Plant community response following the removal of the invasive Lupinus arboreus in a coastal dune system: Community response following L. arboreus removal

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RESEARCH ARTICLE

Plant community response following the removal of the invasive *Lupinus arboreus* in a coastal dune system

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The removal of invasive species is common in restoration projects, yet the long-term effects of pest management programs are seldom assessed. We present results of a long-term program to remove the invasive species *Lupinus arboreus* (lupin) from sand dunes in New Zealand. We evaluate the response of plant communities to lupin removal, by comparing total plant cover, the cover of non-native and native plant species, and species richness between sand dune sites where lupin removal has occurred, not occurred, and where lupin has never been present. Neither lupin presence nor removal had a significant impact on the foredune environment. Following removal, total and other non-native plant cover remained higher, and the cover of several native sand dune species remained lower compared with uninvaded sites in the deflation and backdune environments. These changes can be attributed to persistent effects associated with the invasion of lupin, but have also developed in response to lupin removal. The results of this study have implications for restoration projects in sand dunes. Pest management alone is unlikely to be sufficient to restore plant communities. Given the difficulties in restoring plant communities once an invasive species has established, managers should prioritize actions to prevent the spread of invasive species into uninvaded areas of sand dunes. Finally, the response to lupin invasion and removal differed between dune habitats. This highlights the importance of tailoring a pest management program to restoration goals by, for example, prioritizing areas in which the impacts of the invading species are greatest.

Key words: chemical control, invasive species, New Zealand, pest management, restoration, sand dune

Implications for Practice

- Chemical removal of lupin has been effective at reducing lupin cover in sand dune habitat in southern New Zealand, but has not reestablished the pre-lupin plant communities, 6 years following management.
- Lupin caused changes to plant communities that have persisted following lupin removal. Removing lupin by broad-scale application of herbicide resulted in further undesirable changes to plant communities.
- Additional and/or complementary management is required to the restoration goal of restoring the pre-lupin plant communities at the study site, namely the replanting of native species and measures to limit the growth of non-native grasses.

Introduction

The invasion of plant communities by non-native plants is associated with adverse effects on native taxa; through competition (Mack et al. 2000), modification to ecosystem processes (e.g. nutrient and hydrological cycles) (Richardson et al. 2007; Ehrenfeld 2010), or interruption of mutualistic networks (e.g. pollination and dispersal) (Pyšek et al. 2012). Consequently, managers frequently prioritize the removal of invasive species when aiming to restore modified ecosystems (Corbin & D'Antonio 2012). Monitoring progress toward restoration goals following pest management is, however, less frequent and has tended to focus on the response of key species, with the assumption that removing the invading species will automatically lead to the recovery of original biodiversity values (Reid et al. 2009; Kettenring & Adams 2011). In New Zealand, for example, only 16% of government-run pest management projects involved outcome monitoring, compared with 82% of projects that monitored the decline of the invasive species (Clayton & Cowan 2010). In addition, most studies report species response to management over short time spans (typically <2 years) (Kettenring & Adams 2011), even though ecosystems may take decades to respond (Blossey 1999; Reid et al. 2009).

Invasive species removal, however, does not always lead to recovery of original biodiversity values. Biological, chemical, or physical changes related to the invading species often persist following species removal (Corbin & D'Antonio 2012). Removal of the invading species can also lead to secondary, non-desirable, environmental changes, such as the increase in previously unnoticed species or secondary invasions by new pest species (Emery et al. 2013). Clearly there is a need to examine the long-term impacts of removing an invasive species from

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particular ecosystems, beyond simply monitoring density of the target species, to ensure that the desired restoration endpoints are achieved.

This paper provides a long-term, landscape-scale, assessment of ecosystem recovery over a period of 6 years following the removal of *Lupinus arboreus* Sims. (lupin) during restoration of coastal sand dune habitat in New Zealand. Lupin is a fast growing, short lived, perennial shrub in the family Fabaceae, native to the southern and central coast of California (Pickart 2004). Lupin was introduced to New Zealand in the late 1800s to assist in the stabilization of mobile dune systems (Gadgil & Ede 1998). Despite an extensive dieback across New Zealand in the late 1980s, attributed to the fungus *Colletotrichum gleosporoides* (Molloy et al. 1991), lupin is now widespread. This is of concern, as lupin may degrade native dunal plant communities. Lupin alters dune soil structure and chemistry through the accumulation of litter and release of nitrogen (Pickart et al. 1998); facilitates the invasion of other introduced and native species (Reynolds et al. 2001); and can decrease sand mobility, which may allow opportunistic non-native and native plant species to establish (Pickart 2004). Collectively these impacts can result in the conversion of sparsely vegetated dune ecosystems, dominated by native plant species, with a moderate-to-high tolerance of sand mobility, to stable, densely vegetated systems dominated by non-native plant species.

In response to the threat lupin poses to native plant communities, the Department of Conservation (DoC) initiated a multi-year pest management program in 2007 to remove lupin from the Kaitorete Spit Scientific Reserve in Southern New Zealand. This reserve is nationally and internationally significant. It is an unusually large, relatively unmodified, example of a dry dune system; it retains outstanding populations of rare dune flora and fauna; and local endemism is high (DoC 2002). The goal of DoC's management program is to restore the dune plant communities to a pre-lupin state, with particular emphasis on the recovery of native sand dune plant species. This study evaluates this management program in relation to this aim. Is lupin removal sufficient to restore the pre-lupin plant communities? If not, what management practices are required to achieve restoration? The implications of this study for the management of dune systems elsewhere are considered.

Methods

Study Area

Kaitorete Spit is a south facing late-Holocene progradational barrier located on the east coast of the South Island, New Zealand (latitude 43.8°S, longitude 172.6°E). The contemporary dune landscape comprises a modern foredune with hinterland deflation surfaces and backdune elements associated with stabilized parabolic dunes. Some aeolian sedimentation still occurs during southerly storm events; however, the current landscape and dune forms are essentially inherited from a phase of transgressive dune activity that likely occurred in the late nineteenth century or early twentieth century (Soons et al. 1997). These landform elements are more or less continuous alongshore.

Distinct plant communities are associated with these landforms (Widodo 1997). Native plant communities in the foredune environment, where salinity and aeolian sedimentation is relatively high, are dominated by *Ficinia spiralis*. The deflation surfaces behind the foredune are characterized by the native cushion plant *Raoulia australis* with scattered *F. spiralis*, *Carex arenaria*, and *Scleranthus uniflorus*. The backdune environment, the trailing arms and depositional lobes of the now stable parabolic dunes, contains isolated populations of *Muehlenbeckia complexa* and *Pteridium esculentum* with widespread *F. spiralis*. Several non-native European grasses (*Holcus lanatus*, *Dactylis glomerata*, *Bromus mollis*) and forb species are widespread through all three environments. These non-native species are of pastoral origin and have probably self-introduced to the dunes at Kaitorete Spit from the surrounding farmlands. The Mediterranean grass, *Lagurus ovatus*, is also widespread. All three dune environments contained dense lupin prior to management with average cover of 53–63%.

The site is characterized by low annual rainfall (400–600 mm/year) and high summer temperatures (often exceeding 30°C) (Freeman 1994). The dune soils comprise unusually coarse sand (0.2–2 mm) with gravels and stones up to 20 cm in the deflation environment (Peace 1975; Widodo 1997). Organic matter content is low (<3.3%) (Peace 1975). This, coupled with the coarse base material and dry climate, makes the area very drought prone.

Restoration Program

Lupin has been present at Kaitorete Spit since the late 1960s. By 2006, lupin formed a semi-continuous canopy across 93 ha near the center of the spit (20% of the dune habitat), and was continuing to spread downwind (Hilton et al. 2006). In October 2007, a 39-ha section of the active dunes was sprayed with a 2% solution of the herbicide Versatil™ (active ingredient clopyralid as the amine salt) at a rate of 4 L/ha. This herbicide was selected for use, after field trials, because it is particularly effective on legumes at low concentrations and application rates and did not stress *F. spiralis* when applied in a 2% solution. Herbicide was first applied by helicopter, with surviving plants and re-growth sprayed using vehicle-mounted pumps in January 2008. Few plants survived the combined aerial and ground-based application of herbicide; but the germination of a large lupin seedbank necessitated the reapplication of herbicide to the treatment area by helicopter in October 2009, followed by a further ground-based application in 2010. This cycle of a biennial aerial application of herbicide to control seedlings followed by a ground-based operation has continued until the present. In 2012, the program was expanded to encompass the remaining dunes dominated by lupin, apart from a 1-ha section immediately adjacent to the original 39 ha treatment area.

Sampling Strategy

We conducted a field-based comparative study in May 2013 to infer the response of the aboveground plant communities to lupin removal. Three adjacent areas were selected within the scientific reserve based on the density of lupin and management history. The "managed" site consisted of the 39 ha treatment area. Lupin has been present in this area since at least 1980 and, when management commenced, formed a dense cover over large sections of the study site. Two different types of "control sites" were used, in order to infer changes in community composition resulting from lupin invasion, and changes resulting from lupin management. The "unmanaged" control site consisted of the 1 ha section of the reserve adjacent to the herbicide-treated area, where lupin has not yet been controlled. Lupin density and invasion history was similar between the managed and unmanaged sites prior to management, allowing the response of the native plant communities to management to be evaluated. The "uninvaded" control site was at the eastern end of the scientific reserve where lupin has never established, so this site provided reference plant communities against which the success of the pest management could be measured.

Plant cover was measured in 390 0.5 m^2 quadrats located randomly within a 20-m swathe centered on transects established through the center of the former parabolic dunes, from the foredune to the inland limit of the dunes in each of the three sampling areas. Five transects were established in each of the managed and uninvaded areas. Three transects were established in the unmanaged site due to limited sampling space resulting from the expansion of the spray program in 2012. Sampling was stratified between the three landforms—foredune, backdune, and deflation surfaces—to examine the relationship between dune environment and plant community response. Ten quadrats per landform were located regularly along each transect (30 quadrats per transect) to achieve uniform coverage. The cover of individual species was estimated using the point intercept method. A 0.5×0.5 m quadrat, subdivided by cross-wires into 25 10×10 cm squares, was centered parallel to the transect line and the cross wire intersections used to provide a 16-point sampling frame in each quadrat for cover analysis (Kent & Coker 1996).

Analyses of variance (ANOVAs) were conducted using MINITAB 13 to compare species richness, total plant cover, percentage cover of native plant species, and the percentage cover of non-native plant species (excluding lupin) between sites. The full model included site, dune landform, and interaction terms. The most parsimonious models were selected by iteratively removing non-significant higher order interactions from the model. Comparisons between sites for main effects were then made within each dune environment using one-way ANOVA followed by Tukey post-hoc means comparison tests. All variables were tested for normality and equality of variance prior to analysis and logit transformed as necessary (Warton & Hui 2011).

Overall species richness is important when considering the role that plant diversity plays in ecosystem function; however, the abundance of key species and the structural complexity of the vegetation is also important (Emery et al. 2013). Therefore, the average percentage cover of each species for each landform per treatment area was also calculated to examine potential shifts in dominance of individual species. This individualistic, species-centric, approach to determining the impact of a restoration program, to our mind, provides more practically useful information on progress toward achieving management goals than dimension-reducing community-centric approaches that typically capture less than 50% of differences between sites surveyed.

Results

A significant interaction between treatment and dune environment was detected for all variables measured when the unmanaged and managed sites were compared with the uninvaded sites (Table 1). Comparisons between unmanaged and uninvaded sites indicated that lupin invasion has altered plant communities in deflation and backdune environments, but no significant differences were detected between sites in the foredune environment (Fig. 1). The magnitude of impact differed between deflation and backdune environments. Total plant cover and non-native (excluding lupin) cover were both significantly higher in unmanaged sites compared with uninvaded sites in the deflation and backdune environments (Fig. 1A & 1C). Species richness and native plant cover did not differ between unmanaged and uninvaded sites in the backdune environments, but were significantly higher and significantly lower, respectively, in unmanaged sites than in uninvaded sites in the deflation environment (Fig. 1B & 1D).

Differences between the unmanaged and managed sites show the effect of removing lupin; specifically if lupin removal was aiding the restoration of plant communities, managed sites should show increased similarity to uninvaded compared with unmanaged sites. Instead, managed sites did not differ significantly from unmanaged sites for any of the measured variables in any dune environment. Species richness and non-native plant cover in managed sites remained significantly higher compared

Table 1. Results of GLMs showing differences in total plant cover, species richness, non-native plant cover (excluding lupin), and native plant cover in relation to dune environment and site type (unmanaged, managed, uninvaded) 6 years following lupin management. Statistically significant results are indicated by an asterisk (*$p < 0.05$). *df*, degrees of freedom.

Dependent Variable	*df*	*F*	*p*
Total cover			
Environment	2	9.40	0.000*
Treatment	2	9.20	0.000*
Environment × treatment	4	4.16	0.003*
Species richness			
Environment	2	11.07	0.000*
Treatment	2	3.80	0.023*
Environment × treatment	4	3.56	0.007*
Non-native			
Environment	2	11.84	0.000*
Treatment	2	23.07	0.000*
Environment × treatment	4	17.25	0.000*
Native			
Environment	2	29.98	0.000*
Treatment	2	1.96	0.066
Environment × treatment	4	3.19	0.027*

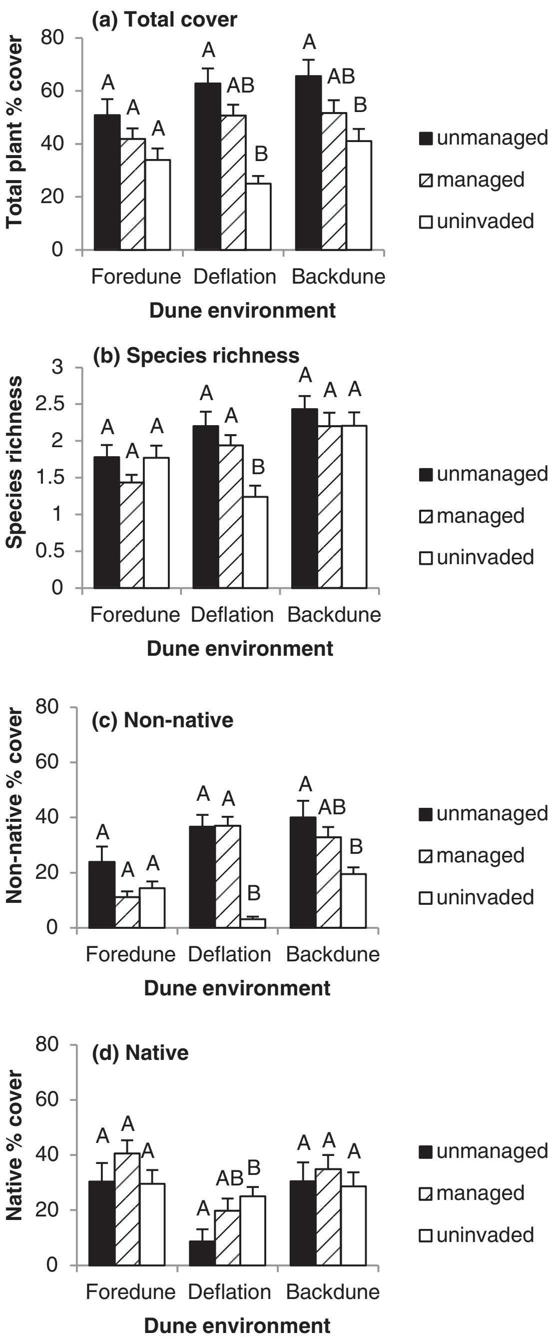

Figure 1. Change in (A) total plant cover, (B) species richness, (C) non-native (excluding lupin) cover, and (D) native plant cover between managed, unmanaged, and uninvaded sites in relation to dune environment. Different letters represent significant differences at $p < 0.05$ using post-hoc Tukey comparisons. Error bars represent +1 SE from the mean.

with uninvaded sites in the deflation environment (Fig. 1B & 1C). Total plant cover in the deflation and backdune environments, non-native plant cover in the backdune environment, and native plant cover in the deflation environment, however, were intermediate between unmanaged and unmanaged sites (Fig. 1A, 1C, & 1D).

The increased total plant cover associated with lupin invasion appears to be driven by an increase in lupin cover and an increase in the cover of other non-native graminoid and forb species (Table 2). In contrast, the cover of most native plant species was similar in the unmanaged and uninvaded sites except in the deflation environment where lupin invasion appears to be associated with a decrease in *Carex pumila*, *Raoulia australis*, and *Scleranthus uniflorus*, and an increase in *Ficinia spiralis* and bryophyte cover (Table 2). Bryophyte cover in the backdune environment was also slightly higher in managed sites compared with uninvaded sites.

The effect on native plant cover of removing lupin differed among species, but was relatively consistent across the three dune environments (Table 2). The cover of both native graminoid species was higher in all managed sites compared with unmanaged sites, and there was little difference in the cover of most native forb and woody species. The exception was *Calystegia soldanella*, which, along with bryophytes, showed slightly lower cover values in managed sites compared with unmanaged sites. The cover values of *C. pumila*, bryophytes, and *Acaena novae-zelandiae* have changed in the desired direction following lupin removal; however, the cover of these native plant species in the managed sites still differs from that of the uninvaded sites. For other native species (*F. spiralis*, *C. soldanella*), cover in the uninvaded sites was more similar to that of the unmanaged sites than the managed sites (Table 2). The process of lupin removal appears to have resulted in undesirable shifts in the cover of these native plant species away from that of the reference site.

The response of non-native plant species to lupin removal differed with species and dune environment. *Lagurus ovatus* cover decreased to levels similar to that of the uninvaded site following lupin removal in the foredune environment, but increased in the deflation and backdune environments (Table 2). The cover of other grasses decreased following lupin removal, but only to levels similar to that of the uninvaded site in the foredune environment. The cover of *Hypochaeris radicata* was lower in the managed sites than in both the unmanaged and uninvaded sites, as was *Rumex acetosella* cover in the foredune environment. *R. acetosella* cover in the deflation environment was slightly lower after lupin removal than that of the unmanaged site, but in the other dune environments remained higher than in the uninvaded site.

Lupin cover in the unmanaged site averaged 5–11% when measured in 2013 (Table 2), much lower than the average cover values (53–63%) measured in 2007, prior to control. The decline in lupin cover prior to lupin management at Kaitorete Spit has been attributed to cyclic outbreaks of *Colletotrichum gleosporoides* (Molloy et al. 1991). This fungus has reduced lupin cover for short periods of time (1–3 years); however, the effect of *C. gleosporoides* is neither sufficiently severe nor persistent to have any long-term effects on lupin at Kaitorete Spit. It is believed that at least two outbreaks of *C. gleosporoides* occurred between 2007 and 2013 (S. Fowler 2013, Landcare Research, Lincoln, New Zealand, personal communication).

Table 2. Mean percentage and standard deviation of species cover across sites and dune environments, 6 years following lupin management.

		Foredune			Deflation			Backdune		
		Unmanaged	*Managed*	*Uninvaded*	*Unmanaged*	*Managed*	*Uninvaded*	*Unmanaged*	*Managed*	*Uninvaded*
Native graminoids	*Carex pumila*				0.4 ± 0.4	6.1 ± 2.2	8.0 ± 2.5			
	Ficinia spiralis	25.5 ± 5.1	38.6 ± 5.8	26.3 ± 5.4	6.8 ± 3.5	10.3 ± 4.2	0.6 ± 0.7	14.9 ± 2.6	20.2 ± 5.0	14.0 ± 4.0
Native forbs	*Acaena novae-zelendiae*							0.5 ± 0.5	0.9 ± 0.8	3.0 ± 2.7
	Calystegia soldanella	4.9 ± 1.3	1.0 ± 0.7	3.3 ± 1.1	1.4 ± 1.0	0.9 ± 0.5	1.5 ± 0.9	0.8 ± 0.7	0.3 ± 0.2	1.0 ± 0.4
	Raoulia australis						12.8 ± 2.8	0.5 ± 0.6		1.1 ± 0.9
	Scleranthus uniflorus						2.1 ± 1.4			
Native woody species	*Muehlenbeckia complexa*							10.4 ± 4.6	13.0 ± 3.2	9.0 ± 4.1
Other native species	Bryophytes				4.1 ± 0.6	2.6 ± 2.3		4.0 ± 1.2	2.3 ± 1.3	1.1 ± 1.3
Non-native graminoids	*Lagurus ovatus*	15.3 ± 2.7	9.5 ± 2.0	9.2 ± 2.1	8.4 ± 1.9	23.6 ± 2.4	1.4 ± 0.9	12.9 ± 3.1	18.1 ± 3.3	10.1 ± 2.0
	Other grasses	2.8 ± 1.4	0.6 ± 0.6	0.1 ± 0.1	13.4 ± 3.6	4.0 ± 1.9		15.6 ± 3.9	3.8 ± 1.7	1.3 ± 0.9
Non-native forbs	*Hypochoeris radicata*	3.6 ± 1.9		0.2 ± 0.2	0.7 ± 0.5	0.1 ± 0.1	0.4 ± 0.2	4.0 ± 1.9	1.4 ± 0.7	2.0 ± 0.9
	Rumex acetosella	5.6 ± 3.1	0.1 ± 0.1	1.4 ± 0.6	12.8 ± 2.9	9.5 ± 2.5	1.3 ± 0.5	4.4 ± 2.0	7.1 ± 1.8	4.3 ± 1.1
Non-native woody species	*Lupinus arboreus*	5.4 ± 1.2	0.1 ± 0.1		10.8 ± 4.2	0.6 ± 0.5		9.4 ± 3.3	3.9 ± 2.0	

Discussion

The New Zealand Department of Conservation's stated management goal for Kaitorete Scientific Reserve is to restore plant communities adversely affected by the establishment of lupin. The removal of lupin in a small portion of the reserve has been the first and, to date, only step taken toward this goal. This study indicates that lupin is associated with significant changes to plant communities at Kaitorete Spit, but only in the deflation and backdune environments. No significant differences in any of the measured values were observed in the foredune environment. In the deflation and backdune environments, the desired restoration of plant communities has yet to be achieved 6 years after the project commenced. While removing lupin has increased the similarity of our managed and uninvaded sites for some measured variables, key differences still exist—namely an increased plant cover, increased cover of the non-native grass *Lagurus ovatus* and native sand sedge *Ficinia spiralis*, and a decreased cover of several native forbs. Furthermore, plant community response to lupin removal varied among the deflation and backdune environments. None of the plant community attributes measured except for total cover showed a trend in the managed site toward that of the uninvaded site across both dune environments.

Some of the differences between the managed and uninvaded sites can be attributed to changes in plant communities associated with lupin that have persisted 6 years after lupin removal. Lupin is associated with an increase in the cover of several non-native species: *Rumex acetosella* and several grass species, for example. The cover of these species remains somewhat higher in managed sites than in the uninvaded sites when measured in 2013. We also recorded changes in plant communities arising from lupin removal, some of which shifted the cover of species away from the desired reference plant community (e.g. an increase in *F. spiralis* and *L. ovatus*). Although the cover and range of some non-native species has increased, all the non-native species recorded in the managed and unmanaged sites were present in the uninvaded sites. This result is encouraging as it indicates that lupin invasion and removal is not facilitating the invasion of new non-native species at Kaitorete Spit.

Some of these persistent and "surprise effects" (after Emery et al. 2013) following lupin removal are likely related, at least in part, to soil enrichment during both the growth of lupin and its post-herbicide decay. Lupin has been associated with the invasion of non-native grasses and forbs through enhanced soil productivity in the dune system at Bodega Bay, California (Maron & Connors 1996; Maron & Jefferies 2001). A similar increase in non-native grasses and forbs in dune systems in Humboldt Bay, California, was found to further enrich the soil (Pickart et al. 1998). The higher cover of non-native species in our unmanaged sites compared with our uninvaded sites suggests that lupin may be having a similar effect in the Kaitorete dunes. Lupin is also likely to have had an ameliorating effect on the microclimate of the spit, allowing less drought-tolerant species such as the European pasture grasses to establish.

The decay of lupin also releases large amounts of plant-available nitrogen (Maron & Connors 1996). This rapid increase in soil productivity may explain the inferred increase of graminoids following lupin management, as the plants were left to decay in situ after herbicide was applied. Graminoids usually respond to nutrient enhancement to the detriment of broad-leaf plants (Hobbs & Huenneke 1992). These increases in soil productivity from lupin growth and decay can persist following lupin removal for at least 5 years and up to 25 years (Maron & Jefferies 2001), potentially explaining why differences between uninvaded and managed sites still exist at Kaitorete Spit.

Lupin invasion and removal impacted native plant communities differently, depending on species and dune environment. Those species dominant in the foredune and backdune environments (*F. spiralis*, *Muehlenbeckia complexa*) displayed no adverse response to either lupin invasion or its removal, whereas species characteristic of the deflation habitat (*Raoulia australis*, *Scleranthus uniflorus*) declined with lupin invasion and did not recover following lupin removal.

We identify two possible mechanisms for the lack of native plant recovery in the deflation environment. First, persistent seed banks in dune habitats are typically rare (Leicht-Young et al. 2009). Once native plants are lost from the system, it may be difficult for them to recolonize. The paucity of propagules may explain the poor response of native forb populations in managed areas, compared with native graminoids, particularly *F. spiralis*, which spreads rapidly through vegetative means. Alternatively, there is some evidence that lupin invasion and removal may have resulted in ecosystem level changes in the deflation environment that are providing a permanent barrier to recovery of the native plant community. Cushion species such as *R. australis* and *S. uniflorus* are naturally found only in areas of low total plant cover and may not be able to colonize the well-vegetated, nutrient-rich, deflation surface of the managed Kaitorete dunes. Similar changes in the soil related to other invasive plants prevent the reestablishment of native dune plants in parts of Spain (Novoa et al. 2013) and California (Magnoli et al. 2013). The lack of recovery of native plant species in the deflation environment is likely to be due to some combination of both these mechanisms. Regardless, it is apparent that the combination of lupin invasion and management has converted a sparsely vegetated deflation environment dominated by native forbs to one more typical of a sand dune environment characterized by native sand-binding graminoids.

At Kaitorete Spit, there have been persistent and profound changes to the plant communities associated with lupin invasion and removal in the deflation and backdune environments. Despite a shift in values toward the reference site for some plant community attributes, it seems unlikely that the current management strategy of lupin removal through the application of herbicide will be successful in restoring plant communities to their pre-lupin state without additional interventions. This result is not entirely unexpected. Removal of invasive species alone can, in some cases, result in a restoration of pre-disturbance communities (Benayas et al. 2009). More often, however, pest management does not lead to the recovery of desired ecosystem properties (Corbin & D'Antonio 2012), particularly when the invasive species is capable of altering resource pools in the ecosystem soil properties, and when the species has been present for many years at the restoration site. Lupin at Kaitorete Spit meets both these conditions.

DoC has several management options. The presence of a long-term seed bank means that the removal of lupin from the management area must continue if the current low cover of this species is to be maintained. Consideration, however, could be given to alternative or complimentary methods of lupin removal. Herbicide was initially applied from a helicopter because large areas could be treated at relatively low cost. However, more intensive methods, including manual removal or selective ground-based application of herbicide, should be evaluated. These have been shown to produce better long-term biodiversity outcomes following the removal of a nitrogen fixing shrub (*Chrysanthemoides monilifera* spp. *rotundata*) from sand dunes in Southeast Australia (Mason & French 2007). Although more costly initially, these methods may prove to be more efficient in the long term, particularly if they limit the need for additional management following lupin removal.

The increase in non-native species following lupin control is a concern. We have suggested that these species may be limiting the recovery of the native dune species, but have no data to support this hypothesis. Regardless, it is likely that the increased ground cover related to these species is contributing to the increased stability of this dune system. Increased stability is generally associated with a decline in dune biodiversity in New Zealand (Hilton 2006). Furthermore, Kaitorete Spit is valued for its scenic and "wilderness" values, which are threatened by the invasion of lupin and non-native grass species (DoC 2002). Consequently, DoC may wish to consider controlling the spread of grass species. This may be achieved, indirectly, by maintaining lupin at close to zero density, a precondition for natural reactivation of dune mobility at some time in the future. Dune mobility and enhanced sedimentation should favor native dune species and reduce the habitat for exotic grasses.

In the short term, exotic grass cover could be reduced through the application of a grass-specific herbicide. In addition, assuming that some of the differences identified between the managed and reference sites result from an increase in soil productivity following the decay of the treated lupin plants, steps could be taken to minimize this effect. For example, nitrogen availability could potentially be decreased through the addition of a carbon source (Alpert & Maron 2000; D'Antonio & Meyerson 2002). Removing the dead lupin biomass and associated litter reduced the establishment of non-native grasses in dunes in coastal California (Pickart et al. 1998). This latter method also reduced the recruitment of new lupin seedlings. Trials would need to be conducted to prove the success of these methods in the Kaitorete dunes.

A post-removal revegetation plan for some native species also seems necessary, particularly if post-lupin recovery is limited by seed availability. Even if the spread of grass species is limiting reestablishment, replanting after removal of grass species will likely hasten their recovery.

Plant invasions are a leading cause of habitat loss in dune ecosystems; and the removal of invasive species is a commonly used approach in restoration projects (Lithgow et al. 2013). Many target species which, similar to lupin, favor the establishment of other non-native species over the native dune flora through changes in microclimate, soil nutrient cycles, or increases in dune stability (e.g. Ens & French 2008; Marchante et al. 2008; Emery et al. 2013; Magnoli et al. 2013). Our study has implications for such projects in dune systems worldwide. First, species removal alone is unlikely to be sufficient to restore plant communities in sand dunes, particularly when the invading species alters soil properties. Managers should plan additional post-removal actions and instigate long-term monitoring to ensure that the desired restoration goals are being achieved. Second, given the difficulties in restoring plant communities once an invasive species has established, managers should prioritize preventing the spread of invasive species into uninvaded areas of sand dunes over species removal from invaded sites. The removal of the target invasive species from densely invaded sites may still be required, where they are serving as a source of propagules facilitating spread to uninvaded sites, for example. Third, this study found that the impact of invasive plant species may depend, in part at least, on the associated dune environment. Lupin at Kaitorete Spit had the greatest impact on the deflation environment, while the foredune environment was largely unaffected. Equally, some plant species and communities in dune environments elsewhere may respond more positively to the removal of invasive species than we have seen here. Knowledge of environment- and species-specific responses provides an opportunity to prioritize and/or schedule management interventions in those environments where positive outcomes are likely to be greatest. Lastly, change in total plant cover was not a useful measure of community response to lupin removal. The importance of species–environment–treatment interactions and the individualistic nature of species' responses were identified only when the cover of individual species was compared between sites. We recommend that individual species responses, rather than measures of community cover or species richness, be considered when assessing the efficacy of restoration programs.

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