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New Zealand Journal of Botany

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t918982741>

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Online publication date: 06 April 2010

To cite this Article Rogers, Geoffrey M. and Wiser, Susan K.(2010) 'Environment, composition and conservation of coastal turfs of mainland New Zealand', New Zealand Journal of Botany, 48: 1, 1 – 14

To link to this Article: DOI: 10.1080/00288251003640002

URL: <http://dx.doi.org/10.1080/00288251003640002>

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Environment, composition and conservation of coastal turfs of mainland New Zealand

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(Received 23 July 2009; final version received 3 November 2009)

Coastal turfs are communities of tightly interlaced, ground-smothering, short-statured herbs, grasses and sedges occupying shoreline rock landforms exposed to persistent salt-laden onshore winds. They are recorded from eight mainland New Zealand regions along the west and south coasts of North and South Islands. They display regional compositional distinctiveness best explained by geographic location, landform shape and substrate type. There is evidence that the predominant direction of onshore winds delivering aerial salt is aligned obliquely and not perpendicular to the coastline, and that the topographic aspect of turfs is correspondingly skewed in the opposing direction. Significant differences in soil salinity and pH were found between turfs of native herbs and those of exotic grasses and herbs on the same uniform landform. Turfs support 9 threatened and 24 uncommon plants, with all but 1 of the 33 being herbs, and 21 being recorded from just one region. Turfs exposed to ungulate (mostly farm stock) disturbance showed greater vegetation cover than those without ungulates. Conservation priorities should mostly be set intra-regionally and cautiously view ungulate disturbance as a beneficial management tool.

Keywords: coast; exotic plants; halophytes; littoral zone; salinity; threatened plants; ungulate disturbance; vegetation–environment relationships

Introduction

Short-statured plants often predominate in sites of climatic extremes, especially cold temperatures and high winds, sites of edaphic extremes in mineralogy or inundation, and sites of heavy use by herbivorous vertebrates. Drawing upon the concept of ‘turf’ in Johnson & Gerbeaux (2004), Johnson & Rogers (2003) and Wardle (1991), coastal turfs are an ecosystem of halophytic herbs, sedges and grasses, seldom growing to more than 50 mm tall, with the herb component dominated by much-branched, creeping, rooting succulents forming a tightly interlaced, dense ground cover. Physiographically, they occupy coastal promontories of hard rock landforms and, infrequently, consolidated sand and gravel, exposed to the maritime

influences of persistent wind and heavy salt deposition. They have been reported from parts of the New Zealand mainland’s central and southern coastal zones, characterized by persistent strong westerly winds. Recognized as coastal-moor in southern Otago by Cockayne (1909, 1958), as dense turf by Mark et al. (1988), as saline wetland by Wardle (1991), as lower maritime turf by Meurk et al. (1994a) and as coastal turf by Wright & Cameron (1985) and Johnson (1993), they were accorded conservation priority by Rogers & Walker (2002) and Williams et al. (2007) as a threatened rare ecosystem. The term ‘coastal turf’ does not appear to have an overseas following. Of the vegetation class terms of Atkinson (1985), ‘herbfield’ is the most applicable for

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this coastal community, but we adopt the term 'turf' for the varying mix of the three plant groups. Although coastal turfs share some dominant plants with those of estuarine marshes (Johnson 1993; Partridge & Wilson 1987; Thannheiser & Holland 1994) and dune slacks (Drobner et al. 1995; Johnson & Rogers 2006), notably *Selliera radicans*, *Samolus repens*, *Sarcocornia quinqueflora*, *Triglochin striata* and *Leptinella dioica*, they differ functionally from estuarine marshes by the aerial, rather than tidal, delivery of salt. They differ from dune slacks in occupying stable substrates and consolidated soils or gravels on promontories rather than unstable sands in dune hollows. Aerial salt is delivered either in dry crystalline form or in solution in the drift of saltwater spume and spray.

Broadly, this study sought to document and understand the geographical vegetation pattern and environmental drivers of coastal turfs of mainland New Zealand. Because of the assumed importance of wind and salt delivery, and in the absence of a direct measure of salt deposition, we sought first to develop a suitable model for onshore winds at the sites. Less salt is likely to be deposited on headland terraces where coastal cliffs generate turbulent vortices in perpendicular winds compared with less turbulence when wind is directed obliquely over the cliff obstruction. Because of this, we examined the hypothesis that turfs tend to develop where the onshore winds that deliver salt arrive at predominantly oblique and not perpendicular angles to the coastline. We then used the vegetation and environment data to ask the following questions:

1. Are there regional variations in coastal turf communities and can these be attributed to environmental differences among their locations?
2. Do exotic species colonize similar sites to the native turf communities or are they restricted to less extreme environments?
3. Do ungulates influence overall vegetation cover and the relative importance of exotic versus native species?

Finally, we use our analysis to develop a template for setting priorities for protection for conservation and conservation management.

Methods

Data collection

Regional coastlines previously reported to contain turfs were comprehensively surveyed on foot. Other regional coasts with hard rock landforms and reputed to receive strong onshore winds were surveyed from the air, with follow-up ground survey to 'ground-truth' aerial observations of turf. For sampling purposes, turfs were divided into sectors mostly by virtue of their confinement to individual headlands; some sectors, however, were arbitrarily delimited where turfs were more or less continuous along intervening bays between adjacent headlands. Vegetation composition and structure, and associated geographical factors were described from 116 variable-area plots following the RECCE method of Allen (1992). Plots were subjectively located at the approximate centroid of homogeneous landform units within each sector. Where sectors spanned more than one landform, the spatially dominant landform unit was selected for plot sampling. Plot area varied to accommodate the limits of vascular plant richness within each homogeneous landform unit and ranged from 15 to 42 m².

Plot variables that differed from those of Allen (1992) are as follows. Topographic position was described using the nine-unit land-surface model of Dalrymple et al. (1968). Soil drainage was described using the seven-unit classification of Taylor & Pohlen (1970). Because turfs often appeared to occupy parts of headlands lying at aspects offset from the perpendicular to the coastline, three measures of topographic aspect were recorded: the dip direction of the headland landform, the direction of the perpendicular of the coastline and the plot aspect. Two measures of an offset angle of the plot were then calculated for use in modelling the directions of onshore winds with respect to topography: the difference between

the dip direction of the headland landform and the plot aspect, and the difference between the perpendicular to the coastline and the plot aspect. Headland dip direction was recorded where the primary landforms were composed of sedimentary rock but was not recorded for those composed of intrusive volcanics.

In the absence of a direct measure of the deposition of aerial salt on turfs, an estimate was compiled of the distance salt is transported to turfs from the shoreline. This variable used the hypotenuse of a right-angle triangle formed by the horizontal distance between the approximate mean high water mark and the plot centroid, on the one hand, and the elevation (m.a.s.l.) of the plot, on the other hand.

Soil parent material was classed as follows: cc, Cretaceous sandstones and conglomerates principally of the Te Taitapu coast, west Nelson; mu, Tertiary calcareous sandstone, siltstone and mudstone; sa, Tertiary, non-calcareous breccias, sandstone and gravels of Otago, Southland, Fiordland and south Westland; it, intrusive granite, gabbro and ultramafic rocks of Southland; li, richly calcareous limestone and dolomite of the Te Taitapu and north Westland coasts; at, tephra, lahars and magnetite sands of Taranaki; ba, basalt of the Otago Peninsula; and pe, peat.

To compare soil pH and salinity between indigenous turfs and vegetation comprising exotic grasses and herbs in close proximity on the same landform unit, we collected soil samples from five subjectively selected sectors: one from Taranaki, one from Nelson, two from Otago and one from Southland. Soils were collected from three to five subjectively located 1 × 1 m plots beneath both indigenous turf and exotic communities at variable distances inland within single 10 m wide belt transects aligned perpendicular to the coast on homogeneous landform units. Vegetation composition was classed as predominantly indigenous turf (combined cover of indigenous plants >75%) or predominantly exotic sward (combined cover of exotic grasses >75%) based on the sum of cover estimates of all vascular species in 5% cover classes at each plot. Soil samples

consisted of at least 15 aggregated soil plugs of 15 mm diameter to 30 mm depth. Samples were analysed for pH and electrical conductivity (as a measure of soluble salts) using the methods described by Blakemore et al. (1987).

Data analysis

To examine the hypothesis that the onshore winds that deliver salt to turfs arrive at predominantly oblique and not perpendicular angles to the coastline, we first obtained wind direction and run data from the coastal weather station closest to each plot (<https://secure.niwa.co.nz/climate-explorer/home.do>). Wind data are in 10° directional and 10 km/h run increments for various sample periods over the last 30 years. For each plot, we computed the direction of the greatest mean wind run by:

1. compiling the total wind run time for each 10° directional arc by summing the time for each 10 km/h increment;
2. compiling the mean wind speed for each 10° directional arc by summing the product of wind run time and the mid-point of speed of each wind speed segment (the 1–10 km/h speed segment was assigned a value of 5, the 10–20 km/h segment a value of 15, etc.) and dividing by the total wind run time;
3. retaining data for the onshore component of the wind only ($\pm 90^\circ$ of the perpendicular to the coast); and
4. selecting the 10° directional segment with the greatest mean wind speed and computing the mean direction as the mid-point of the upper and lower limits of that segment.

The direction of the greatest mean wind speed was then correlated with the plot aspect using the Spearman rank correlation. Two other correlations were performed between the deviation of the direction of the greatest mean wind speed from the perpendicular to the coastline with the plot offset from the landform dip direction and the plot offset from the perpendicular to the coastline.

Plant compositional data were classified using a modification of two-way indicator

species analysis (TWINSPAN; Hill et al. 1975) that allows an uneven partition of vegetation clusters (Roleček et al. 2009). We then used the OPTIMCLASS routine to determine the optimal number of classes for the data. This routine measures the quality of the classification by the total count of diagnostic species across all clusters of that classification and the count of clusters that contain at least a specified number of diagnostic species. Broad-scale relationships between species cover, the cover of aggregate plant groups (native, exotic, herb, grass, fern, sedge and subshrub), the classified plot groups and environmental variables were explored using multidimensional scaling. Modified TWINSPAN and OPTIMCLASS were calculated using the program JUICE 6.4 (Tichý 2002) and multidimensional scaling was calculated using PC-Ord (McCune & Mefford 1999).

Results

Distribution and physiography

Turfs were located and inventoried from two North Island and six South Island regions (Fig. 1) using the RECCE data available on the National Vegetation Survey (NVS) database (<http://nvs.landcareresearch.co.nz/>). Taranaki turfs predominate on the Taranaki Bight coastline from just north of Cape Egmont south to Waverley. An additional turf occurs at Pukearuhe in north Taranaki (C Ogle personal communication 1997) but it was not sampled. No turfs were recorded on Wellington’s Cook Strait coast, whereas they occur along a restricted section of the east Wairarapa coast from the Oterei River to the Waitetuna Stream. Turfs on the Te Taitapu coast of west Nelson extend from just south of Farewell Spit to Kahurangi Point. Small patches of turf may occur at Wekakura Point, north of the Heaphy River mouth (S Courtney personal communication 2003) but these were not observed from the air and were not further investigated. Westland has turfs in two widely disjunct districts. North Westland turfs extend from Point Elizabeth to Cape Foulwind. No turfs were encountered in central Westland and only two patches were inventoried south of Haast at Callery Creek and Spoon River in

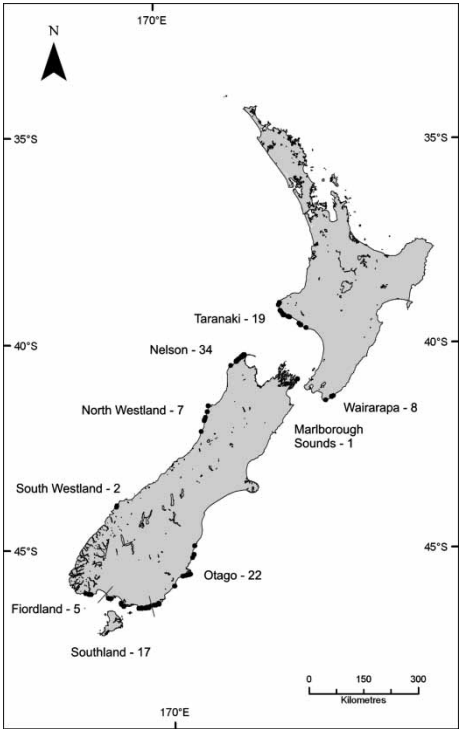


Fig. 1 Regional zones of sampled coastal turfs of mainland New Zealand. Numbers of plots per region are shown.

south Westland. Fiordland turfs are restricted to the sedimentary landforms of the Foveaux Strait coast east of Lake Hakapoua and Big River from the Grant Burn to Crombie Stream. Puysegur Point has small areas on human thoroughfares only but these were not sampled. Southland has the greatest spatial area and coastal extent of turf of all regions that extend from near Riverton in the west to Waipapa Point in the east. Otago turfs occur on most Catlins coast promontories and on scattered headlands from there north to Katiki Point south of Oamaru. On the remainder of the South Island east coast, only one patch of turf was located at Cape Koamaru on north-eastern Arapawa Island on the Cook Strait coast of the Marlborough Sounds. Other Marlborough Sounds islands may support turf but they were not investigated.

Topographically, most turfs occupied landforms of sedimentary rocks or lahar strata,

with dip direction more or less perpendicular to the coast and dip at moderate angles (mean slope = $14^\circ \pm 14$). Sedimentary strata of low-grade metamorphism and aligned perpendicular to the coast produce discordant coastlines (French 1997) of cliffed headlands and bays along retreating coastlines. Turfs are concentrated on the exposed headlands, which can accelerate wind speeds, but on the most wind-exposed coastlines they occur sporadically along the intervening straight or embayed sections. They also occur within clefts, ledges and fall-faces of cliffs facing the sea. Landform exceptions to sedimentary and lahar strata are two sites on intrusive granites in Westland, others on gabbro, granite and ultramafic rocks around Bluff, Southland and two on basalt flows of the Otago Peninsula. Turfs have a mean elevation of 15 ± 13 m.a.s.l., but one Fiordland and two Taranaki examples are atop 40 and 60 m high headlands, respectively. Turfs have a mean distance inland of 19 ± 15 m and a mean patch size of 0.17 ± 0.28 ha, and are commonly bordered by farm pasture following clearance of previous probably woody native vegetation on their inland boundary (Fig. 2). Fiordland turfs are the exception, forming part of a coastal, native vegetation sequence from seaward turf via scrub to low forest, with feral deer common throughout. Some Taranaki, Southland and Otago examples were exposed to vehicular traffic, although of this was of limited detrimental impact if the turfs occupied well-drained soils. The total estimated extent of patches from the single, predominant landform that was sampled was 19.2 ha. Even with an

estimated doubling to account for secondary landform classes not sampled, at ~ 40 ha, coastal turf is an exceptionally rare ecosystem.

Floristic composition

The total sampled vascular flora consisted of 171 taxa, plus three aggregate categories for native liverworts, mosses and lichens. Thirty-two taxa were exotic and 139 were native. The 139 native vascular plants represent 5.8% of the ~ 2400 New Zealand native species. Widespread and abundant native species included *Selliera radicans*, *Samolus repens*, *Leptinella dioica*, *Centella uniflora*, *Apium prostratum*, *Colobanthus muelleri*, *Isolepis cernua* and *Hydrocotyle novae-zeelandiae* var. *montana*. Widespread exotic species were *Cerastium fontanum*, *Hypochoeris radicata*, *Plantago coronopus*, *Sagina procumbens*, *Agrostis stolonifera*, *Holcus lanatus* and several clovers (particularly *Trifolium* spp. and *Lotus* spp.). The most species-rich native genera of turfs were *Crassula* (8), *Leptinella* (6), *Ranunculus* (5), *Myosotis* (4), *Epilobium* (3), *Mazus* (3) and *Nertera* (3), which are all herbaceous genera.

Classification

Twelve vegetation associations were recognized at level 3 of the modified TWINSPAN classification (Fig. 3). The first level of the classification splits turfs of Otago, Southland and Fiordland from those of more northern regions on the exclusive presence of *Poa astonii* and *Gentianella saxosa*. Within this branch, the majority of Southland turfs are separated into three associations (10, 11 and 12) at level 2 by the presence of *Plantago triandra*. The alternative branch at level 2 has *Sarcocornia quinquefolia* and *Disphyma australe* as indicator species and further lower level branching uses similar farm stock-susceptible species such as *Lepidium flexicaule*, *Senecio carnosulus* and *Trichomanes strictum*. The southern South Island endemic *Senecio carnosulus* is the indicator species of a predominantly Otago association (6) that includes one Marlborough turf. Fiordland turfs form one of the associations having high regional fidelity based on the presence of *Gunnera monoica* (9), although



Fig. 2 Geographic setting and vegetation physiognomy of a coastal turf atop a promontory at Tunnel Beach, Otago Peninsula.

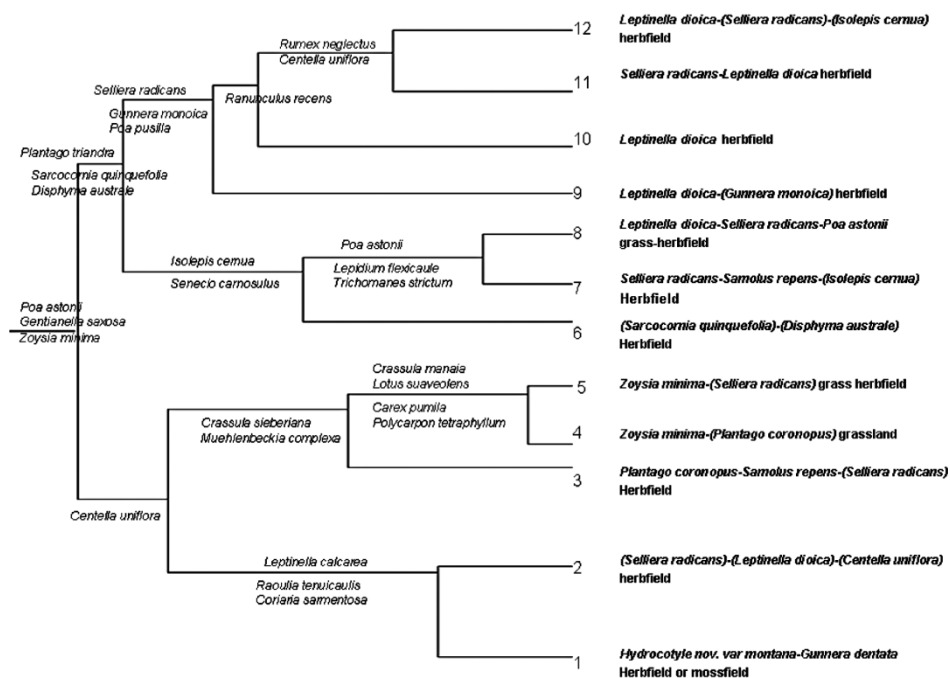


Fig. 3 Indicator species for successive divisions in a weighted two-way indicator species analysis (TWINSpan) of coastal turf vegetation.

that species was recorded in one Nelson and one Taranaki turf as well.

The alternative level 1 branch has the indicator *Zoysia minima*, a mat-forming grass of Taranaki, Wairarapa, Nelson and Westland turfs. At levels 3 and 4 of that branch, Taranaki turfs on andesitic tephra (association 5) are segregated from the Wairarapa turfs on sandstone (association 4). *Leptinella calcarea*, a Nelson regional endemic, separates 28 of the 34 Nelson turfs and 1 Westland turf (association 2) from the 2 south Westland turfs, with their semi-woody subshrub indicator species, *Raoulia tenuicaulis* and *Coriaria sarmentosa* (association 1). The northern Westland turfs are spread throughout associations 2, 7, 11 and 12. Three associations were confined to a particular parent material: association 5, confined to Taranaki, entirely occupies andesitic tephra, while the Wairarapa-dominated associations 3 and 4 are confined to sandstone. The remaining associations did not show fidelity to parent material. There were no relationships

between TWINSpan associations and the topographic or drainage variables.

Ordination

A three-dimensional depiction of ordination axes 1, 2 and 3 shows separation of TWINSpan groups 2, 3, 4, 5, 6, 8 and 9, but overlap of groups 7, 10, 11 and 12 (Fig. 4a). The ordination of the plots by region shows clear separation of those of Fiordland, Marlborough, Nelson and Taranaki and overlap of those of Wairarapa, Westland, Otago and Southland (Fig. 4b). The strongest geographic and environmental gradients related to the ordination are easting, northing, mean wind direction, deviation of the direction of greatest wind speed from the perpendicular of the coastline, offset angle, landform direction and vegetation and herb cover, with the best depiction of their relationships with the vegetation groups shown on a plot of axis 2 versus axis 3 (Fig. 4c). Salt delivery distance was not found

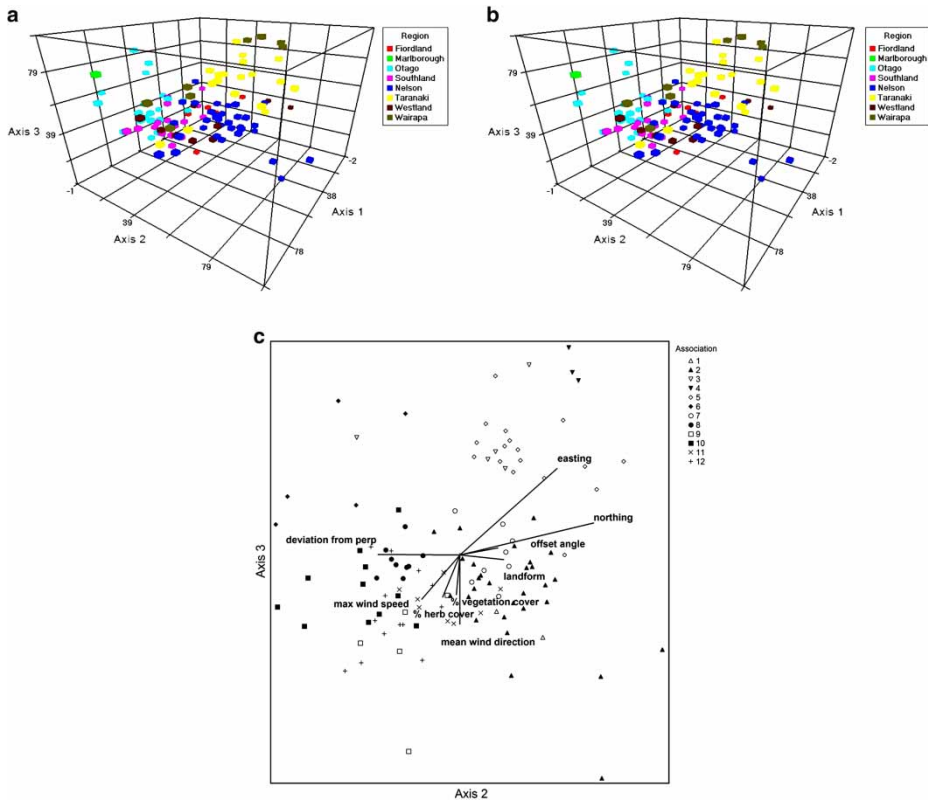


Fig. 4 Multidimensional scaling ordination of vegetation composition data collected from 116 coastal turf plots. (a) Plots coded by two-way indicator species analysis (TWINSpan) association; (b) plots coded by geographic region; (c) environmental vectors. Offset angle is the angular difference between the plot aspect and the perpendicular of the coastline.

to be influential in composition. Clearly, the strongest environmental influences are those that have a strong geographic component.

Soils

Most turfs occupied free-draining loamy soils of 370 ± 150 mm mean depth formed from a wide range of parent materials. Turfs extended on to poorly drained, humic soils east of Waipapa Point, Southland, and a Catlins coast example occupied peat soils. There were significant differences between soils supporting predominantly indigenous turfs and those of predominantly exotic composition in terms of pH (mean indigenous = 6.06, mean exotic = 6.44; $t_{35} = -2.5$, $P = 0.017$) and electrical conductivity (mean indigenous = 0.95, mean

exotic = 0.41; $t_{35} = 3.7$, $P < 0.0007$). There was no relationship between distance inland and pH and electrical conductivity for indigenous turfs or exotic communities or for the two associations combined.

Wind direction

We found a significant correlation between the direction of the greatest mean wind speed and the plot aspect (0.55 , $P < 0.0001$). There were significant correlations between the deviation of the direction of the greatest mean wind speed from the perpendicular to the coastline with both the plot offset from the landform dip direction (0.41 , $P < 0.0001$) and the plot offset from the perpendicular to the coastline (0.65 , $P < 0.0001$).

Threatened and uncommon plants

Sample plots of coastal turfs contained 33 threatened and uncommon plants from the list of de Lange et al. (2009) (Table 1). Almost all are short-statured herbs. Taranaki turfs with 12, Nelson with 11, Southland with 12 and Otago with 10 contain the bulk of those 33 taxa. Of the 33 taxa, 9 are included in the Threatened category and 24 in the At Risk category. The majority of the species have narrow regional turf distributions: 21, or two-thirds are restricted to one region and just 3 species occur in four or more regions (Table 1). *Lepidium naufragorum*, ranked Threatened, Nationally Vulnerable by de Lange et al. (2009), can occupy turf (Garnock-Jones & Norton 1995) but it was not encountered in our study.

Herbivory

Ungulates (farm stock and feral deer) had access to 71% of the sampled turfs. There was a significant difference in total vegetation cover between plots exposed to disturbance by ungulates and those not (mean with ungulates = 85%, mean without ungulates = 76%; $t_{112} = 1.85$, $P = 0.033$). Further statistical tests showed no significant differences in the proportional cover of native plants and the proportional cover of herbs in plots with and without ungulate disturbance.

Discussion

Environment

We found quite high regional distinctiveness in the composition of coastal turfs partly influenced by the high count of threatened and uncommon plants restricted to just one region. There were few physical environmental factors that were statistically associated with this variability. This might reflect the difficulties of sampling the physical environment, particularly landform shape and the limits of our RECCE-based sampling regime. Although a wide range of geological substrates and soil types support turfs and some are confined to one region such as Taranaki's volcanic substrates, the strongest ordination separation was

on grid reference. From this limitation, we offer terraced headlands, especially those associated with discordant coastlines and subject to strong onshore winds directed at predominantly oblique angles to the coast, as a generic set of physical factors controlling the development of coastal turf. Key physiological influences on this distinct vegetation physiognomy are probably wind exposure and edaphic and aerial salt.

Turfs occur in central and southern New Zealand, the zone influenced by the circumpolar westerly vortex of atmospheric circulation and persistent westerly winds. New Zealand's north, where turfs are largely absent, extends into the subtropical ridge of high pressures (McGlone et al. 1993) and less westerly wind. Headlands accelerate winds and the resulting exposure, manifest as mechanical damage, reduced temperatures and desiccation stress (all limiting CO₂ assimilation), selects for ground-hugging plants. Soil-soluble salts in coastal turfs have been found to be within the range of and in some instances higher than those reported for inland saline soils of Otago (cf. Rogers 1999, appendix 2; New Zealand Soil Bureau 1968, table 7.1.2), the latter supporting sparse halophytic vegetation and a flora partly overlapping with that of coastal turfs (cf. Allen & MacIntosh 1997; Rogers 1999). Meurk et al. (1994a) recorded a steeply declining Na ion gradient in precipitation from 2507 to 187 kg/ha/y over 5.5 km on Campbell Island, which they showed had a marked influence on floristic structure and productivity patterns. Wilson & Cullen (1986) found that soil salinity declined vertically on Catlins' coast cliffs, with the flora of the lowermost portions dominated by the common turf constituents *Selliera radicans*, *Samolus repens*, *Sarcocornia quinqueflora* and *Schoenus nitens*. The last three of those species show high tolerance to salinity as salt marsh constituents (Partridge & Wilson 1987). Native species compositional gradients perpendicular to the coast may well exist for coastal turfs but this was not investigated in this study. From a palaeoclimatic perspective, we predict that coastal turfs probably had a greater presence during the last glaciation when temperatures were lower and cold westerly winds more frequent (Shulmeister et al. 2004).

Table 1 Threatened and uncommon vascular plants recorded in coastal turfs of mainland regions of New Zealand (classification from de Lange et al. 2009)**Threatened**

1. Nationally Critical

Crassula peduncularis Taranaki*Gentianella scopulorum* [*Gentiana* aff. *Saxosa*]
(AK 7316; Charlston)] Westland

2. Nationally Endangered

Myosotis pygmaea var. *minutiflora* Taranaki

3. Nationally Vulnerable

Crassula manaia Taranaki*Lepidium flexicaule* Taranaki, Nelson, Westland*Mazus novaezeelandiae* subsp. *Impolitus* f. *impolitus* Nelson**At Risk**

1. Declining

Eryngium vesiculosum Wairarapa, Nelson, Otago*Lepidium tenuicaule* Southland, Otago*Myosotis pygmaea* var. *pygmaea* Taranaki, Nelson, Westland, Southland, Otago*Ranunculus recens* Taranaki, Nelson, Southland, Otago*Selliera rotundifolia* Taranaki*Tetrachondra hamiltonii* Southland

3. Relict

Sonchus kirkii Taranaki, Wairarapa, Fiordland

4. Naturally Uncommon

Acaena microphylla var. *pauciglochidiata* Southland*Anisotome lyallii* Fiordland, Otago*Atriplex buechananii* Otago*Crassula helmsii* Nelson*Crassula mataikona* Taranaki*Euphrasia repens* Southland*Leptinella calcarea* Nelson*Leptinella dispersa* subsp. *dispersa* Southland*Leptinella trailii* subsp. *pulchella* Southland*Mazus arenarius* Southland*Myosotis rakiura* Southland, Otago*Poranthera microphylla* Nelson*Puccinellia walker* Southland, Otago*Senecio carnosula* Otago*Wahlenbergia congesta* subsp. *Congesta* Nelson, Westland**Taxonomically Indeterminate****Threatened**

1. Nationally Critical

Limosella (b) (CHR 515038; Manutahi) Taranaki

3. Nationally Vulnerable

Kirkianella aff. *Novae-zelandiae* (CHR 84044; 'glaucous') Marlborough*Pimelea* aff. *Arenaria* (AK 216133; southern Taranaki, Nelson)

New Zealand)

At Risk

4. Naturally Uncommon

Celmisia aff. *Major* (AK 255352; Pupu) Nelson*Chaerophyllum* (a) (CHR 364086; 'minute flower') Taranaki, Nelson, Southland, Otago*Oreomyrrhis* (a) (CHR 364086; 'minute flower')]

The absence of turfs from most of west and southwest Fiordland, most of central and south Westland, Nelson south of Kahurangi Point and from Wellington to south Taranaki probably results from an absence of headland landforms, insufficient strong onshore winds arriving at oblique angles to the coast and dilution of aerial and edaphic salt by frequent precipitation. For example, detailed botanical survey failed to report turfs from one of the mainland's windiest onshore environments, West Cape, Fiordland (Wardle et al. 1973), likely caused by onshore salinity being diluted by frequent precipitation. Further south, just one patch of coastal turf was reported from the Muttonbird Islands, southwest of Stewart (Rakiura) Island (Fineran 1973), and none from two Foveaux Strait islands (Fineran 1966; Johnson 1976), although a few patches occur about northwest Stewart (Rakiura) Island (B Rance personal communication 2005). A rare northern North Island record of coastal turf on 50–70° coastal rock slopes on north-eastern Great Barrier Island (Wright & Cameron 1985) was not sampled in the current study.

Literature references to coastline turfs beyond the New Zealand archipelago are rare but include a tortoise-browsed and close-cropped turf on limestone substrates on an atoll west of Madagascar (Huntik 1980), turfs within dune-lands of the Isles of Scilly in the English Channel (Randell 2004) and an island headland off the coast of Brittany, France (Kerbiou & Juliard 2007). The Gaelic word 'machair' or 'machar' refers to a fertile low-lying and wind-swept grassy plain found on some of the north-west coastlines of Ireland and Scotland, in particular the Outer Hebrides (Mate 1992), that bear some resemblance to New Zealand's coastal turfs. Vertebrate herbivory is common to all these maritime sites but their onshore wind component is unknown to the authors.

Exotics versus natives

Soil chemistry data suggest that native plants of coastal turfs have a greater tolerance of edaphic salinity than do communities of predominantly exotic grasses on equivalent landforms and soils. Tolerance of aerial crystalline salt is likely to be equally important. Most of the cover

dominants of native turfs are prostrate succulents. Their thick fleshy leaves with waxed cuticles probably provide resistance to salt crystals penetrating the cuticle, and their enhanced foliar water storage would confer drought tolerance when the osmotic potential of salty soils reduces moisture uptake by roots. The succulent growth form is largely absent from the exotic flora within and bordering turfs in farm pasture, where more foliaceous grasses and rosette and scrambling herbs such as *Plantago* spp. and clovers predominate (Appendix 2 in Rogers 1999). This difference in the predominant foliar traits provides a physiognomic contrast between coastal turfs comprised of native plants and those dominated by exotic plants. Although it was not reflected in our examination of edaphic salinity, there must be an inland gradient of decreasing edaphic and aerial salinity (for chloride see Blakemore 1953) that would influence the interplay or transition zone between the predominantly coastal natives and the more inland exotics that we observed in the field.

Ungulate herbivory

Our data provided a limited opportunity to test whether ungulates influence overall vegetation cover and the relative importance of exotic versus native species. Plots with ungulate disturbance had significantly greater vegetation cover than plots without that influence. Although the proportional cover of herbs does show a relationship to the ordination axes, other tests provided no evidence that ungulates might advantage natives ahead of exotics or herbs ahead of other plant types. However, our field observations suggested that excluding ungulates can lead to change in native communities from early-successional, prostrate, commonplace herbs such as *Selliera radicans*, *Samolus repens* and *Leptinella dioica* to the taller succulents *Sarcocornia quinqueflora*, *Disphyma australe* and *Senecio lautus* or to grasses such as *Poa cita* or *Poa astonii*. Further successional change to subshrubs and lianes can also occur, at least at the rearward extent of turfs. In addition, species richness appeared to be promoted by ungulate disturbance in native turfs, apparently benefitting the

maintenance of several threatened and uncommon herbs such as *Lepidium flexicaule*, *L. tenuicaule*, *Ranunculus recens*, *Myosotis pygmaea* var. *minutiflora*, *Crassula manaia*, *C. mataikona* and *Eryngium vesiculosum* (GM Rogers unpublished data). Their persistence may depend on disturbance-induced early successional community states. Nevertheless, cattle (*Bos taurus*) can fracture turfs on poorly drained soils, restricting turf to the sides and tops of pedestals within a matrix of trampled, pugged depressions.

In prehuman times, the dominant avian processes on New Zealand's turfs would have been nutrient input from faeces, herbivory (predominantly grazing but including browsing of subshrubs) and disturbance from trampling and ground scarification (Lee et al. 2010). A wide range of birds would have grazed or otherwise impacted coastal turfs namely moa (Dinornithiformes), geese and ducks (Anseriformes), rails (Rallidae), kakapo (*Strigops habroptilus*), parakeets (Platycercidae), albatross (Diomedidae), gulls (Laridae), shags (Phalacrocoracidae), dotterels (Charadriidae), quail (*Coturnix novaezelandiae*) and perhaps burrow-nesting petrels and shearwaters (Procellariidae). Seals (Phocidae) and sea lions (Otariidae) also would have heavily impacted turfs as haul-out habitat by crushing vegetation and boosting nutrient states as they apparently currently do at Kaihoka Lakes, Nelson, at Long Point in the Catlins, Otago, at Cape Foulwind, Westland and on subantarctic islands (B Rance personal communication 1997; GM Rogers personal observations). Apart from light trampling, today's bird impacts on turfs are limited to rare nesting events by red-billed gulls (*Larus novaehollandiae scopulinus*) and southern black-backed gulls (*Larus dominicanus*) (GM Rogers personal observations), while red-crowned parakeets (*Cyanoramphus novaezelandiae novaezelandiae*) have been observed feeding upon turfs of Southeast (Rangitira) Island in the Chatham Islands (S Courtney personal communication 2007) and Enderby Island in the Auckland Islands (P Johnson personal communication 2001). Paradise ducks (*Tadorna variegata*) have been observed roosting on Waitutu turfs (Ogle 1988).

Accordingly, prehuman avian disturbance has today been lost entirely or largely replaced by ungulate disturbance. The rearward range of native turfs appears to be extended by ungulate grazing, especially where land clearance has removed inland borders of native woody communities and replaced it with farm pasture. Conversely, we expect that native turfs would have contracted shoreward ranges in the absence of ungulate herbivory and the resulting competitive expansion of taller exotic grasses and herbs. Therefore, an ecosystem-based understanding of the community dynamics and spatial extent of mixed native and exotic turfs would need to integrate the abiotic stress gradient (salinity and exposure) with ungulate disturbance. As Meurk et al. (1994b) observed on Campbell Island, productive but low-statured coastal vegetation is a 'compromise between fertility and disturbance', where stature- and productivity-promoting fertility derived from aerosol-borne cations is counteracted by detrimental exposure and toxic levels of salt.

Coastal turfs have been observed on New Zealand's near- and off-shore islands, the latter including Chatham Island (S Courtney personal communication 2007; GM Rogers personal observations 2008), Stewart (Rakiura) Island (B Rance personal communication 2005) and the subantarctic islands (B Rance personal communication 2005). Meurk et al. (1994b) record littoral fringe turfs on Campbell Island that may be used as marine mammal wallows. These were not included in the current study but they offer opportunities to study the disturbance and nutrient inputs from marine mammals and seabirds largely lost from mainland turfs.

Protection priorities

In areal extent, coastal turfs in New Zealand exist as one of the most restricted ecosystems, yet their current extent probably exceeds their prehuman extent because land clearance has relaxed competition from taller vegetation. Turfs have received little protection and conservation management attention (but see Bridge & Clarkson 2004 in Taranaki), partly owing to the preponderance of private tenure.

Overall, 23% of sample sites occur on Crown conservation land, with those of Otago and Westland having the greatest frequency (41 and 56%, respectively) and Nelson, Southland and Wairarapa the least (all <14%). The classification and ordination of the current study can inform the setting of conservation priorities. The ordination shows that the environmental influences on turf composition are regionally distinct and the classification argues for separate sets of within-region priorities for Taranaki, Nelson, south Westland and Fiordland. The composition of TWINSPAN groups 7, 9, 10, 11 and 12 suggests conservation priorities could be rationalized across subsets of Wairarapa, Otago, Southland and north Westland. Other criteria such as plant richness, diversity and rarity, and site naturalness, viability, size and buffering will further inform priorities (Myers et al. 1987). The large list of threatened and uncommon plants, many confined to just one region, would rank highly in those criteria. Further, given the likely key role of avian herbivory in prehuman turfs and no strong quantitative or observational evidence to the contrary, we tentatively recommend ungulate herbivory in turf management, at least on well-drained soils, with sheep (*Ovis aries*) preferred ahead of cattle.

Acknowledgements

We warmly thank Carol West, Brian Rance, Shannel Courtney, Brian Patrick, Peter de Lange, Bill Lee, Colin Ogle, Peter Johnson, David Norton, Albert Rebergen, Lisa Sinclair, Graeme la Cock, Jim Clarkson, Greg Rine, Simon Walls, Don Neale, Phil Knightbridge, John Barkla, Betty and Eric Rogers and Mary Bruce for planning advice and/or field help. We thank Andrew Tait and NIWA for wind run data. Two anonymous journal referees made helpful comments on the manuscript. This research was funded, in part, by the New Zealand Foundation for Research, Science and Technology Contract C09X0503. The data from this study are archived in the National Vegetation Survey Database: <http://nvs.landcareresearch.co.nz/>.

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