Effects of lowered water table and agricultural practices on a remnant restiad bog over four decades

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SUMMARY

Peatlands are important contributors to global biodiversity, yet drainage and land management practices continue to affect many. We studied changes in a 114-ha raised bog remnant in northern New Zealand by assessing the vegetation and peat from 1974 to 2017, a period of agricultural conversion and intensification, and by comparing it with an intact bog. Over 43 years the remnant experienced significant water table drawdown, resulting in changes in vegetation composition and extirpation of species. However, the keystone peat-forming restiads (Restionaceae), *Empodisma robustum* and *Sporadanthus ferrugineus*, are still present. Between 1997 and 2017, concentrations in peat of N and K increased significantly but the concentration of P which, initially, was already higher than in the intact bog, did not increase. Foliar analysis of the ericoid mycorrhizal shrub *Epacris pauciflora* revealed significantly higher N and P, lower N/P and less depleted $\delta^{15}N$ compared with the intact bog. Although raised bogs are inherently P-limited, the nature of the limitation appears to be changing at the remnant, with P becoming less limiting, a likely side effect of local fertiliser application. An ecological tipping point may be imminent, accompanied by a switch to higher productivity and expansion of woody species which are better adapted to lowered water table and increased nutrients.

KEY WORDS: biodiversity, New Zealand, peat, plant nutrients, raised bog, vegetation

INTRODUCTION

Peatlands provide multiple ecosystem services; however, the two that stand out for their global significance are carbon storage and biodiversity conservation (Joosten 2016). While increased carbon storage has clear implications for mitigating global climate change (Frolking & Roulet 2007, Bonn *et al.* 2016), the value to humans of peatland biodiversity is less well understood. Yet the two services are intricately linked in peatlands, as the biota and carbon storage properties are mutually interdependent through the process of peat formation (Minayeva *et al.* 2017). Typically, peatlands are species-poor compared with other ecosystems in the same biogeographical region (Joosten 2016). However, their species are highly specialised, being uniquely adapted to the waterlogged, acidic, low-nutrient conditions, and are usually not found in other habitats (Rydin & Jeglum 2013). Thus, the contribution of peatlands to global biodiversity is extremely important, irrespective of whether peatlands are dominant or rare features of the landscape (Minayeva *et al.* 2017).

Despite their importance, many peatlands in both the Old World and the New World have been destroyed or degraded through conversion to agriculture (Joosten & Clarke 2002). Ongoing drainage of agricultural peats lowers water tables and increases peat oxidation (Pronger *et al.* 2014) which, together with fertiliser additions, can lead to drier, nutrient-enriched natural habitats (Heathwaite *et al.* 1993, Bonn *et al.* 2016). Agricultural modifications result in loss of biodiversity and functional processes, along with associated ecosystem services (Zedler & Kercher 2005, Rydin & Jeglum 2013, Joosten 2016). Despite this, small remnants may retain good populations of regionally rare and threatened biota (Richardson *et al.* 2014, Watts *et al.* 2020).

Rates and patterns of change in vegetation composition and structure have been quantified for anthropogenically modified peatlands in the Northern Hemisphere. Studies have involved real-time monitoring of post-drainage changes, e.g. in Russia (Grabovik 2012), and surveys at sites with different drainage histories, e.g. in Finland (Laine *et al.* 1995) and Canada (Pellerin & Lavoie 1999). These showed that changes in plant communities were small and/or slow in ombrotrophic peatlands (i.e. receiving inputs solely from precipitation, hereafter referred to as bogs) impacted by water table lowering (Laine & Vanha-Majamaa 1992, Laine *et al.* 1995). Comparatively little research has been published on drained peatlands in the Southern

Hemisphere, which are much less extensive but often floristically (non-*Sphagnum*) and physiognomically distinct (Clarkson *et al.* 2017); however, we anticipate similarly slow changes.

In New Zealand, bogs are mostly dominated by rush-like Restionaceae (restiads). They originally covered 153,000 ha, but 74 % of bogs have been lost in the last 100–150 years, the main phase of European settlement, when large tracts were drained and converted to pasture (Ausseil *et al.* 2011). Many now exist as isolated remnants in agricultural landscapes and are highly exposed to surrounding land management practices. Drainage-affected remnants are also vulnerable to drought (Goodrich *et al.* 2017). The long-term effects of both influences on biodiversity are unclear.

The aim of this study was to assess the responses of a remnant raised bog to ongoing environmental changes on three occasions (1974, 1997, 2017) during a 43-year period of agricultural intensification. This was achieved by comparison with a relatively intact reference bog system, measured in 1997 and 2017. Specifically, we focused on the rates and patterns of change in vegetation composition, peat and foliage nutrients, and peat physicochemical properties in the remnant. We hypothesised that decreases in plant species richness and restiad cover, and increases in peat nutrients, would occur at gradual rates in the affected bog, which would slowly diverge from the reference site.

METHODS

Study sites

Our drainage-affected site is Moanatuatua (37.926 °S, 175.369 °E, altitude 65 m) and our reference site is Kopuatai (37.40 °S, 175.55 °E, altitude 5 m). They are located 50 km apart in the lowland zone of the Waikato region, northern New Zealand (Figure 1). Both were initiated 13,000–15,000 years ago in the early post-glacial period (Hogg *et al.* 1987) and eventually formed raised bogs dominated by the restiads *Sporadanthus ferrugineus* (de Lange *et al.* 1999; henceforth *Sporadanthus*) and *Empodisma robustum* (Wagstaff & Clarkson 2012; henceforth *Empodisma*). They currently experience a mild climate with moderate temperatures (annual means 13.6 °C and 14.3 °C for Moanatuatua and Kopuatai, respectively), high annual mean humidity (83 % and 80 %), and moderate annual rainfall (1,252 mm and 1,339 mm) (New Zealand Meteorological Service 1973).

Moanatuatua comprises a 114-ha rectangular-shaped remnant of a bog that originally covered 7,500 ha, with peat depths up to 12 m (Taylor & Grange 1939). Although peripheral drainage at Moanatuatua began in the late 1800s, agricultural development of the deep peats was not successful until after 1939 (Cranwell 1939). Conversion to pastoral agriculture gathered pace following World War II (1945) and in 1959 only a central core of 3,500 ha still retained the original bog vegetation (NZMS1 Sheet N65 topographic map). In 1974, the area of bog vegetation was estimated as 1,250 ha around a central core, based on 1974 aerial photography (NZ Mapping Service SN 3730 L/12). At that time, drainage and development greatly accelerated with the completion of a bisecting road, and much of the peatland neighbouring the current remnant was in various stages of conversion to pasture. By 1997, raised bog vegetation had been reduced to less than 140 ha in two adjacent remnants, the larger of which (114 ha) is legally protected as Moanatuatua Peat Scientific Reserve. Moanatuatua is currently ring-drained, surrounded by dairy farms, and its long-term ecological viability is unclear.

In contrast, Kopuatai is essentially intact, covering an area of 10,500 ha with peat up to 12 m deep (Newnham *et al.* 1995). It is the largest raised bog in New Zealand and designated as a Government Purpose Reserve and Ramsar site.

Sampling

The vegetation and peat at Moanatuatua were sampled in the late spring–midsummer seasons of 1974, 1997 and 2017. Sampling was extended to Kopuatai 1997 and 2017, in early midsummer. The methodology and sampling design were based on the first survey of vegetation at Moanatuatua in 1974 (Dickinson 1974), with the addition of peat nutrient analysis in 1997 (Clarkson *et al.* 2004a) and of plant nutrients in 2017 (presented here). Monitoring periods are thus 43, 20, and 0 ('present day'; 2017) years for the modified site, and 20 and 0 years for the reference site. Plant species lists were compiled from reconnaissance surveys during sampling, with nomenclature following Ngā Tipu o Aotearoa (2019).

In 1974, a 750 m transect was established from the margin to the centre of Moanatuatua, through late-successional bog vegetation dominated by *Sporadanthus* and *Empodisma* (Dickinson 1974). Vegetation (vascular and non-vascular species cover, richness, maximum height) and water table data were collected from a total of eight temporary 2 m × 2 m plots located 50–100 m apart along the transect. Peat decomposition was scored using the 10-class von Post humification scale (von Post & Granland 1926), and peat pH was determined in the laboratory (Dickinson 1974).

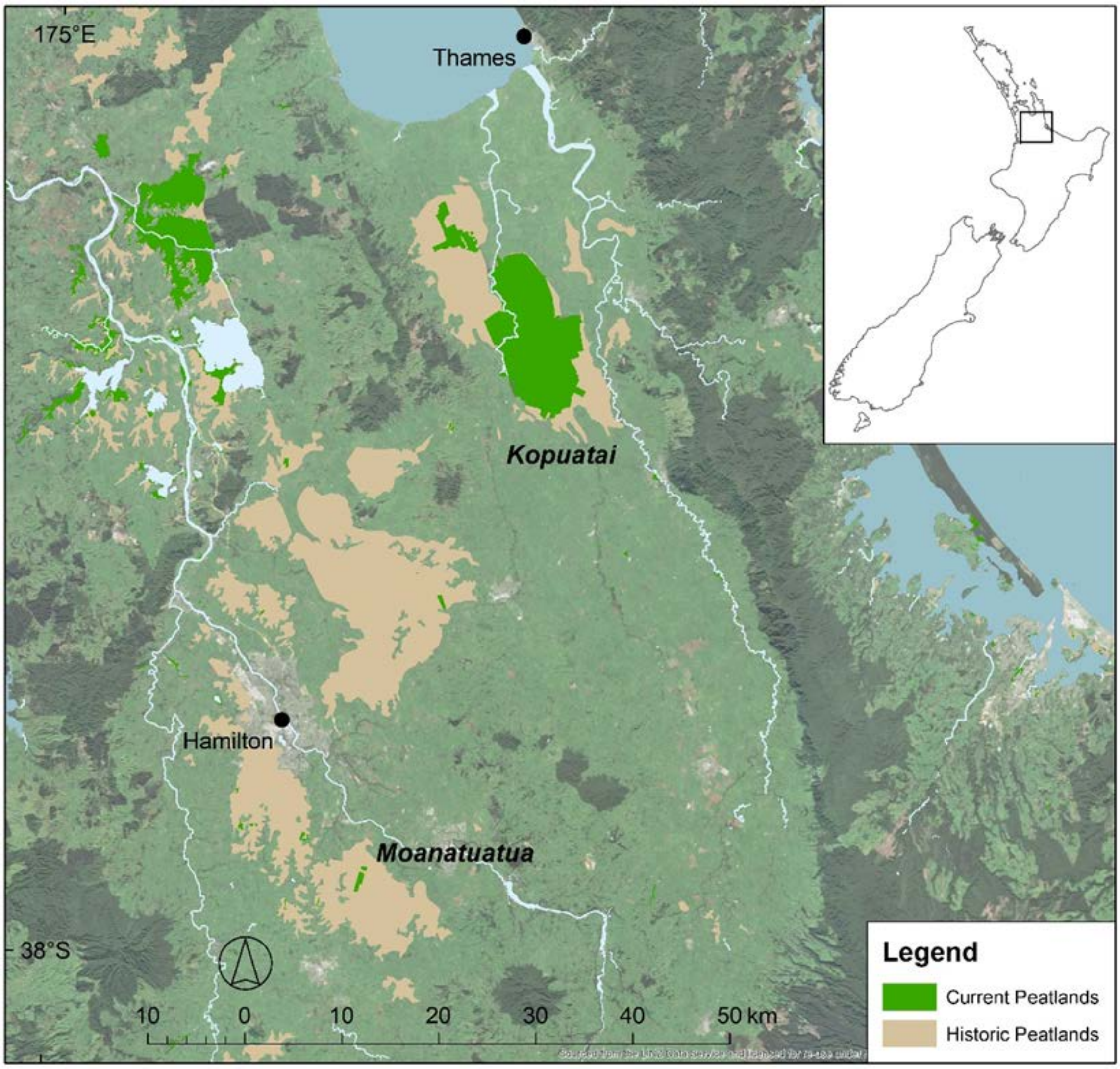

Figure 1. Location of modified bog, Moanatuatua, and relatively intact bog, Kopuatai, in the Waikato region, North Island, New Zealand. A separate bog remnant lies north-west of Kopuatai. Grey indicates hillshade.

By 1997, the Moanatuatua remnant had been reduced to its current size with new drains along the eastern and western boundaries. A second transect was established close to the original transect but across the east–west short axis (by then reduced to 650 m wide) to enable assessment of post-drainage changes. The vegetation and peat were sampled as above in seven temporary plots of size 2 m × 2 m and at 100 m intervals, commencing at 5 m in from the western boundary (Clarkson *et al.* 2004a). In addition, at each plot two peat samples were obtained from the surface layer using steel soil core sample rings (100 mm diameter by 75 mm deep). One core was analysed for bulk density and water content, the other for pH, total nitrogen (N), total phosphorus (P), and total potassium (K) at the Landcare Research Environmental Chemistry Laboratory, Palmerston North, following Blakemore *et al.* (1987). At the larger Kopuatai bog in 1997, a 1.2 km transect was established in late successional *Sporadanthus/ Empodisma* vegetation, and eight plots were similarly set up and sampled (Clarkson *et al.* 2004a).

In 2017, for this study, eight permanently marked plots of size 2 m × 2 m were established at 50–150 m intervals along an east–west transect at Moanatuatua, commencing at the same plot as in 1997 and on the same transect line. Plot locations were determined by newly installed water-level data loggers, to provide long-term vegetation and water-table monitoring data. At Kopuatai (the reference site) we were unable to access the original transect, so we established five permanent 2 × 2 m plots along a new 1.0 km transect parallel to the first but 500 m south. The plots were in the same late-successional vegetation type as in 1997 and had consistent vegetation composition and structure in order to provide an overall reference state for Waikato restiad bogs. At each plot, the vegetation and peat were sampled and analysed as outlined above, with the inclusion of total carbon (C). Additionally, at both sites, foliage samples of the three dominant plant species, the restiads *Empodisma* and *Sporadanthus*, and the heath shrub *Epacris pauciflora* (henceforth *Epacris*; Ericaceae), were collected. About 5 g of newly mature culms or leaves exposed to the sun were oven-dried for 24 h at 60 °C and analysed for N, P, K and C at the Environmental Chemistry Laboratory, and for $\delta^{15}N$ at the University of Waikato Stable Isotope Unit, Hamilton.

Data analysis

Due to the unbalanced design, vegetation, hydrological and peat physico-chemical data were analysed using residual maximum likelihood (REML) in Genstat 19 (VSN International 2017). The model comprised fixed effects for factors Site, Year, and the Site by Year interaction. No random effects were included in the model. Residual plots were inspected for departures from the assumptions of normality and constant variance. Before analysis, peat total C and peat C/N were natural-log transformed to stabilise the variance. Site by Year means were compared using Fisher's unprotected least significant differences at the 5 % level.

The data on foliage chemical composition of the three dominant plant species collected in 2017 were similarly analysed using REML but with fixed effects for factors Site, Species, and the Site by Species interaction. The Site by Species means were compared using Fisher's unprotected least significant differences at the 5 % level.

RESULTS

Vegetation and hydrological changes 1974–2017

In 1974, the vegetation at Moanatuatua was dominated by cane-like clumps of *Sporadanthus* up to 1.6 m tall scattered above sprawling *Empodisma* up to 1.1 m in height (Dickinson 1974, de Lange *et al*. 1999). Occasional heath shrubs of *Epacris* and *Leptospermum scoparium* were also present in the canopy, with the sedge *Machaerina teretifolia*, the fern *Gleichenia dicarpa* and *Empodisma* common in the understorey. The ground cover was characterised by small carnivorous herbs (*Utricularia delicatula*, *Drosera* spp.), lycopods (*Lycopodiella serpentina*, *L. lateralis*), mosses (*Campylopus acuminatus* var. *kirkii*, *Sphagnum cristatum*) and liverworts (e.g., *Goebelobryum unguiculatum*), which grew in the water-saturated peats. Vascular species richness at Moanatuatua was initially similar to that at Kopuatai (Table 1), but decreased from 1974 to 1997, after which it remained stable but significantly lower. Vegetation height and von Post peat decomposition at the remnant were also originally similar to the reference site values but had significantly increased by 2017. Vegetation height at Kopuatai also increased over this 20-year period, perhaps due to recovery after fire in the mid-1970s (de Lange *et al.* 1999) (Table 1). The lowered water table at the reference site was probably a result of the exceptionally dry 2016–2017 summer season recorded in northern New Zealand (NIWA 2017), and the water table at Kopuatai has since returned to its former, higher levels, whereas the water table at Moanatuatua remains low (BRC unpublished data).

Vegetation changes over time at Moanatuatua were marked. In 1997 the same canopy and understorey species were present (Figure 2A; species height frequency diagrams of representative plots are in de Lange *et al.* 1999) but the vegetation had nearly doubled in height (Table 1), mainly due to the increased height of *Epacris* shrubs. Additionally, the understorey was becoming very dense, and many ground cover species such as *U. delicatula*, *S. cristatum* and *L. serpentina* had become scarce or were extirpated. In 2017, *Sporadanthus* cover had decreased across the bog remnant (Table 1), whereas *Empodisma* had increased (Figure 2B), resulting in relatively constant restiad cover. *Epacris* cover had not changed significantly but *Epacris* shrubs were typically the tallest canopy plants (whereas *Sporadanthus* were the tallest plants in 1974). *Machaerina teretifolia* and *G. dicarpa* persisted locally in the understorey. Although vascular species richness was similar to that in 1997, a few 'dryland' and non-bog species such as *Pteridium esculentum* and *Histiopteris incisa* had spread or established in plots at or near the new margins of the bog. In particular, the westernmost plot, located 5 m from the margin, was dominated by *Pteridium esculentum* (88 %), which largely contributed to the increase in overall mean for that species in transect plots during the period 1997–2017 (Figure 2C). Non-native species were very scarce and typically restricted to peripheral areas.

The Moanatuatua restiad bog flora, compiled from reconnaissance surveys and plot data, initially comprised 23 species, of which 17 were vascular and six non-vascular (Table 2). In 1997, at least six short-statured species were not encountered at the remnant, and in 2017 a further five short species were not recorded. Over the 43 years, this represents a loss of 35 % of vascular and 83 % of non-vascular species, and 48 % of the total restiad bog flora. In contrast, the flora at Kopuatai remained unchanged over time.

Table 1. Mean vegetation, hydrological and peat physico-chemical properties, from the residual maximum likelihood (REML) analysis, for modified (Moanatuatua) and reference (Kopuatai) bogs in 1974, 1997 and 2017. Water table is depth from bog surface. SEM is standard error of the mean. For each property, means without a letter in common are significantly different.

	Site	Year	Vascular species (n)	*Sporadanthus* cover (%)	*Empodisma* cover (%)	*Epacris* cover (%)	Restiad cover (%)	Vegetation height (m)	Water table (mm)	Water content (%)	von Post	pH
Means	Moanatuatua	1974	6.0	21.5	37.9	11.2	59.4	1.4	227	1188	1.6	4.3
	Moanatuatua	1997	4.3	50.0	22.9	13.7	72.9	2.6	293	342	1.9	4.4
	Moanatuatua	2017	4.4	6.6	54.4	13.8	60.9	2.6	785	289	3.0	4.4
	Kopuatai	1997	6.6	11.6	56.6	2.3	68.2	1.4	49	1682	1.6	4.8
	Kopuatai	2017	6.4	23.2	43.8	12.0	67.0	2.1	216	1441	2.2	4.5
SEMs	Moanatuatua	1974	0.4	7.1	7.5	4.6	4.5	0.1	38	78	0.2	0.1
	Moanatuatua	1997	0.4	7.1	7.5	4.6	4.5	0.1	38	78	0.2	0.1
	Moanatuatua	2017	0.3	6.6	7.0	4.3	4.2	0.1	36	73	0.2	0.1
	Kopuatai	1997	0.3	6.6	7.0	4.3	4.2	0.1	36	73	0.2	0.1
	Kopuatai	2017	0.4	8.4	8.9	5.4	5.3	0.2	46	92	0.2	0.1
Letters	Moanatuatua	1974	b	a	ab	a	a	a	b	b	a	a
	Moanatuatua	1997	a	b	a	a	a	c	b	a	ab	a
	Moanatuatua	2017	a	a	b	a	a	c	c	a	c	a
	Kopuatai	1997	b	a	b	a	a	a	a	d	a	b
	Kopuatai	2017	b	a	ab	a	a	b	b	c	b	a

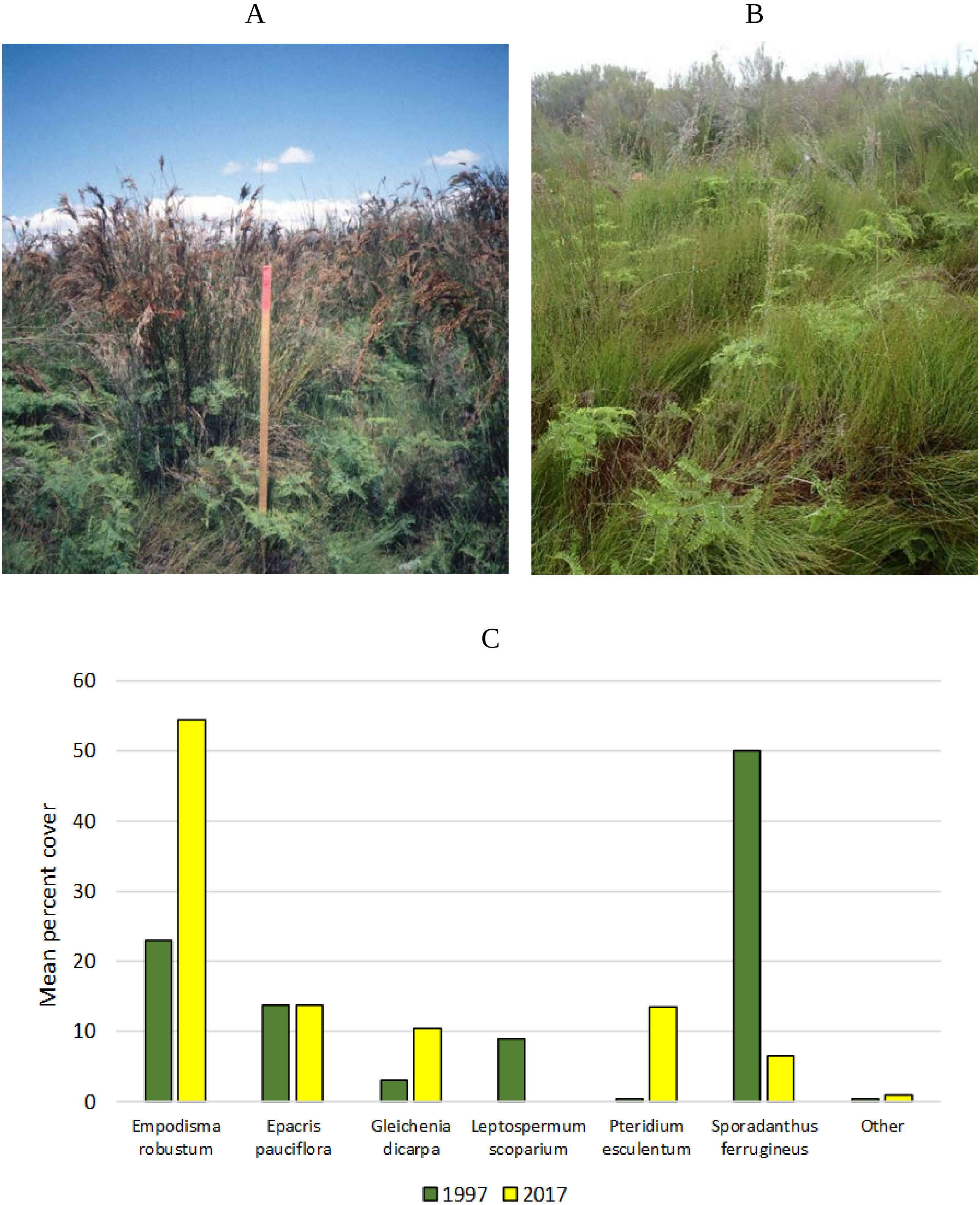

Figure 2. A: Moanatuatua vegetation in 1997 dominated by *Empodisma* and *Gleichenia dicarpa* in foreground, and the taller *Sporadanthus* in background. The wooden stake is 2 m tall. B: Moanatuatua vegetation in the same general area in 2017 showing *Empodisma* and *Gleichenia dicarpa* in foreground and *Epacris* shrubs in background, with scattered culms of *Sporadanthus* (e.g., upper mid left), recognisable by the tall brown rush-like flower heads. C: Clustered column chart of transect species mean percent cover at Moanatuatua in 1997 and 2017; 'Other' = *Drosera binata* (1997), *Histiopteris incisa* (2017) and *Hypolepis distans* (2017).

Table 2. List of restiad species and plant functional types recorded in Moanatuatua Bog in 1974, 1997 and 2017. Height categories: Short < 0.3 m, Medium 0.3–1.0 m, Tall > 1.0 m

Species	Family	Plant Functional Type	Height Category	1974[1]	1997[2]	2017
Vascular						
Corybas carsei	Orchidaceae	Orchid	Short	✓		
Drosera binata	Droseraceae	Forb	Short	✓	✓	✓
Drosera spatulata	Droseraceae	Forb	Short	✓	✓	✓
Empodisma robustum	Restionaceae	Restiad	Tall	✓	✓	✓
Epacris pauciflora	Ericaceae	Shrub	Tall	✓	✓	✓
Machaerina teretifolia	Cyperaceae	Sedge	Medium	✓	✓	✓
Gleichenia dicarpa	Gleicheniaceae	Fern	Medium	✓	✓	✓
Leptospermum scoparium	Myrtaceae	Shrub	Tall	✓	✓	✓
Lycopodiella lateralis	Lycopodiaceae	Club moss	Short	✓		
Lycopodiella serpentina	Lycopodiaceae	Club moss	Short	✓		
Microtis unifolia	Orchidaceae	Orchid	Short	✓	✓	✓
Schizaea fistulosa	Schizaeaceae	Fern	Short	✓	?	
Schoenus brevifolius	Cyperaceae	Sedge	Medium	✓	✓	✓
Sporadanthus ferrugineus	Restionaceae	Restiad	Tall	✓	✓	✓
Thelymitra cyanea	Orchidaceae	Orchid	Short	✓	✓	✓
Utricularia delicatula	Lentibulariaceae	Forb	Short	✓		
Utricularia dichotoma	Lentibulariaceae	Forb	Short	✓		
Non-vascular						
Campylopus acuminatus var. *kirkii*	Leucobryaceae	Moss	Short	✓	✓	
Goebelobryum unguiculatum	Acrobolbaceae	Liverwort	Short	✓	✓	
Lepidozia sp.	Lepidoziaceae	Liverwort	Short	✓	✓	
Riccardia crassa	Aneuraceae	Liverwort	Short	✓	✓	
Sphagnum cristatum	Sphagnaceae	Moss	Short	✓		
Sphagnum falcatulum[3]	Sphagnaceae	Moss	Short	✓	✓	✓
Total				23	16	12

[1] Dickinson 1974, Clarkson *et al*. 1999; [2]Clarkson *et al*. 1999; [3] Present only in marginal ditch in 1997–2017.

Chemistry changes 1997–2017

Comparisons of the Moanatuatua peat analyses (Table 3) between 1997 and 2017 revealed significant increases in K (mean increase 200 %) and N (mean increase 71 %). While there were no significant changes in bulk density or P in the intervening 20 years, both of these were already significantly higher than at the Kopuatai reference site. In addition, in 2017, total carbon was significantly higher at Moanatuatua compared with Kopuatai, and C/N was lower.

Foliage chemical composition in 2017 varied between the shrub and restiads and between sites. (Table 4). At Moanatuatua, compared with the reference site, *Epacris* had significantly increased levels of N and P and lower N/P. On the other hand, both restiad species showed little change in N or P. *Empodisma* had lower N/P whereas *Sporadanthus* N/P values did not change significantly. For all three species, values for C and K were significantly different from each other, but not between sites. Compared with the Kopuatai reference site, $\delta^{15}N$ stable isotope signatures at Moanatuatua were significantly less depleted for *Epacris* and *Sporadanthus*, whereas *Empodisma* signatures were more depleted.

Table 3. Means (± standard error) for peat nutrients and associated variables (bulk density (BD), total nitrogen (TN), total potassium (TK), total phosphorus (TP), total carbon (TC) and carbon/nitrogen quotient (C/N)), from the residual maximum likelihood (REML) analysis, for modified (Moanatuatua) and reference (Kopuatai) bogs in 1997 and 2017. For the natural log transformed total carbon and C/N, the back-transformed mean is given (in parentheses). For each variable, means without a letter in common are significantly different.

Site	Year	BD ($g\ cm^{-3}$)	TN (%)	TK (%)	TP (m)	log(TC)	TC (%)	log(C/N)	C/N (%)
Moanatuatua	1997	0.072 ± 0.005 b	0.95 ± 0.10 a	0.02 ± 0.01 a	0.034 ± 0.004 b				
Moanatuatua	2017	0.068 ± 0.004 b	1.63 ± 0.09 b	0.06 ± 0.01 bc	0.038 ± 0.004 b	4.01 ± 0.01 b	(55.3)	3.54 ± 0.07 a	(34.3)
Kopuatai	1997	0.042 ± 0.004 a	0.98 ± 0.09 a	0.04 ± 0.01 ab	0.014 ± 0.004 a				
Kopuatai	2017	0.045 ± 0.006 a	0.90 ± 0.12 a	0.09 ± 0.01 c	0.014 ± 0.005 a	3.94 ± 0.01 a	(51.4)	4.06 ± 0.09 b	(58.2)

Table 4. Mean (± standard error) for plant foliage isotopic and chemical composition (total carbon (TC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), $\delta^{15}N$ and nitrogen/phosphorus quotient (N/P)), from the residual maximum likelihood (REML) analysis, for modified (Moanatuatua) and reference (Kopuatai) bogs in 2017. For each variable, means without a letter in common are significantly different.

Site	Species	TC (%)	TN (%)	TP (%)	TK (%)	$\delta^{15}N$ (‰)	N/P
Moanatuatua	*Epacris*	53.5 ± 0.1 c	1.34 ± 0.04 d	0.043 ± 0.002 c	0.35 ± 0.03 a	-6.55 ± 0.42 b	31.9 ± 1.1 a
Moanatuatua	*Empodisma*	49.2 ± 0.1 b	0.79 ± 0.04 bc	0.022 ± 0.002 ab	0.59 ± 0.03 b	-3.56 ± 0.42 c	35.9 ± 1.1 b
Moanatuatua	*Sporadanthus*	48.6 ± 0.1 a	0.73 ± 0.04 abc	0.026 ± 0.002 b	0.86 ± 0.03 c	-1.93 ± 0.45 d	28.5 ± 1.2 a
Kopuatai	*Epacris*	53.4 ± 0.2 c	0.88 ± 0.06 c	0.021 ± 0.002 ab	0.31 ± 0.04 a	-15.35 ± 0.68 a	42.5 ± 1.8 c
Kopuatai	*Empodisma*	49.2 ± 0.1 b	0.70 ± 0.05 ab	0.017 ± 0.002 a	0.60 ± 0.03 b	-0.18 ± 0.53 e	41.6 ± 1.4 c
Kopuatai	*Sporadanthus*	48.2 ± 0.1 a	0.65 ± 0.05 a	0.022 ± 0.002 ab	0.78 ± 0.03 c	-6.81 ± 0.53 b	29.2 ± 1.4 a

DISCUSSION

Vegetation and hydrological changes

Over the 43-year monitoring period, Moanatuatua Peat Scientific Reserve has experienced major hydrological modifications which have resulted in significant changes in vegetation structure and composition, and loss of species. In 1974, although more than 80 % of the original bog had been drained and developed, the extant 114-ha remnant was buffered within 1,250 ha of natural bog habitat and not greatly impacted by peripheral drainage. When our monitoring began in 1974, Moanatuatua still retained the essential and original bog hydrological characteristics and flora as described by Cranwell (1939), Campbell (1964) and Butcher (1965). All the 23 ombrotrophic bog species (17 vascular, 3 mosses, 3 liverworts) recorded by Butcher (1965) were still present in 1974 (Clarkson *et al.* 1999). Such minimal changes in plant communities in the early post-drainage years are also observed in ombrotrophic sites in Finland (Laine *et al.* 1995).

Changes to the bog ecosystem began to be observed in the 23 years between 1974 and 1997. The area of natural bog was reduced to the current 114-ha remnant (plus a 21-ha modified outlier 300 m to the north), deep drains were dug around the entire perimeter, and surrounding land converted to pasture for dairying. In 1997, the remnant had significantly lower water table and taller, denser vegetation, which together resulted in a loss of several small-statured species adapted to high water table and/or open habitat, e.g., *Utricularia* spp., *Lycopodiella* spp., *Sphagnum cristatum*. Small populations of the remaining non-vascular species were limited to isolated pockets in wetter parts of the remnant. Similar losses or reductions of species adapted to wet conditions (*Sphagnum* spp., *Vaccinium oxycoccus*) and associated increases in plant productivity and shrub growth have been reported with water-table lowering in northern bogs (Minkkinen *et al.* 1999, Murphy *et al.* 2009, Talbot *et al.* 2010).

By 2017, the rate of vascular species loss in the remnant plots had slowed or halted and, compared with 1997, vascular species richness was unchanged. All non-vascular species had disappeared apart from rare occurrences of *Sphagnum falcatulum* in the deepest parts of the marginal ditch. Vegetation height was also unchanged, but canopy composition had shifted to increased cover of *Empodisma* and *Epacris* (Ratcliffe *et al.* 2019 at the expense of *Sporadanthus*. Given the overtopping of the canopy vegetation and thickening of the understorey, these differences may be accounted for by competition for niche resources, including light, and species-specific adaptations to lowered water tables (Clarkson *et al.* 2009, Ratcliffe *et al.* 2019). Water table fluctuations and range, as well as water table drawdown, are also important drivers of compositional and structural shifts in vegetation. For example, pronounced water table fluctuations at Moanatuatua (up to 704 mm recorded), together with the overall low water table, have favoured *Empodisma* dominance and the recent expansion of *Epacris* shrubs (Ratcliffe *et al.* 2019). In Finnish bogs, Laine *et al.* (2019) also demonstrated that magnitude of water table change was a primary driver of vegetation change, with the flooding regime controlling shifts from non-forested to forested peatland.

Nutrient changes

Peat nutrient levels have increased at Moanatuatua over the past 20 years; however, the patterns and rates of change differed among N, P and K. In 1997, total P was already significantly higher at Moanatuatua than in the reference Kopuatai site and remained significantly higher in 2017. Although we do not have pre-development levels of total P for Moanatuatua, these were likely to have been similar to current levels at Kopuatai, as all Waikato raw peats were known to be extremely deficient in P and other major elements required for plant growth (Grange *et al.* 1939). Applying heavy rates of phosphates (e.g., 1 t ha^{-1} of superphosphate in the first year; van der Elst 1958) was standard agricultural practice in the early post-development years of the Waikato Basin, making aerial drift of P fertiliser applied to the surrounding land a likely cause of enrichment of Moanatuatua peats. In contrast, N levels at Moanatuatua and Kopuatai were similar in 1997 and did not markedly diverge until later. Application of artificial N was not originally recommended as standard farm practice as it was very costly (van der Elst 1958). Manufacturing of locally sourced urea fertiliser began in 1983, and application of N in Waikato increased by more than 50 % during the period 2002–2017 (Statistics New Zealand 2019). Nowadays, clouds of fertiliser drifting over the Moanatuatua reserve from adjacent farms are not uncommonly observed when fertiliser application is in progress. Total K levels also increased at Moanatuatua over the last 20 years, but they are currently not significantly different from those at Kopuatai. The naturally higher K content of Kopuatai peat may be the result of K-enriched coastal winds, as high inputs of wind-transported oceanic ions, including K, have been measured on subantarctic Campbell Island (Meurk *et al.* 1994). The Kopuatai sampling site is 15 km from the ocean, whereas Moanatuatua is 52 km inland and more sheltered.

Drainage (lowered water table, reduced peat water content) also increases the depth of the oxic layer, leading to peat shrinkage and faster decomposition (higher von Post index), which increases rates of mineralisation and amounts of available nutrients (Rydin & Jeglum 2013).

Foliage N and P levels for *Epacris*, the main shrub species at Moanatuatua in 2017, were significantly higher than at Kopuatai (reference site). *Epacris* is an ericoid mycorrhizal shrub (Reed 1987), and its foliar nutrients have been shown to strongly reflect peat nutrient status across nutrient gradients in bogs in a similar manner to its close relative *Dracophyllum scoparium* (Clarkson *et al*. 2004b, BRC unpublished). N and P are the most important nutrients in restiad bog development (Clarkson *et al.* 2004a), with wetlands switching from N limitation in early succession to P limitation in late succession (i.e., becoming bogs; Verhoeven *et al.* 1996). Plant N/P can reflect the nature of the limitation at community level, with $N/P < 14$ indicating N limitation and $N/P > 16$ P limitation in European wetlands (Koerselman & Meuleman 1996). For the three dominant species at both of our sites, all N/P values were greater than 16, indicating P limitation (Table 4). Plant $\delta^{15}N$ signatures can be used as indicators of P or N limitation; $\delta^{15}N$ becomes more depleted with increasing N availability and with increasing P limitation (McKee *et al*. 2002, Clarkson *et al.* 2005). The higher *Epacris* nutrient concentrations suggest that Moanatuatua has become enriched in N and P, a likely side effect of fertiliser applications to the surrounding land. Additionally, the lower N/P and less depleted $\delta^{15}N$ signatures indicate the site is changing from being strongly P limited (as at Kopuatai) to less so.

Foliage nutrient trends for the restiad species at Moanatuatua in 2017 were less clear. N and P levels were nearly 50 % lower in *Empodisma* and *Sporadanthus* than in co-habiting *Epacris* and were not significantly different from the Kopuatai values. The nutrient contrasts between woody and restiad species have been attributed to fundamental species-specific differences in nutrient requirements and nutrient acquisition mechanisms (Clarkson *et al.* 2005). The restiad species are non-mycorrhizal, have extremely efficient nutrient-acquiring cluster roots (Lamont 1982) and are very conservative nutrient users, highly adapted to extremely low nutrient levels (Meney & Pate 1999). Restiad species could be considered to have strong stoichiometric homeostasis, characterised by low N and P concentrations, high N/P and the ability to maintain high N/P despite variation in nutrient availability or abundance (Yu *et al.* 2011). In contrast, *Epacris* displays weaker homeostasis and, because it has the potential to absorb more nutrients when available, its nutrient levels can change accordingly.

Ecosystem processes

Moanatuatua has become drier and nutrient-enriched, and several species have been lost; however, basic ecosystem processes appear to be maintained. The key restiad species are still present and, although *Sporadanthus* has declined in extent, the main peat former *Empodisma* has become the dominant species. *Empodisma* is considered to be the ecosystem engineer in the fen–bog transition zone in New Zealand, playing a similar role to the *Sphagnum* in northern bogs (Hodges & Rapson 2010). It has distinctive structural and physiological adaptations to a range of environmental conditions, including tolerance of high, low, and fluctuating water tables (Ratcliffe *et al.* 2019), extremely low decomposition rates (Clarkson *et al.* 2014), and strict physiological controls over evaporation (Campbell & Williamson 1997). Studies of carbon fluxes at Moanatuatua have shown that the site remains a moderate sink for CO_2, sequestering 69 g C m^{-2} yr^{-1} (Ratcliffe *et al.* 2019). However, this was attributed to increased gross primary productivity caused by chronically low water table and expansion of (woody) *Epacris* cover; rather than by typical peat-forming processes as at Kopuatai, where the rate of C sequestration was 203 g m^{-2} yr^{-1} (Ratcliffe *et al.* 2019). Productivity would also be influenced by increased P levels, as demonstrated in fertilisation studies by Güsewell (2004).

The long-term ecological prognosis for Moanatuatua is unclear. It may be reaching an ecological tipping point where ongoing water table drawdown and nutrient inputs tip the balance to favour expansion of faster growing nutrient-demanding plants. Also, the increased woody content and drier conditions make the site extremely vulnerable to fire. Expansion of shrubs such as *Epacris* in the short term (Ratcliffe *et al.* 2019), and probably taller oligotrophic forest species in the long term, as has happened in drained bogs elsewhere in the world (Laine *et al.* 1995, Minkkinen *et al.* 1999, Weltzin *et al.* 2003, Talbot *et al.* 2010) are likely to occur under current land management. Raising and stabilising the water table is an immediate priority for increasing the resilience of the remnant, but restoration of the former bog extent should also be seriously considered, given the emerging importance of restoring agriculturally modified peatlands as safety nets in the face of global climate change (Leifeld & Menichetti 2018), and to maintain global biodiversity and other essential ecosystem services (Bonn *et al.* 2016, Minayeva *et al.* 2017).

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AUTHOR CONTRIBUTIONS

BRC developed the study design and objectives; BRC, CHW, DT and NBF conducted the field research; and VMC undertook the data analysis. BRC and VMC wrote the draft manuscript and all authors contributed to refinement and editing.

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