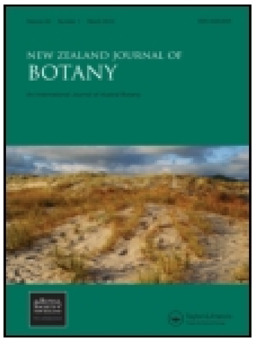

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Big Hellfire Dune on the western coast of Stewart Island/Rakiura, New Zealand, is an unusual dune climbing 220 m in altitude on the Ruggedy Range, to dissipate on the leeward side of Hellfire Pass. To record vegetation and environmental characters we ran six transects parallel to the coast, at 50-m altitudinal intervals up the dune. Topography reflected substrate and sand deposition patterns. Wind speed was higher further up the dune, and conductivity and water content were lower, while organic matter and pH did not change. The dune has a rich native flora, with very few exotic species. Analysis defined four plant communities, reflecting openness, and cover of *Ficinia spiralis*, extent of marginal shrubland of *Brachyglottis rotundifolia*, and presence of some forest species. The adaptive ability of dune plants was investigated in relation to altitude, using leaf traits. The most widespread species *B. rotundifolia* and *F. spiralis* adapt with thicker, shorter, wider leaves, shorter petioles and lower specific leaf areas closer to the coast, and again at the Pass. Vegetation patterns appear to be driven by rainfall and the stability of the fine, even-sized sand, not by altitude. Anthropogenic disturbances from invading weeds and trampling from exotic mammals threaten Big Hellfire Dune, requiring monitoring to protect this unusual climbing dune.

Keywords: altitude; duneland; exposure; muttonbird scrub; pīngao; salt; specific leaf area; spray; sand; succession; topography; trait; wind

In New Zealand, sand dunes cover an estimated 39,000 ha, an area reduced to 30% of 1900's values by anthropic activities (Hilton et al. 2000). The remaining dunelands are rarely in their natural state, with most now dominated by exotic plants, such as *Ammophila arenaria* (marram grass) and *Lupinus arboreus* (Wardle 1991; Partridge 1992a; Johnson 1992; Hilton et al. 2000; nomenclature follows Ngā Tipu o Aotearoa [http://nzflora.landcareresearch.co.nz] except where noted). The most natural dunes remaining are remote from human disturbance, and only a few have had their vegetation well documented (Asplin & Fuller 1985; Smith et al. 1985; Sykes & Wilson 1987, 1991; Partridge 1992a; Drobner et al. 1995; Pegman & Rapson 2005). Climbing dunes, where sand piles up against natural obstacles, are rare, but occur at Castlepoint and Cape Reinga, North Island, and East Ruggedy Beach, Stewart Island. None has been extensively documented. Here, we describe an almost pristine confined climbing dune on Stewart Island/Rakiura, which rises up to 200 m in altitude, crossing a pass.

Many of New Zealand's best remaining dunes are on Stewart Island/Rakiura, the third largest and most southerly island in the archipelago. It has a wet, oceanic temperate climate, with an annual rainfall range of 1000–3000 mm. Mean monthly temperatures range from 6.1 °C

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in July to 13.4 °C in both January and February (NIWA 2011). The prevailing wind is from the west, due to the island's position on the circumpolar wind belt (Brenstrum 1998). Reserved since 1907, Rakiura National Park covers 85% of the island, at 157 kha, and has nine dunelands of national significance (Hilton et al. 2000). The dominant native dune plant is the endemic sand-binding sedge pīngao (*Ficinia spiralis*, AKA *Desmoschoenus spiralis* (A. Rich.) Hook. f. 1853; Muasya & de Lange 2010), often occurring in association with the grass *Poa billardierei* (HD Wilson 1987). On stable dunes, pīngao is often replaced by *Ficinia nodosa* and adaptable native shrubs such as *Coprosma acerosa*, *Pernettya macrostigma* and *Ozothamnus leptophyllus* (HD Wilson 1987). At the rear of the dunes, 'muttonbird scrub', dominated by *Brachyglottis*, *Dracophyllum* and *Olearia* spp., is often present, transitioning into native forest dominated by *Weinmannia racemosa* with *Metrosideros umbellata* and the emergent podocarp *Dacrydium cupressinum* (HD Wilson 1987).

Big Hellfire Beach (Latitude 46°46′23″S, Longitude 167°44′35″E), also a nationally significant duneland (Hilton et al. 2000; Fig. 1), is 800 m long, and ranges from 50 to 100 m wide (averaging c. 70 m), extending up a narrow, otherwise rocky, valley on the coastal Ruggedy Range (Fig. 2). It reaches an altitude of 220 m, entering Stewart Island's montane zone (HD Wilson 1987), and extends 50 m vertically over the ridge (Big Hellfire Pass), towards Freshwater Swamp, before dissipating into forest, below the Hellfire Pass Hut, a tramping destination on the 'Northern Circuit'. The aims of this article are to describe the floristics and patterns in plant communities present on this unusual climbing dune, and to examine gradients in adaptation of leaf traits as aids to understanding the dune's ecology.

Methods

Detailed surveys for environmental variables, vegetation composition and individual plant leaf traits were made on six cross transects, placed at 50-m altitudinal intervals up Big Hellfire Dune (Fig. 3). The first transect (T20) was 20 m in altitude above the high tide mark, with other transects at 70, 120, 170 and 220 m (the top of the dune). A further transect line (TFW) was placed on the leeward side of the Pass towards Freshwater Swamp at 170 m. Transects ran on a north–north–west aspect (316–338°), extending a few metres into the muttonbird scrub on either side. Transect topography was surveyed at 1-m intervals, starting 0.5 m along each transect, and expressed relative to the lowest point of each transect, then graphed against topographic maps and GPS locations.

Three sets of comparative wind readings were taken at the centre of each transect, with a hand-held anemometer over a 1-min period. Wind direction was also recorded. Because it took 30 min to visit all transects, parallel reference wind readings were taken in the centre of T220, with values for other transects standardized against those. These were compared against daily and 5-yearly wind speeds from South West Cape, at the bottom of Stewart Island.

Sand movement was measured by placing five sand traps spaced evenly along each transect. Traps consisted of 1.5-L plastic bottles, with a 5-cm diameter hole cut in the side. Capped bottles were buried upside-down, with the lowest portion of the hole just above the sand surface, facing the coast. On transect T170, five additional sand traps were placed behind the first five, but facing inland, to record sand movement down the dune. The amount of sand collected was measured after 5.0 days by placing samples into a reference tube, wetting all samples equally (as some were wetter than others), and recording sand volume after a 5-min settling period.

Sand samples were collected at three points in mobile substrate along each transect, near the three central sand traps. A 5-cm diameter corer was used to collect samples 0–5 cm and 20–25 cm deep. Samples were stored at 4 °C, then thoroughly mixed prior to analyses.

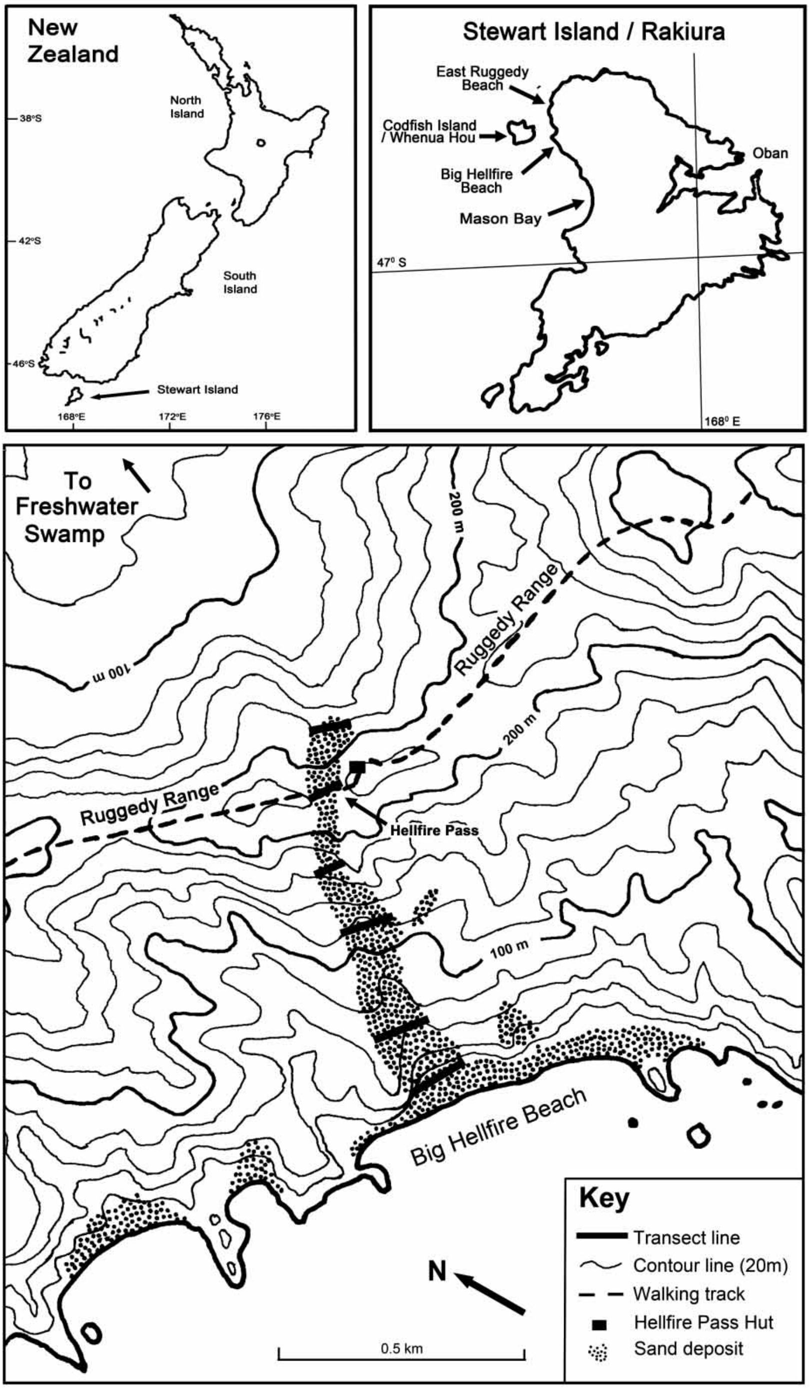

Figure 1 Location of Stewart Island, Big Hellfire Dune and other features referred to, and topography of landforms around Big Hellfire Dune.

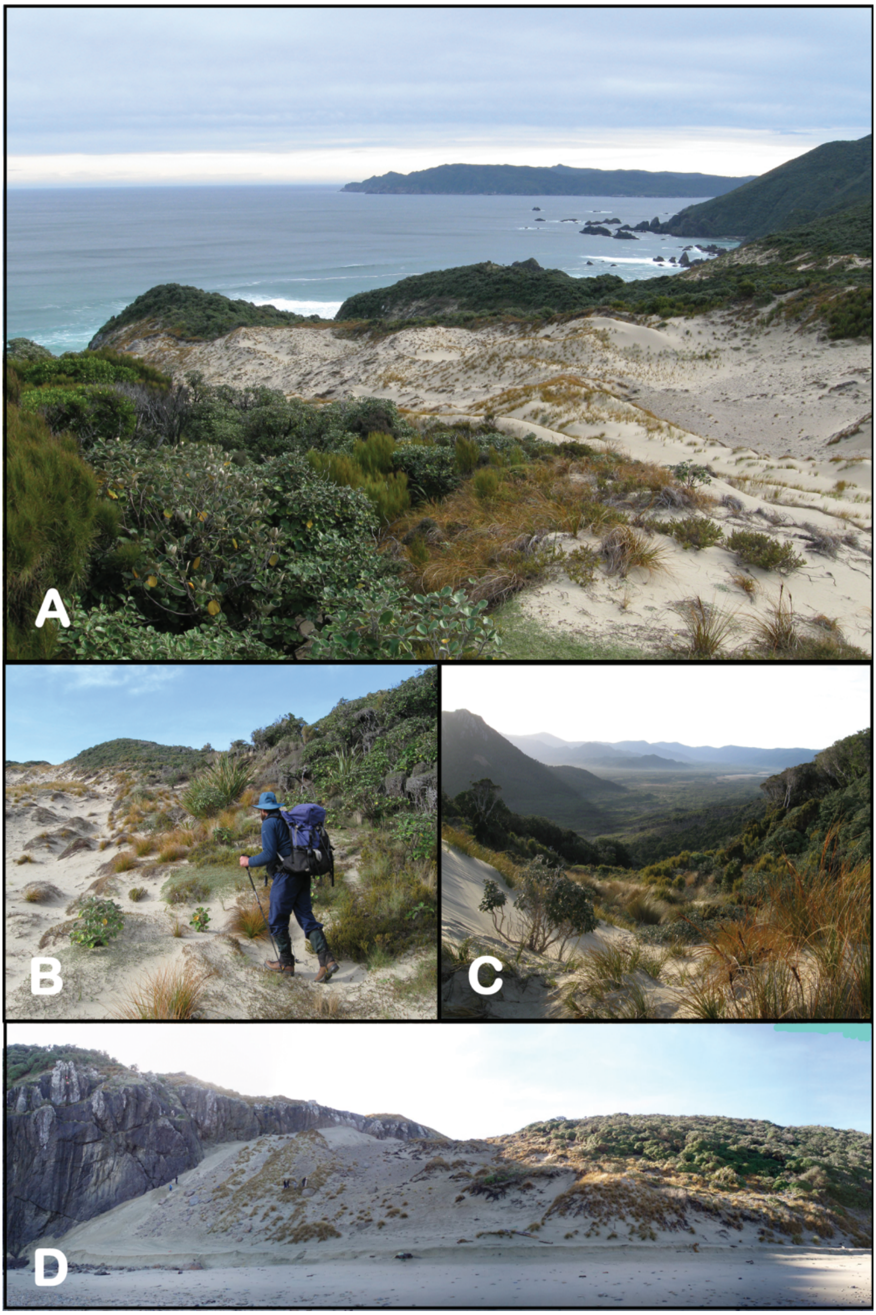

Figure 2 Images of Big Hellfire Dune. **A,** Middle part of the dune, looking west towards Codfish Island/ Whenua Hou from near T170. **B,** Dune Shrubland community adjacent to more open stable dune vegetation, looking towards the Pass (lowest point on skyline) from near T120. **C,** Leeward side of the dune dissipating into forest, looking over TFW towards Freshwater Swamp from the Pass. **D,** Wide-angle view along transect T20, 20 m above sea level, where authors are working, with the cliff at the northern end; no other transect is visible in this view.

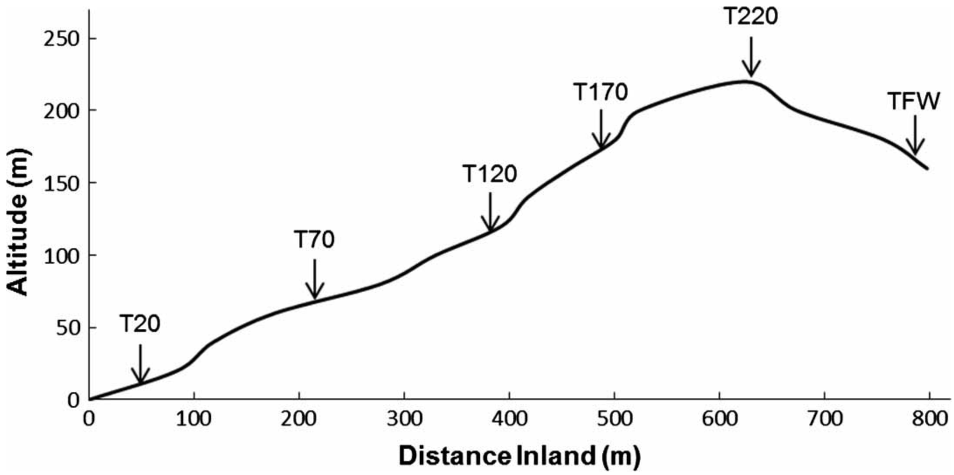

Figure 3 Profile of Big Hellfire Dune, from the coast to the Pass, with positions of the six transects sampled.

A 50-g subsample was stirred with 250 cm^3 distilled water for 2 min, and left to settle for 2 min, before a Cyberscan meter (Eutech Instrumentals, Vernon Hills) was used to measure pH and conductivity. Water content (% wet weight of sand) was derived by weighing another subsample, drying for 70 h at 80 °C, and reweighing. The dry sand was then split into two portions, one of which was sieved and weighed into six size categories (see Results for details) to measure the range of sand sizes, while the other portion was burnt at 500 °C for 5 h, and reweighed, to calculate organic matter content, expressed per unit dry weight of sand containing carbon.

Sand particle size classes, carbon content, pH and conductivity were analysed in Minitab 16 (Minitab Inc.), using an analysis of variance (ANOVA) model with transect, depth and transect by depth as factors. Differences between factors were compared using Tukey pairwise tests.

Vegetation and site characteristics were sampled at 4-m intervals along each transect, using 2 m $\times$ 2 m quadrats. Height along the transect was taken as the average of the two topography measurements per quadrat. Slopes and aspects were recorded (the latter expressed as northings and eastings using the sine and cosine of each angle in radians so that values could be averaged), along the line of maximum slope of each quadrat. Maximum standing vegetation height was also recorded for each quadrat, along with percentage covers for sand ($<$ 2 mm diameter), stones ($<$ 2 cm diameter), rocks ($\geq$ 2 cm diameter), wood, live and dead vegetation. Cover was estimated for each individual plant species as the vertical projection of all foliage of a single species onto a horizontal surface, effectively recording the shadow of that species under solar zenith.

To group the plots into similar vegetation types, here designated communities, analysis was carried out on the square root transformed cover data. Cluster analysis was conducted using SYSTAT (Systat 1998), to give a dendrogram based on Euclidean distance and Ward Linkage metrics, which was pruned to give four vegetation groups. A principal component analysis (PCA, which also uses Euclidean distance; Legendre & Gallagher 2001) was produced via Canoco (ter Braak & Smilauer 2002). The four communities from the cluster analysis were superimposed onto the ordination space. The average species composition and environmental variables of each community were tabulated.

To survey adaptational variation in morphological traits, nine abundant and widespread plant species were selected: herbs, *Acaena microphylla* var. *pauciglochidiata*, *Craspedia robusta* var. *pedicellata* and *Hydrocotyle novae-zeelandiae* var. *montana*; shrubs, *Brachyglottis rotundifolia*, *Coprosma acerosa* and *Pernettya macrostigma*; and monocotyledons *F. spiralis*, *Poa astonii* and *P. billardierei*. Ten leaves of each species were collected haphazardly along each transect, where present. Lamina thickness was measured with a slipping clutch micrometer in the field and samples were then pressed for transport. In the laboratory, lamina length and width (at the widest point), and petiole or sheath length were measured, as was leaf weight following drying at 80 °C for 72 h. To determine specific leaf areas, leaf areas of herbs and shrubs were measured using the pixel counter on posterized scanned images in Adobe Photoshop (Adobe Systems, San Jose). For monocots, leaf length and width (at 0.5 cm above the ligule) were used to calculate leaf area based on an isosceles triangle. As leaves of *P. astonii* and *P. billardierei* were rolled, the circumference of the base of the leaf cylinder was taken as the leaf width. From these measurements other combinations and ratios were calculated (see Results).

Individual trait variables were analysed by ANOVA using SYSTAT. Because not all species occurred on every transect, two analyses were completed, one using all species but excluding transects without some of those species, and the other using all transects but excluding species not found on all transects. These were used for species effects and transect effects respectively. For the species by transect interactions, the presented ANOVA table is for the tests using the full complement of transects, since species differences are to be expected anyhow, and so are less interesting. Range tests were applied to significant variates using Tukey's measure.

Results

Environmental variables

The topography of Big Hellfire Dune is unusual. The dune had an average slope of 20° (Fig. 3). There is no foredune, and no footprint of a dissipated foredune between the dune proper and the foreshore. Rather there is a steep slope (c. 40°), the bottom of which has been cut into by the sea, forming a 1-m high sand cliff. The coastal portion of the dune is narrow (c. 50 m) with one side bordered by a 20-m tall cliff. Above the height of the cliff is a wider and flatter area of mobile hummocky sand mounds and deflation pockets. Next, altitudinally, the dune has a valley shape which is likely to follow the topography of the bedrock it covers, augmented by higher, but thinner deposits of sand near the lateral dune edges. This zone gives way to a broad (c. 110 m wide) deflation flat at 150–350 m from the coast, with steep sand slopes rising on either side of it. The south-facing slopes of the transects averaged c. 19°, 62% more than those facing north, creating a slightly one-sided valley. Halfway up this flat, a small pocket of bare sand, surrounded by shrubland, occupies a side branch of the valley, and is vegetationally comparable to the main dune (data not presented). Next the dune narrows and steepens, and large accumulations of sand fill the neck (c. 60 m wide). Near the ridge crest, sand deposits overlie a steep section with patches of exposed bedrock. At the Pass (25 m wide, and crossed by a tramping track) small sand dunes surround a semi-rocky flat used for helicopter landings. Inland from the Pass is a smooth well-vegetated slope leading on to a flat open area, below which on a steep slope bordered by a small creek, the sand dune dissipates under forest.

Sand pH averaged 6.74 (range 6.27–7.71), but was unaffected by transect position, depth or their interaction (Table 1), similar to results for organic matter content of dry sand (mean 0.44%; range 0.20%–1.76%). The lower layer

Table 1 *P*-values from the general linear model for sand characteristics.

	Transect	Depth	Transect × depth	Error M.S.	Error d.f.
Ph	0.89	0.96	0.50	0.15	24
Water content	**0.02**	**0.00**	0.80	0.68	24
Organic content	0.39	0.17	0.61	0.06	23
Conductivity	**0.00**	**0.00**	**0.00**	12.33	24
Substrate size classes					
1.1–2 mm	0.30	0.27	0.70	14.71	24
601 μm–1 mm	**0.04**	0.46	0.80	0.82	24
250–600 μm	0.12	0.18	0.80	0.34	24
125–249 μm	**0.00**	0.07	0.30	24.17	24
45–124 μm	**0.00**	0.07	0.40	6.75	24
< 45 μm	**0.00**	0.15	0.20	0.00	24

Note: Significant values ($P \leq 0.05$) are given in bold. M.S., mean square; d.f., degrees of freedom.

of sand was 53% wetter than the top layer. T220 was about half as wet as T20 ($P = 0.028$), while all other relationships were non-significant. Conductivity in T20 was 2.5 times higher than the mean of all other transects (Table 1; $P < 0.001$), which did not differ significantly. Overall, the top 5 cm of sand had 61% higher conductivity than the deeper 20–25 cm layer, being a maximum of 225% higher on T20, the transect closest to the sea (Table 2). Sand grains 125–249 μm in diameter were by far the most common (mean 91.3% by weight), followed by those in the 45–124-μm size class (mean 6.05%). There were only small differences in size classes between transects, with T120 having more larger particles, and T20 more very fine ones. Particles ≥ 2 mm in size were only present in three samples on T120 and one on T20, with an average of 10.3% cover of the substrate. There was no significant interaction between transect and depth for any particle size (Table 1). Analyses of the sand trap data showed no overall patterns, although maximum movement of 3.6 $cm^3\,cm^{-2}\,day^{-1}$ occurred on T170, the transect on the steepest part of the dune. This was a much higher rate than on the other transects (mean 0.81 $cm^3\,cm^{-2}\,day^{-1}$).

Wind speeds were generally moderate over the time sampled, being just under 7 $m\ s^{-1}$, which equates to 25 $km\,h^{-1}$, although the

Table 2 Results for sand analysis for variates with significant values by depth or transect.

	Conductivity (μS)			Substrate size classes			
Transect or depth	Top	Bottom	Water content (%)	601 μm–1 mm	125–249 μm	45–124 μm	< 45 μm
T20	50.1	22.2	3.30^{b}	0.10^{a}	81.85^{a}	14.57	0.19^{b}
T70	13.4^{a}	9.4^{a}	2.31^{ab}	0.00^{a}	93.40^{b}	6.46^{ab}	0.04^{a}
T120	14.2^{a}	8.6^{a}	2.95^{ab}	1.56	88.45^{ab}	5.54^{ab}	0.12^{ab}
T170	8.8^{a}	8.3^{a}	2.93^{ab}	0.00^{a}	92.52^{b}	7.40^{b}	0.04^{a}
T220	14.5^{a}	10.9^{a}	1.71^{a}	0.00^{a}	93.98^{b}	2.66^{a}	0.01^{a}
TFW	9.2^{a}	7.6^{a}	3.16^{b}	0.04^{a}	94.52^{b}	4.45^{ab}	0.07^{a}
Top	18.3	–	2.15	0.40	89.74	7.68	0.09
Bottom	–	11.2	3.30	0.17	92.84	6.02	0.06

Note: Values in the same column followed by the same letter do not differ significantly according to Tukey's test. Top, 0–5 cm deep; Bottom, 20–25 cm deep.

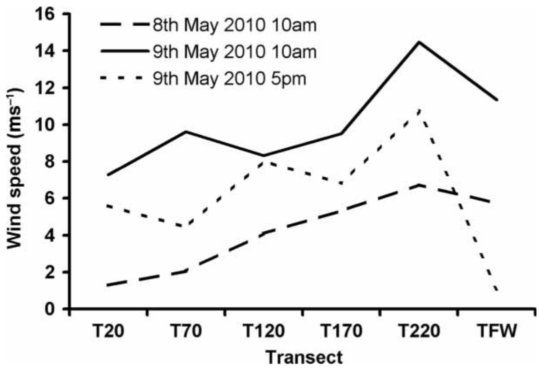

Figure 4 Wind speed variation with altitude up Big Hellfire Pass dune on three occasions. Lines are to clarify, not interpolate.

windiest value at the Pass was double that at 14.4 m s^{-1}. Wind speeds were lowest at the coast (Fig. 4; 4.8 m s^{-1}), increasing progressively up the dune to the Pass (10.6 m s^{-1}) and declining over the Pass. The 5-year average wind speed at South West Cape was 10.5 m s^{-1}, very close to the 10.8 m s^{-1} recorded there on the two days we sampled. Wind directions were mostly from the ocean to the land, although on one occasion wind blew from Freshwater Swamp towards the coast. In the evening and early morning, the air could be very still.

Plant community composition

Ten quadrats on Big Hellfire Dune contained only bare sand (Table 3). In total 86 plant species were identified from the remaining

Table 3 Means of environmental variables, and quadrat coverage of different substrates and organic matter, for each community, and for the quadrats containing only bare sand.

	Bare sand	Open Dune	Pīngao Dune	Stable Dune	Dune Shrubland
Number of quadrats	10	49	16	37	14
Total species present	0	20	23	72	46
Mean quadrat richness	0	3.24	3.88	12.35	7.93
Maximum quadrat richness	0	6	13	20	12
Proportion of species which are native	–	0.95	0.87	0.96	0.98
Mean maximum vegetation height (cm)	–	34.5	57.1	128.1	195.3
Mean relative height on transect (m)	2.49	3.11	3.35	6.37	5.99
Mean slope angle (°)	23.9	21.0	25.0	20.2	26.4
Mean northings (sine of angle in radians)	−0.23	−0.32	−0.24	0.00	−0.03
Mean eastings (cosine of angle in radians)	−0.54	−0.43	−0.31	−0.09	−0.44
Mean sand cover (%)	93.6	91.0	80.7	38.0	52.2
Mean stone cover (%)	3.9	4.7	0.1	0.0	0.0
Mean rock cover (%)	1.4	0.4	0.2	0.0	0.0
Mean wood cover (%)	0.2	0.2	0.1	1.4	3.8
Mean litter cover (%)	1.2	1.2	0.9	7.7	22.9
Mean vegetation cover (%)	0.0	4.4	20.3	72.2	79.9

116 quadrats sampled. Three (*Anthoxanthum odoratum*, *Hypochaeris radicata* and *Leontodon taraxacoides*) were exotics, occupying < 2.5% of any quadrat, and averaging 0.2% cover. Quadrats had a mean species richness of 6.8, while each species occurred, on average, in 9.6 quadrats. The most common species was the sedge *F. spiralis*, found in 71% of quadrats. The shrub *C. acerosa* and grass *P. billardierei* were also abundant, each found in 48% of quadrats. The tree daisy *B. rotundifolia*, sedge *F. nodosa*, and herbs *Wahlenbergia albomarginata* and *Craspedia robusta* var. *pedicellata* and the exotic *Hypochaeris radicata* were each found in more than 25% of quadrats. Twelve other species were found in at least 20 quadrats, while 18 species were found only once.

Species common throughout the dune included *B. rotundifolia*, *F. spiralis* and *P. billardierei*, as well as the widespread shrub of backs of foredunes, *C. acerosa*. Species much more common near the coast than inland were *Craspedia robusta*, *Myosotis pygmaea* and the exotic *Hypochaeris radicata*. Species restricted to or more common in the three top transects were mostly components of the rātā/rimu/kāmahi forest, such as *Metrosideros umbellata*, *Helichrysum filicaule*, *Hymenophyllum revolutum* and a number of lichens. There are no alpine or montane specialists, except for *Gunnera dentata*, which is a prostrate herb, found only at the Pass (T220) and over (TFW).

The main split (Table 4) of the dendrogram represented a distinction between shrubby dune edge communities and the more mobile dune communities, occupying relatively high and low parts of each of the transects respectively (Table 3). These were further divided into two communities each, differing in stability. PCA depicted the two communities of mobile dune (Open Dune and Pīngao Dune) as relatively similar, while the stable dune community was the most variable in composition (Figs 5, 6). The first four axes of the analysis explained 49.8% of the variation in the data.

Ficinia spiralis was present in all communities (Table 4) and was at highest cover in the Pīngao Dune community. Eight of the ten listed herb species had their highest covers in the Stable Dune community. Tree species were generally most common in Dune Shrubland. Only two species, the herbs *Myosotis pygmaea* var. *pygmaea* and *Uncinia uncinata*, were restricted to one community, i.e., the Dune Shrubland, which had a much higher canopy openness than nearby forest.

The Open Dune community was the most common at Big Hellfire Dune, making up 38% of the sampled quadrats. It had very low vegetation cover (4.4%), and consequently the highest covers of sand, stone and rock. Species richness averaged only 3.2 species per quadrat (maximum 6). Of the 20 plant species found, the most common was *F. spiralis*, with others being the monocots *P. billardierei* and *F. nodosa*, as well as the herb *A. microphylla* var. *pauciglochidiata* and small shrubs such as *C. acerosa* (Table 4).

The Pīngao Dune community was found in 12% of quadrats, and while it had a 4.6 times higher vegetation cover than the Open Dune, it had similar species richness (mean 3.9; maximum 13). A total of 23 species were found, with vegetation cover being 20.3%. *Ficinia spiralis* was dominant along with other species found in the Open Dune community. The monocot *P. astonii* and the herb *Apium prostratum* were also important in this community, though at low cover. This community had the highest proportion of exotic species (13% of the flora), with *Hypochaeris radicata* having the highest mean cover (0.2%).

The Stable Dune community comprised 29% of quadrats sampled, and had the highest mean species richness (12.4 species per quadrat) and the highest number of plants found in any community (72 species). It was also found on the flattest topography (average slope of 20.2°). Vegetation cover (72.2%) was high, and surficial stones and rocks were absent. The dominant species were the shrubs *D. longifolium*, *Ozothamnus leptophyllus*, *Pernettya macrostigma* and *B. rotundifolia*, interspersed with monocots, of which *F. spiralis* was the most abundant (mean 5.2% cover).

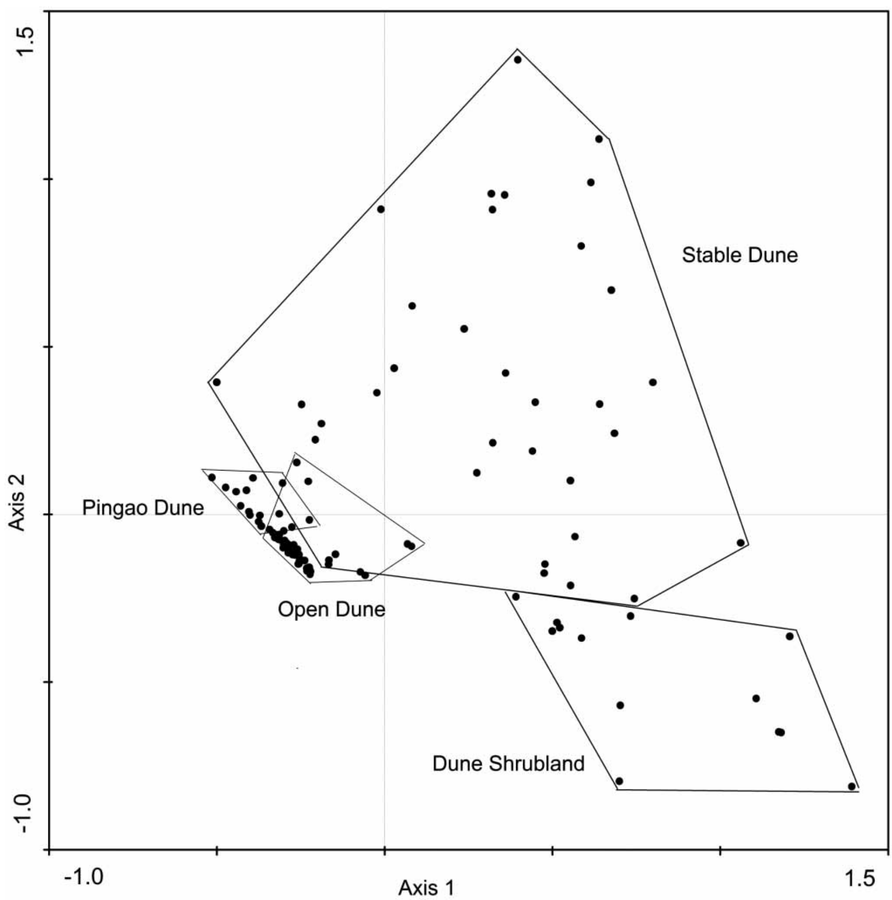

Figure 5 Principal components analysis of the sampling sites with best fit polygons surrounding each community, as identified by the dendrogram (see Table 4).

The Dune Shrubland made up 11% of quadrats at Big Hellfire Dune, and was the tallest community (Table 3). Less diverse than the Stable Dune community, it had only 7.9 species per quadrat and 46 species overall. It also had the highest proportion, cover-wise, of native plant species (98%), and the highest wood and litter covers (3.8% and 22.9%, respectively). This community was dominated by the tree daisy *B. rotundifolia* and the divaricating shrub *C. rhamnoides* (total of 55.5% cover). Other species included *D. longifolium*, *Leptecophylla juniperina*, *Myrsine australis*, *Olearia colensoi* and some incipient forest species, such as *Dacrydium cupressinum*, *Weinnmania racemosa* and *Metrosideros umbellata*, standing over an understorey of ferns, monocotyledons, smaller shrubs and herbs.

Communities mapped along transect profiles (Fig. 7) showed the Open Dune occupied the centre of the lower dune transects, but was rare around the Pass. Pīngao Dune was scattered on all coast-facing transects, often peripheral to the Open Dune community, but was absent on TFW. The Stable Dune community was mostly found only near the transect margins, but it dominated the length of the inland transect (TFW). Dune Shrubland was found mostly at the edges of transects, but was found more centrally on T20, T120 and TFW, as patches on higher ground.

Table 4 Mean percentage cover of the most interesting or dominant plant species in each community.

Species	Habit	Open Dune	Pīngao Dune	Stable Dune	Dune Shrubland
Acaena microphylla var. *pauciglochidiata*	h	0.05	0.06	1.99	0.04
Apium prostratum	h	0.08	0.31	–	0.04
Blechnum discolor	f	0.01	–	0.35	2.50
Brachyglottis rotundifolia	s	0.40	–	5.27	32.18*
Coprosma acerosa	s	0.81	0.63	3.80	0.79
Coprosma propinqua	s	0.06	–	2.82	–
Coprosma rhamnoides	s	0.04	–	2.05	23.32*
Craspedia robusta var. *pedicellata*	h	0.15	0.19	0.30	0.14
Dracophyllum longifolium	s	0.14	–	7.23*	0.39
Elymus tenuis	m	–	–	0.16	0.11
Ficinia nodosa	m	0.04	1.03	0.69	3.29
Ficinia spiralis	m	2.01*	16.38*	5.24	0.54
Gunnera dentata	h	0.02	–	0.30	–
Hydrocotyle novae-zeelandiae var. *montana*	h	0.01	0.03	0.18	0.04
Hypochaeris radicata†	h	0.21	0.19	0.32	0.14
Leptinella traillii	h	0.01	0.13	0.64	0.29
Leptecophylla juniperina	s	0.02	–	1.15	3.57
Leptospermum scoparium	t	0.01	–	0.32	–
Leucopogon fraseri	s	0.02	–	0.89	0.07
Luzula banksiana var. *acra*	m	0.01	0.03	0.19	0.04
Metrosideros umbellata	t	0.05	–	2.73	0.21
Microsorum pustulatum	f	–	–	0.11	0.25
Myosotis pygmaea var. *pygmaea*	h	0.13	–	–	–
Myrsine australis	t	0.01	–	0.27	4.07
Olearia colensoi var. *grandis*	s	0.03	–	1.35	2.14
Olearia oporina	s	0.02	–	0.96	–
Ozothamnus leptophyllus	s	0.27	0.06	7.66*	0.36
Pernettya macrostigma	s	0.18	–	7.88*	0.18
Phormium tenax	m	0.06	–	3.14	–
Pimelea lyallii	s	–	0.06	0.22	0.36
Poa astonii	m	0.04	0.53	1.73	0.07
Poa billardierei	m	0.52	0.25	0.66	0.71
Pratia angulata	s	–	0.03	0.16	0.32
Pseudocyphellaria coronata	l	0.01	–	0.32	0.07
Ranunculus acaulis	h	0.03	0.03	0.12	0.07
Stereocaulon ramulosum	l	0.01	–	0.70	–
Uncinia uncinata	m	–	–	0.07	–
Wahlenbergia albomarginata	h	0.07	0.09	0.57	0.21
Weinnmania racemosa	t	0.01	–	0.72	0.71

Note: Habit categories: b, bryophyte; f, fern; h, herb; l, lichen; m, monocot; s, shrub; t, tree. †Exotic. Dominant species in each community are marked with an asterisk.

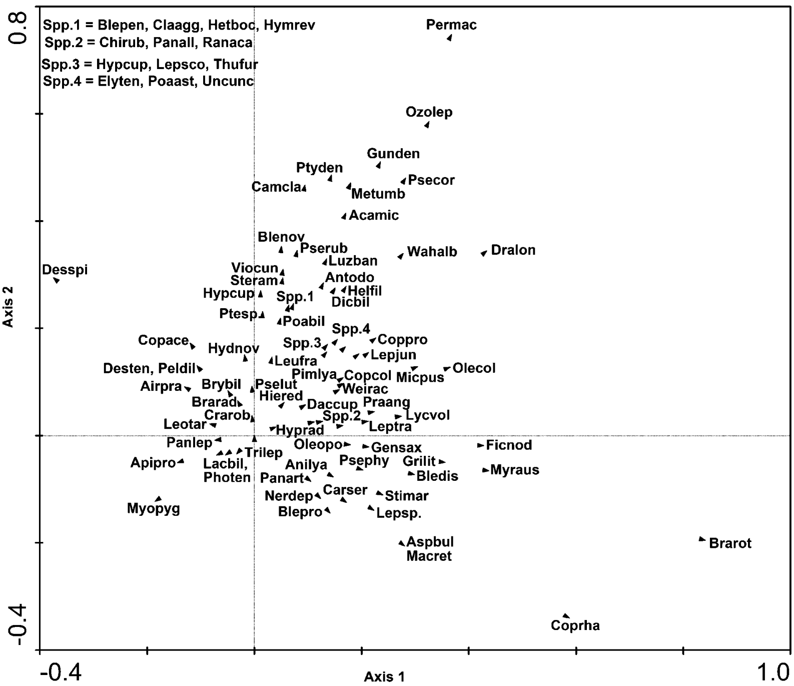

Figure 6 Principal components analysis of the species found on Big Hellfire Dune. Codes: Acamic, *Acaena microphylla* var. *pauciglochidiata*; Acrchl, *Acrocladium chlamydophyllum*; Airpra, *Aira praecox*; Anilya, *Anisotome lyallii*; Antodo, *Anthoxanthum odoratum*; Apipro, *Apium prostratum*; Aspbul, *Asplenium bulbiferum*; Bledis, *Blechnum discolor*; Blenov, *Blechnum novae-zelandiae*; Blepen, *Blechnum penna-marina*; Blepro, *Blechnum procerum*; Brarad, *Brachyscome radicata*; Brarot, *Brachyglottis rotundifolia*; Brybil, *Bryum billardierei*; Camcla, *Campylopus clavatus*; Carser, *Carpodetus serratus*; Chinov, *Chiloscyphus novaezeelandiae*; Chisem, *Chiloscyphus semiteres* var. *semiteres*; Chirub, *Chionochloa rubra*; Claagg, *Cladia aggregata*; Copace, *Coprosma acerosa*; Copcol, *Coprosma colensoi*; Coppro, *Coprosma propinqua*; Coprha, *Coprosma rhamnoides*; Crarob, *Craspedia robusta* var. *pedicellata*; Daccup, *Dacrydium cupressinum*; Desten, *Deschampsia tenella*; Dicbil, *Dicranoloma billardierei*; Dralon, *Dracophyllum longifolium*; Elyten, *Elymus tenuis*; Ficnod, *Ficinia nodosa*; Ficspi, *Ficinia spiralis*; Gensax, *Gentianella saxosa*; Grilit, *Griselinia littoralis*; Gunden, *Gunnera dentata*; Helfil, *Helichrysum filicaule*; Hetboc, *Heterostylus bociliatus*; Hiered, *Hierachloe redolens*; Hydnov, *Hydrocotyle novae-zeelandiae* var. *montana*; Hymrev, *Hymenophyllum revolutum*; Hypcup, *Hypnum cupressiforme* var. *cupressiforme*; Hyprad, *Hypochaeris radicata*; Lacbil, *Lachnagrostis billardierei*; Leotar, *Leontodon taraxacoides*; Lepjun, *Leptecophylla juniperina*; Lepsp., *Leptogium* sp.; Lepsco, *Leptospermum scoparium*; Leptra, *Leptinella traillii*; Leufra, *Leucopogon fraseri*; Luzban, *Luzula banksiana* var. *acra*; Lycvol, *Lycopodium volubile*; Macret, *Macromitrium retusum*; Metumb, *Metrosideros umbellata*; Micpus, *Microsorum pustulatum*; Myopyg, *Myosotis pygmaea* var. *pygmaea*; Myraus, *Myrsine australis*; Nerdep, *Nertera depressa*; Olecol, *Olearia colensoi* var. *grandis*; Oleopo, *Olearia oporina*; Ozolep, *Ozothamnus leptophyllus*; Panall, *Pannaria allorhiza*; Panart, *Pannaria arthroophylla*; Panlep, *Pannaria leproloma*; Peldil, *Peltigera dilacerata*; Permac, *Pernettya macrostigma*; Photen, *Phormium tenax*; Pimlya, *Pimelea lyallii*; Poaast, *Poa astonii*; Poabil, *Poa billardierei*; Praang, *Pratia angulata*; Psecor, *Pseudocyphellaria coronata*; Psephy, *Pseudocyphellaria physciospora*; Pserub, *Pseudocyphellaria rubella*; Pselut, *Pseudognaphalium luteo-album*; Ptesp., *Pterostylis* sp.; Ptyden, *Ptychomnion densifolium*; Ranaca, *Ranunculus acaulis*; Steram, *Stereocaulon ramulosum*; Stimar, *Sticta martinii*; Thufur, *Thuidium furfurosum*; Trilep, *Trisetum lepidium*; Uncunc, *Uncinia uncinata*; Viocun, *Viola cunninghamii*; Wahalb, *Wahlenbergia albomarginata*; Weirac, *Weinnmania racemosa*.

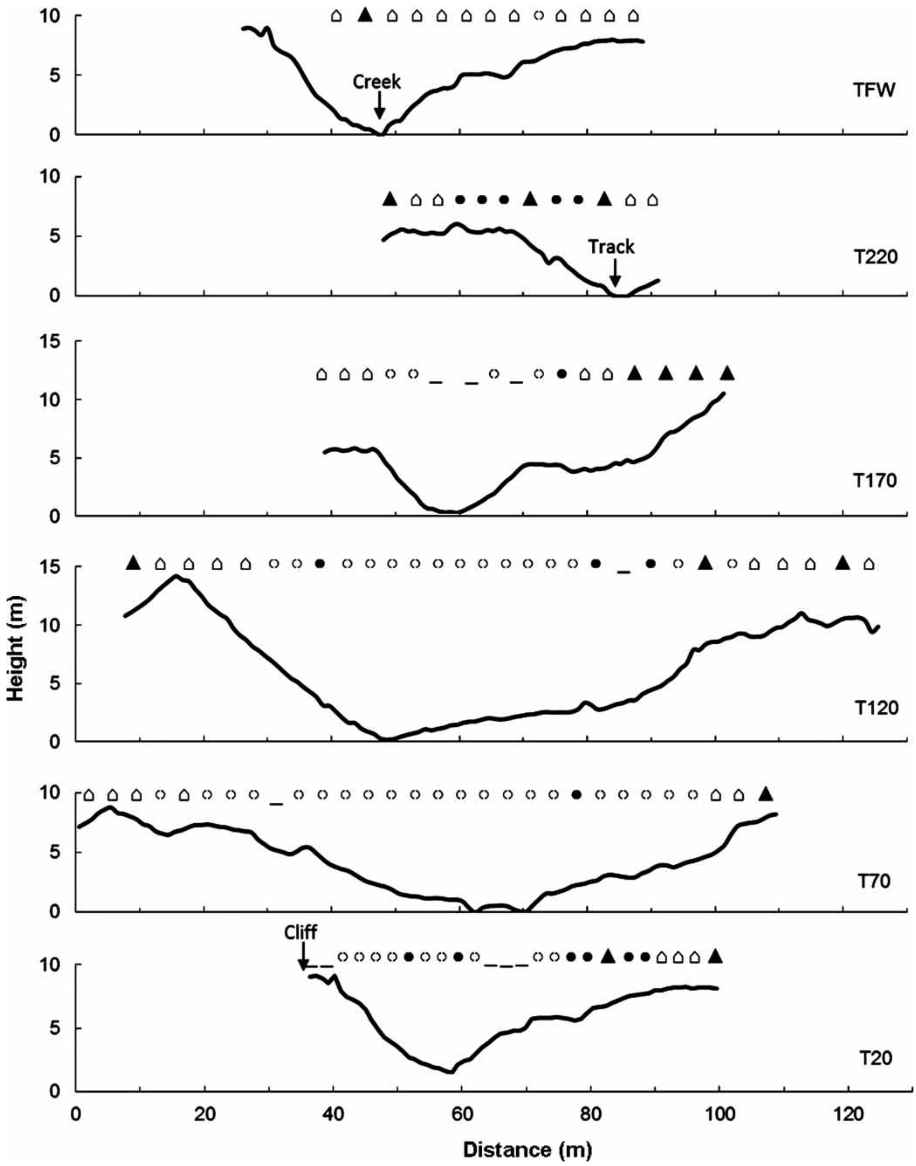

Figure 7 Profile diagram of the six transects surveyed on Big Hellfire Dune, with plant communities (bare sand _, open dune ○, pīngao dune ●, stable dune △, dune shrubland ▲) and notable features mapped. The vertical alignment of transects reflects the orientation of the dune.

Plant traits

Pernettya macrostigma was not found in the transect closest to the coast (T20), while *H. novae-zeelandiae* var. *montana* was not present over the Pass (TFW). Only one species, *A. microphylla* var. *pauciglochidiata*, has leaflets (6.2 per leaf, each with an area of 0.037 cm^2), with no significant differences between transects ($P = 0.23$). All other traits examined showed significant differences between species, as expected (Table 5), and most also showed significant differences between transects, and significant species by transect interactions.

Table 5 Significance values for leaf traits, which are significant for at least one of the two analyses, of seven species located on all six transects, and of the nine species found on four transects.

	Transect differences ($n = 6$) examined using seven species				Species differences ($n = 9$) examined using four transects		
	Transect effects	Species × transect	Error M.S.	Error d.f.	Species effects	Error M.S.	Error d.f.
Lamina thickness	**0.000**	**0.000**	0.023	349	**0.000**	0.023	301
Lamina length	0.072	**0.000**	32.519	351	**0.000**	22.520	302
Petiole length	**0.000**	**0.003**	4.468	342	**0.000**	4.414	294
Leaf length	**0.028**	**0.014**	47.766	351	**0.000**	36.434	302
Lamina width	0.484	**0.003**	0.214	351	**0.000**	0.200	302
Lamina width/ length	**0.000**	**0.000**	0.004	351	**0.000**	0.005	302
Lamina/petiole length	**0.000**	**0.000**	10.631	342	**0.000**	7.736	294
Lamina area	0.110	**0.001**	19.954	352	**0.000**	18.056	303
Leaf dry weight	0.152	**0.000**	0.025	352	**0.000**	0.021	303
Specific leaf area	**0.014**	**0.000**	995.07	352	**0.000**	613.61	303

Note: Petiole length includes the sheaths of monocots. Significant values ($P \leq 0.05$) are given in bold. M.S., mean square; d.f., degrees of freedom.

Of the species' traits, the herbs *A. microphylla* var. *pauciglochidiata* and *H. novae-zeelandiae* var. *montana*, and the prostrate shrubs *C. acerosa* and *Pernettya macrostigma* all had very small, thin leaves. *Brachyglottis rotundifolia* had the thickest, roundest, largest leaves, with highest dry weights and relatively low specific leaf areas (SLA; Table 6). *Craspedia robusta* var. *pedicellata* had intermediate values for size; its hairiness resulted in a high lamina thickness though its SLA was quite low. The poads had the longest, narrowest leaves, with greatest leaf areas, and relatively thick leaves.

The two largest values for lamina thickness were found in the two transects closest to the coast, with thinnest leaves in the top three transects (Table 7). Leaf length was significantly greater at T170 than any other transect, largely due to the long petioles, though laminae were also very wide there, and at the lowest transect. Petioles were shortest at TFW and T20, the two extreme transects. Laminae were widest per unit length at the lowest transects, becoming narrower upslope. Specific leaf area was lower in the lower transects.

In terms of the different ways in which species adapted to the different transects, 10 traits show significant interactions, though leaf length and lamina length were highly correlated ($r = 0.98$), and only the latter is reported. Short petioles were found in T20 for some species tested, and in TFW for others (Table 8). Species' values for all traits were variable at TFW (Table 8; Fig. 8), while size measurements for T170 were large. The transect closest to the coast was the most extreme in terms of small leaf areas and dry weights for *Craspedia robusta* var. *pedicellata*, *F. spiralis* and *P. astonii*. By contrast *B. rotundifolia* was relatively invariant trait-wise, except that leaf area and dry weight were greatest in this most exposed transect. Between transects, *H. novae-zeelandiae* var. *montana*, *Craspedia robusta* var. *pedicellata* and *Pernettya macrostigma* were the least variable (as a proportion of their largest values) for most traits, while the poads *P. billardierei* and *F. spiralis* were the most variable (Table 8; Fig. 8). The mid-dune environment produced the greatest values of leaf dry weight and petiole and lamina lengths for *P. astonii*,

Table 6 Values of the traits with significant differences per species, averaged over all four transects where all nine species were found.

	Acaena microphylla	*Brachyglottis rotundifolia*	*Coprosma acerosa*	*Craspedia robusta*	*Ficinia spiralis*	*Hydrocotyle novae-zeelandiae*	*Pernettya macrostigma*	*Poa astonii*	*Poa billardierei*
n	53	60	60	41	60	42	46	60	60
Lamina thickness (mm)	0.29^{a}	1.12	0.41^{b}	0.92	1.23	0.35^{a}	0.54^{c}	0.51^{c}	0.44^{b}
Lamina length (cm)	0.83^{a}	5.87	1.02^{a}	2.86	44.41	0.74^{a}	1.04^{a}	16.44	25.03
Petiole or sheath length (cm)	0.61^{a}	2.82^{b}	0.14^{a}	2.44^{b}	4.99	1.73	0.14^{a}	6.63	10.72
Leaf length (cm)	1.44^{a}	8.69	1.16^{a}	5.30	48.44	2.47^{a}	1.18^{a}	23.07	35.75
Lamina width (cm)	0.52^{b}	5.01	0.10^{a}	1.09	0.36^{b}	0.86	0.20^{a}	0.12^{a}	0.12^{a}
Lamina width/length	0.644	0.862	0.104	0.407	0.008^{a}	1.153	0.198	0.009^{a}	0.005^{a}
Lamina/petiole length	2.076^{ab}	2.141^{ab}	8.921	1.609^{a}	10.056	0.529	7.942	2.880^{b}	2.614^{ab}
Leaf dry weight (g)	0.002^{a}	0.834	0.001^{a}	0.038^{a}	0.340	0.005^{a}	0.002^{a}	0.028^{a}	0.045^{a}
Leaf area (cm^2)	0.24^{a}	24.63	0.09^{a}	1.99	9.11	0.52^{a}	0.16^{a}	1.01^{a}	1.54^{a}
Specific leaf area ($cm^2\,g^{-1}$)	146.9	30.1^{a}	109.0	56.2	27.6^{a}	128.2	71.1	39.9^{b}	41.3^{b}

Note: Values in the same row followed by the same letter are not significantly different according to Tukey's test. *n*, number of measurements.

Table 7 The values of the traits with significant differences per transect, averaged over all six transects in which seven species were found.

	Transects					
	T20	T70	T120	T170	T220	TFW
Lamina thickness (mm)	0.749^{c}	0.769^{c}	0.726^{b}	0.655^{a}	0.655^{a}	0.660^{a}
Petiole length (cm)	3.2^{a}	3.8^{b}	3.9^{b}	4.6^{c}	3.9^{b}	2.9^{a}
Leaf length (cm)	16.0^{a}	17.3^{ab}	16.0^{a}	19.1^{b}	18.4a^{b}	15.6^{a}
Lamina width (cm)	1.11^{b}	1.08^{ab}	1.00^{a}	1.10^{b}	1.00^{a}	1.03^{ab}
Lamina width/length	0.30^{b}	0.32^{b}	0.27^{a}	0.28^{a}	0.29^{ab}	0.28^{a}
Lamina/petiole length	6.33^{c}	4.23^{a}	4.08^{a}	3.74^{a}	5.27^{b}	5.36^{b}
Specific leaf area ($cm^2\,g^{-1}$)	63.2^{a}	63.1^{a}	57.7^{a}	64.0^{a}	72.9^{b}	76.4^{b}

Note: Values in the same row followed by the same letter are not significantly different according to Tukey's test. $n = 36$.

P. billardierei and *C. acerosa* (Fig. 8). By contrast, *F. spiralis* tended to show greater values, so that sheaths were longer, laminae wider and dry weights greater at higher altitude, although leaf thickness showed the reverse effect. Similarly, *A. microphylla* var. *pauciglochidiata* had higher leaf dry weights further from the sea. Except for *B. rotundifolia*, which is largely trait-invariant, and *F. spiralis*, which has an unusually low SLA at T220, plants, especially *C. acerosa* and *H. novae-zeelandiae* var. *montana*, built larger leaf areas per unit of leaf dry weight (SLA) further from the coast (Fig. 8).

Discussion

Geomorphology and environment

This study of patterns in vegetation, environment and leaf traits on Big Hellfire Dune provided an opportunity to assess an unusual climbing dune of Stewart Island. The study suggests that such deposits affect coastal vegetation patterns differently from those of sand dunes formed on planar surfaces, and that dune-based influences largely over-ride altitudinal effects in such an extreme environment.

The maximum altitude (220 m) of the dune is high compared with other New Zealand dunes. Nearby Mason Bay dunefield does not attain heights greater than 15 m (Hilton et al. 2005), though Big Sand Hill is 156 m. To the north, Smokey Beach has dunes to 30 m and East Ruggedy Beach to c. 100 m (GLR, pers. obs.). In the North Island, the extensive prograding Manawatu dunes are up to c. 15 m (Esler 1978), while the vast Te Paki dunefield reaches heights of 100 m (Hilton et al. 2000). Thus Big Hellfire Dune appears to be New Zealand's tallest active sand deposit, even reaching into the upper montane zone which starts at c. 200 m on Stewart Island (HD Wilson 1987), and so is within the range of aeolian transport of sand.

Big Hellfire Dune has remarkably uniform patterns of sand size, resulting in uniform rates of evaporation and water infiltration due to pore sizes between sand grains (Tsoar 2005). Similar proportions of fine grains (<250 μm) are found on the mobile prograding beach of Whatipu, northern North Island (Pegman & Rapson 2005), but the relatively stable Chrystall's Beach, South Otago (Drobner et al. 1995) has larger grains. Rock types contributing sand to Big Hellfire Dune are Ruggedy Granite, the bedrock under the dune, with coarse grain sizes of 7–10 mm, and Codfish Granite, which comprises the beach below Big Hellfire Dune, and has a medium grain size of 2–5 mm (Allibone 1991). Wind preferentially mobilizes smaller particles but there is no apparent sorting at Big Hellfire Dune, since a 2-m deep pit dug in the centre of the dune revealed no obvious layering.

The level of moisture on a sand dune is affected by wind, topography and weather patterns (Sykes and Wilson 1991), and in turn influences sand dune vegetation. Stewart Island is cold and windy with moderately high precipitation (annual average of 1467 mm), falling every other day (NZMS 1980; Peat 2000; NIWA 2011). But compared with 4.5% of wet weight at Chrystall's Beach (Drobner et al. 1995), and 9.7% at Whatipu (Pegman & Rapson 2005), moisture content of Big Hellfire Dune's sand was low (average 2.7%) and was 65% less moist on the surface than at depth. This vertical zonation of moisture is consistent with other studies (Zhang, 1996; Ozcan et al. 2010), but is not apparently stressing vegetation in this high rainfall regime.

Sea spray adds solutes to the sand, and T20 was the most saline transect. Solutes normally accumulate due to leaching (Tsoar 2005), to give higher conductivity at greater substrate depth (Olff et al. 1993; Ozcan et al. 2010), although on Big Hellfire Dune conductivity was higher in the upper layer. A similar pattern occurred at Cole Creek, South Island (Sykes & Wilson 1991), another high rainfall area (4500 mm year^{-1}). Compared with Sykes & Wilson (1988, 1989) salt concentration is probably not influencing vegetation on our upper transects due to high rainfall regimes.

Table 8 Values for variates with significant species × transect interactions.

	Acaena microphylla	*Brachyglottis rotundifolia*	*Coprosma acerosa*	*Craspedia robusta*	*Ficinia spiralis*	*Hydrocotyle novae-zeelandiae*	*Pernettya macrostigma*	*Poa astonii*	*Poa billardierei*
	$n = 4–10$	$n = 10$	$n = 10$	$n = 3–10$	$n = 10$	$n = 6–10$	$n = 7–10$	$n = 10$	$n = 10$
Petiole length (cm)									
T20	0.46	3.58	0.10	1.81	2.38	1.70	–	5.71	8.10
T70	0.48	2.69	0.15	2.25	5.15	1.67	0.16	6.42	9.35
T120	0.78	2.64	0.12	2.84	5.03	1.84	0.13	6.83	9.33
T170	0.47	3.14	0.14	1.85	6.20	1.78	0.14	7.42	13.15
T220	0.73	2.82	0.17	2.84	3.61	1.63	0.13	5.85	11.03
TFW	0.24	2.92	0.10	2.08	3.71	–	0.11	4.12	7.16
Lamina width (cm)									
T20	0.54	5.70	0.12	0.91	0.22	1.02	–	0.12	0.17
T70	0.49	5.24	0.11	1.16	0.30	0.77	0.20	0.12	0.17
T120	0.47	4.72	0.10	1.13	0.31	0.98	0.22	0.13	0.10
T170	0.61	5.62	0.10	0.80	0.42	0.94	0.20	0.12	0.10
T220	0.51	4.47	0.09	1.29	0.40	0.75	0.21	0.11	0.10
TFW	0.44	5.31	0.09	0.84	0.30	–	0.19	0.11	0.13
Lamina width/length									
T20	0.690	0.777	0.111	0.513	0.006	1.091	–	0.012	0.008
T70	0.684	0.913	0.122	0.500	0.008	1.122	0.186	0.008	0.006
T120	0.540	0.865	0.105	0.349	0.009	1.212	0.225	0.010	0.005
T170	0.631	0.818	0.112	0.396	0.009	1.186	0.190	0.010	0.004
T220	0.723	0.853	0.075	0.382	0.008	1.092	0.191	0.007	0.005
TFW	0.593	0.832	0.103	0.385	0.007	–	0.218	0.008	0.005
Lamina/petiole length									
T20	2.174	2.156	12.542	1.042	20.749	0.626	–	2.468	3.195
T70	1.793	2.215	10.325	1.166	7.656	0.483	7.112	3.324	3.116
T120	1.302	2.154	10.110	1.558	7.877	0.577	8.177	2.856	2.669
T170	2.914	2.270	6.713	1.426	8.572	0.530	7.733	2.155	2.101
T220	2.294	1.924	8.536	2.284	16.119	0.526	8.747	3.185	2.570
TFW	3.291	2.253	11.643	1.141	12.294	–	8.776	3.341	3.536

Table 8 (*Continued*)

	Acaena microphylla	*Brachyglottis rotundifolia*	*Coprosma acerosa*	*Craspedia robusta*	*Ficinia spiralis*	*Hydrocotyle novae-zeelandiae*	*Pernettya macrostigma*	*Poa astonii*	*Poa billardierei*
	$n=4$–10	$n=10$	$n=10$	$n=3$–10	$n=10$	$n=6$–10	$n=7$–10	$n=10$	$n=10$
Leaf area (cm^2)									
T20	0.219	32.850	0.108	1.261	5.891	0.776	–	0.721	2.481
T70	0.186	25.551	0.093	1.826	9.094	0.432	0.159	1.117	2.365
T120	0.243	21.701	0.091	2.657	8.916	0.677	0.158	1.101	1.200
T170	0.316	31.409	0.071	1.283	10.881	0.590	0.165	0.976	1.371
T220	0.212	19.865	0.092	2.190	7.556	0.397	0.168	0.861	1.203
TFW	0.204	26.119	0.070	1.443	7.276	–	0.139	0.753	1.909

Note: Some species were not present on some transects. *n* is given over the range of transects in which the species was present. Dash, no species located at this transect. T20–TFW, transects (see text for details).

Organic matter aids in the retention of moisture and nutrients, and ameliorates the substrate for plant species (Olff et al. 1993). The mean organic matter content was comparable with those at Cole Creek (Sykes & Wilson 1991) and Whatipu (Pegman & Rapson 2005), although lacking the higher values found at those sites, perhaps because of the absence of organic-rich dune slacks (winter-wet hollows; e.g. Roxburgh et al. 1994). The presence of high levels of organic matter is also a sign of a more advanced successional stage, as woody species contribute debris to the upper sand layers, especially compared with the deeper layers (Smith et al. 1985; Olff et al. 1993; Ozcan et al. 2010). On Big Hellfire Dune the very low level of organic matter, and its spatial and depth-wise uniformity, indicate that the sand is probably blown on top of the shrubland, rather than the shrubland growing on the dune, developing an organic soil as does so. This phenomenon is not restricted to Big Hellfire Dune, as coastal muttonbird scrub and the rātā/rimu/kāmahi forest which form further inland both contain aeolian dustings of sand, applied during storm events. Sometimes these dustings accumulate into dune fragments, similar to the side dunes mentioned above.

Positioned on the circumpolar wind belt, the prevailing Stewart Island wind is westerly (Brenstrum 1998). The average wind speed for the Big Hellfire Dune was 7 m s^{-1} on the three occasions it was possible to measure the entire dune, and this is probably typical, although little sand movement was recorded at those speeds. In comparison, New Zealand's windiest location, Wharite Peak in the Manawatu, has a mean daily wind speed of 44 km h^{-1} (Burgess 1989), only 1.8 times faster. Winds encounter Codfish Island/Whenua Hou (250 m in altitude), located 4 km northwest of Big Hellfire Beach, and are redirected around the island, depositing sand in the vicinity of Big Hellfire Beach. The topography of Ruggedy Range is very steep, facilitating formation of an altitudinally elongated sand deposit, given adequate sand supply and transport.

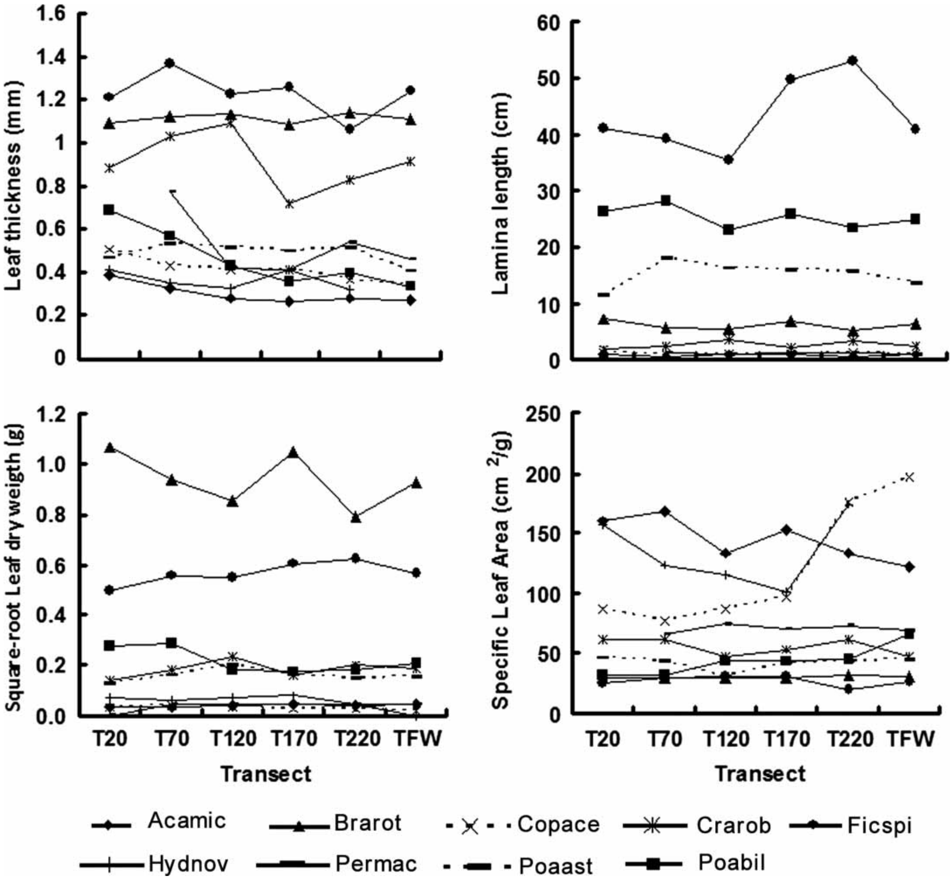

Figure 8 Species by transect interactions for leaf characters with large, significant effects. **A,** Leaf thickness. **B,** Lamina length. **C,** Square-root of dry leaf weight. **D,** Specific leaf area. Abbreviations: Acamic, *Acaena microphylla*; Brarot, *Brachyglottis rotundifolia*; Copace, *Coprosma acerosa*; Crarob, *Craspedia robusta*; Ficspi, *Ficinia spiralis*; Hydnov, *Hydrocotyle novae-zeelandiae*; Permac, *Pernettya macrostigma*; Poaast, *Poa astonii*; Poabil, *Poa billardierei*.

When winds hit the cliff located immediately north of the base of Big Hellfire Dune they are further funnelled up the gully to the Pass, losing sand progressively with altitude. This combination of phenomena may be responsible for the formation and maintenance of Big Hellfire Dune.

Floristics and vegetation

Big Hellfire Dune had a very diverse flora, with 86 species recorded, including 3 exotic and 13 forest species, a much greater diversity than most other New Zealand dunelands. The Tangimoana dunes in Manawatu, North Island, have 49 native species (Ogle & Singers 2001), while Chrystall's Beach, southern South Island, has 33 (Drobner et al. 1995). Cole Creek, Fiordland has around 58 species, disregarding those of rear dune forest (Sykes & Wilson 1991). Many native dune species, including the foredune sand binder *Spinifex sericeus* and the sand daphne *Pimelea arenaria* (Dawson et al. 2005) are not naturally present on Stewart Island, making its observed diversity even more unexpected. This supports Hilton et al.'s (2000) suggestion that many dunes on the larger New Zealand islands have suffered from species' loss due to anthropogenic disturbances and introduction of exotic species. Alternatively, the environments of Big Hellfire Dune, and similarly of Cole Creek, may be especially compatible with high floristic diversity, suggesting a role for high rainfall in ameliorating coastal influences.

Both Chrystall's Beach and Tangimoana dunes have significant numbers of exotic plant species (42%–64% of the flora; Drobner et al. 1995; Ogle & Singers 2001). Of the three exotic species identified on Big Hellfire Dune (< 5% of the flora), none was abundant. *Hypochaeris radicata*, a common plant on dunes in both its natural European range and New Zealand (Roxburgh et al. 1994), is scattered throughout the more open communities at Big Hellfire Dune, but appears unable to penetrate the local forest. It may not directly compete with native dune species (following Stanisci et al. 2010). The exotic sand binder *Ammophila arenaria* (marram), deliberately planted throughout New Zealand (McKelvey 1999), destabilizes foredunes through its inability to grow downslope, and excludes native sand-binders (Hilton et al. 2005), which cannot compete during summer droughts (Dixon et al. 2004). Not currently present in the study area, marram fragments disperse in large storm events (Hilton et al. 2005), and so Big Hellfire Dune is at ongoing risk of invasion.

Dune vegetation often experiences sand burial, wind blast, sea spray and salt deposition (Sykes & Wilson 1989, 1990a, 1990b; Udo & Takewaka 2007; Ogura & Yura 2008). The effects of salt have been shown to be more important than burial for some dune species (JB Wilson & Sykes 1999), and where developed, soil characteristics are more important than other factors (Lane et al. 2008), while sand blast appears to exacerbate the effects of salt spray (Ogura & Yura 2008). Trait analysis can give some understanding of the degree of adaptation of plants to their local environment, either by genetic means or via plasticity (Bradshaw 1973). Plant traits of sand dune species often change clinally with respect to distance from coast, reflecting severity of coastal influences (Smith et al. 1985; Stanisci et al. 2010), although some species are unresponsive (Garcia-Mora et al. 1999).

Open vegetation is the pioneering community of dunes (Esler 1978; Sykes & Wilson 1991; Widodo 1997; Hilton et al. 2000; Dixon et al. 2004; Pegman & Rapson 2005). The Open Dune community of Big Hellfire Dune is the most barren (95.6% bare ground), and has the lowest species richness. A more mature successional stage, where more species are able to establish as other influences, such as sand, wind and salt spray are reduced (Kennedy 1978; Partridge 1983, 1992b; Widodo 1997; Hay et al. 2004), is the Pīngao Dune community. It contains a range of herbs and shrubs, including *C. acerosa*, widespread on dunes throughout New Zealand, *P. astonii*, associated with coastal vegetation from Otago Peninsula to the Snares Islands, south of Stewart Island (Kennedy 1978; Partridge 1983; Hay et al. 2004) and *Apium prostratum* which inhabits coastal areas of the lower South Island, and can persist under high salinity, moderate alkalinity and high conductivity (Allen et al. 1997). Both the Open Dune and Pīngao Dune communities are dominated by *F. spiralis* with traits showing it as adaptable to transects characterized by strong winds, low sand stability and salty substrates, i.e., closer to the coast. However, its SLA is low at the Pass, perhaps a result of drier conditions there (following Hoffman et al. 2005). In terms of leaf traits, *P. astonii* is only slightly less stressed at medium and high altitude transects than it is at the coast. This suggests salt spray is having little effect on leaf morphology through water loss and osmoregulatory processes (Maun 1994; Ogura & Yura 2008). Similarly *P. billardierei*, which is now extremely rare on mainland New Zealand (Johnson 1992; Partridge 1992a), is present on open sand in all communities. Unaffected by salt spray (Sykes & Wilson 1988), its growth is negatively affected by total, although not partial, burial (Sykes & Wilson 1990a), suggesting it can cope with relatively mobile dunes. This coincides with our results, which found it growing bigger leaves in the most coastal transects.

The Stable Dune community had the highest species richness, with three dominant shrub species. *Ozothamnus leptophyllus* occurs in vegetation ranging from stabilized dunes to montane shrubland (Esler 1978; Bergin 2008). Although *D. longifolium* associates with muttonbird scrub (Hawke & Newman 2007), it also occurs in montane plant communities (HD Wilson 1982; Onipchenko et al. 2005). With a similar range from coast to alpine (HD Wilson 1982), *Pernettya macrostigma* was also common in the Stable Dune community, although on sand dunes at Chrystall's Beach it is usually associated with cushion communities (Drobner et al. 1995). Like *B. rotundifolia*, *Pernettya macrostigma* is remarkably trait-invariant (although leaf areas are very small in TFW), and it is unlikely to be nearing its altitudinal limit. *Brachyglottis rotundifolia* is more abundant in Dune Shrubland which has taller shrubs, a higher proportion of vegetation cover, and is the only community in which ferns occur. It also has the highest proportion recorded of species typical of Stewart Island forests, such as *Dacrydium cupressinum* and *Weinnmania racemosa*, as well as foliose lichens, which are positively related to tree size (Buckley 2011). Although wind velocity and sand transportation rate are significantly reduced in densely vegetated areas (Udo & Takewaka 2007), leaves are generally expected be smaller in windier environments (Parkhurst & Louck 1972). This applies at Hellfire Pass Dune, where species have their smallest leaves at or over the Pass (especially *C. acerosa*, *H. novae-zeelandiae* and the largely invariant *B. rotundifolia*). Overall, the species in the Dune Shrubland community are a mixture of dune-specialists (as for the Open Dune communities), forest-specialists and species that have wide ecological amplitudes. Thus facilitation is likely the driver of succession on this dune, a general conclusion reached in most dune studies (Avis & Lubke 1996).

Unlike most other New Zealand sand dunes, Big Hellfire Dune does not display the typical dune forest succession running in bands parallel to the coast, such as those seen at Big Bay, northern Fiordland (Wardle 1991), Cole Creek, Westland (Sykes & Wilson 1991) and Tautuku Beach, south Otago (Smith et al. 1985). International dune studies also find vegetation gradients perpendicular to the coast (Keddy 1982; Lane et al. 2008). Instead, at Big Hellfire Dune, the vegetation bands are perpendicular to the coast along most of the length of the dune, to become parabolic towards and over the Pass, where sand supply is restricted. Despite its vegetation patterns, Big Hellfire Dune is clearly not a parabolic dune, which would form on a planar surface, after collapse of the foredune (Pye 1982). While the trailing arms of elongate parabolic dunes are formed of deep deposits of sand, at Big Hellfire Dune the margins are higher simply because of the gully's topography, and the sand there is actually shallow. Nor is there a nose, a crescent-shaped sand deposit on the leeward of a parabolic dune (Pye 1982), and instead the end of Big Hellfire Dune is a carpet and/or shelf of sand (possibly several metres deep) lying on the leeward side of Hellfire Pass. This dune is the most extreme example of a confined climbing dune known in New Zealand, and the only one which crosses a pass, suggesting the depositional regime to Big Hellfire Beach is very unusual.

Conclusions

The environmental conditions at the base of Big Hellfire Dune are similar to dunes elsewhere in New Zealand and the world (Sykes & Wilson 1991; Zhang, 1996; Hilton et al. 2000; Dixon et al. 2004; Pegman & Rapson 2005; Ozcan et al. 2010). While the top of the dune is at a montane altitude, plant associations common to coastal vegetation in New Zealand are still encountered, so coastal and dune patterns prevail over altitudinal ones. The only potential montane specialist we found, restricted to TFW, is *Gunnera dentata* (Mark & Adams, 1973), which appears a distinct taxon from the more coastal *Gunnera arenaria* (c.f. HD Wilson 1982), found on flatter areas of the dune, though not in any of our quadrats. Around the Pass the presence of *B. rotundifolia*, *C. acerosa*, *F. spiralis* and *P. billardierei* attests to the dune-like nature of the environment, caused by aeolian processes but ameliorated by high rainfall.

Human and deer trampling, deer browse and regular helicopter landings at the Hellfire Pass are likely to destabilize sand, which may negatively impact stable communities and lead to an increase in mobile dune communities (Smale et al. 1995; Hesp 2000; Lemauviel & Roze 2003). There are no bush tracks leading to the beach. Red deer (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*), which were introduced to Stewart Island for recreational hunting in the early 1900s, and human visitors make their own way down the dune through the low and sparsely vegetated Open Dune and Pīngao Dune communities. Trampling is less likely to be a problem for the stable dune and Dune Shrubland communities as these are difficult to penetrate. While the level and influence of trampling is unknown and further studies of the dune are required to determine their importance, it is unlikely there has been sufficient trampling to artificially perpetuate the Open Dune and Pīngao Dune communities, which instead probably owe their existence to ongoing sand deposition.

Though dunes were formerly common throughout New Zealand, few are as natural today as that of Big Hellfire Dune. Given the importance of this dune nationally, all threats to the Big Hellfire Dune should be minimized.

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