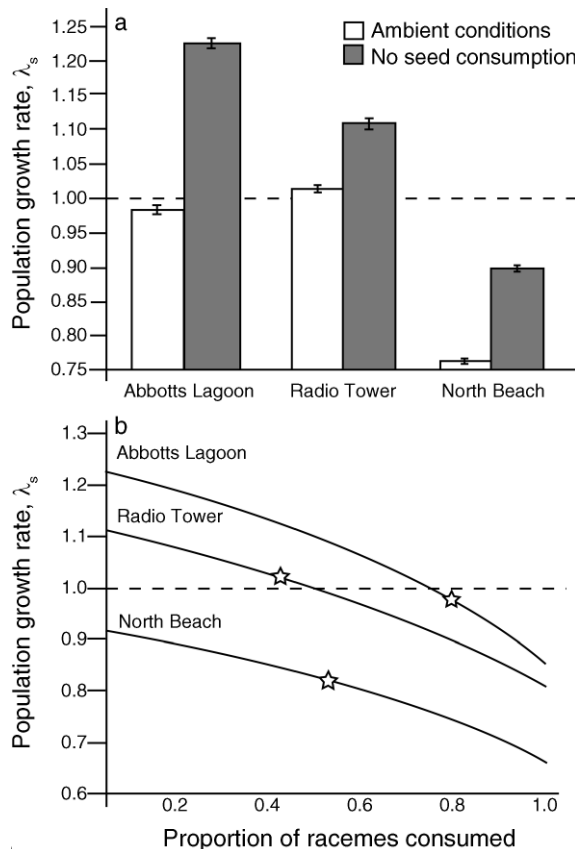
FIG. 4. (a) Stochastic matrix model projections of population growth rate (λ_s) are significantly higher when no seed consumption is assumed compared to ambient conditions. We present mean and 95% confidence intervals from 50 000 bootstrap estimates. (b) Stochastic matrix model projections of population growth rate in three populations of *Lupinus tidestromii* across a gradient of pre-dispersal seed consumption. Current, ambient consumption rates are denoted by an open star.

increasing distance from *A. arenaria* (logistic regression: $n = 136$ fruiting racemes, odds ratio = 0.964 [95% CI: 0.947–0.979], $P < 0.001$).

Population-level effects of consumption

Vital rates differed greatly among the three populations (Appendix A). Stochastic matrix model growth-rate projections were higher in the absence of consumption in all cases (Fig. 4a). Fig. 4b illustrates projected population growth rates at levels of seed consumption ranging from 0 to 1. A slight reduction in consumption is projected to bring λ above 1 at Abbotts Lagoon. The North Beach population is projected to decline over all levels of consumption.

Elasticity analysis showed that survival of reproductive individuals has the largest effect on projected population growth rate in all three populations (Table 1). The rankings of elasticity values did not qualitatively change across years within each population (Appendix B).

Life-table response experiment

The three vital rates affected by consumption, reproductive stage-to-seed bank 1, reproductive stage-to-seed bank 2, and reproductive stage-to-seedling stage, contribute differently to the difference in λ between the ambient-conditions matrix and the no-consumption matrix (Table 2). In all three populations, the reproductive stage-to-seed bank 1 transition is the most important contributor to the observed difference in λ between these two matrices.

DISCUSSION

Our results, together with those of others, demonstrate the general importance of apparent competition in species invasions. Invasive plant species can cause high consumer densities (Pitts and Barbor 1979, Meiners 2007, Orrock et al. 2008a), increased seed consumption (Boyd 1988), decreased establishment of native plant species mediated by consumers (Orrock et al. 2008a), and reduced survival and reproduction via increased herbivory (Sessions and Kelly 2002). We show that apparent competition between an invasive plant and a native plant can cause declines in long-term population growth. Specifically, the introduced grass, *Ammophila arenaria*, negatively affects the population viability of the native species, *Lupinus tidestromii*, via elevated seed consumption by *Peromyscus maniculatus*.

Consumers do not necessarily have population-level effects, even if they cause significant loss of fecundity. Seed consumption will only affect population dynamics if it influences a vital rate to which population growth rate is sensitive (Mills and Lindberg 2002, Ehrlén 2003, Ehrlén et al. 2005), if population growth is not already limited by the availability of safe sites for germination, and if density-dependent seedling survival does not compensate for loss of seed to consumers (Eriksson and Ehrlén 1992, Louda and Potvin 1995). In our study, the population growth rate of *L. tidestromii* was moderately sensitive to transitions from the reproductive stage to seed or seedling stages, which are affected by consumption. Loss of fecundity to consumers affects these transitions and thus population growth rate. Consumers are predicted to disproportionately affect short-lived perennial plants that have no or limited seed banks, and thus rely heavily on current seed rain (Louda and Potvin 1995, Maron and Crone 2006). Seed banks have been thought to buffer plant populations against negative effects of consumers (Harper 1977, Crawley 1989, 1990) but may also retain a "memory" of accumulated seed loss over time, especially with increased longevity of the seed bank (Maron and Gardner 2000). Our study species is a short-lived perennial plant with a seed bank. Since it germinates on open sand dunes and occurs at low densities, it is likely seed limited rather than microsite limited, and density-dependent seedling mortality likely does not compensate for seed losses to predation.

Our model might be conservative in its estimate of population growth rate for two reasons. First, the model

TABLE 1. Average elasticity matrices for each population of *Lupinus tidestromii*, an endangered coastal dune plant of northern California, USA.

Stage at year $t + 1$	Plant stage at year t				
	SB2	SB1	Sdlg	Non	Rep
Abbotts Lagoon					
SB2	0	0	0	0	0.0320
SB1	0.0320	0	0	0	0.0704
Sdlg	0	0.1025	0	0	0.0229
Non	0	0	0.0793	0.0086	0.0164
Rep	0	0	0.0461	0.0957	0.4939
Radio Tower					
SB2	0	0	0	0	0.0378
SB1	0.0378	0	0	0	0.0858
Sdlg	0	0.1235	0	0	0.0289
Non	0	0	0.1446	0.1003	0.0430
Rep	0	0	0.0078	0.1876	0.2032
North Beach					
SB2	0	0	0	0	0.0427
SB1	0.0427	0	0	0	0.0761
Sdlg	0	0.1189	0	0	0.0201
Non	0	0	0.0543	0.1843	0.0487
Rep	0	0	0.0846	0.1030	0.2243

Note: Key to abbreviations: SB2, seeds in the seed bank that will germinate in two years; SB1, seeds in the seed bank that will germinate in one year; Sdlg, seedling; Non, nonreproductive; Rep, reproductive.

assumes that once seeds are removed from the plant, they do not germinate. It is conceivable that seeds in cached fruits may escape consumption (e.g., squirrel caches of acorns); however, personal observations of fruit caches found that all fruits and their seeds were completely consumed. Additionally, most caches are found underneath shrubs and other dense vegetation that might not be suitable germination sites for *L. tidestromii* seeds. Second, we do not explicitly include post-dispersal seed predation. Seeds within racemes that escape pre-dispersal seed predation might still be vulnerable to post-dispersal predation. Predation risk

of these seeds should occur in a relatively restricted time period, between the time of fruit dehiscence and the time of burial by sand such that they are hidden from predators.

Our model assumes that *L. tidestromii* seeds that do not germinate within three years are dead. While seeds are capable of surviving much longer than this in the seed bank, we believe that this assumption still provides a realistic picture of the population dynamics of *L. tidestromii* for several reasons. Most importantly, sand dune stabilization by invasive grasses eliminates disturbances that would naturally bring old seeds to the

TABLE 2. Life-table response experiment for three populations of *Lupinus tidestromii*.

Matrix element	a_{ij}^{NC}	a_{ij}^{A}	$a_{ij}^{NC} - a_{ij}^{A}$	s_{ij}	Contribution
Abbotts Lagoon					
Rep. to seed bank 2	1.2101	0.2904	0.9197	0.0563	0.0518
Rep. to seed bank 1	2.6922	0.6461	2.0460	0.0640	0.1309
Rep. to seedling	0.8874	0.2130	0.6744	0.0727	0.0490
Radio Tower					
Rep. to seed bank 2	0.6943	0.4087	0.2855	0.0743	0.0258
Rep. to seed bank 1	1.5445	0.9093	0.6353	0.0795	0.0611
Rep. to seedling	0.5091	0.2997	0.2094	0.0850	0.0214
North Beach					
Rep. to seed bank 2	0.4493	0.1882	0.2611	0.1317	0.0344
Rep. to seed bank 1	0.9997	0.4187	0.5809	0.1144	0.0665
Rep. to seedling	0.3295	0.1380	0.1915	0.0993	0.0190

Notes: "Rep." stands for reproductive individual. We used the mean matrix across all years for each population and consumption type (ambient or no consumption). The expression $a_{ij}^{NC} - a_{ij}^{A}$ is the difference between matrix elements when no seed consumption is assumed (NC) and when ambient levels of seed consumption occur (A); s_{ij} is the sensitivity of the population growth rate to changes in each matrix element. The contribution of each vital rate to the difference in population growth rates between ambient consumption and no consumption is the product of $a_{ij}^{NC} - a_{ij}^{A}$ and s_{ij}. A large contribution indicates that the matrix element plays a disproportionate role in the difference in population growth rate between NC and A matrices.

PLATE 1. Native dune vegetation, including the endangered *Lupinus tidestromii* (foreground), has been replaced along much of the California coast (USA) by the invasive *Ammophila arenaria*, which forms dense stands across the coastal dune ecosystem (background). Photo credit: E. A. Pardini.

surface and allow them to germinate. Natural sand dunes in California and elsewhere are a dynamic ecosystem that is shaped by disturbance from wind storms; these storms uproot current vegetation and move the top layer of sand, exposing seeds in the seed bank. Historically, *L. tidestromii* seeds probably germinated and thrived in these conditions. We have observed that in small sand blowouts, *L. tidestromii* seedlings are one of the first species to appear in the newly formed early successional habitat. However, the presence of the invasive grass, *A. arenaria*, stabilizes sand dunes and prevents large-scale movement of sand during storms (Wiedemann and Pickart 1996). Therefore, *L. tidestromii* seeds that do not germinate within the first three years will become buried by sand and will likely never have the opportunity to germinate. In our seed-germination study, we found that most germination occurs in the first two years; only one new seedling was found in the final year of our study.

Our results contribute to a growing body of literature suggesting that spatial and temporal variation in seed predation can affect plant abundance, distribution, and population dynamics (see Maron and Crone 2006) but that the outcomes of seed consumption may vary depending on the environmental context (Kolb et al. 2007a). Variable seed predation has been found to alter plant abundance over large spatial scales, as documented with the California shrub *Haplopappus squarrosus*,

which increases across an altitudinal gradient as a result of decreasing seed predation (Louda 1982). Seed predation has also been shown to drive plant abundance across smaller spatial scales, including gradients between sun and shade (Louda and Rodman 1996) and canopy cover (Kolb et al. 2007b). Differences in seed predation contribute to differences observed in population dynamics of our *L. tidestromii* populations. However, the population receiving the lowest level of predation (North Beach) was also the smallest population. The low population growth rate and abundance of this population is likely due to other environmental factors that are pronounced at this site, such as cattle grazing and heavy encroachment by another nonnative plant species (iceplant; *Carpobrotus* spp.). Invasive plants and apparent competition might have the capacity to change the spatial scale at which gradients of seed predation are observed. It is possible that gradients in predation at smaller spatial scales disappear once invasive plants establish and become a homogenizing force resulting in high levels of predation across all sites; larger scale gradients in predation may be driven by whether or not the invasive plant has established.

The interactions between the invasive grass *A. arenaria* and the native herb *L. tidestromii* are an example of a widespread phenomenon of the synergistic negative effects of plant invaders on native species, communities, and ecosystems. *Lupinus tidestromii* is

affected in a multitude of ways by the invasive grass, *A. arenaria*: *A. arenaria* directly outcompetes *L. tidestromii* and other native vegetation (e.g., Barbour et al. 1976, Pavlik 1985, Boyd 1988) and it houses higher densities of the seed predator *Peromyscus maniculatus*, than does native vegetation (Pitts and Barbour 1979). Additionally, *A. arenaria* alters the structure of the dunes and decreases sand flow to interior dunes (Wiedemann and Pickart 1996), which likely reduces seed scarification and thus germination, as well as reducing the availability of open blowout microsites available for native-plant establishment. Another well-documented example of synergistic effects of plant invaders is the case of the grass–fire cycle set in motion by *Bromus tectorum* (cheatgrass) in sagebrush steppe communities in western North America (D'Antonio and Vitousek 1992). *Bromus tectorum* is highly flammable and increases vertical continuity in fuel load, which increases fire to a frequency at which native shrubs and perennial grasses cannot recover (Whisenant 1990). Furthermore, cheatgrass possesses traits that allow it to exploit soil resources and thus recover more rapidly than native species following fire: *B. tectorum* competes with native species for water and negatively affects their water status and productivity (Melgoza et al. 1990). Direct competition with native plants and ecosystem engineering create a positive invasion-feedback loop that shifts community dominance toward *B. tectorum* (D'Antonio and Vitousek 1992, Brooks et al. 2004).

In cases where apparent competition is an important mechanism by which invasive species cause extinction of natives, large-scale restoration will be necessary to remove the negative effects of the invasive species and to restore consumer populations to natural densities due to the larger foraging ranges of the rodent consumers (see also Orrock et al. 2008b). For *L. tidestromii* it is notable that the Abbotts Lagoon population requires only a slight reduction in pre-dispersal seed predation to allow projected population increase. We predict that removal of *A. arenaria* will be accompanied by a subsequent decline or redistribution of *P. maniculatus* populations because there will be fewer refugia available to them. Large-scale removal of *A. arenaria* is likely to benefit other native plant species by reducing direct competition for resources, reducing consumption by native predators, and restoring open, dynamic, sand-dune habitat that favors recruitment and establishment by federally listed native plants such as *L. tidestromii* and *Layia carnosa*.

In addition to affecting individual native species, invasive species have the potential to cause biotic homogenization of natural communities. "Biotic homogenization" is the process by which the composition of species in communities becomes more similar after invasion (McKinney and Lockwood 1999, Olden 2006). To date, most studies have described the pattern of biotic homogenization by comparing community similarity through time (reviewed by Olden [2006]), and have

not explicitly studied the mechanisms that cause this pattern (but see theoretical study by Olden and Poff [2003]). Here, we suggest a novel mechanism that might result in biotic homogenization. When invasive plants compete strongly with native plant communities via apparent competition, native species preferred by consumers are selectively eliminated from the community. As a result, invaded communities will ultimately contain a more homogenous plant-species composition that is not preferred by consumers. There are many examples where changes in the abundance of an herbivore or introduction of an exotic herbivore changes plant community composition toward less preferred species. Throughout eastern North America, white-tailed deer have increased in density due to habitat fragmentation, supplemental food sources, and the eradication of large carnivores; this in turn causes a reduction in the relative abundance of their preferred plant species (Augustine and McNaughton 1998). In addition, the introduction of exotic cattle to American landscapes similarly shifts plant communities toward those species that are not preferred (Fleischner 1994). Further examination of these mechanisms involving predator preferences will improve our understanding of the documented patterns of biotic homogenization and our ability to predict future patterns of homogenization.

Invasive species are the second greatest threat to threatened species (Wilson 1992, Wilcove et al. 1998), yet we have little quantitative evaluation of their effects on decline and extinction of native species. This might be due in part to the long time to extinction for declining native plant species (Sax and Gaines 2008). If similar extinction threats are present at all populations of a species, then understanding local population dynamics will inform extinction risk of the entire species (Morris and Doak 2002). Studies such as our present one, which employ field experiments and demographic population models, can project long-term population dynamics and growth rates and elucidate the mechanisms by which invasive species threaten native plant species (Byers et al. 2002, Thomson 2005b). We need additional population viability analyses to understand the dynamics of rare and threatened plants in advance of severe decline or extinction and to ultimately reverse such trajectories.

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APPENDIX A

Estimates of vital rates and ambient consumption for three study populations of *Lupinus tidestromii* at Point Reyes National Seashore (*Ecological Archives* E091-161-A1).

APPENDIX B

Transition matrices and elasticity matrices for all years and all populations (*Ecological Archives* E091-161-A2).