

Turf wars: experimental tests for alternative stable states in a two-phase coastal ecosystem

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Abstract. Alternative stable states have long been thought to exist in natural communities, but direct evidence for their presence and for the environmental switches that cause them has been scarce. Using a combination of greenhouse and field experiments, we investigated the environmental drivers associated with two distinctive herbaceous communities in coastal ecosystems in New Zealand.

In a mosaic unrelated to micro-topography, a community dominated largely by native turf species (notably *Leptinella dioica*, *Samolus repens*, and *Selliera radicans*) alternates with vegetation comprising exotic (i.e., nonnative) pasture species (notably *Agrostis stolonifera*, *Holcus lanatus*, *Lolium perenne*, and *Trifolium repens*). The species of these two communities differ in functional characters related to leaf longevity and growth rate, and occupy soils of differing nitrogen levels.

Both spatial and environmental factors influenced the species composition locally. Reciprocal transplants of soil, with and without associated vegetation, showed that a native turf community developed when sward or soil from either community was bounded by turf, and a pasture community developed when sward or soil from either community was surrounded by pasture. In artificial mixed communities in the greenhouse, turf was able to invade the pasture community where the vegetation was clipped to simulate grazing, and also where *Trifolium* was removed and/or salt spray was applied. The pasture community invaded the turf where *Trifolium* was present or nitrogen was added. These results were supported by trends in experimentally manipulated field plots, where the amount of turf cover increased when nitrogen was kept low and when salt spray was applied, whereas pasture cover increased in the absence of salt spray.

Thus, persistence of the native turf community is dependent on grazing, both directly and via its effect on keeping nitrogen levels low by excluding the exotic, nitrogen-fixing *Trifolium*, and by exposing the vegetation to salt spray. If any of these factors change, there could be a state change to pasture dominance that might be resistant to reversion to turf. Managing such coastal herbaceous communities therefore requires an understanding of the environmental and species characteristics that maintain alternative states.

Key words: alternative stable state; coastal turf ecosystems; Dunedin, South Island, New Zealand; functional traits; grazing; invasion; nitrogen; positive feedback switch; salt spray; *Trifolium repens*; vegetation mosaic.

INTRODUCTION

The paradigm of alternative stable states provides a framework for explaining sharp spatial and temporal shifts in ecological communities. These arise when small initial differences in the environment lead to divergent pathways of community composition. Central to this theory is the concept of a controlling variable reaching some threshold or tipping point (the ball-in-cup analogy of Scheffer 1990). It has been suggested that for alternative states to be stable, there must be an

associated positive-feedback switch, with the community modifying its environment to facilitate persistence of the new species assembly (Wilson and Agnew 1992). Recently, ecosystem models built around alternative stable states have been advanced as providing a framework for ecological management and restoration (Bestelmeyer 2006, Suding and Hobbs 2009). For these models to inform management decisions, the drivers of the alternative states must be known. However, direct experimental evidence for alternative stable states, and for the switches that cause them, remains sparse (Schröder et al. 2005, Mason et al. 2007).

Evidence for alternative stable states and for their ecological drivers has been sought in freshwater

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(Scheffer et al. 2001, Dent et al. 2002, Chase 2003) marine (van de Koppel et al. 2001, Konar and Estes 2003, Petraitis et al. 2009), and terrestrial systems (Noy-Meir 1975, May 1977, McCune and Allen 1985, Rietkerk and van de Koppel 1997). Many potential biotic and abiotic drivers of switches, and thus of alternative stable states, have been proposed, such as nutrient pulses (Dent et al. 2002), change in sedimentation (van de Koppel et al. 2001), or light levels (Tsuyuzaki and Haraguchi 2009). However, controversy has developed about how common alternative stable state situations are, and the types of ecosystem in which they are most likely to be found (Didham et al. 2005, Mason et al. 2007).

The criteria for demonstrating the existence of alternative stable states in a system have been much debated (see reviews by Beisner et al. 2003, Knowlton 2004, Petraitis and Dudgeon 2004), but there is agreement that testing at both temporal and spatial scales is important (Connell and Sousa 1983, Peterson 1984, Petraitis and Latham 1999). Although the existence of alternative stable states can be suspected when we see a mosaic of different communities in an apparently homogeneous environment, experimental evidence is needed to show that two different self-maintaining communities could potentially occupy the same site (Peterson 1984). Such evidence is difficult to obtain. A review by Schröder et al. (2005) of research from a wide range of environments found that of the 21 studies that used an appropriate experimental approach, only nine involved field experiments to test for alternative stable states, and only two of them showed positive evidence of alternative stable states.

In the present study, we examine two herbaceous plant communities that are frequent across exposed coastal headlands in the South Island of New Zealand. These communities often occur in mosaics of two apparently distinct stable states: a native turf community and a pasture community dominated by exotic species. The relatively small scale of the mosaic (1–300 m² patches), fast species growth rates, and ease of manipulation of the communities make this an ideal system for examining alternative stable states and for experimentally determining the possible drivers of a state change.

The primary drivers of the transition between such coastal turf and pasture communities are untested, but those that have been suggested include: (1) disturbance, particularly grazing defoliation by introduced mammals, (2) exposure to salt spray, and (3) soil fertility (Rogers and Wisser 2010). Grazing disturbance can create and maintain vegetation mosaics, allowing new individuals to become established (Sousa 1984), thus changing the competitive balance between species (Al-Mufti et al. 1977, Veblen and Young 2010). Since European settlement 150 years ago, the investigated site has been grazed by stock, which may constrain pasture and favor the spread of turf. In coastal ecosystems, salt spray is an

important factor in determining the distribution and growth form of plants (Sykes and Wilson 1988, Yura and Ogura 2006), and differences in height and physical structure of the communities may play a role in minimizing or magnifying its effects. Soil fertility can be modified through anthropogenic inputs (Weiss 1999, Prober et al. 2005) and contributions by animals (Steinauer and Collins 2001). Plant feedbacks can affect soil nutrient status by influencing soil microbial processes via litter input (Buckeridge and Jefferies 2007, Orwin et al. 2010), and by nitrogen fixation associated with, e.g., legumes (Gylfadottir et al. 2007). These changes in nutrient input have the potential to mediate a positive feedback switch (Wilson and Agnew 1992, HilleRisLambers et al. 2010), as discovered in juniper–sagebrush communities in the western United States (Roberts and Jones 2000). Such drivers may function independently or synergistically to control what seem to be alternative stable states.

Here we combine vegetation analysis and manipulative experiments to: (1) test for alternative stable states in our coastal headland ecosystem, and (2) quantify the relative importance of proposed drivers in controlling different states (Fig. 1). With a combination of field survey, laboratory analysis, field experiments, and a greenhouse experiment, we test three main hypotheses about the composition, stability and drivers of the communities (Fig. 1). Our hypotheses are:

- 1) The two vegetation states (phases) exist on the site with distinct (a) plant species, (b) morphological plant traits, (c) plant nutrient status, and (d) soil nutrient status. Field sampling and nutrient analyses were used to measure these four components across the systems.
- 2) The two states are alternative stable states (with the alternative hypotheses that they are dependent on soil differences or on spatial mass flow of propagules). We tested this with a field reciprocal transplant experiment and controlled experiments under different abiotic conditions.
- 3) Shifts between the alternative states are driven by different community-level responses to abiotic and biotic factors. We examined the role of grazing, salt spray, and nitrogen. Further hypotheses about these drivers are as follows.

The grazing hypothesis is that ungulate grazing favors the native turf community in the face of invasion by exotic pasture species by reducing the dominance and regeneration of pasture. We test this experimentally by removing biomass (with mowing or clipping as surrogates for grazing) from the system in the greenhouse and field manipulation experiments.

The next hypothesis is that salt spray weakens exotic pasture species, thereby favoring the native turf community. We test this experimentally by adding salt spray to the system in both the greenhouse and field experiments.

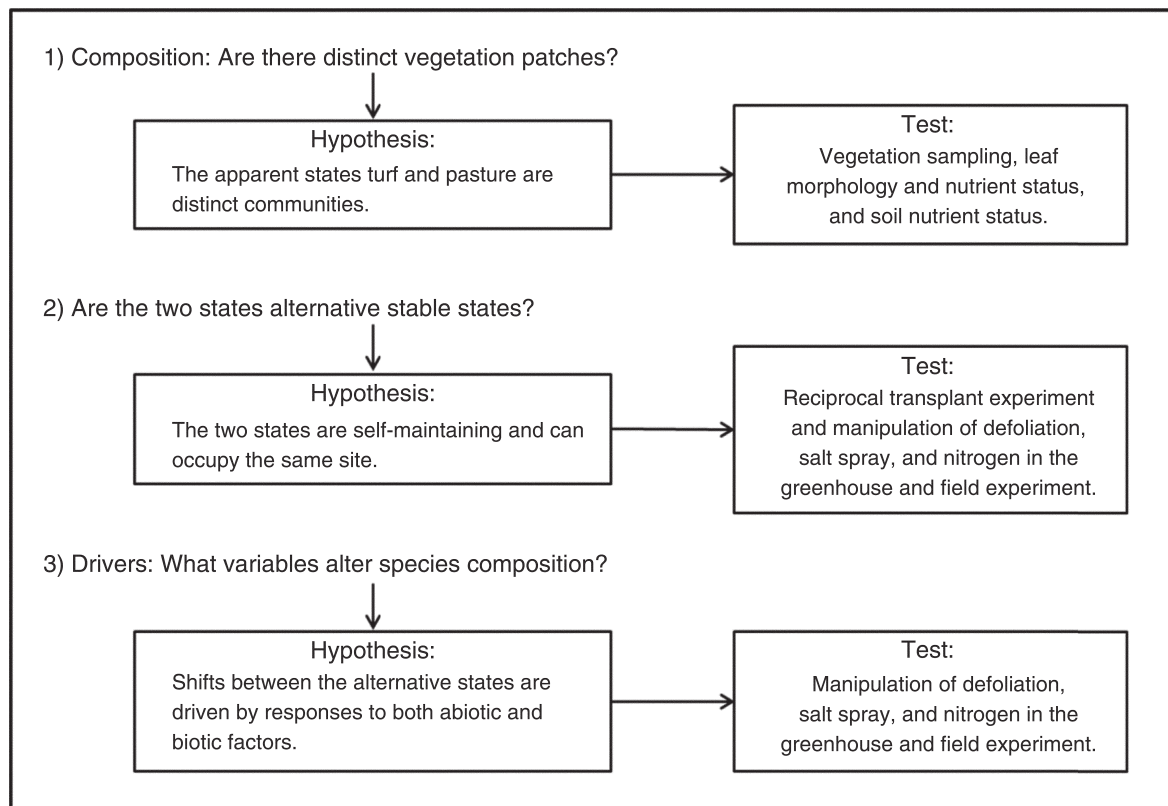


FIG. 1. Conceptual framework for examining alternative stable states employed here to study two herbaceous communities (native turf and exotic pasture) in coastal ecosystems in New Zealand. The questions are numbered 1–3, with the associated hypotheses and tests in this study in boxes.

The nitrogen hypothesis is that an increase in plant-available nitrogen caused by *Trifolium repens* mediates the switch, and a change in nitrogen status can drive a change between the states. We test this experimentally by altering nitrogen availability and, in the greenhouse experiments, by removing *T. repens*.

MATERIALS AND METHODS

Study site

The field site was located on an exposed headland above Smaills Beach (45°54'29.31" S, 170°33'56.61" E, elevation 50 m above mean sea level) near Dunedin, South Island, New Zealand (see Plate 1). Mean annual rainfall is 80 cm, with 5–8 cm of rain in all months. During the warmest month (January), mean daily maximum temperature is 19°C and mean daily minimum temperature is 11°C; during the coldest month (July), the mean daily maximum temperature is 10°C and mean daily minimum temperature is 3°C, based on a 30-year record from the National Institute of Water and Atmospheric Research (NIWA) Musselburgh weather station, 4 km east of the study site. The experiments were carried out between October 2006 and January 2010. The vegetation across the headland was a two-phase mosaic of native low-growing halophytes vs.

exotic grassland (Appendix: Fig. A2). Along the headland, patches of each community ranged in size from 1 to 300 m², with a total of 40 vascular species recorded from both communities. Nomenclature follows the Landcare Research Key to Flowering Plant Genera of New Zealand (Glenny et al. 2012).

Defining the communities

To formally define species composition and distinctness of the communities, we sampled 10 randomly selected 20 × 20 cm plots from each apparent vegetation phase. In each plot, the subquadrat shoot frequency (Wilson 2011) of each species was calculated in a 20 × 20 cm grid of 400 1 × 1 cm contiguous subquadrats.

Soil characters

Five soil samples (at 1–10 cm depth) were collected at random positions from the central area of the largest patches (>10 m²) of each community, and were analyzed for pH, soluble salts, carbon, nitrogen, and phosphate content by ECLab at Landcare Research, Palmerston North, New Zealand. We determined pH using a 1:5 suspension of soil in water shaken for 30 minutes, allowed to settle, and then measured with a pH electrode. Conductivity was measured on the same suspension using a temperature-compensated probe

(Blakemore et al. 1997). Total carbon and total nitrogen were determined by heating in a stream of high-purity oxygen in a LECO CNS2000 furnace (LECO, St. Joseph, Michigan, USA), with infrared detection of the CO₂ for carbon, and reduction to N₂ and measurement by thermal conductivity for nitrogen (LECO). Mineral nitrogen was extracted from the soil using 2 mol/L KCl (1:10 soil:extractant, 1 hour shaking), and nitrate and ammonium determined colorimetrically using a flow-injection analyzer (Lachat Instruments Division, Zellweger Analytics, Milwaukee, Wisconsin, USA). To estimate Olsen plant-available phosphate, soil samples were shaken for 30 minutes in a 1:20 ratio suspension with 0.5 mol/L sodium hydrogen carbonate adjusted to pH 8.5, filtered, and then phosphate was determined colorimetrically using a flow-injection analyzer (Lachat Instruments). Soil nutrient data are included in the Supplement.

Leaf traits

We measured leaf functional traits underlying resource use and stress tolerance strategies that could reflect plant response to different biotic and abiotic drivers. Leaf size (area, length), thickness, dry matter content (LDMC), specific leaf area (SLA), and nutrient concentrations are variously linked to growth rate, leaf life span, environmental stress and disturbance, and nutrient limitation (Cornelissen et al. 2003). These traits were measured for 13 species on 10 leaf samples collected at random positions across each community in which the species occurred (*Agrostis stolonifera*, *Apium prostratum*, *Cerastium fontanum*, *Crassula moschata*, *Holcus lanatus*, *Hypochaeris radicata*, *Leptinella dioica*, *Lolium perenne*, *Plantago lanceolata*, *Poa astonii*, *Samolus repens*, *Selliera radicans*, and *Trifolium repens*). Leaves were stored in sealed plastic bags for a maximum of one hour for fresh leaf measurements. Following the methods of Cornelissen et al. (2003), leaf area and length were measured using WinFOLIA Pro 2005b (Regent Instruments, Quebec, Canada), and leaf thickness was measured using digital calipers on fresh leaves. Fresh mass and dry mass of leaves were measured and used to calculate SLA and LDMC.

To establish species-level means for leaf nutrient content (nitrogen, phosphorus, potassium, calcium, and magnesium), three replicate samples of each of 10 species (*Agrostis stolonifera*, *Apium prostratum*, *Cerastium fontanum*, *Holcus lanatus*, *Leptinella dioica*, *Lolium perenne*, *Plantago lanceolata*, *Samolus repens*, *Selliera radicans*, and *Trifolium repens*) were collected at random positions from the community in which the species was most abundant. Each sample comprised 3–40 leaves (depending on the size of the leaf) from one plant. Samples were dried at 60°C (giving ~20 µg dried material) and were analyzed by ECLab at Landcare Research, Palmerston North, New Zealand. Samples were block-digested using a Kjeldahl wet oxidation process (Blakemore et al. 1987). Nitrogen and phos-

phorus were determined colorimetrically on a flow-injection analyzer (Lachat Instruments), and potassium, calcium, and magnesium by atomic absorption spectrometry on a Varian SpectrAA FS-220 (Varian, Mulgrave, Victoria, Australia).

Abundance-weighted trait means for each community were calculated following Ackerly and Cornwell (2007), using the species subquadrat shoot frequency obtained as previously described in *Defining the communities* with 20 plots from each community.

Leaf trait data are included in the Supplement.

Reciprocal transplant experiment

To test whether the mosaic pattern across the headland was driven by: (1) soil differences, e.g., in nutrients and/or seed bank, and/or (2) strong inertia in the soil/vegetation system, and/or (3) the influence of the surrounding vegetation, e.g., propagule input or modification of salt spray, we established 10 blocks, each 3 × 1.5 m, straddling the turf/pasture community ecotone, each replicate being 2 m apart (Fig. 2). Alternate blocks were fenced to exclude grazers (rabbits and sheep). Within each block, two 60 × 60 cm (i.e., 3600 cm²) plots were marked out, one in turf and the other in pasture. Each plot was divided into four subplots (each 30 × 30 cm, i.e., 900 cm²), with the following randomly assigned treatments: turf sward, pasture sward, turf soil, or pasture soil. For turf and pasture sward treatments, a 30 × 30 × 20 cm deep sward of vegetation plus soil was removed so as not to disturb the vegetation, and was transplanted into a randomly assigned subplot within the block, either of the community from which the sward had been removed (these are considered to be the methodological controls, allowing for transplantation disturbance), or of the other community. For the turf soil and pasture soil treatments, a similar-sized area was dug up, the soil was sieved (2 mm) to remove large roots and rhizomes, and was then replaced in a randomly assigned subplot within the block, either in the community from which it came or in the other community.

In order to assess vegetation change, species shoot frequency in the subquadrats was calculated from species presence/absence in a 20 × 20 cm grid of 400 1 × 1 cm contiguous subquadrats centered within each 900-cm² subplot. Sampling was performed immediately after the transplants and soil insertion were performed, and again 3, 6, and 12 months later.

Reciprocal transplant data are included in the Supplement.

Test of switch drivers: greenhouse

A greenhouse community-manipulation experiment under controlled conditions was conducted to examine the influences on the invasion rate of the pasture and turf communities of (1) defoliation (as a surrogate for grazing), (2) salt spray, and (3) manipulation of the soil nitrogen status (addition of N, and *Trifolium repens*

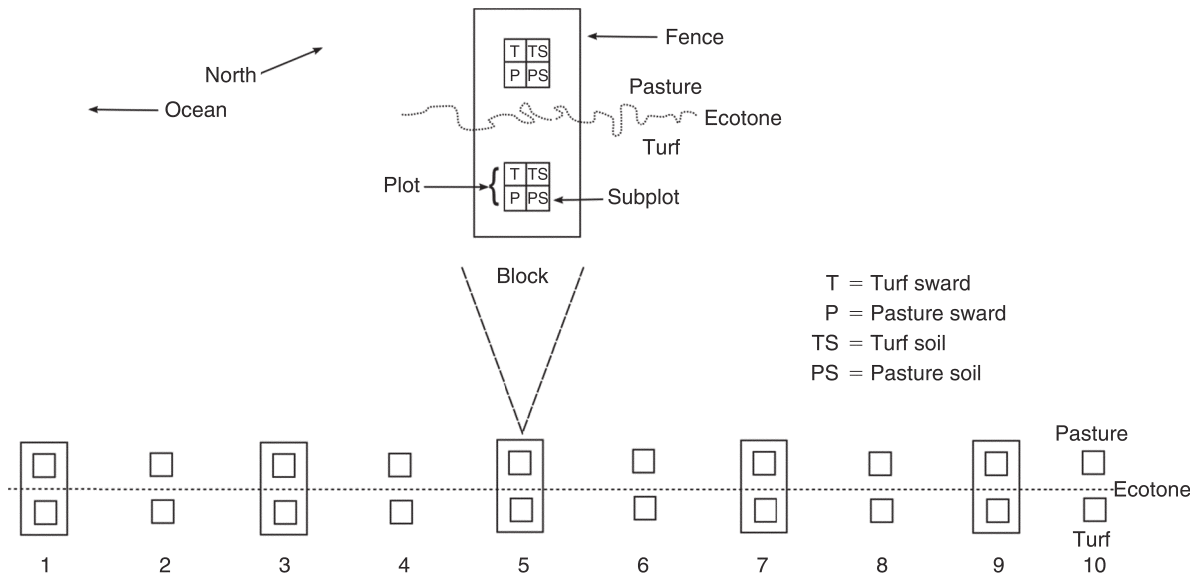


FIG. 2. Illustration of the experimental layout for the reciprocal transplant experiment. Each block (10 blocks in total, numbered from 1 to 10, each replicate block 2 m apart) straddles the ecotone (dotted line) to include both turf- and pasture-dominated areas. Alternate blocks were fenced to exclude grazing (due to the ecotone being nearly perpendicular to the ocean). One block is detailed in the inset; the locations of each treatment were randomized within each plot. Each block is 3×1.5 m; within each block are two 60×60 cm plots, each divided into four subplots (30×30 cm).

removal). The experiment was carried out in a greenhouse of the Department of Botany, University of Otago, Dunedin, during the summer of 2007/2008 between mid-October and mid-January. Natural light and day length were used, with temperature maintained at $\sim 18^\circ\text{C}$.

Ten 50×50 cm randomly chosen swards from each community were split into $17 \times 8.5 \times 8.5$ cm deep sections, randomly paired, and placed side-by-side in plastic containers ($17 \times 17 \times 19$ cm deep) so that vegetation from each community, turf and pasture, occupied one-half of the container. The swards were placed in each container over 7 cm depth of 50:50 mixture of unfertilized commercial potting mix and quartz sand layered over 3 cm of washed drainage gravel.

One of 16 treatments (four factors in a full factorial design: clipping, salt spray, nitrogen enrichment, and *Trifolium* removal) was randomly assigned to each container, with five replicates of each treatment. Nitrogen enrichment was achieved by the addition of 0.3 g urea per container every 20 days, urea being used to match sheep micturition. In the *Trifolium* removal treatment, all *Trifolium* was removed by hand at the start, and subsequently as needed (after three weeks, no further *Trifolium* appeared). The salt spray treatments consisted of spraying from all sides with 75 mL of either filtered seawater (containing ~ 2.6 g of sea salt) or freshwater (control) every 14 days; the salt treatment was chosen to represent the more extreme events in the coastal environment (Barbour 1978), with similar salt concentrations as a longer-term study in the same region

(Sykes and Wilson 1988). Clipped treatments had all biomass above 3 cm removed every seven days.

After three months, aboveground biomass of each community (as defined by the original 50:50 split of the container) was clipped at soil level. Invasion was classified as the shoot biomass of species that had rooted in a community from which they did not originate. All plant material was oven-dried for three days at 60°C and weighed. Percentage invasion was calculated as the amount of invader biomass divided by the total biomass of the pot.

Data files for testing switch drivers in the greenhouse experiment are included in the Supplement.

Test of switch drivers: field

The field experiment aimed to test the findings from the greenhouse experiment. In transition zones, where both communities were present as small patches, five 15×5 m blocks were laid out. Within in each block, 11 combinations of three treatments were assigned at random to 1×1 m plots as (1) mowing (as a surrogate for grazing), with plots mown monthly during the growing season (i.e., from October to May) to 3 cm high (i.e., above turf canopy height), vs. un-mown plots; (2) salt spray, with 1 L/m^2 of filtered saltwater vs. freshwater sprayed over the plot (the amount applied was the same per area as the greenhouse experiment); and (3) nitrogen: high nitrogen with 10 g/m^2 of N in the form of urea added monthly, vs. reduced nitrogen with the addition of 42.1 g/m^2 carbon in the form of sucrose added monthly (following Baer and Blair 2008), vs. control with no addition of urea or sucrose.

TABLE 1. Mean local frequency of each species in the two study communities (native turf and exotic pasture) in coastal ecosystems in New Zealand, as defined by the cluster analysis.

Species	Native or exotic?	Turf	Pasture
<i>Agrostis stolonifera</i>	E	<5%	67.5%
<i>Bromus hordeaceus</i>	E		<5%
<i>Cirsium arvense</i>	E		<5%
<i>Colobanthus muelleri</i>	N	<5%	
<i>Coronopus didymus</i>	E		<5%
<i>Leptinella dioica</i>	N	90%	
<i>Lolium perenne</i>	E	<5%	50%
<i>Plantago lanceolata</i>	E	<5%	<5%
<i>Poa pratensis</i>	E		<5%
<i>Sagina procumbens</i>	E	<5%	
<i>Samolus repens</i>	N	25%	
<i>Selliera radicans</i>	N	74%	
<i>Spergularia marina</i>	E	<5%	
<i>Trifolium repens</i>	E	<5%	60%

Notes: Blank cells indicate that the species was not present in that community. Indicator species determined by Dufrene-Legendre Indicator Species Analysis are shown in boldface.

To assess change, species cover was calculated using 100 point quadrats, i.e., all live plant shoot material hit by a 2.3 mm diameter laser point. The 100 point quadrats were evenly spaced over the center 50 × 50 cm of each 1-m² plot to minimize edge effects. Sampling was performed at the start (i.e., immediately after the treatments were applied), and then six and 14 months later.

Data files for testing switch drivers in the field study are included in the Supplement.

Statistical analyses

Unless otherwise stated, all statistical procedures were performed using the R statistical software platform v. 2.12 (R Development Core Team 2011) and associated packages. To define the communities, hierarchical cluster analysis (using the core stats package hclust function, with average agglomeration) on a Bray-Curtis dissimilarity matrix of species (using vegan package 2.0 vegdist function; Oksanen et al. 2011) was performed on the 10 plots sampled from each vegetation phase. Indicator value analysis (Dufrene and Legendre 1997) was used to define indicator species for each community.

Differences between pasture and turf in soil nutrients and in species abundance-weighted leaf traits were examined with a one-way ANOVA. Data were log transformed where violations of the assumptions of these parametric tests were found (i.e., for leaf thickness, leaf area, leaf dry matter content, leaf phosphorus, and leaf magnesium); the geometric means are presented in these cases. In one case (leaf potassium) log-transformed data did not satisfy the assumptions of a parametric ANOVA, and a Kruskal-Wallis rank-sum test was used. To take into account the correlational structure between traits, PERMANOVA (vegan package 2.0 adonis function) was used to test for differences between

communities with all leaf traits combined and all soil traits combined.

To formally test the hypothesis that location and grazing affected community composition, split-split-plot permutational multivariate analysis of variance analyses (PERMANOVA+ version 1.0.5 in Primer 6 version 6.1.15; Primer-E, Lutton, Ivybridge, UK) were applied separately for each of the four transplant types: turf swards, turf soil, pasture swards, and pasture soil. To examine the relationship between the treatment plots and the methodological controls through time, the CAP routine in Primer was used to perform discriminant analysis (Anderson and Willis 2003), using PERMANOVA+ version 1.0.5 in Primer 6 version 6.1.15. The data were split into two sets: the methodological controls and the treatment plots. For the methodological control data set, the a priori turf and pasture groups were assessed using canonical analysis of principal coordinates (CAP). Treatment plots were then classified into either the “turf” or “pasture” group using this CAP model. We used the default selection for number of meaningful axes (i.e., m , in this case, 1) and tested the significance of the trace statistic and the squared canonical correlation by permutation ($n = 999$). In addition, we performed leave-one-out allocation of observations for cross-validation. For both the PERMANOVA and CAP analyses, zero-adjusted Bray-Curtis similarities were used because initial soil plots were bare (Clarke et al. 2006). To visualize the relationships between treatments and their controls, we plotted the mean distance of each treatment to the corresponding methodological control (i.e., turf replanted in turf and pasture replanted in pasture) at each time point using the distances to group centroid given by the CAP routine.

To examine the drivers of state changes between communities in the greenhouse and field experiments, we applied analysis of variance (ANOVA) to linear models using type II SS (car package 2.0 Anova function; Fox and Weisberg 2011)

RESULTS

Defining the communities

Using the 20 plots sampled across the site, the cluster analysis identified two clear vegetation communities on the headland, with 90% average dissimilarity at the main split (Appendix: Fig. A1). These matched the two communities identified in the field and are named here “turf” and “pasture.” Indicator species for the turf community were the native forbs *Leptinella dioica*, *Samolus repens*, and *Selliera radicans*. Indicator species for the pasture community were all exotic, namely the grasses *Agrostis stolonifera* and *Lolium perenne*, and the nitrogen-fixer *Trifolium repens* (Table 1; see Appendix: Table A1 for a complete species list for the entire headland).

The plants growing in the turf community were largely natives, characterized by significantly smaller,

TABLE 2. Abundance-weighted leaf trait means for each community, calculated using the species' subquadrat shoot frequency in 20 plots from each community.

Leaf trait	Units	Turf community	Pasture community
Area	cm ²	0.65 ± 0.268	3.11 ± 0.74
Length	cm	16.56 ± 3.12	90.75 ± 3.16
Thickness	mm	0.84 ± 0.079	0.23 ± 0.05
LDMC	mg/g	15.6 ± 1.94	27.20 ± 4.59
SLA	cm ² /g	141.1 ± 15.62	242.65 ± 18.26
Nitrogen	%	2.32 ± 0.05	3.74 ± 0.08
Phosphorus	%	0.45 ± 0.01	0.30 ± 0.01
Potassium	%	2.03 ± 0.05	2.20 ± 0.02
Calcium	%	0.75 ± 0.01	0.28 ± 0.02
Magnesium	%	0.98 ± 0.05	0.39 ± 0.01

Notes: Values are mean ± SE; here all traits differ significantly ($P < 0.05$) between communities. LDMC is leaf dry matter content, and SLA is specific leaf area.

thicker leaves than those in the pasture community, and correspondingly lower SLA (Table 2; Appendix: Table A2). In foliar chemistry, turf community species contained less nitrogen and potassium than species growing in the pasture, but greater concentrations of the other nutrients (P, Ca, Mg). When the leaf traits were analyzed together by PERMANOVA, the turf and pasture communities were significantly different ($P_{\text{perm}} = 0.001$; Appendix: Table A4).

Soil in the turf community had lower concentrations of total nitrogen and nitrate than that in the pasture community (Table 3; Appendix: Table A3), paralleling the difference in nitrogen content in the plants, but had higher total carbon. Phosphorus (total and available), pH, soluble salts, and ammonium were not significantly different between the two soil types. When the soil nutrients were analyzed together by PERMANOVA, the turf and pasture communities were not significantly different ($P_{\text{perm}} = 0.8$; Appendix: Table A4).

Reciprocal transplant experiment

The CAP analysis placed the turf and pasture methodological controls into two distinct groups, with 97% of the variation explained by the first axis. The leave-one-out cross-validation allocated observations to groups correctly 100% of the time. Over the 12-month field experiment, entire transplanted swards of turf and

pasture gradually become more similar to the surrounding community, i.e., distance decreased (Fig. 3). The similarity in species composition between turf swards planted into the pasture community and pasture swards replanted into pasture (the latter being the pasture methodological control) increased, so that at 12 months, turf swards planted into the pasture community were classified as pasture (Fig. 3; location × date, pseudo- $F_{3,79} = 21.67$, $P_{\text{perm}} \leq 0.001$; Appendix: Tables A5 and A6). The similarity in species composition between pasture swards planted into the turf community and turf swards replanted into turf (the latter being the turf methodological control) showed similar trends, although with a slower convergence to the controls, and at 12 months the pasture swards planted into the turf community were still classified as pasture (Fig. 3; location, pseudo- $F_{1,79} = 1.801$, $P_{\text{perm}} = 0.138$; Appendix: Tables A5 and A6). These trends were similar both with and without grazing.

There was little effect of soil type on colonization of the turf or pasture bare soils. Initially, regardless of location or soil source, plant recolonization was predominantly by the fast-growing exotic annual species *Coronopus didymus* and *Anagallis arvensis*, both of which had very low abundance in either of the original communities. However, by 12 months, the surrounding community (location: turf or pasture) had started to colonize the soil patches (for turf soil, location × date pseudo- $F_{3,79} = 5.509$, $P_{\text{perm}} \leq 0.001$; for pasture soil, location × date pseudo- $F_{3,79} = 3.144$, $P_{\text{perm}} \leq 0.001$; Fig. 3; Appendix: Figs. A5 and A6). The rate of colonization was not dependent on the source of the soil, e.g., turf soil transplanted among pasture became like the pasture community no more slowly than pasture soil transplanted among pasture (Fig. 3). Likewise, pasture soil transplanted among turf became like the turf community hardly more slowly than turf soil transplanted among turf (Fig. 3).

Test of switch drivers: greenhouse experiment

In the greenhouse experiment, conditions that favored turf invasion tended to inhibit pasture invasion, and vice versa, as was expected (although when the data were examined for nonindependence, the negative correlation

TABLE 3. Soil factors for the turf and pasture communities.

Soil factor	Units	Turf community	Pasture community
pH		6.22 ± 0.07	6.20 ± 0.09
Conductivity	mS/cm	0.54 ± 0.09	0.43 ± 0.06
Total carbon*	%	4.33 ± 0.31	5.56 ± 0.28
Total nitrogen*	%	0.32 ± 0.02	0.45 ± 0.02
Nitrate*	ppm	0.62 ± 0.3	13.73 ± 2.2
Ammonium	ppm	5.82 ± 2.87	7.89 ± 1.82
Available phosphorus	ppm	16.18 ± 1.54	13.51 ± 1.25
Organic phosphorus	ppm	1091.35 ± 61.49	1106.5 ± 24.87

Notes: Values are mean ± SE ($n =$ five samples from each community); an asterisk indicates a significant difference ($P < 0.05$) between communities for the nutrient.

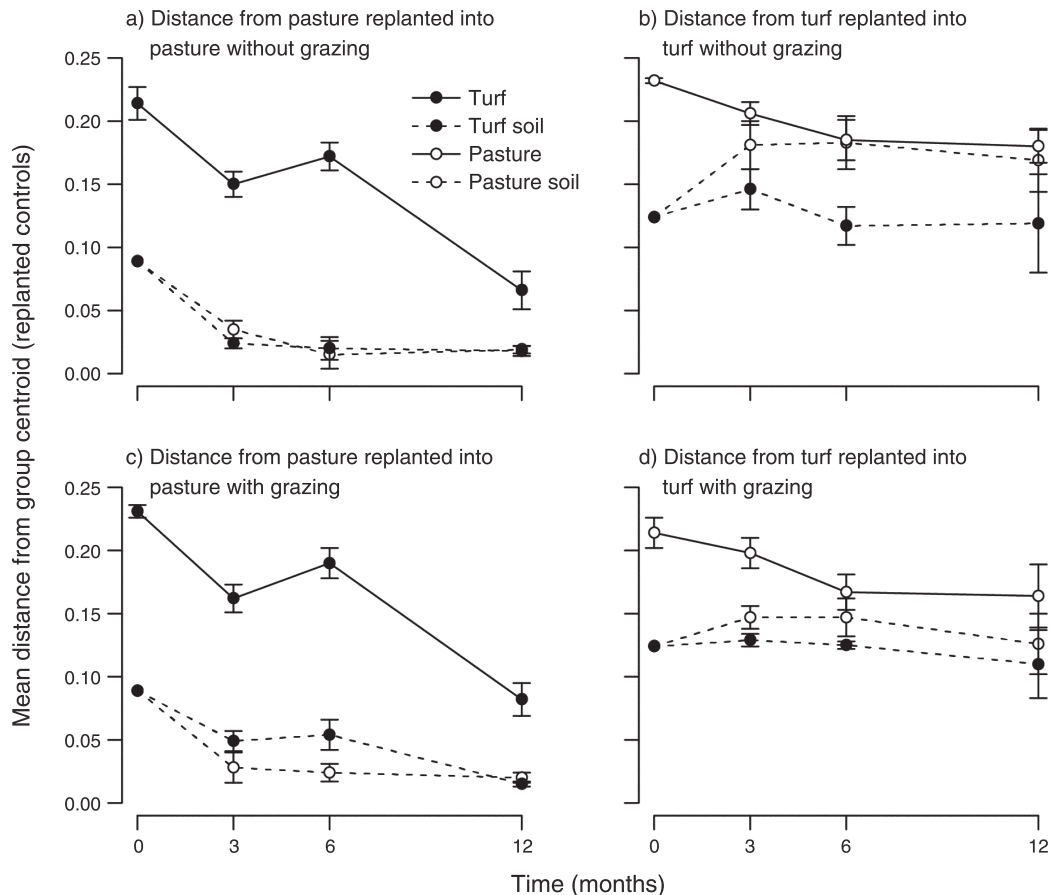


FIG. 3. Reciprocal transplant experiment: distance (mean \pm SE) of treatment plots (transplanted swards and soils) to the group centroid (methodological controls or replanted swards) vs. time since transfer or replanting of swards or soil. (a, c) The left-hand panels show the methodological control of pasture replanted into pasture. (b, d) The right-hand panels show the methodological control of turf replanted into turf. In the upper panels, grazers are excluded by fences; the lower panels include effects of grazing. Distance to the centroid was determined by canonical analysis of principal coordinates (CAP). Over the 12-month field experiment, entire transplanted swards of turf and pasture gradually become more similar to the surrounding community, i.e., distance decreased.

was not strong; $r = -0.277$). Thus, clipping, salt spray, no additional nitrogen, and the removal of *Trifolium repens* all resulted in increased invasion by turf species into the adjacent pasture community (Fig. 4a). The greatest amount of pasture invasion (10%) occurred with no clipping, no salt added, and *Trifolium repens* present (Fig. 4b). Clipping alone, i.e., with no salt spray, no added N, and no *Trifolium repens* removal, compared to unclipped, resulted in a sixfold increase in turf invasion (Fig. 4a; $F_{1,64} = 150.42$, $P < 0.001$; Appendix: Table A7). Salt spray alone, i.e., with no added N, no clipping, and no *Trifolium repens* removal, compared to freshwater, resulted in a sixfold increase in turf invasion (Fig. 4a), and caused a fivefold reduction in pasture invasion (Fig. 4b; $F_{1,64} = 29.10$, $P < 0.001$; Appendix: Table A7). The combination of salt spray and clipping (compared to freshwater and unclipped) resulted in a 15-fold increase in turf invasion (salt effect, $F_{1,64} = 31.89$, $P < 0.001$; clipping \times salt interaction $F_{1,64} = 30.65$, $P <$

0.001; Appendix: Table A7). The pasture species showed the largest amount of invasion into the turf community when *Trifolium repens* was present, a fivefold increase compared to *Trifolium repens* removal. Elimination of *Trifolium repens* together with clipping resulted in a 10-fold increase in turf invasion (main effect $F_{1,64} = 6.14$, $P = 0.016$; *Trifolium repens* \times clipping $F_{1,64} = 9.26$, $P = 0.003$; Appendix: Table A7). The greatest amount of turf invasion (22%) occurred with clipping, salt spray, *Trifolium repens* removal, and no nitrogen addition (Fig. 4a).

Test of switch drivers: field experiment

Reduced nitrogen resulted in a slight increase (5%) in turf cover in the mixed communities in the field, whereas the high-nitrogen treatment resulted in the greatest loss (nearly 100%) of turf cover (Fig. 5a; $F_{2,44} = 26.59$, $P < 0.001$; Appendix: Table A8). The addition of salt spray also increased the percentage of turf cover in the field

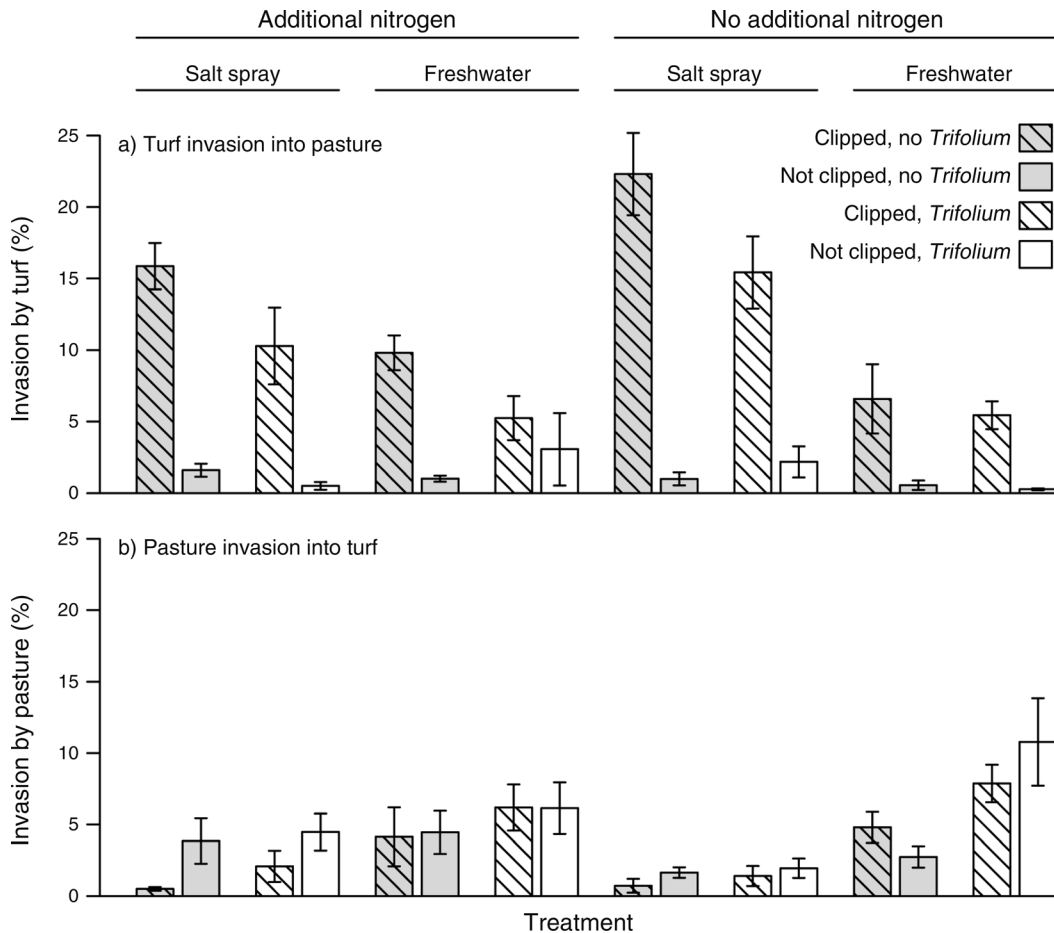


FIG. 4. Test of drivers: greenhouse experiment, showing (a) percentage (mean \pm SE) turf invasion into pasture community and (b) percentage (mean \pm SE) pasture invasion into turf community. Invasion is measured as invader biomass as a percentage of the total biomass of the community in the half pot. Treatments include: additional nitrogen (0.3 g urea); salt spray (75 mL filtered sea water spray); freshwater (75 mL freshwater spray); clipped (biomass above 3 cm removed); no *Trifolium* (all *Trifolium repens* plants removed). Further details of the treatments can be found in the *Material and methods: Test of switch drivers: greenhouse* section.

($F_{1,44} = 13.30$, $P < 0.001$; Fig. 5a; Appendix: Table A8). Pasture cover remained constant over the 14 months in the salt spray treatment (a reduction of just 1%), whereas the freshwater control treatment resulted in an increase of 33% (Fig. 5b; $F_{2,44} = 32.02$, $P < 0.001$; Appendix: Table A8). The combination of reduced nitrogen, mowing, and salt spray resulted in the largest reduction in percent cover of pasture species (23%), whereas the largest increase was in the high-nitrogen, freshwater, mown treatment (36%; Fig. 5b).

DISCUSSION

Alternative stable states provide an intuitive framework for explaining sudden spatial and temporal shifts in ecological community composition. However experimental evidence for alternative stable states and their drivers is scarce (Schröder et al. 2005, Mason et al. 2007). In coastal herbaceous communities, we examined the hypotheses that (1) two distinct vegetation states exist

at the site, (2) these two states represent alternative stable states, and (3) shifts between states are driven by community-level response to biomass removal, salt, and nitrogen. To examine hypotheses (1) and (2), we utilized a combination of field surveys and experimental manipulations and showed that our system is defined by two distinct alternative (although not stable) states with contrasting functional traits: one dominated by native turf species, the other by exotic pasture species. Through a combination of field- and greenhouse-based experiments, we examined hypothesis (3) to show that biomass removal, salt spray, and soil nitrogen content are key drivers of this state change and that the application of multiple drivers can alter the magnitude of their effect. We will address each of these key findings in turn, examining first the evidence for alternative stable states, before discussing how the drivers of these alternative states interact with the functional traits of the constituent species to establish these distinct communities.

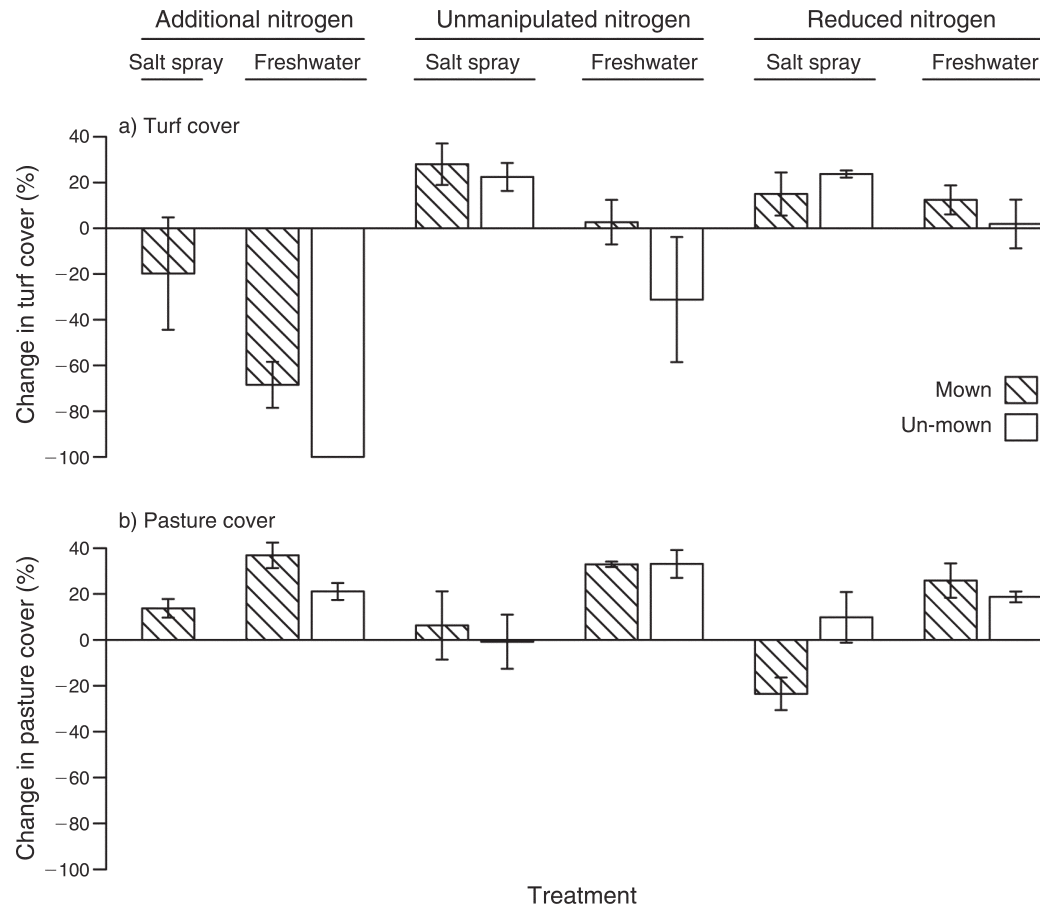


FIG. 5. Test of drivers: field experiment, showing change in percentage (mean \pm SE) of (a) turf cover and (b) pasture cover after 14 months for each treatment. Treatments include: additional nitrogen (10 g N/m^2); reduced nitrogen (42.8 C g/m^2); salt spray (1 L/m^2 filtered sea water spray); freshwater (1 L/m^2 freshwater spray); mowing (biomass above 3 cm removed). Further details of the treatments can be found in the *Material and methods: Test of switch drivers: field* section.

Distinct, co-occurring and self-maintaining states

Demonstration of alternative stable states requires that both states can be initiated from the same point in space and time (Peterson 1984). In our system, both of the communities reestablished on bare soil, indicating that the communities do not represent different successional states. Further evidence that preexisting conditions are not determining the establishment of the communities is that soil origin had no effect on which community recolonized a patch (Fig. 3). Importantly, we show that the system can undergo a bi-directional shift and is capable of moving from turf to pasture and from pasture to turf under the right conditions. In the field experiments, the system moved to a greater degree toward pasture community, whereas in the greenhouse experiment, the system moved more toward turf. In other experimental systems, e.g., testing the state change between *Ascophyllum* stands and mussel beds, the scale of the perturbation influenced the outcome (Petraitis and Latham 1999, Petraitis et al. 2009). In our system, this difference could be because the treatments were

more severe in the greenhouse than those in the field, or because the current climate in the field favored the pasture species more than did conditions in the greenhouse. It seems that both communities can initiate from the same point in time and space, and that, under the appropriate conditions, they can move between states.

The second criterion of alternative stable states is that two (or more) functionally distinct systems occur under the same environmental conditions (Peterson 1984). In our system, the two communities differed markedly in species abundance, leaf functional traits, and soil nutrient characteristics (Tables 1–3), showing that there are discrete phases with discontinuous variation in community structure (Smith 2012). The native turf community is dominated by small-leaved species growing in nitrogen-poor soils (Tables 2 and 3), and is consistent with previous descriptions of this community type as short ($<50 \text{ mm}$ tall), branched halophytic forbs, sedges, and grasses, forming dense ground cover in areas with poorly drained soils and high salt deposition



PLATE 1. The headland above Smaills Beach, South Island, New Zealand. The turf community is lighter than the pasture community, both in the foreground. A color version of the photo can be seen in the Appendix. Photo credit: G. Brownstein.

(Partridge and Wilson 1988*a*, Rogers and Wiser 2010). In contrast, the pasture community comprises tall (100–350 mm) species with larger leaves and higher SLA, and typically higher soil nitrogen requirements than the turf community (Tables 2 and 3; Grime et al. 1988, Buckland et al. 2001). This distinct contrast in functional traits is characteristic of systems where alternative stable states have been shown or are purported to exist, e.g., the alternative savannah/woodland states of Dublin et al. (1990) and the needle-leaved/broad-leaved forest states of Tsuyuzaki and Haraguchi (2009). In both of these examples, the dominant species in the two states differ markedly in life history, functional form, and physiology, and these differences help to modify the environment in favor of the state, creating a positive feedback facilitating the persistence of the alternative stable states (Wilson and Agnew 1992). In our system, the differences in form and function are related to salt tolerance and nutrient requirements of the turf and pasture; and suggest the mechanism for how the state change occurs.

Although our system has most of the hallmarks of alternative stable states (distinct, self-replicating states that can exist in the exact same location), the states do not appear to be stable under the exact same conditions. The shift between states seen in the reciprocal transplant experiment showed that the system lacks an internal stabilizing mechanism needed to maintain patch dom-

inance. It may be that the range of environmental conditions under which both states are stable is so narrow that we missed it with our relatively coarse manipulations, but we think not. Rather, the evidence suggests that there is a very fine cutoff between environmental conditions that favor one state or the other, i.e., the mosaic of the two communities seen is the result of small changes in environmental conditions across the headland (Appendix: Fig. A2). We suggest that this is good evidence that alternative stable states require a positive feedback switch to be stable (cf. Wilson and Agnew 1992). However, this hypothesis is not universally accepted (e.g., Petraitis and Hoffman 2010).

Drivers of alternative states

Here the manipulations of environmental drivers (defoliation, salt spray, and nitrogen addition) had opposing effects on the two communities. Defoliation, added salt, and low nitrogen favored development and invasion of the native turf community, whereas the exotic pasture community was favored in the opposite conditions (i.e., no defoliation, no added salt, and high nitrogen). Further, we showed a greater change in species abundances when multiple drivers were present, and a smaller change when drivers favoring opposing communities were applied (e.g., high nitrogen combined with high salt). Here we address each of these drivers,

with a specific focus on how the functional traits of the species in these communities might play a role in establishing (and perhaps maintaining) the alternative states.

Drivers of alternative states: defoliation

Experimental defoliation (in the form of grazing, clipping, or mowing) resulted in a greater cover of turf species and reduced cover of pasture species (Figs. 3 and 4). Repeated removal of the upper canopy helps to eliminate the asymmetry in light interception and the associated positive feedback loop of taller species intercepting more light and thus growing taller (Mitchley and Grubb 1986, Mitchley 1988, Zobel et al. 1996). Biomass removal also potentially reduces the amount of litter added to the system, reducing its shading of the lower strata (Al-Mufti et al. 1977). It may also expose the lower strata to direct salt spray, and thus promote (or perhaps reinforce) the turf state. The effects here parallel conclusions made for sites elsewhere, that biomass removal promotes short-stature natives (Huenneke et al. 1990, Weiss 1999), and grazing creates and maintains vegetation mosaics (Steinauer and Collins 2001, Veblen and Young 2010). The experiments on our system indicate that defoliation plays an important role in maintaining native turf communities, especially when combined with salt spray and in areas with low plant-available soil nitrogen.

Drivers of alternative states: salt

Salt spray also played a role in controlling the state changes between pasture and turf communities, which can be related to community differences in functional traits. The turf species have traits that are associated with salt tolerance: thicker, smaller leaves. These species are characteristic of salt marshes, and are salt tolerant (Partridge and Wilson 1987, 1988b, Sykes and Wilson 1988). In contrast, the pasture species have traits indicative of faster growth rates: higher SLA and larger leaves (Table 2). The resulting mosaic of these two communities across the headland can be seen as illustrating the trade-off between stress tolerance and competitive ability (Grime 1974). The turf species were present in higher abundance in treatments with low nitrogen and high salt spray, whereas pasture species performed best in treatments with no salt spray and high nitrogen. In other systems (e.g., Haraguchi et al. 2003, Kleinebecker et al. 2008), the taller plants and litter provide enough protection from salt deposition for the less salt tolerant species to establish. Here the short stature of most turf species provides little protection and may enable them to maintain their hold in areas of periodic salt spray.

Drivers of alternative states: nitrogen

The most rapid and obvious environmental driver of a state change from turf to pasture community was nitrogen (added in the form of urea); in plots where

soil nitrogen was added, the abundance of pasture species also increased. This result supports the suggested importance of nitrogen as a key factor in increased invasion by exotics and in changes from native- to exotic-dominated communities elsewhere (Huenneke et al. 1990, Weiss 1999, Prober et al. 2005). The finding that the presence of *Trifolium repens*, an exotic N-fixing species found in the pasture community, can facilitate this change provides additional evidence that plant-available nitrogen is an important driver of these alternative states.

Soil sampling showed that, across the headland, soil nitrogen was higher under the pasture community than under turf (Table 2). Because the transplant experiment showed no effect of soil type on recolonization, the difference seems to be transient, probably due to the presence of the nitrogen-fixer *Trifolium repens* in the pasture. *Trifolium repens* has been shown to supply a significant portion of the nitrogen used by plants in many grasslands (Gylfadottir et al. 2007); at our site, it may be facilitating the growth of exotic grasses with high nutrient requirements. The greenhouse invasion experiment, which showed that removal of *Trifolium repens* reduced the pasture invasion by two-thirds (Fig. 4), provides direct experimental evidence of this. In order to effect a state change back to turf, a reduction in nitrogen levels was required (Fig. 5a).

CONCLUSIONS

Using information from a combination of species characters and environmental factors, we demonstrate that it is possible to effect a state change between a native turf community and an exotic pasture community by experimentally modifying three important drivers of community assembly. We hypothesize that pasture establishes when there is an input of nitrogen (e.g., from animal input), and the presence of *Trifolium repens* within the pasture maintains the higher nitrogen level. Turf, on the other hand, establishes when there is an input of salt spray (e.g., from storms) sufficiently large to kill the less tolerant pasture species. It appears that once the nonnative pasture species are established under the current natural conditions, a change back to a turf community requires a combination of factors, including salt spray and grazing. Although these two distinct communities are present at the same time in essentially the same place and can replace each other, they are not stable under exactly the same set of conditions. Our experimental manipulation of these two communities illustrates the importance of investigating multiple aspects of ecological stability when experimentally testing alternative stable states, and it highlights the difficulty in finding natural ecological systems that conform to theory.

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SUPPLEMENTAL MATERIAL

Appendix

Image of study area (color version of Plate 1) and detailed results from the cluster analysis, PERMANOVA, CAP analysis, and ANOVAs ([Ecological Archives E095-036-A1](#)).

Supplement

Data files for abundance-weighted leaf traits, soil nutrient data, data for defining community composition, and reciprocal transplant experiment data, along with data from the test of switch drivers for the greenhouse experiment and the field experiment ([Ecological Archives E095-036-S1](#)).