



# Created dune slack wetlands effectively host rare early successional turf communities in a dynamic dunefield, New Zealand

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## Abstract

Dune slack wetlands should be relatively unhindered by challenges in recovering the hydrology, geochemistry and biological structure affecting other created habitats, thus presenting a simple exemplar of restoration's success. The Manawatū coast, New Zealand, has one of the most actively prograding parabolic dunefields in the world. In 1992 a study of Tawhirihoe Scientific Reserve, Tangimoana, first described three significant wetlands in dune slacks, the floor of these wetlands containing several rare perennial turf-forming species (<4 cm tall), which were in decline. A practical experiment creating wetlands in 1996 resulted in appropriate turf habitat, and was repeated on a larger scale in 2008. A survey of the vegetation and environment of the 3 natural and 3 created wetlands was conducted in 2009–2010 summer. Seven vegetation communities were identified, the three earliest successional communities containing rare turf species. The largest wetland contained the broadest range of communities, but other natural wetlands were successional older. The most recently created wetland has only the earliest successional phase. All wetlands progressively infill with aeolian sand over the decades, rates depending on their locations and sizes, accelerating succession to exotic vegetation. Turf communities containing rare wetland plants appear to exist for only about two decades, highlighting their temporary nature. Deliberate wetland creation remains the most promising management strategy for their perpetuation in small reserves within dynamic dunelands, but even in these simple environments, restoration impediments are easy neither to predict nor to forestall.

**Keywords** Community · Dynamic · Dune slack · Excavation · Turf · Wetland

## Introduction

Wetland creation is common (terminology for origin of wetlands from Moreno-Mateos et al. 2012), though mostly for fresh-water macrophytes used for waste-water treatment or mitigation of pollution (e.g., Vymazal 2014; Wu et al. 2015; Wiegleb et al. 2017). Creation, re-creation or restoration of

wetlands for habitat provision is less common, and evaluation of success is generally with respect to changes over time (e.g., Craft et al. 2002; Kearney et al. 2013), with most studies indicating progressive improvement with respect to the functioning of reference wetlands (e.g., Campbell et al. 2002; Seabloom and van der Valk 2003; Zampella and Laidig 2003; Spieles 2005). However Moreno-Mateos et al.'s (2012) review of wetland restoration reported widespread failure of biological structure and geochemistry to reach levels similar to reference sites, even after decades, though hydrology was usually engineered appropriately.

Dunes have naturally high levels of dynamism with mobile substrates and strong, on/off-shore winds (Ranwell 1960; Hesp 2001). Consequently dune wetlands have simple hydrology while their geochemistry is largely that of pure sand (i.e., uniform and nutrient-poor), obviating these challenges to successful restoration. The remaining challenge, biological structure, is mitigated by possession of small floras of specialists, so that created dune wetlands are the simplest test of restoration success. While studies

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**Nomenclature** Follows Nga Tipu o Aotearoa (<http://nzflora.landcareresearch.co.nz>). Families are given only for turf species.

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of created dune wetlands are rare, Parikh and Gale (1998) reported on 3.2 ha in depressions in aeolian sand amongst sage scrub over heterogeneous rock (Anderson et al. 2015) in California's coastal ranges. The created depressions were lined with topsoil from "reclaimed" wetlands, adding both a seed bank and organic matter (referred to as "soil"). Natural hydrology was recreated well, and hand-seeding with native wetland and upland species recovered biological structure while abundance values converged on those of the reference wetlands (Parikh and Gale 1998).

An ideal situation to further test the efficacy of dune wetland creation is in New Zealand. The Manawatū dunefield, on the south-western side of the North Island, is the second-largest active dunefield in New Zealand at 16627 km<sup>2</sup>. Coastal and particularly dune areas of New Zealand have been extensively damaged by humans. Manawatū has lost the largest proportion (81.3%) of active dunelands in New Zealand, with only 2.3 kha remaining (Hilton et al. 2000). In addition to a number of rare habitats (Williams et al. 2007), the Manawatū dunefield hosts four rare plant species, and several rare bird species also use the area, generating unique conservation imperatives.

Manawatū's foredunes are actively prograding (Cowie 1963; McKelvey 1999) with annual rates of coastal accretion exceeding 1 m (Patrick Hesp pers. comm.). Sediment is contributed by the three big rivers draining the lower North Island, the Manawatū, Rangitikei and Whanganui Rivers, which debouch onto the coast within 45 km of each other (Esler 1970; McEwen 1987). In the last 150 years deforestation-activated erosion from the Tararua, Ruahine and Kaimanawa Mountain Ranges has increased supply of sediment to the coast. In addition, extensive use of the coast as a stock-droving route from 1840s to early 1900s (Saunders 1968; Hesp 2001; the beach is still a legal road today), resulted in destabilisation of the dunes by grazing (Esler 1969, 1970). Since the 1940s an extensive campaign of dune stabilisation planted pine forests (*Pinus radiata*, an exotic) on the hinterland, and *Ammophila arenaria* (marram, an exotic) on the foredunes (Esler 1969; McKelvey 1999). More recently stabilisation of foredune vegetation has changed to planting of the dominant native dune builder (silvery sand grass; *Spinifex sericeus*), superior due to its downward-growing stolons (Esler 1970).

Dunes on Manawatū's prograding coast are considered among the most migratory in the world (Hesp and Shepherd 2003). Where foredune vegetation is lost or disrupted, the prevailing on-shore wind erodes a "blowout". Hesp (2002) recorded 20 blowouts per km of unstabilised foredune along the coast near Foxton. Mobilised sand blows inland, the bulk of the dune rolling grain by grain over any vegetation, even tall pine trees (Rapson pers. obs.), either to stabilise into a toe-dune where the wind energy has subsided, or to dissipate over the hinterland. Muckersie and Shepherd (1995) reported

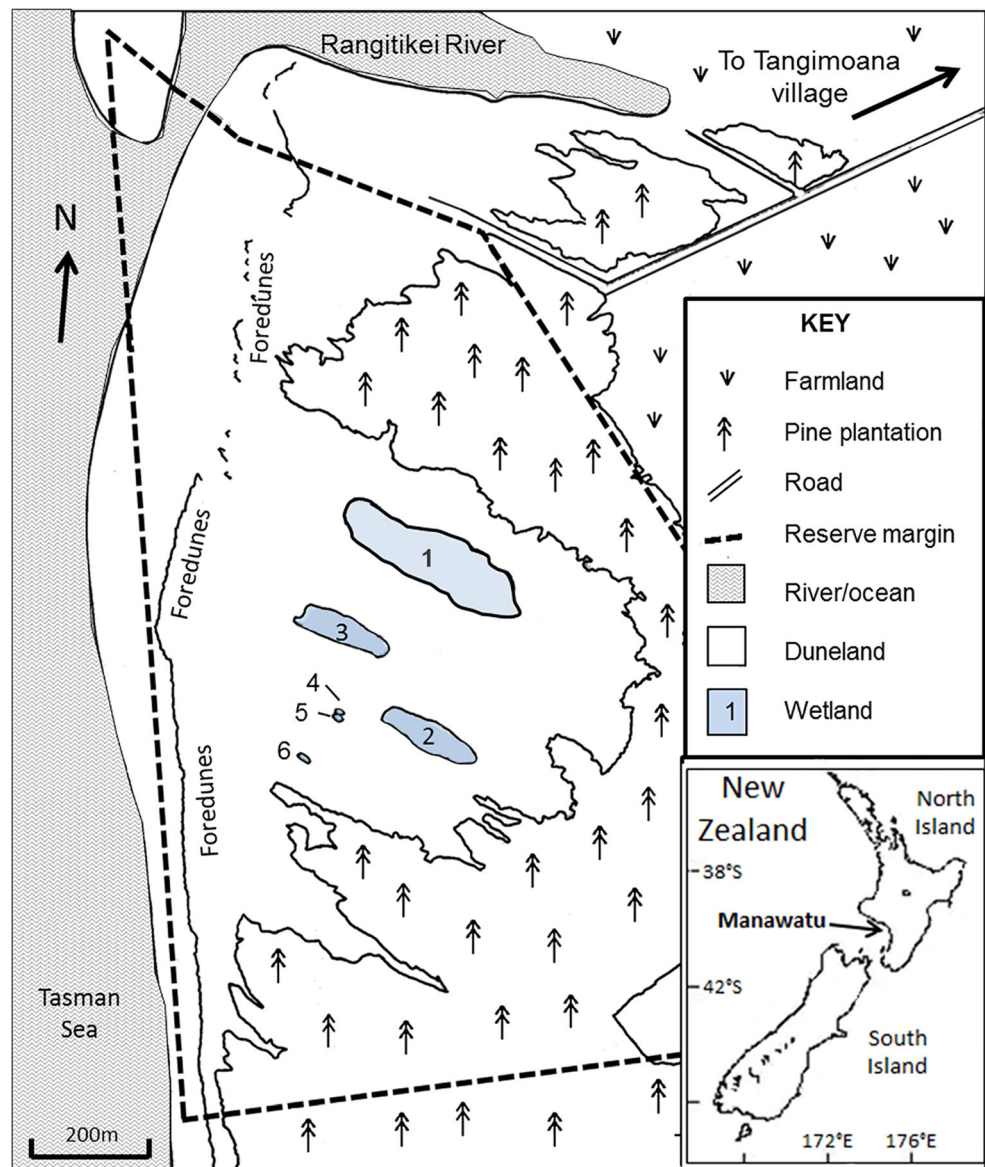
longitudinal migration rates of dunes as 1.5–5.1 m/yr as the norm, with small dunes capable of moving at 17 m/yr, while low sand ridges can roll over pasture at up to 400 m/yr (Hesp and Shepherd 2003). During migration, slower turn-over rates of sand at the more sheltered sides of the foredune blow-out result in formation of attenuated parabolic dunes (term of Semeniuk and Semeniuk 2011), which have long sand ridges trailing seawards ("horns"; Reitz et al. 2010). Oriented by the prevailing wind (Cowie 1963; Esler 1969), in Manawatū the parabolas form at 247 degrees true North (Esler 1969), and so slightly deviate from right-angled to the coast.

As the blown-out dune moves inland along the bearing of the prevailing wind it leaves behind a depression or dune slack, formed by ablation (aeolian stripping of sand from the depression; Esler 1969; Shepherd and Lees 1987). Ablation will generally occur down to the year's lowest water table, i.e., the summer's in New Zealand. In the winter the water table rises, filling the depression with water, and generating a wetland (Tansley 1949; Roxburgh et al. 1994; Singers 1997). In an exceptionally dry and windy summer, the floor of the depression may be stripped well below the normal water table, creating a wetland which has standing water even during average summers. The foredune gradually repairs itself as sand-binding plants establish, so the wetland is protected from blowouts for at least a few years.

Swales are depressions between beach ridges elongated parallel with the shore (Bates and Jackson 1987; Otvos 2000). The term "slack" is derived from the Old Norse word "slakki", and in dunelands means "damp or wet hollows left between the dune ridges" (Tansley 1949; Ranwell 1960), where the water table fluctuates seasonally (Grootjans et al. 1991; Curreli et al. 2013; Jones et al. 2017). Dargie (2000) noted these occur primarily in hind-shore systems, equivalent to the  $\beta$  slacks of Semeniuk and Semeniuk (2011). Ranwell's (1960) slacks all contain soil, and Wilson and Gitay (1995) describe a slack in the South Island of New Zealand as "a relatively flat area between dune ridges, with a humified sand substrate and with the water table above the surface for some part of the year". Most dune wetlands along the Manawatū coast are in relatively small, seasonally-wet depressions, almost at right angles to the shore, so can be regarded as slacks even though they are not humified.

The least stabilised, and most mobile, coastal dune system remaining in the Foxton Ecological District (Ravine 1992), Tawhirihoe (Scientific Reserve (pronounced "tar-firry-ho-e"; 40°15'10"S, 175°14'10"E; Fig. 1), was gazetted in 1999, management passing to the government's Department of Conservation (DoC). Located immediately south of the Rangitikei River mouth, near the township of Tangimoana and 45 km north-west of the city of Palmerston North, the reserve is roughly triangular, approximately 45 ha in size, with 1000 m of coastline, and extending up to 800 m inland. It is fronted by coastal foredunes, though near the river-mouth

**Fig. 1** Location of Tawhiriho Scientific Reserve, Manawātū, lower North Island, New Zealand, and of three natural (Wetlands 1–3) and three created (Wetlands 4–6) wetlands



these are continually being eroded by the mouth's ongoing southwards drift due to the southerly long-shore currents (Clement et al. 2010), this drift being periodically reset by flood events. The fine-grained sand (<0.5 mm) is feldspar and quartz, with a pH in the youngest dune phases of 6.4–7.8 (Syers and Walker 1969).

A broad-scale assessment of Tawhiriho's vegetation was carried out in 1992, prior to the establishment of the Reserve (Ravine 1992), and a more in-depth study by Singers (1997) focussing on three natural wetlands was conducted in the mid 1990's as part of a study of a rare wetland turf species, *Eleocharis neozelandica*, or sand-spiked sedge (Cyperaceae; Fig. 2; Given 1981). While exotic plants dominated many parts of the reserve, a diverse range of natives was present, including several nationally threatened species, such as the increasingly rare rear-dune shrub *Pimelea villosa* ssp.

*arenaria* (Thymeleaceae; Dawson et al. 2005; Burrows 2009). In the wetlands were perennial turf species generally less than 4 cm tall, forming form dense carpets or turves, either speciose or monotypic. These turves included the rare species *Eleocharis neozelandica*, *Isolepis basilaris* (Cyperaceae) and *Selliera rotundifolia* (Goodeniaceae; Fig. 2), this last a Manawātū endemic restricted to the Foxtangi coast (i.e., the coast between Foxtong Beach, on the Manawātū River's estuary, and the village of Tangimoana, near the Rangitikei River mouth; Fig. 1; Heenan 1997; Singers 1997; Rapson 2018b). The "Nationally Critical" species *Pimelea actea* (Thymeleaceae; Burrows 2008; de Lange et al. 2013; Rapson 2018b), a sub-shrub of open dune slacks, was planted at Tawhiriho in late 1995 (Singers 1998), as most of its remaining range further north had been subsumed into exotic forest during the Santoft dune stabilisation scheme (McKelvey 1999).



**Fig. 2** The specialist turf species of the dune slack wetlands. Scale bars are 1 cm high

In the 1990's concern grew that wetlands in the degraded Manawatū dunefield appeared to be “drying out” (technically, infilling with aeolian sand) to the detriment of the rare wetland turf species, and that there was an apparent absence of on-going formation of natural wetlands. Two experimental wetlands were created in January 1996 (Singers 1998), in bowl form following the interpretation of Cowie (1963). With the deepest end closest to the coast, and comparable with the water table of nearby natural wetlands, they were over-steepened at 30 m long and 6 m wide (Singers 1998). In each of the two created wetlands eighteen plants of *Eleocharis neozelandica* and 12 of *Isolepis cernua* (Cyperaceae), a common sedge, were planted prior to natural succession commencing (from Singers 1997). By the millennium, these created wetlands offered the only habitat sufficiently open to house the rare turf species. In June 2008 DoC excavated a larger wetland nearby to provide more habitat. It was dug *c.* 1.3 m deep to create a wetland 40 cm below the local water table (i.e. to be summer-wet) and was twice as long as earlier creations; the deep end was placed inland, following observations and logic re infilling patterns.

Dune wetlands offer a situation lacking most of the impediments to successful restoration noted by Moreno-Mateos et al. (2012), i.e. they have simple hydrology, vegetation and geochemistry. In this, the first reported study in such a dynamic environment hosting a turf flora, the lack of true replication and absence of continuous monitoring necessitates an inferential technique informed by three decades of observations on the dunelands. We assess the efficacy of management through comparison of natural and created wetlands via their environments, vegetation patterns and successional dynamics.

## Methods

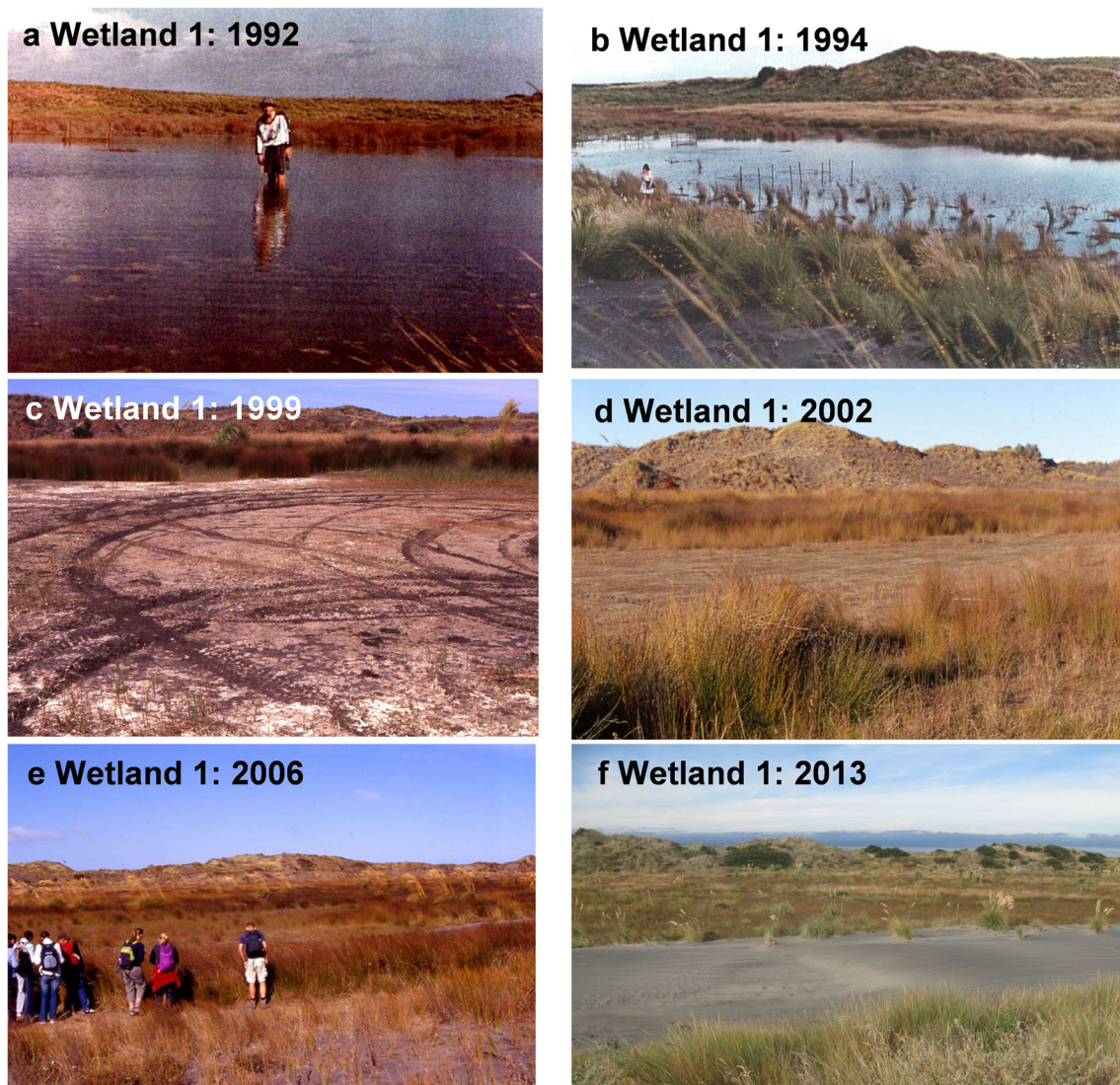
Six dune slack wetlands at Tawhirihoe Reserve are the focus of this study, three natural, numbered 1–3, and three created, numbered 4–6 (Fig. 1). Two of the three large, natural wetlands (Wetlands 1–2; Fig. 3) were the focus of work by Singers (1997), who excavated two of the created wetlands (4, 5).

## Environment

Rabbits are an exotic feral pest in these systems, which evolved in the absence of mammalian herbivory (King 1990). Their impacts were examined using Wetlands 1 and 2 as model systems for all the dune slacks. A 1.5 × 1.5 m enclosure plot in each wetland had wire mesh 1 m high but buried 10 cm into the substrate. These were compared with three-sided enclosures, open on the downwind side, to mitigate any sand trapping by the structure. Vegetation cover was assessed between January 1995 and March 1997 and trends plotted (Singers 1997).

Hydrological trends are likely applicable across all wetlands given the regional nature of the porous sandy substrate. They were measured in Wetlands 1 and 2 using, respectively, 8 and 11 porous tubes 1 m long and inserted 70 cm into the substrate. Water depth was recorded monthly for 2.4 years from June 1994 (Singers 1997, 1998). Results were averaged across each wetland, there being no robust trends within.

Since strong, often uni-directional environmental gradients impact on dune floras (Sykes and Wilson 1987, 1991), a transect was laid through the lowest portion of each wetland and along the long axis, with a shorter transect crossing the long one at right angles, both ending arbitrarily within largely exotic vegetation on higher ground. To increase the sample size



**Fig. 3** Changes in natural wetlands over time, with communities identified from past observations. *Wetland 1*: **a** 1992, measuring wetland depth, looking sou-west; **b** 1994, a full wetland with emergent enclosure plots, looking sou-east; **c** March 1999, the dry lowest-lying area in summer, with algal coating and off-road vehicle tracks, looking south; **d** May 2002, Turfed Wetland persisting in the lowest-lying area, looking sou-west; **e** March 2006, some central Rush Wetland surrounded by Mixed Rushland and, in front of the viewers, Oioi Rushland, looking

south; **f** March 2013; in the Oioi Rushland sward the lowest-lying area is on the far right, partly inundated by transgressive sand dunes, looking sou-west. *Wetland 2* (overleaf); **g** 1994, a full wetland, looking sou-west; **h** March 2000, standing water along the disturbed northern margin of an almost complete Oioi Rushland sward, looking sou-west; **i** October 2003; looking west over oioi (*Apodasmia similis*) with tufts of *Ficinia nodosa*; **j** March 2006, Oioi Rushland surrounded by Exotic Grassland, looking sou-west. Images: GL Rapson, NJD Singers

at Wetland 5, a small, high-value wetland created in 1996, an additional cross-transect was laid parallel to the coast. In the summer of January 2010, topography was surveyed using a level and staff, starting at 0.5 m along each transect, crossing the natural wetlands and Wetland 6 at 1 m intervals, and the smaller Wetlands 4 and 5 at 0.5 m intervals. Wetland area was derived from length and width for an ellipse.

### Plant communities

Because the full temporal or spatial range of plant communities was not known from within any one wetland, both natural

and created wetlands were analysed simultaneously to derive the successional sequence (an approach which implies restoration was successful). 328 quadrats containing vegetation were sampled in January 2010. Along the transect lines, but without overlap with the cross transect, contiguous 1 × 1 m quadrats were sampled in the created wetlands, while the larger natural wetlands were sampled contiguously only through the lowest elevations of the transects to focus on the relatively small areas of turf species, and every 5–10 m in other areas.

Within each quadrat, the maximum standing vegetation height, and percentage covers of exposed sand (<2 mm diameter), stones (≥2 mm diameter), wood, rabbit pellets, and live

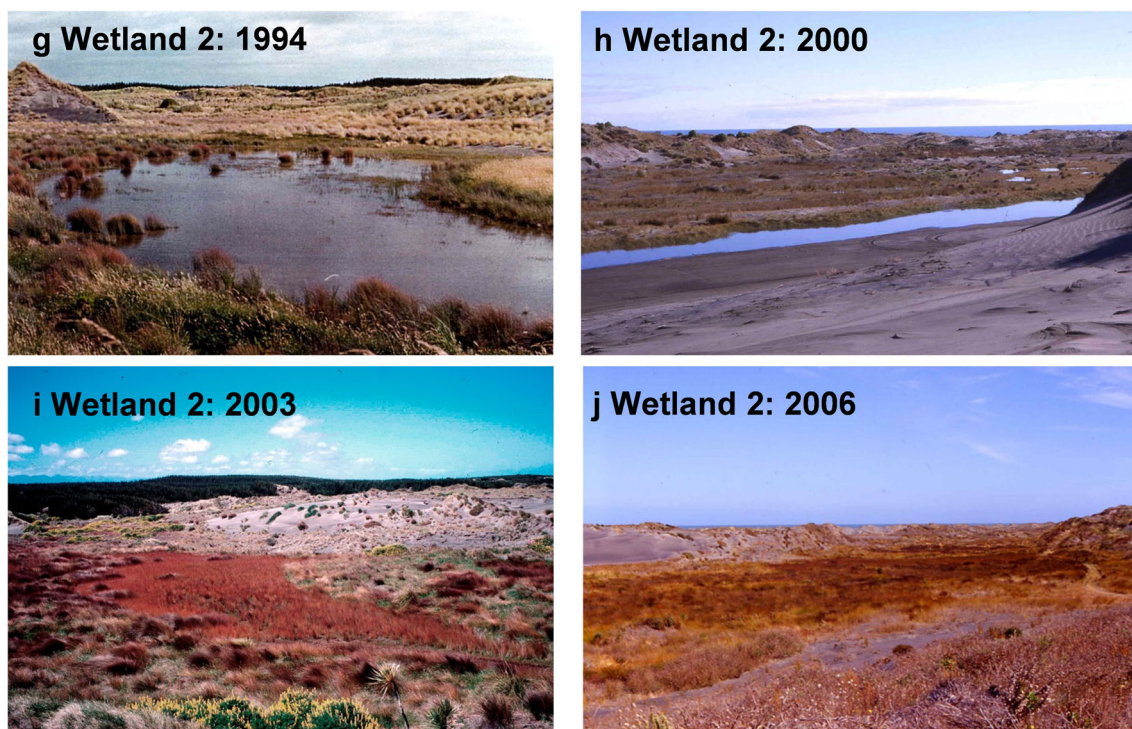


Fig. 3 (continued)

and unattached dead vegetation were recorded, as well as cover of each individual plant species. Cover was estimated as the vertical projection of all material or foliage of a single species onto a horizontal surface, effectively recording its shadow under solar zenith (Rapson 2018a). Very rare species were given an arbitrary value of 0.5%. Soil moisture was categorised as 0 (dry at surface) to 4 (wet). Depth of any standing water was measured, and defined as the wetland's water table. Topographic data were used to calculate the water table's distance below ground in the drier (higher) quadrats of the wetland assuming the water table was regional, giving positive (water table above the ground surface) to negative values (water table below). The water table's depth was inferred for drier wetlands by excavation or with respect to known water tables nearby. To facilitate comparisons despite the wetlands' various sizes, the position (Posi) of each sampled quadrat was expressed as the proportionate height above each transect's low-point (0), with the highest point of the transects assigned an arbitrary 1.

Structure in the species  $\times$  quadrat data matrix was examined using the Simprof routine in Primer 7 (Clarke and Gorley 2015). Vegetation types were identified using multivariate analyses, with preliminary analysis indicating percent cover data benefitted from square root transformation (c.f. Wilson 2007). Cluster analysis using SYSTAT (Systat 1998) based on Euclidean distance and Ward linkage metrics created a dendrogram which was pruned to give six groups, the most disparate of which was subdivided further, resulting in seven designated "communities", named descriptively. The

significance of all accepted nodes was examined using the procedure Simprof in the package "Clustsig" by Whitaker and Christman (2015) in the R computing environment (R Core Team 2014), employing the Ward-D metric (following Murtagh and Legendre 2014). A canonical correspondence analysis (CCA) of the quadrats using Canoco (ter Braak and Smilauer 2002) requires the species' scores to be linearly constrained by the imposed environmental variables, appropriate when the vegetation is strongly responsive to a limited number of factors (ter Braak and Smilauer 2002). The five uncorrelated variables (with Pearson correlations  $<|0.6|$  in SYSTAT) selected as constraining vectors were position with respect to the wetland's margins (Posi; see above), depth of the water table, percent sand cover, vegetation height, and proportion of vegetation cover in natives. The strengths of the axes were tested using 999 random permutations. The communities from the cluster analysis were superimposed on the CCA plot to clarify overlap, and successional trends identified.

### Natural v. created wetlands

The average species' composition and environmental variables of each wetland and each community were tabulated, as were the mean topographical and environmental variables. For the three created wetlands contour diagrams were drawn from the data, with communities plotted thereon. For the natural wetlands, where the topography between transects is less predictable, profile diagrams were used. Differences attributable to wetland origin were explored.

## Results

### Environment

All wetlands are within the Holocene dune field (Shepherd and Lees 1987; Muckersie and Shepherd 1995; Hesp 2001; inevitably so according to Semeniuk and Semeniuk 2011), extending 500–800 m from the current shoreline, and oriented west-sou-west with the prevailing wind (Table 1). The natural wetlands studied were larger (>20 times) than the created wetlands, and Wetland 1 is >55% longer than the other two natural wetlands. Natural wetlands tended to be bowl-shaped, with their lowest points midway or slightly closer to the coast (Fig. 3). The vegetation patterns over the wetlands form elliptic bands around the lowest point (pers. obs.).

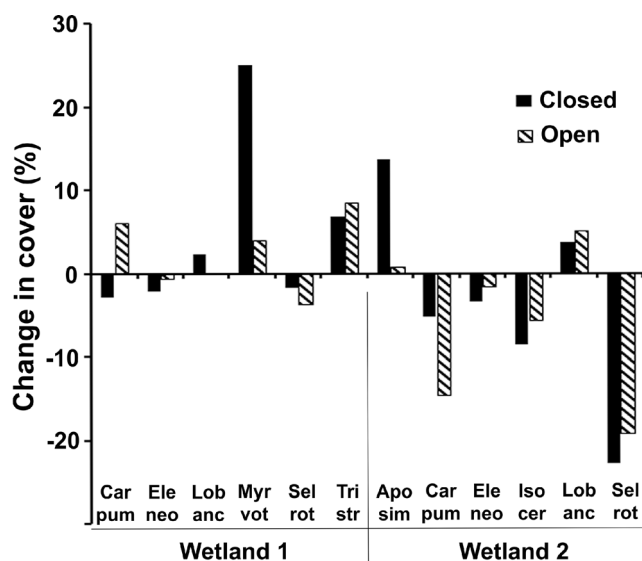
Vegetative cover increased in the herbivory plots of Wetland 1 by 20%, and decreased by 30% in Wetland 2 (Fig. 4). In Wetland 1 the open plot had a 50% smaller increase in vegetation cover than the plot which excluded herbivory. For Wetland 2 the closed plot had only 60% of the cover loss of the open plot. The only species which appeared to be reduced in the presence of herbivores were the restiad *Apodasmia similis* (named oioi, as in “oil”, by the indigenous Māori people; Fig. 7f) and the semi-aquatic *Myriophyllum votschii* (<2 cm tall; Haloragaceae; Fig. 2).

In the 1990’s both Wetlands 1 and 2 had standing water >30 cm for at least 5 wintery months in most years (Figs. 3, 5, and 6). The water table was planar between measuring pipes, never went below 50 cm deep even in summer, and was generally within 10 cm of the surface or higher for most of the

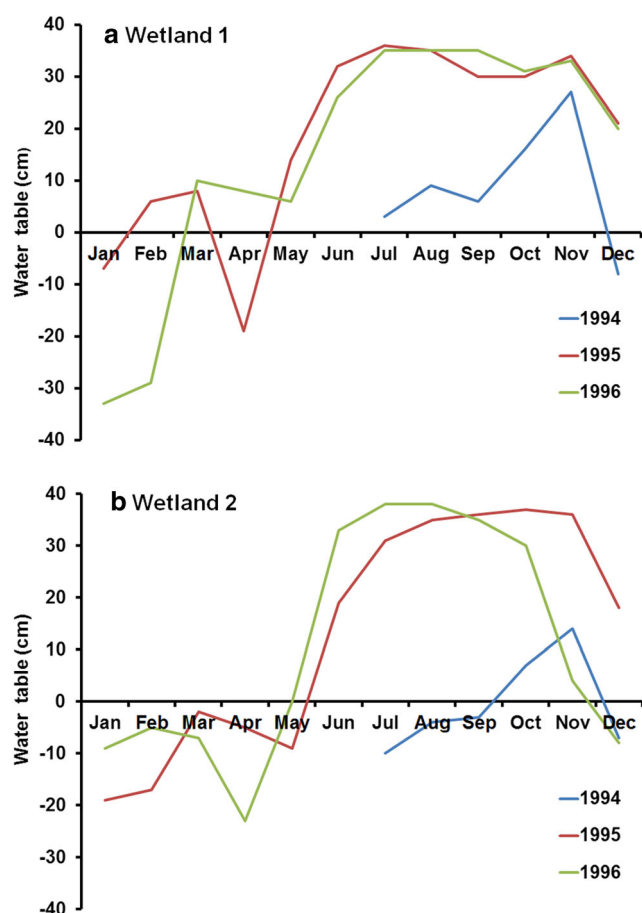
**Table 1** Wetland descriptors, mean environmental variables, and % coverages per quadrat of substrate, vegetative matter, turf species and other important species for each of the six wetlands sampled

Wetland	1	2	3	4	5	6
Origin or date of construction	Natural	Natural	Natural	1996	1996	2008
Wetland length (m)	290	180	150	27	23	50
Wetland width (m)	150	60	60	14	9	20
Wetland area (m <sup>2</sup> )	34,165	8482	7069	297	318	1571
Distance from coast (m)	300	530	325	380	380	350
Number of quadrats sampled	87	82	56	36	41	26
Mean height above water level (cm)*	12	49	32	2	−6	−29 <sup>#</sup>
Maximum depth of standing water (cm)	20	−8	−8	8	16	116
Vegetation height (m)	1.17	1.10	0.93	0.75	0.46	0.35
Soil moisture (scale: 0 = wet - 4 = dry)	1.6	1.7	1.5	2.9	2.8	3.2
Sand cover (%)	14.5	14.5	8.3	25.4	51.1	67.3
Stone cover (%)	0.1	0.0	0.0	4.2	13.9	30.3
Cover of live vegetation (%)	81.7	84.9	76.2	74.9	39.4	1.3
Cover of dead material (%)	6.4	3.3	23.0	3.7	0.8	0.2
Cover of turf spp. (%)	0.1	0.4	0.0	5.0	13.9	0.1
Number of turf spp.	5	4	0	4	4	2
Total number of species	49	47	35	24	24	21
Native cover (%)	54.3	67.2	54.3	65.1	27.8	0.8
Exotic cover (%)	29.7	21.0	24.9	14.6	14.4	1.4
Porportion of cover in natives	0.6	0.7	0.7	0.8	0.6	0.5
<i>Apodasmia similis</i>	35.2	45.7	11.1	18.1	6.3	0
<i>Coprosma acerosa</i>	0.4	1.2	1.3	0	0	0.04
<i>Eleocharis neozelandica</i>	0	0	0	0	0.9	0
<i>Ficinia nodosa</i>	9.1	6.4	17.4	5.6	1.7	0.5
<i>Isolepis basilaris</i>	0	0.01	0	0	0	0
<i>Isolepis cernua</i>	0.01	0	0	0.2	0.8	0.04
<i>Lilaeopsis novae-zelandiae</i>	0.01	0	0	0.07	0	0
<i>Myriophyllum votschii</i>	0.01	0.1	0	3.8	6.4	0
<i>Schoenus nitens</i>	4.5	11.1	20	33.9	4.2	0
<i>Selliera radicans</i>	0.02	0.2	0	0	0	0
<i>Selliera rotundifolia</i>	0.03	0.02	0	0.8	5.8	0.08
<i>Triglochin striata</i>	0	0	0	0.3	0.5	0

\*Height above water table was measured at time of sampling; negative values indicate water table below the surface. # - values include the 56 unvegetated quadrats



**Fig. 4** Herbivore-related change in percent cover of vegetation over time for Open and Closed plots in Wetlands 1 and 2. Species' codes are as per Table 2. Positive values indicate increase in cover



**Fig. 5** Seasonal water table changes over time, with respect to the ground surface (the 0 line) for Wetlands 1 and 2

year. By January 2010 the summer water table of Wetland 1 was still above the lowest point of the surface, but for Wetland 2 it was 8 cm below ground (Table 1), though still comparable with the summer ranges seen two decades earlier (Fig. 5).

Originally permanently wet, by 2005 Wetland 1's northern side and part of the remaining open wetland became overwhelmed by a mobile dune, creating an abrupt start to the cross transect (Fig. 3, Wetland 1: 2013). Over the subsequent decade, this accelerated the infilling of the whole depression. By 2010 Wetland 1's topographical variation was *c.* 1.2 m (Fig. 6), also featuring transgressive dunes deposited as crescents across its surface during dry, windy periods (Rapson, pers. obs.) and visible as highpoints at 60, 78, 165 and 210 m on the long transect of Wetland 1 and 35, 60 and 120 m on the cross transect (Fig. 6a, b). Originally the deepest of the three natural wetlands with respect to the water table, and still containing water in the summer of 2010, by 2015 even the lowest point was above the summer water table (Rapson pers. obs.). By March 2016 the centre of the wetland had been engulfed by the mobile dune, resulting in the loss of all turf vegetation.

Wetland 2 had a similar water regime to Wetland 1 in the 1990's (Figs. 5 and 6), but it appeared to infill much more quickly (Fig. 3, Wetland 2). However the presence, down its northern side (5 m along cross transect), of an active off-road vehicle track kept that edge open and compressed. Wetland 3 was little studied by Singers (1997), due to its relative paucity of turf vegetation (Table 1); even in the 1990's it appeared higher and drier than the other wetlands.

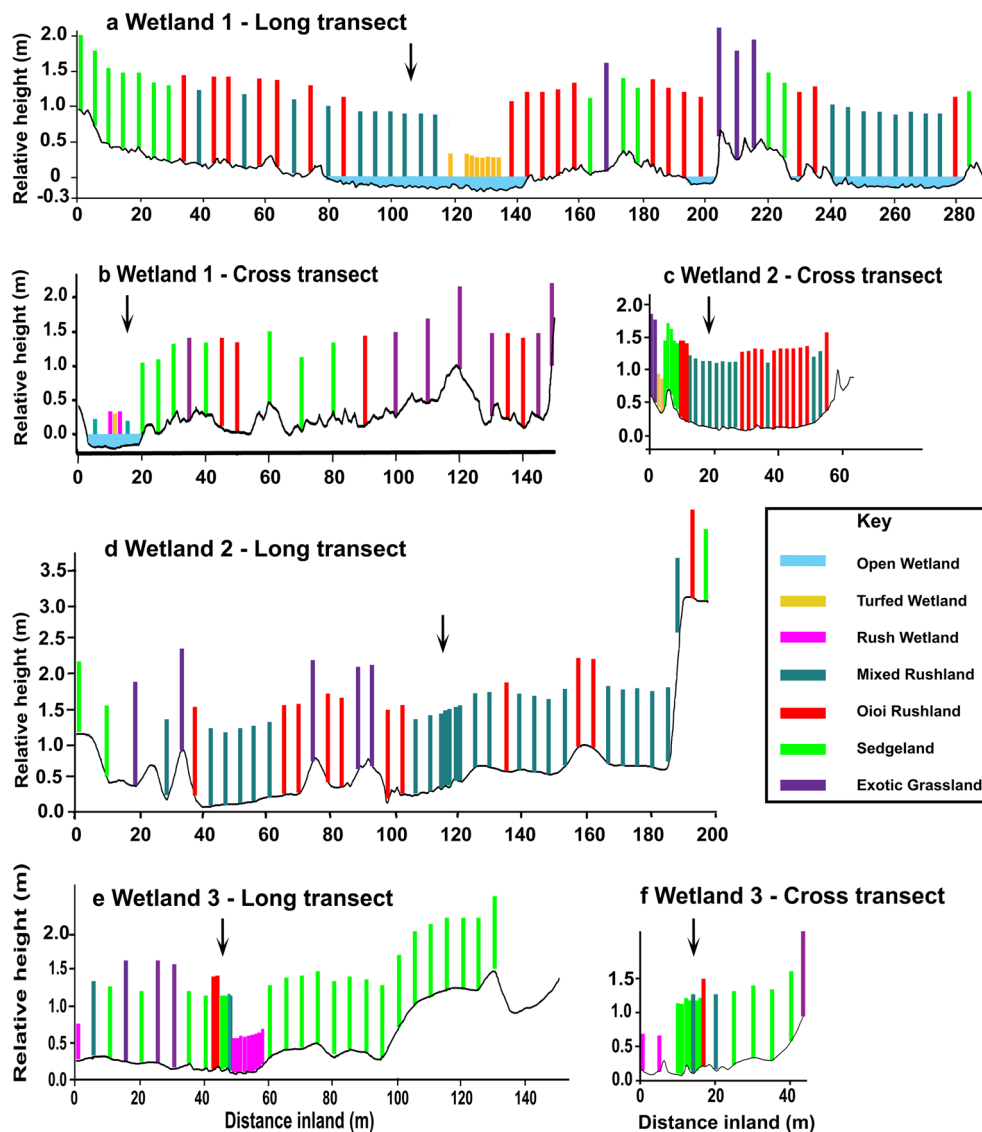
During the 2010 survey the two older created wetlands (4 and 5) were both relatively shallow, with height variation of *c.* 0.4–0.5 m below the general plane of the surrounding area (Table 1; Figs. 7 and 8). In mid-summer of 2010 they both had standing water, 7 cm deep in the case of Wetland 4, and 16 cm for Wetland 5, although they dried out by late summer (Rapson pers. obs.). Both still had extensive bare sand in 2010, and their location on a stony plain (probably an old river mouth of the Rangitikei) meant they had a high proportion of round river cobbles present (mean cover 9%; Table 1). Wetland 4 was the drier of the two, and by March 2016 was lacking bare sand. While about 5% bare sand remained in Wetland 5, patches of *Apodasmia similis* were widespread (Fig. 7). Wetland 6 was the deepest (1.16 m standing water was recorded in mid-December 2009; Table 1; Figs. 8 and 9), with standing water year-round (Rapson pers. obs.). By 2015 its water depth had decreased to about 70 cm, due to aeolian infilling and water-borne re-shaping of the depression.

## Vegetation analysis

A total of 70 species was sampled in the wetlands in 2010, with 40 (57%) being exotic (Table 2). Native species accounted for 42% of the vegetation cover and exotics 23%, the rest being bare sand.



**Fig. 6** Profile diagrams (both long-ways and cross-ways) of natural Wetlands 1–3, with the communities plotted along the transect lines in the same colours as for the CCA (Fig. 10a) and as bars of their average maximum heights. Light blue - water. Arrows - positions where transects cross; positions for Wetland 2 inferred



The Simprof analysis revealed there was significant structure in the data ( $p < 0.001$ ). Seven vegetation types, called “communities”, differing in both vegetation cover and species’ diversity were identified and named (Table 2), all being significantly different at the  $<5\%$  level. The dendrogram places the two short-statured communities adjacent (Open Wetland and Turfed Wetland are subdivisions of a single dendrogram branch), and closest to the Rush Wetland. Mixed Rushland and Oioi Rushland form the last cluster. The first two axes of the ordination explain 74% of the variation ( $p < 0.001$  by randomisation test), and support the Rushland cluster as distinctive (Fig. 10a). So the branch order linking the Wetland communities with the Sedgeland and Exotic Grassland clusters is attributed to the swamping effect of the dominant *Apodasmia similis* and discounted, to simplify interpretation.

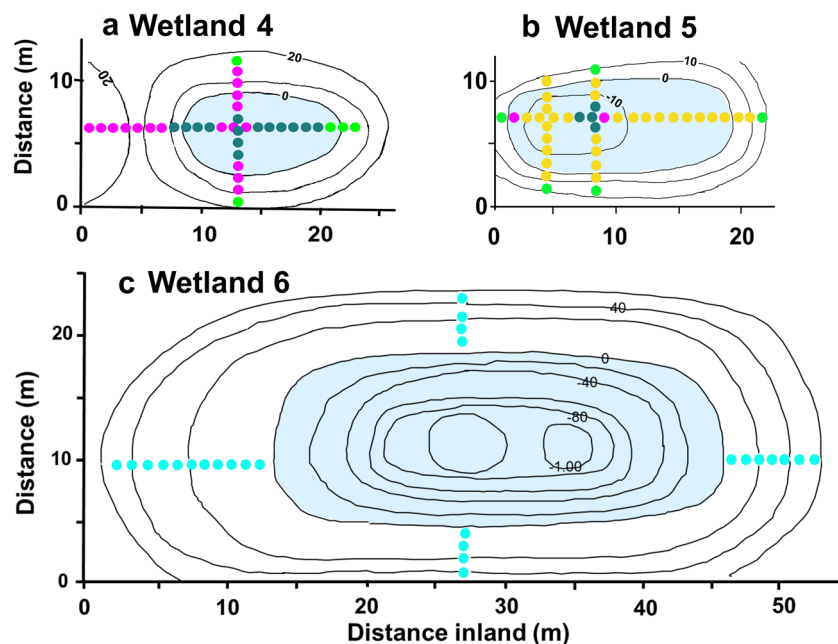
The ordination separates the applied environmental vectors, with sand cover and maximum vegetation height strongly opposed on Axis 1 (Fig. 10a). The height vector is strongly

associated with the presence of the native rear-dune shrubs *Coprosma acerosa*, *Coprosma propinqua* and *Pimelea villosa* spp. *arenaria*, as well as the arborescent monocot, *Cordyline australis*, which is still only present as “saplings” (Fig. 10b). High sand cover is associated with the wetland turf species *Eleocharis neozelandica*, *Lilaeopsis novae-zelandiae* (Apiaceae) and *Isolepis cernua*, along with *Carex pumila*, a small sedge ( $<20$  cm here) capable of building low dunes, but also equally tolerant of shallow wetlands, and consequently relatively widespread. *Epilobium billardioreanum*, *Lobelia anceps*, *Myriophyllum votschii* and *Schoenus nitens* are the natives associated with deeper water. The vector describing the proportionate coverage of natives (Axis 2; Fig. 10a) is opposed by the position of each quadrat with respect to the transect’s low-point (Posi). High values of Posi are associated with the exotic dune builder *Ammophila arenaria*, and a range of other exotic grasses and forbs, and low values with the wetland or estuarine species *Selliera radicans* and *Samolus repens* (Fig. 10b).

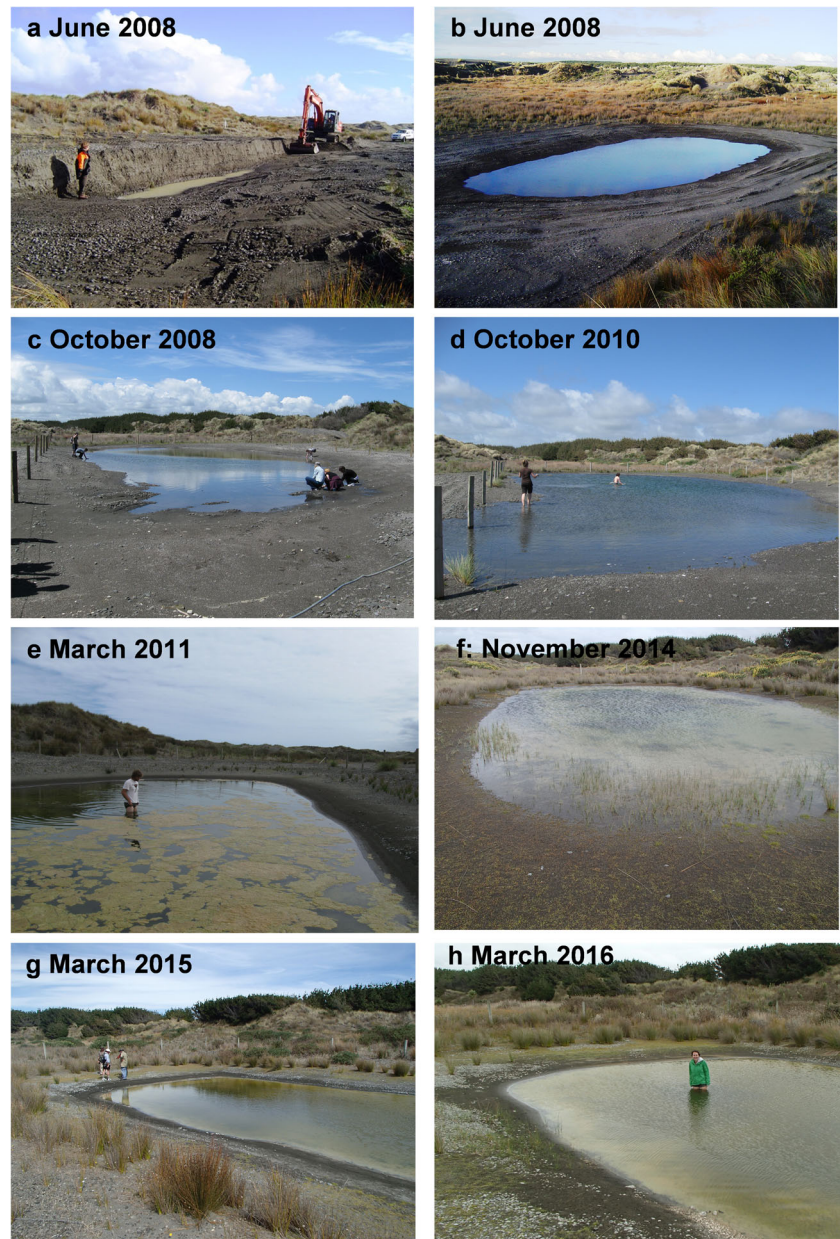
**Fig. 7** Changes in created wetlands over time. **a** 1992, excavation of Wetland 5 in a sand plain with occasional tussocks of *Ficinia nodosa*, looking sou-east; **b** 1992, wetland excavation against a foreground of scattered *Carex pumila*, looking sou-west; **c** 1998, across Wetland 4 to the adjacent Wetland 5, with sparse turf in the depressions, looking sou-east; **d** January 2010, Wetland 5, i.e., the depression running from top left to middle right in the image is dry with Turfed Wetland containing *Eleocharis neozelandica*, looking sou-west; **e** March 2010, half a dozen plants of *Eleocharis neozelandica* (at finger ends) remain amongst Rush Wetland in Wetland 5, looking north; **f** May 2015, *Apodasmia similis* dominating Oioi Rushland during winter high-water in Wetland 5, looking west. Images: GL Rapson



**Fig. 8** Contour plots of created Wetlands 4, 5 and 6, with the community types plotted as dots along the transect lines. The community types are plotted in the same colours as for the CCA (Fig. 10a). Contour lines are 20 cm apart vertically, and interpolated between transects using field observations



**Fig. 9** Changes in the largest created wetland (Wetland 6) over time: **a** June 2008, wetland under excavation, looking west; **b** June 2008, the newly finished wetland, looking nor-east; **c** October 2008, the wetland stabilises, looking east; **d** October 2010, depression full after winter with patches of *Selliera rotundifolia* forming an Open Wetland, looking west; **e** March 2011, peripheral ring of sedges establishing around the wetland, looking east; **f** November 2014, extensive carpet of *Selliera rotundifolia* with patches of *Isolepis basilaris* in a Turfed Wetland, the emergents being an unexpected stand of *Schoenoplectus pungens*, an estuarine plant, looking west; **g** *Isolepis basilaris* patches common close to the water-line, March 2015, looking sou-west; **h** March 2016, water table dropping during summer, exposing extensive Turfed Wetland, looking east-sou-east. Images: GL Rapson



## Plant communities

Of the seven communities depicted in the ordination, Open Wetland has the most bare substrate (Table 2; Fig. 10a). Its very low vegetation cover is of natives, and particularly *Isolepis cernua* and *Selliera rotundifolia*, the two most locally common turf species. Some exotics, including nitrogen-fixers, and the native sedge, *Ficinia nodosa*, are also present at low covers. The Turfed Wetland community has the highest cover of wetland turf species at 13%. It is dominated by *Myriophyllum votschii* and *Selliera rotundifolia*, although another three turf species are present, including the extremely rare *Eleocharis*

*neozelandica*, which is mostly found here (Table 2). The community is associated with high cover of bare sand and wet substrates, water being 8 cm above the ground surface on average. Vegetation is generally short, and species-rich though variable in composition. The Rush Wetland community is tightly linked to the vector for high depths of standing water, and is always close to the water table. Vegetation covers 67% of each quadrat, dominated by the small native sedge, *Schoenus nitens*, <15 cm tall in this environment. A large number of wetland turf species are present, though at low cover, including *Lilaeopsis novae-zelandiae* and tiny amounts of *Eleocharis neozelandica* (Table 2; Fig. 10a).

**Table 2** Mean environmental variables and species' covers of the most abundant or interesting species, for each of the seven communities identified from the wetland survey. Species' six-letter codes (see Fig. 10a) are of 3 letters from each of the generic and specific names. Standing water as in Table 1

Community name	Open Wetland	Turfed Wetland	Rush Wetland	Mixed Rushland	Oioi Rushland	Sedgeland	Exotic Grassland
Relative distance from transect lowpoint	0.85	0.42	0.39	0.42	0.42	0.62	0.62
Mean height above water level (cm)	34	-8	6	17	23	43	54
Maximum depth of standing water (cm)	4	20	18	16	14	1	-18
Vegetation height (cm)	35	46	60	102	123	106	123
Soil moisture (Scale: 0 = wet - 4 = dry)	1.42	2.75	2.60	2.10	1.90	1.26	1.23
Sand cover (%)	67.3	60.0	23.7	16.3	10.0	11.0	3.5
Stone cover (%)	30.3	7.0	4.0	1.3	0.0	2.7	0.0
Cover of live vegetation (%)	1.3	35.5	67.3	82.3	89.0	79.3	85.6
Cover of dead material (%)	0.2	2.1	13.6	3.2	4.0	12.5	15.5
Cover of turf species (%)	0.1	13.0	4.5	1.2	0.0	0.2	0.0
Total number of turf species	2	5	5	6	0	2	0
Total number of species	21	31	35	45	33	47	23
Species' number per quadrat	3.5	8.3	8.5	7.1	6.2	7.6	5.5
Native cover (%)	0.8	24.3	59.3	78.8	75.0	46.3	11.2
Exotic cover (%)	1.4	14.5	12.1	7.4	16.4	35.6	75.3
Proportion of cover in natives	0.46	0.59	0.83	0.91	0.83	0.55	0.13
<i>Ammophila arenaria</i> * (ammare)	0.19	0	0	0	0	0	0.23
<i>Apodasmia similis</i> (aposim)	0	5.58	3.16	50.44	64.90	7.81	3.20
<i>Arrhenatherum elatius</i> * (arrela)	0	0.25	1.34	1.02	4.10	4.83	59.55
<i>Austroderia toetoe</i> (austoe)	0	0	0	0.13	0.52	1.08	0
<i>Blechnum novae-zelandiae</i> (blenov)	0	0	0	0	0.10	0	0
<i>Carex pumila</i> (carpum)	0.08	1.25	0.09	0	0	0.01	0
<i>Coprosma acerosa</i> (copace)	0.04	0	0.31	0.08	2.23	1.05	0
<i>Coprosma propinqua</i> (coppro)	0	0	0	0.01	0.02	0.34	0
<i>Cordyline australis</i> (coraus)	0	0	0	0	0	0.47	0
<i>Cortaderia selloana</i> * (corsel)	0	0	0.47	0.35	2.60	0.96	0
<i>Dactylis glomerata</i> * (dacglo)	0	0	0	0	0	2.07	0
<i>Eleocharis acuta</i> (eleacu)	0	2.58	0	0	0	0	0
<b><i>Eleocharis neozelandica</i></b> (elenov)	0	0.86	0.01	0	0	0	0
<i>Epilobium billardiereanum</i> (epibil)	0	0.13	0.34	0.25	0.24	0.13	0
<i>Ficinia nodosa</i> (ficnod)	0.46	0.38	4.60	0.42	2.27	28.32	6.41
<i>Holcus lanatus</i> * (hollan)	0.02	0	0.24	0.42	3.06	8.10	5.18
<i>Hypochaeris radicata</i> * (hyprad)	0.23	1.15	2.20	1.54	1.02	3.53	1.48
<b><i>Isolepis basilaris</i></b> (isobas)	0	0.01	0	0.01	0	0	0
<b><i>Isolepis cernua</i></b> (isocer)	0.04	0.80	0.21	0.04	0	0.01	0
<i>Juncus articulatus</i> * (junart)	0	8.73	3.47	1.57	0.19	0.29	0.18
<i>Juncus caespiticus</i> (juncae)	0	0.16	1.56	0.34	0	0.01	0
<i>Lachnagrostis billardierei</i> (lacbil)	0.04	0.25	0.33	0.15	0.06	0.30	0.16
<i>Leontodon saxatilis</i> * (leosax)	0.04	0	3.30	1.66	0.10	0.28	0
<i>Lepidosperma australe</i> (lepaus)	0	0.20	0.11	0.01	0	0	0
<i>Leptospermum scoparium</i> (lepsco)	0	0	0	0.03	0	0	0
<b><i>Lilaeopsis novae-zelandiae</i></b> (lilnov)	0	0	0.07	0.01	0	0	0
<i>Lobelia anceps</i> (lobanc)	0	0.66	0.76	0.89	0.23	0.28	0
<i>Lotus pedunculatus</i> * (lotped)	0	0	0.01	0.39	6.01	6.69	7.18
<i>Lupinus arboreus</i> * (luparb)	0	0	0	0	0	1.18	0
<i>Medicago lupulina</i> (medlup)	0.23	0.01	0.21	0.17	0.10	2.39	0.14
<b><i>Myriophyllum votschii</i></b> (myrvot)	0	5.66	3.33	0.89	0	0	0

**Table 2** (continued)

Community name	Open Wetland	Turfed Wetland	Rush Wetland	Mixed Rushland	Oioi Rushland	Sedgeland	Exotic Grassland
<i>Oenothera stricta</i> * (oenstr)	0	0	0.01	0	0	0.13	0
<i>Pimelea actea</i> (pimact)	0	0	0	0	0	<i>0.01</i>	0
<i>Pimelea villosa</i> ssp. <i>arenaria</i> (pimvil)	0	0	0	0	<i>0.02</i>	0.01	0
<i>Rubus fruticosus</i> * (rubfru)	0	0	0	0	0.63	3.20	0.41
<i>Samolus repens</i> (samrep)	0	0	0.01	0.04	0.04	0	0
<i>Schoenus nitens</i> (schnit)	0	0.88	<i>42.06</i>	<i>24.09</i>	0.78	4.73	0.52
<b><i>Selliera radicans</i></b> (selrad)	0	0	0	0.24	0	0	0
<b><i>Selliera rotundifolia</i></b> (selrot)	<i>0.08</i>	<i>5.63</i>	0.90	0.05	0	0.18	0
<i>Triglochin striata</i> (tristr)	0	0.44	0.34	0.01	0	0	0
Total number of quadrats sampled	26	40	35	79	52	74	22
Number of quadrats in Wetland 1		9	2	20	24	21	11
Number of quadrats in Wetland 2		2		36	25	12	7
Number of quadrats in Wetland 3			14	4	3	31	4
Number of quadrats in Wetland 4			17	14		5	
Number of quadrats in Wetland 5		29	2	5		5	
Number of quadrats in Wetland 6	26						

Relative distance from transect lowpoint on 0–1 scale = Posi); \* - exotics; bold - turf species; italics in cover values - key species

Mixed Rushland retains a high cover of *Schoenus nitens*, but is dominated by the taller *Apodasmia similis*, at 50% cover, so the average community height is now 1.02 m. There is little bare sand (Table 2). The more common turf species are still present here, and there is a small appearance of *Selliera radicans*, segregated from the local endemic *Selliera rotundifolia* (Heenan 1997), and not usually considered sympatric. The ordination (Fig. 10a) presents this as one of the most tightly structured communities, with a strong relationship to the vectors for a high proportion of natives and to separation of the water table to the sand's surface.

The Oioi Rushland community is strongly related to the vector for vegetation height (Fig. 10a; Table 2). Dominated by *Apodasmia similis*, forming nearly three-quarters of the high cover and to 1.23 m in height, the community still contains 32 other species. It has no wetland turf species and there are only trace amounts of *Schoenus nitens* while *Ficinia nodosa* is frequent along with the rear dune shrub *Coprosma acerosa*. Covers of the exotics *Lotus pedunculatus* and *Holcus lanatus* are relatively high. Sedgeland differs from Rush Wetland by the dominance of *Ficinia nodosa* and low cover of *Schoenus nitens* and bare sand (11% cover). The widespread turf species, *Selliera rotundifolia* and *Isolepis cernua*, occasionally occur. But the community also contains both *Coprosma* and *Pimelea* species, forming a shrubby component along with 8% cover of the exotic grass *Holcus lanatus*. Exotic Grassland is the tallest and driest of the communities, with the highest proportion of exotic cover and a low species' diversity. Dominated to 60% cover by the tall exotic grass

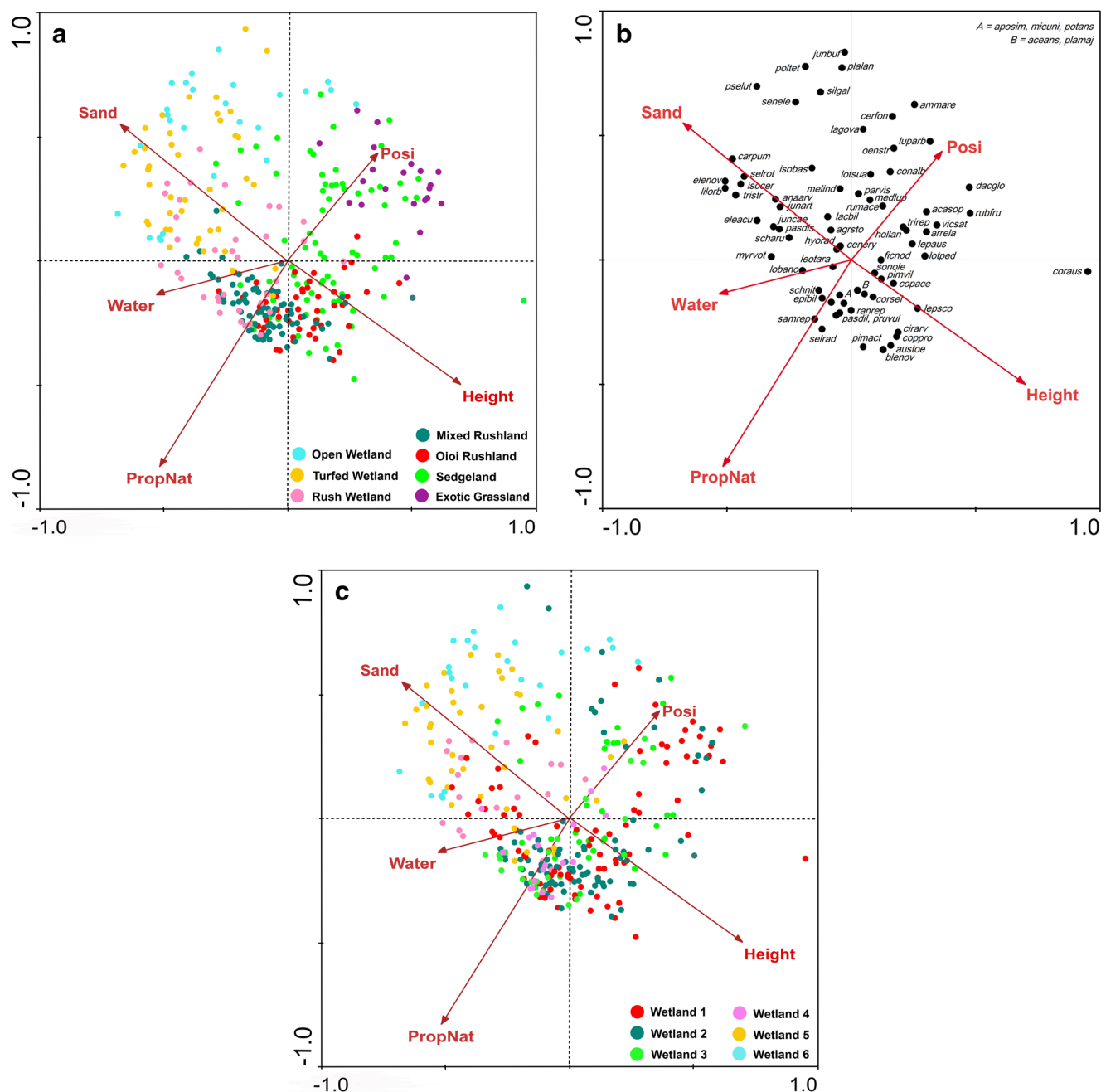
*Arrhenatherum elatius*, the exotics *Ammophila arenaria*, *Holcus lanatus* and *Lotus pedunculatus* have >5% cover.

### Natural v. created wetlands

In 2010, the created wetlands were wetter than the natural wetlands, in terms of maximum water depth and mean height above the water level, and had much greater coverage of bare sand and stones (Table 1). They had lower cover of shorter vegetation, lower coverage of exotics and fewer species.

Thirty eight species were found in created wetlands, to which seven species were restricted, being two otherwise common exotics (no exotics were at >2% cover in created wetlands), and five natives, including *Eleocharis neozelandica* and *Carex pumila*. Of the 63 species found in natural wetlands, 18 exotic species were only found there, as were 14 natives, including *Isolepis basilaris* and *Schoenoplectus pungens*, both subsequently becoming frequent in Wetland 6. The other natives in natural wetlands were mostly plants of shrubland. The most common native, *Apodasmia similis*, was found in all wetlands, but at highest cover in the natural wetlands, though in Wetland 3 it was partially replaced by 16% cover of exotic grasses. Wetland turf species were found in all except Wetland 3, but covers were high ( $\geq 5\%$ ) only in created Wetlands 4 and 5 (Table 1). Four turf species and three other short native herbs were more common in created than natural wetlands.

The ordination of the wetlands (Fig. 10c) separates the 3 created wetlands from each other, based on their sand and



**Fig. 10** **a** Canonical correspondence analysis with constraining vectors plotted over the quadrats sampled, and colours representing the 7 communities; **b** the species sampled, with codes upper right; and **c** with different colours representing the 6 wetlands. Codes, formed from the first 3 letters of the genus and the first 3 of the species, for the interesting species are in Table 2. The other species are: *Acacia sophorae*\*, *Aceana anserinifolia*, *Agrostis stolonifera*\*, *Anagallis arvensis*\*, *Centaurium erythraea*\*, *Cerastium fontanum*\*, *Cirsium arvense*\*, *Erigeron sumatrensis*\*, *Juncus bufonius*\*, *Lagurus ovatus*\*, *Lotus suaveolens*\*, *Melilotus indicus*\*, *Microtis unifolia*, *Parentucellia*

*viscosa*\*, *Paspalum dilatatum*\*, *Paspalum distichum*\*, *Plantago lanceolata*\*, *Plantago major*\*, *Polycarpon tetraphyllum*\*, *Potentilla anserinoides*, *Prunella vulgaris*\*, *Pseudognaphalium luteoalbum*, *Ranunculus repens*\*, *Rumex acetosella*\*, *Schedonorus arundinaceus*\*, *Senecio elegans*\*, *Silene gallica*\*, *Sonchus oleraceus*\*, *Trifolium repens*\*, *Vicia sativa*\*. Vectors are: Height - maximum height of vegetation per quadrat; Posi - the proportionate horizontal position of each quadrat with respect to the transect's low- and high-points (0–1 scale); PropNat - proportionate coverage of natives; Sand - cover of bare sand; Water - distance from the water table to the surface. \* - exotic

and water levels, and from the older, natural wetlands, which are linked by their vegetation heights and low proportionate covers of natives.

Most wetlands host 4–5 communities (Table 2), except Wetland 6 which contains only, and all of, the Open Wetland, which occurs above the summer water table on the

wetland's margins (Figs. 8 and 9). Found in three of the wetlands, Turfed Wetland is commonest in Wetland 5, the successional "younger" of the two wetlands created in 1996. Almost a quarter of the quadrats containing this community are also found in the central portion of Wetland 1 (Fig. 6a, b), and a small patch is found along a rough vehicle track on the cross-transect of Wetland 2 (Fig. 6c). The Rush Wetland community is dispersed through the natural wetlands, commonly so in Wetlands 3, but it also occurs in created Wetland 4. The profiles (Fig. 6) present it as in the damper areas of the older wetlands, though a group of Rush Wetland quadrats occur conspicuously in the dry (water = -10 cm) low-point of the long transect of Wetland 3 (Fig. 6e). The Mixed Rushland community is widespread and forms much of the matrix in the two largest natural wetlands in 2010. Oioi Rushland is most common in Wetlands 1 and 2, but not in the created wetlands. Sedgeland occurs in every wetland except Wetland 6, but is particularly common in Wetlands 1 and 3, where it occurs on the higher and drier margins (Fig. 6). Exotic Grassland is most frequent in Wetlands 1 and 2, and commonly on the higher crests of small transgressive dune ridges.

## Discussion

The apparent lack of on-going natural formation of wetlands resulted in creation of three new wetlands in Tawhiriho Scientific Reserve, all post-dating its natural wetlands. Three decades of observation of dune slack wetlands and their dynamics, facilitated by successional patterns occurring within as well as between wetlands, allow assessment of recovery of biological structure and hydrology in these very simple, geochemically-uniform and short-lived systems.

## Wetland formation

Our results demonstrate the brief longevities of these dune slack wetlands, the turf phases lasting about two decades and the pre-shrubland phases probably only 2–3 more decades, implying constant wetland turnover. One hypothesis for natural wetland formation is that it is continuous as and when suitable dune slacks arise behind foredune blowouts, which would result in a random distribution of wetlands. However this does not seem to be occurring currently, despite the recent appearance of a wet depression beside Wetland 1, as no wetlands have formed coast-wards of our studied wetlands during the last three decades, despite the presence of potential sites. Stabilisation of foredunes, originally via planting and more latterly by unassisted spread of *Ammophila arenaria*, accelerated by re-introduction of the native fore-dune binder, *Spinifex sericeus* (Esler 1969), may have caused the process of wetland formation through foredune blowouts to stall (Singers 1997; Dargie 2000).

A second hypothesis is that, in an environment of unstable dunes, wetlands form episodically during particularly dry, windy weather such as must have occurred during Manawati's history of dune instability and dune building (Cowie 1963; Esler 1969; Muckersie and Shepherd 1995; McKelvey 1999). Given a rapidly prograding coast, this would imply that wetlands should occur in belts along the coast, as they appear to do (Angelina Smith pers. comm.). The location and size range of wetlands along the coast requires determination as a guide to situations under which wetlands form as this has significant implications for wetland management and conservation.

## Wetland dynamics

Wetland infilling rates can be calculated for Wetlands 4 and 5, excavated as replicates in 1996 (Singers 1997). Assuming the surrounding ground surface has not changed in height, of which there is little indication, in 1997 Wetland 4 had a low-point of around 50 cm below the surrounding land (Singers 1998). This has decreased to about 20 cm by 2010 (Fig. 9a), an infilling rate of 2.3 cm/year. Wetland 5, while initially slightly shallower, reduced from 45 cm to 28 cm over 26 years (1.3 cm/year). Singers (1998) attributed the difference in infilling rate to the presence of a small but unstable sand dune (to about 10m<sup>3</sup>) upwind of Wetland 4. Estimating rates for the larger, natural wetlands, Wetland 1 had, on average, 7 cm of standing water for the summer months when first surveyed (from Fig. 5), and its centre half was 0.0 cm below the water table in 2010, indicating an infilling rate of 0.5 cm/year. For Wetland 2 the figure was 3.2 cm/year. The much lower rate for Wetland 1 is probably a consequence of the surrounding dry dunes supplying insufficient aeolian sand to infill such a large area. Additionally Wetland 2 is further from the sea (its seaward edge is the most inland of the natural wetlands), exposing it to a potentially greater volume of mobile sand from the surrounding dunelands. Initially at a similar stage of succession to Wetland 1 (Turfed Wetland), the enclosure plot data indicates that even by 1997 Wetland 2 was losing its turf species and becoming dominated by *Apodasmia similis* (Fig. 4). Wetland 6 was 116 cm deep at the time of our survey, and by March 2016 (peak summer; Fig. 9h) was approximately 74 cm deep, an infilling rate of 7 cm/yr., at least double expectations, especially given the limited sources of mobile sand in the vicinity. Thus as well as continuous infilling, wetlands also experience on-going ablation of dry surfaces during the summer months. The dynamic balance here merits exploration.

Micro-topographical variation within wetlands is due to deposition (presumably during dry periods) of small, highly mobile dunes, which then become vegetated in accordance with the water table (Fig. 6). These dunes customarily form

parabola-like lobes skewed to the south by the prevailing north-westerly wind. They conspicuously appear as a series of lighter-coloured bands of Exotic Grassland between darker crescents of Mixed Rushland or Oioi Rushland on aerial photos (Rapson pers. obs.). Such incursions reduce the surface area and viability of wetlands and hasten succession.

### Dynamics of rare turf species in dune slack wetlands

The two youngest natural wetlands still had 4–5 turf species present at the time of the survey, the almost ubiquitous turf species, *Isolepis cernua*, *Myriophyllum votschii* and *Selliera rotundifolia*, also being present in created Wetlands 4 and 5. *Lilaeopsis novae-zelandiae* was found only in Wetland 4 except for a tiny amount in Wetland 1, and *Eleocharis neozelandica* restricted to Wetland 5 (Fig. 7e), where it was planted in 1996 (Singers 1998). By 2017 all turf species except *Selliera rotundifolia* had disappeared from the wetlands, though the presence of a 4-wheel-drive track on the northern margin of Wetland 2 maintained viable habitat for *Isolepis basilaris*.

A primary incentive for the formation of Tawhirihoe Scientific Reserve was the presence of substantial populations of the tiny sand-spiked sedge, *Eleocharis neozelandica* (Ravine 1992), recorded as “At risk”, data-poor and subject to extreme fluctuations in population size by de Lange et al. (2013). Mostly <4 cm tall, it can grow to 10 cm in Northland and in fertile conditions in glasshouses (Rapson pers. obs.). Singers (1997) reported it as relatively widespread, occurring from Northland to Cape Farewell, and it forms extensive swards in both those areas (Rapson pers. obs.; Melanya Yuhnevich pers. comm.). Burgess (1984) recorded *Eleocharis neozelandica* as common (up to 25% cover) in three wetlands on the Foxtangi coast, but these slacks were subsequently forested. In 1994 Singers (1997) described it as common in Wetlands 1 and 2 and four other areas of Tawhirihoe Scientific Reserve, trapping sand to form raised mounds to 1 m when most common. Steadily declining over the years, the last population, planted in Wetland 5 and present during the survey, had died out by summer 2013. Readily germinating with 10% viability from field-collected seed (Singers 1998), it may persist in the seedbank (Bekker et al. 1999), to reappear when suitable habitat presents, although it is yet to occupy Wetland 6, the deepest of the created wetlands.

*Isolepis basilaris* (<2 cm tall) is classified as “Nationally vulnerable”, range-restricted and sparse by de Lange et al. (2013), though it may be more widespread nationally than thought (Melanya Yuhnevich pers. comm.). In addition to Wetland 2, it is found in several other small patches on open ground around the Reserve, though restricted to the more southern inland portion. Often on off-road-vehicle tracks, it is adapted to the situation of open, damp sand. In March 2016 it had conspicuously appeared beside Wetland 1 in a new depression formed the previous year, along with a few plants

of *Triglochin striata*, *Selliera rotundifolia* and *Lilaeopsis novae-zelandiae*. However it was much slower to enter Wetland 6, taking 6 years, 4 years after the survey. *Isolepis cernua*, its larger and more widespread congener, was scarce in Wetland 1, absent from the other natural wetlands, and present in the created wetlands at low cover.

*Selliera rotundifolia* is a local endemic species (Heenan 1997), probably restricted to the Foxtangi coast (but see Pilkington 2014). It was the earliest plant to invade the created wetlands, and entered Wetland 6 within the first 3 years, possibly from stem fragments moved during excavations, though it occupied the new depression beside Wetland 1 within 1 year. Generally common in slacks, and present in most wetlands during the survey, it persists until late in the succession, suggesting broad ecological tolerances. Its congener, *Selliera radicans*, was recorded from Wetlands 1 and 2 during the survey, but morphotypes can be hard to attribute (Pilkington 2014; Rapson 2018b). Ogden (1974) regarded these as ecotypic differences, though Pilkington (2014) found reproductive isolation in some populations of *Selliera rotundifolia*, and suggested possible polyphyly.

*Lilaeopsis novae-zelandiae*, locally called tape-measure plant because of its segmented leaf-like “phyllodes”, is occasional along the coast, and can grow to 20 cm high in fresh-water (Allan 1961). Common in Wetland 4 and scarce in Wetland 1, it also forms a large patch beside a vehicle track (where it is only occasionally driven over), in a swale about 100 m behind the toe of the foredune. It appeared in the new depression beside Wetland 1 by March 2016.

The aquatic *Myriophyllum votschii* forms dense terrestrial mats like true turf species. During the survey it was common in Wetlands 1, 4 and 5 and scarce in Wetland 2 though it had not occupied Wetland 6 by March 2016. Being extremely small, with leaves to 2 mm, it is probably more common in dune wetlands than realised, and is the most persistent of the turf species. At a prograding beach, Whatipu, Auckland, *Myriophyllum votschii* was found, along with *Limosella lineata*, in the Sand River community, where a fresh-water stream flows over the sand plain (Pegman and Rapson 2005). *Limosella lineata* is missing from Tawhirihoe though it occurs at several other sites along the Foxtangi coast, often forming extensive monotypic and pinkish swards (Angelina Smith pers. comm.). Two other turf species, *Ranunculus acaulis* and *Gunnera dentata*, were not encountered during the survey, but are known from a few other dune slack wetlands along the coast (Esler 1970; Angelina Smith pers. comm.). Their occurrences are very sporadic and their absence from Tawhirihoe Reserve unexplained.

The sward-forming species *Triglochin striata*, to 30 cm tall in estuaries, is present in early communities in the older created wetlands Wetlands 4 and 5, but does not occur at high cover and is <10 cm tall. Other common taller herbs, *Epilobium billardioreanum* and *Lobelia anceps* are regular



participants in dune slack vegetation (Esler 1969), being found occasionally in all older wetlands, and in all communities except Open Wetland and Exotic Grassland.

A native, rhizomatous binder capable of building dunes to 50 cm high, *Carex pumila* forms dense swards to 40 cm tall in other wetlands along the coast (Rapson pers. obs.). Singers (1998) reported that it emerged extensively in Wetlands 4 and 5 six months after their excavation, and in our survey it was most abundant (<2%) in the Turfed Wetland community, though probably dispersed from rhizomes fragmented during excavations. Burgess (1984) and Singers (1998) give it the role of wetland colonisation in dune slacks, but it is not found in any of our natural wetlands. Instead it appears to be a plant of slightly higher zones around wetland margins (see also Esler 1970).

*Pimelea actea* is a small sub-shrub to about 40 cm tall, which is extremely cryptic in the dune environment, though flowering and fruiting prolifically. Its “preferred” habitat seems to be on the still-damp margins of slacks. The species is in the highest category of threat, “Nationally critical” (Burrows 2008; de Lange et al. 2013; Rapson 2018b). Wetland 5 is close to where Singers (1998) planted 22 plants grown from cuttings in 1996, a fifth of which died during a dry period in 1997. Despite subsequent plantings at Tawhiriho (Department of Conservation, Vivienne McGlynn pers. comm.), only a dozen plants of *Pimelea actea* were known in the Reserve in 2015, those adjacent to Wetland 5 probably being natural descendants from Singers’ plantings. But none appear to have survived the hot, dry summer of 2015/2016. The conservation of this species is even more of a priority than for *Eleocharis neozelandica*.

### Natural successional sequence in dune slack wetlands

Pioneering dune slack vegetation from Europe is normally described as basiphilous, speciose and often marshy, with species >20 cm tall (Ranwell 1960; Sival et al. 1997; Barrett-Mold and Burningham 2010; Curreli et al. 2013; Jones et al. 2017; Šilc et al. 2017), very different from the turf vegetation described here. No explanations are obvious.

There are no consistent floristic differences in turf species between wetlands, except that related to age, so recovery of biological functioning is best examined through successional processes. As succession progresses in these dune wetlands, bare ground decreases, with the vegetation cover and height increasing, as well as the height of the surface above the water table. Species’ diversity, species’ richness, the proportions of native species and cover of native vegetation increase initially, but then decrease in the later communities. The successional sequence inferred here is Open Wetland to Turfed Wetland and Rush Wetland, through the Mixed Rushland and Oioi Rushland stages to Sedgeland, before transiting to Exotic Grassland as the sand stabilises (Fig. 11).

The relative height with respect to the mean annual water table of Open Wetland indicates that the depressions’ surface, largely bare sand, is still ablating at this stage of succession, which was not obvious in the field. So the occasional *Ammophila arenaria* or *Ficinia nodosa* here are probably relicts. Esler (1969) and Singers (1998) note *Selliera rotundifolia* as the first species to invade after wetland creation, and *Isolepis cernua*, widespread along the coast, was also an early arrival. Observations suggest that the Open Wetland phase may last 5 years, perhaps longer.

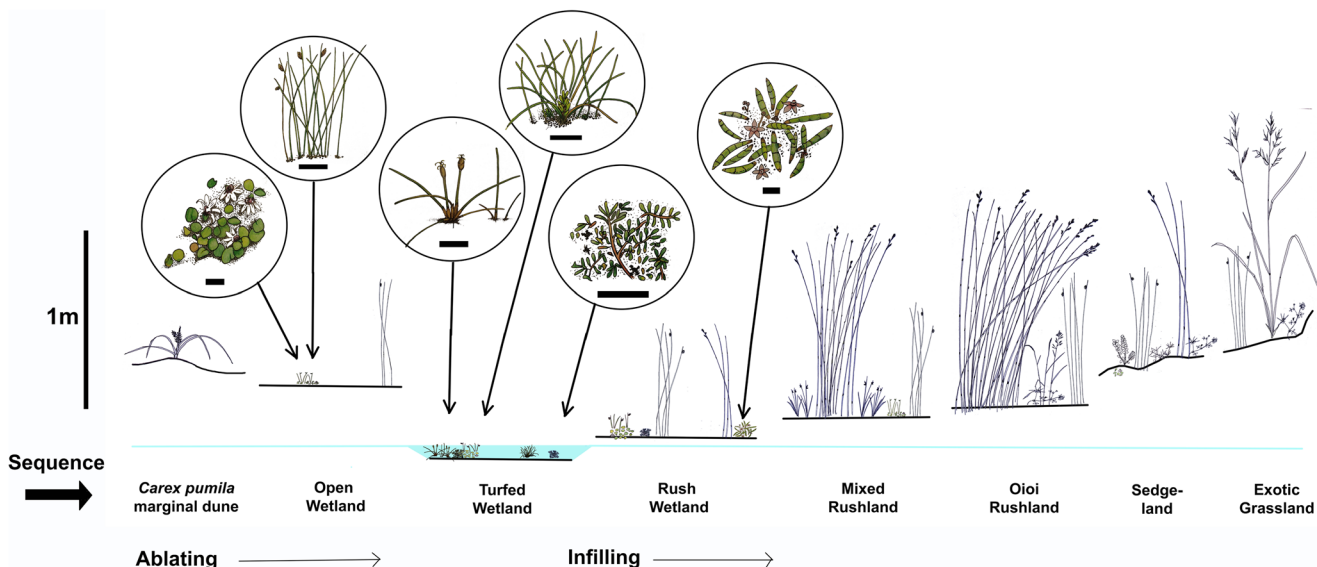


Fig. 11 Diagrammatic representation of the successional sequence of communities of dune slack wetlands through the deflating and infilling phases of wetlands with respect to the water table (blue

line) from left to right. Horizontal distances not to scale. The horizontal bar scale of the plants inside the circles is 1 cm

As a result of ongoing ablation the next community, Turfed Wetland, is the one closest to the mean water table. The earliest invader here is *Isolepis basilaris*, the small, rare sedge, arriving after 6 years. Being aquatic, *Myriophyllum votschii* also invades readily and attains co-dominance with *Selliera rotundifolia*, which has a wide range of water tolerances (Esler 1969). Turfed Wetland has the highest cover of rare *Eleocharis neozelandica*, deliberately introduced into Wetlands 4 and 5 in April 1996, though naturally present in the vicinity. While intolerant of deep water it survived in the middle zone (Singers 1998), and continued to occupy Wetland 5 longer than any other turf species except for *Isolepis cernua*. Cover of *Eleocharis neozelandica* declines within about 5 years (also seen in the herbivore enclosure plots), along with *Selliera rotundifolia*, while *Myriophyllum votschii* and *Triglochin striata* both increase in cover.

Turfed Wetland is followed by Rush Wetland (Fig. 11), where the turf species begin to decline in cover, and the short rush, *Schoenus nitens*, becomes common. This multi-variate construct came as a surprise result of our analyses, the importance of *Schoenus nitens*, a small rush to 15 cm tall, not being obvious in the field, particularly amongst taller vegetation. Although Esler (1969) suggests that the species appears after *Apodasmia similis*, our data give it an earlier place in the successional continuum. A common though variable community, occurring in 10% of our quadrats and all four more mature wetlands, it apparently lasts about 3–5 years.

Rush Wetland is gradually displaced by Mixed Rushland, a widespread and speciose community, as *Apodasmia similis* apparently out-competes the shorter *Schoenus nitens*. This phase, in which the last remnant populations of the even shorter turf species die out, lasts about 3–5 years. Probably the sand-trapping and dispersal abilities of *Apodasmia similis* hasten the succession to Oioi Rushland, a very dense, and hence more species-poor community. In some large wetlands up to 1 km from the coast and lacking supplies of mobile sand for infilling, Oioi Rushland forms extensive swards which appear to persist for many years (Rapson, pers. obs.), perhaps an example of arrested succession (Grootjans et al. 1998; Boyes et al. 2011).

*Ficinia nodosa* attains dominance as sand accumulates and the environment becomes too dry for *Apodasmia*, so that Oioi Rushland transits to Sedgeland. Esler (1969) refers to *Ficinia nodosa* occupying low dunes, and similarly Sykes and Wilson (1987) describe a “Scirpoides/Lupinus [low] dune” community, which is dominated by natives *Ficinia nodosa* and *Coprosma acerosa*. Not unexpectedly, our community is speciose and largely marginal. Where there is ongoing sand supply Oioi Rushland transits to Exotic Grassland under the current invasion regime.

Occupying the margins of our wetlands, our most mature community, Exotic grassland, is not the natural climax of this sere, only *Leontodon saxatilis* being present in 1968 (Esler

1969). Formerly succession from Sedgeland would likely have proceeded through the large monocots *Austroderia toetoe*, *Cordyline australis* and *Phormium tenax*, and shrubs *Coprosma propinqua*, *Leptospermum scoparium* and *Olearia solandri*, all of which are present in our wetlands though *Olearia* was not encountered in sampling. If undisturbed, these sites would presumably have originally hosted podocarp-broadleaved swamp forest of *Dacrydium dacrydioides* and *Laurelia novae-zelandiae*, as in Omarupapako or Round Bush Reserve (DoC; Esler 1978), where tall (25 m) forest nestles between trailing ridges of a dissipated parabolic dune. Natural succession to this stage is now unlikely in our dunes, suitable seed sources being at least 17 km away, even if any requisite separation from coastal influences is obtained (see Pegman and Rapson 2005). The future of our Exotic Grassland community is unknown.

### Successional drivers

The major driver of succession in dune slacks is the increased separation of sand surface and water table over time (Schat 1984; Sykes and Wilson 1987; Bakker et al. 2007), all emergent species, even *Eleocharis neozelandica*, trapping aeolian sand (Singers 1997). Species also differ in their tolerances to submergence (Shumway and Banks 2001; Curreli et al. 2013), though Sykes and Wilson (1987) noted the vegetation patterns of the Mason Bay dune slack to be only generally related to water tables. Also coastal plants differ greatly in their tolerance to both the darkness of burial and the pressure of deposited sand (explored relative to plant height; Sykes and Wilson 1990a, 1990b). Wetland turf species are classically early-successional in that they increase in number and abundance when the sand surface is almost bare, and then decline within two decades. They may even have this as their “preferred” habitat (e.g., Bakker et al. 2007). The turf species, *Isolepis basilaris* and *Myriophyllum votschii* and to a lesser extent, *Eleocharis neozelandica*, appear tolerant of submergence and slight sand deposition (Esler 1969; Singers 1997; Melanya Yukhnevich pers. comm.), but experimental delimitation is required here.

Other drivers have also been implicated for dune slack succession. Roxburgh et al. (1994) looked at a range of southern slacks, and concluded vegetation was strongly related to peat deposits, but none of our wetlands has any organic material, even amongst the upper sand grains. In the initially nutrient-poor environment restrictions on nitrogen uptake and translocation due to root anoxia (Schat 1984), can be critical, especially for early successional species (Plassmann et al. 2008). One of our species, *Schoenus nitens*, is known to exhibit nitrogen limitation, though *Myriophyllum votschii* does not (Champion and Reeves 2009), and indeed exotic fabaceous species are ready invaders, indicating nitrogen-limitation. However nutrient relations are likely secondary in

importance once vegetation becomes tall and dense, and a shift to competition for light occurs (e.g., Bossuyt et al. 2003). Competition experiments between wetland plants would be informative here on both sandy surfaces and those with some organic constituents.

The more isolated dune slacks are from each other, the slower succession will be (Singers 1998; Bossuyt et al. 2003). Dispersal at the coast is often by wind, but water also appears influential. Singers (1998) reported that plants introduced into Wetlands 4 and 5 were supplemented by naturally-spreading siblings within a year or two, as seed and even stem fragments were readily dispersed by water. During rainstorms surface water can temporarily be very high (e.g., Fig. 9d), conjoining nearby wetlands, such as Wetlands 4 and 5, and further dispersing seed. A newly emerged depression adjacent to Wetland 1 hosted 3 turf species and *Triglochin striata* within a year, the source of plants being unknown, but possibly from overflow from Wetland 1. Wading birds might also have a role in dispersal though these are uncommon on this part of the coast, while squamates and other rare fauna may once have dispersed seed in faeces. Comparisons could usefully be made with other local wetlands and dispersion and dispersal of these species merits further investigation.

### Natural v. created wetlands

These wetlands form a non-linear chronosequence through the natural and then the created wetlands in the order Wetlands 3, 2, 1, 4, 5, 6 (Fig. 10c). Though an element of circularity is present, spatial patterns within both natural and created wetlands appear concordant with temporal patterns between wetlands, since the gradients along the profiles (Figs. 6 and 8) match the anti-clockwise successional spiral in the ordination's sequence of the communities (Fig. 10a).

Vegetation height and cover and species' diversity of the natural wetlands were twice that of the created wetlands, while sand and stone covers were lower (Table 1), because the natural wetlands are all inevitably older than the created ones, and thus in later successional phases. Wetland 1, the largest of the natural wetlands, still contained all communities at the time of our survey, except for the Open Wetland community, which was present even before the herbivory experiments (Rapson pers. obs.). Wetland 3 is the furthest along the successional sequence. By 2010 it had a large amount of litter (woody or herbaceous plant detritus), and a relatively low number of native species (only 74% of Wetlands 1 and 2). Originally considered to be as high-value as Wetland 2, if not higher (Vivienne McGlynn pers. comm.), and thus chosen for a planting of the rare subshrub *Pimelea actea*, Wetland 3 has "aged" the quickest of the natural wetlands. Our survey showed it lacking standing water, and having only a small patch of the least open community, Rush Wetland, while *Pimelea actea* had died out. The most likely explanation is a

high rate of infilling due to being in a very narrow slack surrounded by tall dunes (Fig. 6e, f). By contrast, its large size has assisted Wetland 1 to retain some early successional characteristics longer than the other natural wetlands, with wetland turf species resident until 2014. In 2010, Wetland 4 was largely occupied by the Rush Wetland and Mixed Rushland communities, older successional stages than the Turfed Wetland community which dominated the contemporaneous Wetland 5. This difference appears due to their relative rates of infilling, so the micro-location for Wetland 5 was the most suitable. Subsequently Wetland 5 appears to have changed to dominance by Mixed Rushland, and Wetland 4 into the Oioi Rushland phase, still a seral stage behind.

Locations for created wetlands within Tawhirihoe Reserve were limited by the availability of sites lacking conflicting biodiversity values, but close to coastal influences. The wetlands sampled here are generally 300–400 m from the coast, more coastal than those mentioned by Esler (1969) at 600 m inland, even allowing for coastal progradation. No explanation for the difference has been identified.

Natural dune slack wetlands are all in extremely flat depressions, with topographical variations of <1.0 m, even when following the Syke's principle (Roxburgh et al. 1994) and sampling into the surrounding vegetation, generally Exotic Grassland. Created wetlands were excavated to match. Cowie (1968) considered that the lowest point of every slack, i.e., the portion wettest for longest, was coast-wards, and immediately inland of the foredunes. The two wetlands created in 1996 were shaped this way (Singers 1998; Fig. 7). However subsequent observations and advice (Patrick Hesp pers. comm.) suggested that the lowest area would be the most inland third of the slack, as this site is probably as windy as the foredune end, but has less dry sand available to be deposited into the wetland to raise it. Wetland 6, created in 2008, reflects this interpretation (Fig. 9). Yet our profiles (Fig. 8) show the lowest portion of both natural and created wetlands to be roughly central, tending coastwards. This is probably a consequence of internal water dynamics (e.g., fetch) reworking deposited sand. Further, the actual lowest zones of both Wetlands 1 and 2 appear not to have changed in location over the last three decades.

Wetland 2 had a remarkably similar water regime to Wetland 1 in the 1990's (Fig. 5), though it infilled much more quickly (Figs. 3 and 6). Where measured, the below-ground water-tables at Tawhirihoe appear to be horizontal (c.f. Ranwell 1959; Jones et al. 2017), and Singers (1997) notes a dependence on local rainfall levels, 10 mm of rainfall raising the wetlands' water tables by 4.5 mm. This supports the interpretation that the water table is regional and so affecting both natural and created wetlands equally. As expected, water tables at Tawhirihoe fluctuated widely between the seasons, similar to those monitored by Champion and Reeves (2009) and Jones et al. (2017) etc.

Finally, budgetary constraints inevitably affect the size of created wetlands, as well as the requirement to safely emplace the excavated sand. Natural dune slack wetlands can be large, even 5 ha, but are generally <1 ha. Our created wetlands are <22% of the size of natural wetlands. These small sizes probably do affect infilling rates, though no consistent differences were detected here.

### Evaluation of wetland recovery

Given the bare sand substrate, geochemistry should not vary in the early stages of succession, though issues with respect to nutrient dynamics are implied by some of our results. The physical shape of the natural wetlands has been well restored in the created wetlands, but success was more mixed for resultant hydrology.

The water table in natural wetlands was used to define excavation depth for the created wetlands, so independent comparisons are not possible (c.f., Moreno-Mateos et al. 2012). While hydrological recovery was excellent for Wetlands 4 and 5, it was poorer for Wetland 6, the most recently created wetland. By March 2016, 8 years after excavation, Wetland 6 had very low cover of plants in 2010, and appeared to still be entering the Turfed Wetland phase, a phase which should last about 5 years. The only native turf species which had invaded were common to most other wetlands, i.e., the local endemic *Selliera rotundifolia* and the nationally ubiquitous *Isolepis cernua*, both with source populations present only 10 m away. By 2013 their coverage around the margins of the water was increasing, and the welcome addition of three small clumps of *Isolepis basilaris* was noted. With a source population persisting within 20 m of Wetland 6, *Isolepis basilaris* was common by 2015, forming extensive patches by March 2016. But other species have still to reach the wetland, such as *Lilaeopsis novae-zelandiae*, a large population of which is 200 m coastwards of Wetland 6, and *Eleocharis neozelandica*, planted into Wetland 5, about 100 m away, but no longer seen there. Thus Wetland 6's succession is slower than expected. Excavated to give a standing summer water table of about 30 cm deep, it may be too wet to be functioning normally, explaining the uncharacteristic presence of the native estuarine rush, *Schoenoplectus pungens* which invaded late 2013.

Over-steepening in created wetlands is often an issue for the natural formation of zonation (Zampella and Laidig 2003; Roy et al. 2016). This was also shown by Wetland 6 whose depth generated a slope of  $3.6^\circ$ , greater than the largest natural wetland, Wetland 1 (slope of  $0.4^\circ$ ) while the shallower but smaller created Wetlands 4 and 5 (mean of  $1.1^\circ$ ), are functioning more typically.

More unexpectedly, the precise location of created wetlands within the dynamic landscape of the dunes seems

important in determining infilling rates from both aeolian sand and transgressive dunes, affecting wetland longevity. This could be further explored through historic photographic records to track wetlands' sizes, locations, longevity and movements.

Except for idiosyncrasies in the presences of some of the turf species and a few minor exotic species, recovery of biological structure and hence functioning appeared good here, though may well be improved by routine in-planting (following Parikh and Gale 1998). There is no evidence of slower successional processes in the created wetlands, compared with the natural ones, except for aspects readily attributable to wetland size.

Invasion by exotics, particularly those exotics having an important role in dune slacks in their native environment, e.g., *Agrostis stolonifera* and *Holcus lanatus* (Dargie 2000), reduces growth and survival of native seedlings (D'Antonio and Meyerson 2002; Pegman and Rapson 2005; Champion and Reeves 2009). Created wetlands may be particularly invadable (Confer and Niering 1992). Our slacks have high proportions of exotic species, and their relative invadability may be a consequence of the low diversity of natives (Champion and Reeves 2009). If exotic dispersal is at random, then larger and/or older wetlands would be more exposed to chance invasion events anyhow, but our experimental "design" gives no way to disentangle invasion pressure from vulnerability to invasion. However, while occasional throughout, exotics appear unimportant to the functioning of the created wetlands in their early seral stages, although their role in altering the long-term dynamics of wetlands and dunes cannot be under-estimated (Hilton et al. 2005). For example, the invasive exotic *Osmunda regalis* (royal fern), which can completely dominate wetlands (Clarkson 1997), was found and removed from the centre of Wetland 1 during our survey, its first record in the lower North Island. Altering dune dynamics are the aggressive South African *Senecio glastifolius* (pink ragwort), which is widespread along the Foxtangi coast (Beautrais 2013), and *Lilium formosanum*, a nuisance spreading around Foxtan Beach. Protection of wetlands will require appropriate management of such species.

Following Sival et al. (1997), Champion and Reeves (2009) have suggested that an exotic herbivore might be used to manage such wetlands, and we report some indication that rabbits preferentially browse *Apodasmia similis*, though they appear to avoid *Lobelia anceps* (Fig. 4), so that they may actually be serving to decelerate the successional sequence, as desired. However they may also play a role in decline of *Eleocharis neozelandica*, which Singers (1998) reports they target when the wetland surface is dry. Their presence in the dunelands is unsatisfactory.

## Conclusion

The formation of ablation hollows via foredune blowouts appears necessary for the continued presence of the wetland specialists. Historically restoration plans inevitably focussed on the perceived need to stabilise dunes (McKelvey 1999), but without dynamism, especially blowouts, wetlands cannot form naturally, and their natural processes are modified or arrested. However landscape-scale processes are not easily recreated, even in very simple environments.

Although very intrusive, the creation of wetlands within Tawhiriho Scientific Reserve has allowed at least some of the rare turf species to persist and operate in their appropriate successional stages. Wetland 5 is the most successful, and its small size and location close to a small mobile dune appear to be only minor handicaps to wetland longevity. However Wetland 6 is too deep to dry out seasonally as it apparently should, even if only for a month or two, too steep (to date) to allow vegetational gradients to develop, and too remote for adequate dispersal of plant propagules. Restoration success seems more achievable when at least some plant material is deliberately introduced, possibly compensating for anthropically-induced difficulties in dispersal (Parikh and Gale 1998). Overall wetland creation is an effective management strategy, despite the attendant logistic, legal and managerial problems. Indeed future creation of wetlands may be essential to perpetuate these specialist species along the Manawatū coast.

Many other issues remain unanswered in studying these dune slack wetlands. Detailed mapping and study of wetlands all along the coast, both in Manawatū, and in other New Zealand dunefields, might answer questions about their rarity, distribution, relative floristics, water depths and conservation imperatives. Ongoing monitoring of these natural and created wetlands will clarify succession times, and confirm the population dynamics of the rare turf species. Exploration of their environmental tolerances in controlled conditions would assist in understanding their roles in these systems, and hence in strategies for their conservation. Additionally, consideration needs to be given to the likely effects of climate change, both in modifying rates of coastal progradation, and in altering water tables (Grootjans et al. 1991, 1997; Curreli et al. 2013). Impacts of other coastal activities need to be considered, such as increased irrigation for dairying, which can raise local water tables, and potentially eutrophy wetlands (Foote et al. 2015), in contrast to plantation forestry and other anthropogenic activities which can lower water tables (Curreli et al. 2013; Robins et al. 2013). Similarly off-road vehicles appear to maintain open habitat for dune slack species, though increased traffic is detrimental (Kindermann and Gormally 2010; Šilc et al. 2017). And there are many other direct and indirect human pressures on dunes. Dune slack wetlands are under threat from a variety of sources, including their own temporary nature, and, following Moreno-Mateos et al. (2012), even these very simple systems are not easy to restore or create.

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## References

- Allan HH (1961) Flora of New Zealand, volume 1. Government Printer, Wellington
- Anderson RS, Ejarque A, Rice J, Smith SJ, Lebow CG (2015) Historic and Holocene environmental change in the San Antonio Creek basin, mid-coastal California. *Quat Res* 83:273–286
- Bakker C, van Bodegom PM, Nelissen HJM, Aerts R, Ernst WHO (2007) Preference of wet dune species for waterlogged conditions can be explained by adaptations and specific recruitment requirements. *Aquat Bot* 86:37–45
- Barrett-Mold C, Burningham H (2010) Contrasting ecology of prograding coastal dunes on the northwest coast of Ireland. *J Coast Conserv* 14:81–90
- Bates RL, Jackson JA (1987) Glossary of geology. American Geological Institute, Alexandria 788 pp
- Beautrais JR (2013) The geographic distribution of *Senecio glastifolius* in New Zealand: past, current and climatic potential. M.Sc. thesis, Victoria University of Wellington, Wellington, New Zealand
- Bekker RM, Lammerts EJ, Schutter A, Grootjans AP (1999) Vegetation development in dune slacks: the role of persistent seed banks. *J Veg Sci* 10:745–754
- Bossuyt B, Honney O, Hermy M (2003) An island biogeographical view of the successional pathway in wet dune slacks. *J Veg Sci* 14:781–788
- Boyes LJ, Gunton RM, Griffiths ME, Lawes MJ (2011) Causes of arrested succession in coastal dune forest. *Plant Ecol* 212:21–32
- Burgess RE (1984) The life history strategy of *Carex pumila* a rhizomatous perennial pioneer species on the sand plains of the dune system of coastal Manawatu. Ph.D. thesis, Massey University, Palmerston North, New Zealand
- Burrows CJ (2008) Genus *Pimelea* (Thymelaeaceae) in New Zealand 1: the taxonomic treatment of seven endemic, glabrous-leaved species. *N Z J Bot* 45:127–176
- Burrows CJ (2009) Genus *Pimelea* (Thymelaeaceae) in New Zealand 3: the taxonomic treatment of six endemic hairy-leaved species. *N Z J Bot* 47:325–354
- Campbell DA, Cole CA, Brooks RP (2002) A comparison of created and natural wetlands in Pennsylvania, USA. *Wetl Ecol Manag* 10:41–49
- Champion PD, Reeves PN (2009) Factors causing dune ephemeral wetlands to be vulnerable to weed invasion. Research and Development Series 310, Department of Conservation, Wellington, New Zealand

- Clarke KR, Gorley RN (2015) Primer V7: user manual/tutorial. Primer-E, Plymouth
- Clarkson BR (1997) Vegetation recovery following fire in two Waikato peatlands at Whangamarino and Moanatuatua, New Zealand. *N Z J Bot* 35:167–179
- Clement AJ, Sloss CR, Fuller IC (2010) Late Quaternary geomorphology of the Manawatu coastal plain, North Island, New Zealand. *Quat Int* 221:36–45
- Confer SR, Niering WA (1992) Comparison of created and natural freshwater emergent wetlands in Connecticut (USA). *Wet Ecol Manag* 2: 143–156
- Cowie JD (1963) Dune-building phases in the Manawatu district, New Zealand. *N Z J Geol Geophys* 6:268–280
- Cowie JD (1968) Soil-age relationships in the Manawatu District, New Zealand. *Trans 9th Int Soc for Soil Sci* 4:541–549
- Craft C, Broome S, Campbell C (2002) Fifteen years of vegetation and soil development after brackish-water marsh creation. *Restor Ecol* 10:248–258
- Curreli A, Wallace H, Freeman C, Hollingham M, Stratford C, Johnson H, Jones L (2013) Eco-hydrological requirements of dune slack vegetation and the implications of climate change. *Sci Total Environ* 443:910–919
- D'Antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor Ecol* 10:701–713
- Dargie TC (2000) Sand dune vegetation survey of Scotland: national report. Scottish Natural Heritage, Edinburgh
- Dawson PAC, Rapson GL, Robertson AW, Fordham RA (2005) Limitations on recruitment of the rare sand daphne *Pimelea arenaria* (Thymelaeaceae), lower North Island, New Zealand. *N Z J Bot* 43:619–630
- de Lange PJ, Rolfe JR, Champion PD, Courtney SP, Heenan PB, Barkla JW, Cameron EK, Norton DA, Hitchmough RA (2013) Conservation status of New Zealand indigenous vascular plants, 2012. New Zealand threat classification series 3. Department of Conservation, Wellington
- Esler AE (1969) Manawatu sand plain vegetation. *Proc NZ Ecol Soc* 16:32–35
- Esler AE (1970) Manawatu sand dune vegetation. *Proc NZ Ecol Soc* 17: 41–46
- Esler AE (1978) Botany of the Manawatu. DSIR Information Book 127, EC Keating, Government Printer, Wellington, New Zealand
- Footo KJ, Joy MK, Death RG (2015) New Zealand dairy farming: milking our environment for all it's worth. *Environ Manag* 56: 709–720
- Given DR (1981) Rare and endangered plants of New Zealand. Reed, Wellington
- Grootjans AP, Hartog PS, Fresco LFM, Esselink H (1991) Succession and fluctuation in a wet dune slack in relation to hydrological changes. *J Veg Sci* 2:545–554
- Grootjans AP, Esselink H, van Diggelen R, Hartog P, Jager TD, van Hees B, Oude Munnink J (1997) Decline of rare calciphilous dune slack species in relation to decalcification and changes in local hydrological systems. In: Novo FC, Crawford RMM, Diaz Barradas MC (eds) The ecology and conservation of European dunes. Universidad de Savilla, Spain, pp 59–74
- Grootjans AP, Ernst WHO, Stuyfzand PJ (1998) European dune slacks: strong interactions of biology, pedogenesis and hydrology. *Trends Ecol Evol* 13:96–100
- Heenan PB (1997) *Selliera rotundifolia* (Goodeniaceae), a new, round-leaved, species from New Zealand. *N Z J Bot* 35:133–138
- Hesp PA (2001) The Manawatu dunefield: environmental change and human impacts. *N Z Geogr* 57:33–40
- Hesp PA (2002) Foredunes and blowouts: initiation, geomorphology and dynamics. *Geomorphology* 48:245–268
- Hesp PA, Shepherd M (2003) Sandy barriers and coastal dunes. In: Goff JR, Nicol SL, Rouse HL (eds) The New Zealand coast - Te tai o Aotearoa. Dunmore Press and Whitireia Publishing, Auckland, pp 163–189
- Hilton M, Macauley U, Henderson R (2000) Inventory of New Zealand's dunelands. Science for Conservation No. 157, Department of Conservation, Wellington, New Zealand
- Hilton M, Duncan M, Jul A (2005) Processes of *Ammophila arenaria* (marram grass) invasion and indigenous species displacement, Stewart Island, New Zealand. *J Coast Res* 21:175–185
- Jones PS, Farr G, Low R, Etherington JR (2017) Ecohydrological studies of dune slack vegetation at Kenfig dunes, South Wales, UK. *J Coast Conserv* 21:623–630
- Kearney MA, Fickbohm S, Zhu W (2013) Loss of plant biodiversity over a seven-year period in two constructed wetlands in Central New York. *Environ Manag* 51:1067–1076
- Kindermann G, Gormally MJ (2010) Vehicle damage caused by recreational use of coastal dune systems in a special area of conservation (SAC) on the west coast of Ireland. *J Coast Conserv* 14:173–188
- King CM (1990) The handbook of New Zealand mammals. Oxford University Press, Oxford
- McEwen WM (1987) Ecological regions and districts of New Zealand, 3rd revised edition, Sheet 2. NZ Biological Resources Centre Publication No. 5
- McKelvey PJ (1999) Sand forests: a historical perspective of the stabilisation and afforestation of coastal sands in New Zealand. Canterbury University Press, Christchurch
- Moreno-Mateos D, Power ME, Comin FA, Yockteng R (2012) Structural and functional loss in restored wetland ecosystems. *PLoS Biol* 10(1):e1001247
- Muckersie C, Shepherd MJ (1995) Dune phases as time-transgressive phenomena, Manawatu, New Zealand. *Quat Int* 26:61–67
- Murtagh F, Legendre P (2014) Ward's hierarchical agglomerative clustering method: which algorithms implement Ward's criterion? *J Classif* 31:274–295
- Ogden J (1974) Observations on two coastal ecotypes of *Selliera radicans* Cav. (Goodeniaceae) growing in the Manawatu district of New Zealand. *N Z J Bot* 12:541–550
- Otvos EG (2000) Beach ridges - definitions and significance. *Geomorphology* 32:83–108
- Parikh A, Gale N (1998) Vegetation monitoring of created dune swale wetlands, Vandenberg Air Force Base, California. *Restor Ecol* 6:83–93
- Pegman APMK, Rapson GL (2005) Plant succession and dune dynamics on actively prograding dunes, Whatipu Beach, northern New Zealand. *N Z J Bot* 43:223–244
- Pilkington KM (2014) A population genetics approach to species delimitation in the genus *Selliera* (Goodeniaceae). M.Sc. thesis, Massey University, Palmerston North, New Zealand
- Plassmann K, Brown N, Jones MLM, Edwards-Jones G (2008) Can atmospheric input of nitrogen affect seed bank dynamics in habitats of conservation interest? The case of dune slacks. *Appl Veg Sci* 11: 413–420
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna URL <http://www.R-project.org/>
- Ranwell DS (1959) Newborough Warren, Anglesey. I: the dune system and dune slack habitat. *J Ecol* 47:571–601
- Ranwell DS (1960) Newborough Warren, Anglesey. II: plant associates and succession cycles of the sand dune and dune slack vegetation. *J Ecol* 48:117–141
- Rapson GL (2018a) Changing methodology results in operational drift in the meaning of leaf area index, necessitating implementation of foliage layer index. *Ecol Evol* 8:638–644
- Rapson GL (2018b) Endemic plants of the Manawatu dunes. Plains' Science: Inventions, innovations, and discoveries from the Manawatu 3:112–123. (Ed: VE Neall; Publ: Royal Society of New Zealand Manawatu Branch Inc., and Science Centre Inc., Palmerston North.)

- Ravine DA (1992) Foxton Ecological District survey report for the Protected Natural Areas Programme No. 19. Department of Conservation, Whanganui, New Zealand
- Reitz MD, Jerolmack DJ, Ewing RC, Martin RL (2010) Barchan-parabolic dune pattern transition from vegetation stability threshold. *Geophys Res Lett* 37:L19402
- Robins NS, Pye K, Wallace H (2013) Dynamic coastal dune spit: the impact of morphological change on dune slacks at Whiteford Burrows, South Wales, UK. *J Coast Conserv* 17:473–482
- Roxburgh SH, Wilson JB, Gitay H, King WM (1994) Dune slack vegetation in southern New Zealand. *N Z J Ecol* 18:51–64
- Roy MC, Foote L, Ciborowski JJ (2016) Vegetation community composition in wetlands created following oil sand mining in Alberta, Canada. *J Environ Manag* 172:18–28
- Saunders BGR (1968) The physical environment of the Manawatu sand country. *N Z Geogr* 24:133–154
- Schat H (1984) A comparative ecophysiological study on the effects of waterlogging and submergence on dune slack plants: growth, survival and mineral nutrition in sand culture experiments. *Oecologia* 62:279–286
- Seabloom EW, van der Valk AG (2003) Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. *Wetlands* 23:1–12
- Semeniuk CA, Semeniuk V (2011) Dune slacks in Western Australia. *J R Soc West Aust* 94:503–532
- Shepherd MJ, Lees CM (1987) Holocene alluviation and transgressive dune activity in the lower Manawatu Valley, New Zealand. *N Z J Geol Geophys* 30:175–187
- Shumway SW, Banks CR (2001) Species distributions in interdunal swale communities: the effects of soil waterlogging. *Am Midl Nat* 145:137–146
- Šilc U, Caković D, Kuzmič F, Stešević D (2017) Trampling impact on vegetation of embryonic and stabilised sand dunes in Montenegro. *J Coast Conserv* 21:15–21
- Singers NJD (1997) The dynamics of temporary wetlands in dune slacks at Tangimoana, Manawatu, New Zealand, with special reference to the endangered sand-spiked sedge *Eleocharis neozelandica* Kirk (Cyperaceae). M.Sc. Thesis, Massey University, Palmerston North, New Zealand
- Singers NJ (1998) Rare plant conservation at the Tangimoana dunelands. Department of Conservation, Wellington
- Sival FP, Grootjans AP, Stuyfzand PJ, de la Houssaye TV (1997) Variation in groundwater composition and decalcification depth in a dune slack: effects on basiphilous vegetation. *J Coast Conserv* 3:79–86
- Spieles DJ (2005) Vegetation development in created, restored, and enhanced mitigation wetland banks of the United States. *Wetlands* 25:51–63
- Syers JK, Walker TW (1969) Phosphorus transformations in a chronosequence of soils developed on wind-blown sand in New Zealand. *Eur J Soil Sci* 20:57–64
- Sykes MT, Wilson JB (1987) The vegetation of a New Zealand dune slack. *Vegetation* 71:13–19
- Sykes MT, Wilson JB (1990a) Dark tolerance in plants of dunes. *Funct Ecol* 4:799–805
- Sykes MT, Wilson JB (1990b) An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand. *Acta Bot Neerl* 39:171–181
- Sykes MT, Wilson JB (1991) Vegetation of a coastal sand dune system in southern New Zealand. *J Veg Sci* 2:531–538
- Systat (1998) SYSTAT for windows, version 8.0. Systat Inc., Illinois
- Tansley AG (1949) The British Isles and their vegetation. Cambridge University Press, Cambridge
- ter Braak C.J.F., Šmilauer P (2002) Canoco reference manual and Canodraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, New York
- Vymazal J (2014) Created wetlands for treatment of industrial wastewaters: a review. *Ecol Eng* 73:724–751
- Whitaker D, Christman M (2015) Clustsig: significant cluster analysis. R package version. 2014:1.1. <https://cran.r-project.org/web/packages/clustsig/clustsig.pdf>
- Wiegand G, Dahms HU, Byeon WI, Choi G (2017) To what extent can constructed wetlands enhance biodiversity? *International Journal of Environmental Science and Development* 8:561–569
- Williams PA, Wiser S, Clarkson B, Stanley MC (2007) New Zealand's historically rare terrestrial ecosystems set in a physical and physiognomic framework. *N Z J Ecol* 31:119–128
- Wilson JB (2007) Priorities in statistics, the sensitive feet of elephants, and don't transform data. *Folia Geobot* 42:161–167
- Wilson JB, Gitay H (1995) Community structure and assembly rules in a dune slack: variance in richness, guild proportionality, biomass constancy and dominance/diversity relations. *Vegetation* 116:93–106
- Wu H, Zhang J, Ngo HH, Guo W, Hu Z, Liang S, Fan J, Liu H (2015) A review on the sustainability of created wetlands for wastewater treatment: design and operation. *Bioresour Technol* 175:594–601
- Zampella RA, Laidig KJ (2003) Functional equivalency of natural and excavated coastal plain ponds. *Wetlands* 23:860–876