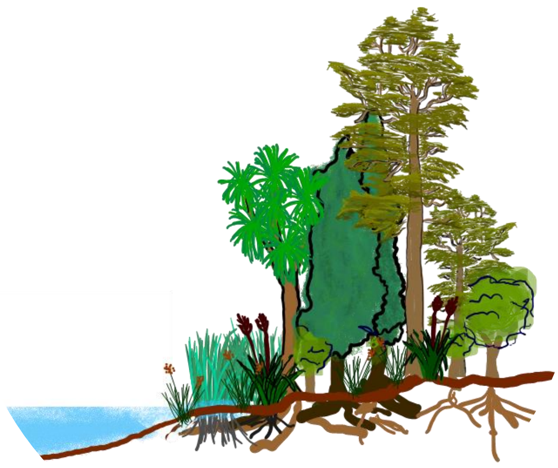
QUANTIFYING SOIL, MICROBIAL, AND PLANT COMMUNITY CHANGES FOLLOWING WETLAND RESTORATION ON PRIVATE LAND



BY

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TE HERENGA WAKA

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He waka eke noa

We are all in this together

- Whakataukī (Māori proverb)

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Abstract

Extensive global and national wetland loss has reduced ecosystem services to people and undermines the sustainability of ecosystems. Restoration projects aim to regain the biophysical conditions of remnant wetlands that produce an abundance of ecosystem services. Ecological restoration practices manipulate community succession to enhance ecological functions, and these different successional stages may be reflected in the soil physio-chemical characteristics, plants, and soil microbes, which in turn produce a variety of ecosystem services. Considerable potential for wetland restoration on private property exists in New Zealand, but it remains unknown how successful restoration is when undertaken through a landholder's own prerogative. Relative to restoration of public land, private restoration projects are often small scale, personally funded and preference driven. In this thesis, I quantify the outcomes of small-scale private wetland restoration projects by measuring changes in plant and soil microbial communities, and soil physiochemical characteristics. I explore the relationships among variation in plant, soil and microbial datasets and test for causes of this variation. Using a paired sampling design, I sampled 18 restored wetlands and 18 unrestored wetlands on private property in the Wairarapa region. I used a Whitaker plot design to sample wetland plant communities at multiple scales and took soil samples that I analysed for physio-chemical properties. Additionally, I quantified the biomass and community composition of the microbes in the soil samples using phospholipid fatty acid analysis. In my second chapter, I use linear mixed-effect models, principal components analysis, and non-metric multidimensional scaling to ask: How does wetland restoration alter the plant community, soil physio-chemical characteristics, and the soil microbial community? In my third chapter, I employ Procrustes analysis to look at the association of variation in plants, microbes, and soil characteristics to explore whether successional processes of these attributes are concurrent within wetlands. I then use hierarchical cluster analysis to determine which of the wetlands are at similar successional stages and identified site contexts and restoration treatments that were in common among similar wetlands. These analyses provide insight to the conditions that advance successional processes in restored wetlands. Specifically, I ask 1) How do plant, microbial, and soil characteristics co-vary during wetland restoration? 2) How do indicators of wetland succession respond to restoration? 3) Are different restoration practices and site contexts influencing wetland outcomes during restoration? Private wetland restoration enhanced succession in plant, soil, and microbial properties towards those more similar to undisturbed wetland conditions. Specifically, restoration added ~13 native plant species, increased total fungal and arbuscular mycorrhizal biomass, and total microbial biomass by 25%. Restoration increased soil moisture by 93%, soil organic carbon by 20%, and saturated hydraulic conductivity by 27%. It also reduced bulk density by 0.19 g^{-1} cm^{3} and plant available phosphorus (Olsen P) by 23%. Procrustes analysis revealed a lack of congruence in the recovery of plant, microbial, and soil indicators of succession, signifying that the plant community succeeded faster than the microbial community and soil characteristics. Variation in soil and microbial properties separated restored wetlands into two groups of early and later succession wetlands, which was independent of the number of years since restoration began at the sites but corresponded to elements of wetland hydrology. Soil and microbial characteristics in hydrologically connected wetlands recovered more quickly following restoration than hydrologically isolated wetlands. Private restoration increased spatial heterogeneity of outcomes at the plot scale, which depended on site factors. My data suggests that private wetland restoration is effective in increasing plant, soil, and microbial characteristics that produce ecosystem services. Additionally, wetland restoration increased environmental heterogeneity and the capacity for ecosystem service delivery, which may contribute to increased resilience of the Wairarapa landscape.

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Table of Contents

List of Tables

List of Figures

List of Abbreviations

A	---	Chance-corrected within-group agreement
F/B	---	Fungi/ bacteria
FA	---	Fatty acid
$Gram^+$ / $Gram^-$	---	Gram-positive bacteria/ Gram-negative bacteria
$Gram^+$	---	Gram-positive bacteria
$Gram^-$	---	Gram-negative bacteria
IV	---	Indicator value
K_S	---	Saturated hydraulic conductivity
MRPP	---	Multi Response Permutation Procedure
N	---	Nitrogen
NMS	---	Nonmetric Multidimensional Scaling
Olsen P	---	Olsen Phosphorus
P	---	Phosphorus
PCA	---	Principal Components Analysis
PLFA	---	Phospholipid fatty acid analysis
POC	---	Particulate organic carbon
PTF	---	Pedotransfer function
SOC	---	Soil organic carbon
SOM	---	Soil organic matter
z	---	Slope of species accumulation curve

Chapter 1 Literature Review, Aims & Questions

Literature Review

Wetland ecosystems exist at the interface of terrestrial and aquatic systems. They are characterised by soils that are submerged by water partially or fully year-round and contain plants that are adapted to exist within anoxic soil conditions. Wetlands can be found in a large array of climates, landscapes, elevations, latitudes, and hydrological systems. Therefore wetlands are diverse in the types of flora, fauna and soil types they contain (Mitsch & Gosselink, 2015). They are highly productive systems, contributing to 10 % of the global terrestrial production despite only covering ~ 6% of the earth's surface (Aselmann & Crutzen, 1989; Fourqurean et al., 2012; Neori & Agami, 2017; X. Xu, Thornton, & Post, 2013). They provide about a quarter of the global value of ecosystem services, producing 10 – 100 fold higher amounts of services per unit area than drylands (Costanza et al., 2014; Kingsford, Basset, & Jackson, 2016). A major ecosystem service they provide is atmospheric regulation because they hold a third of the world's organic carbon in their soils, although contrasting their regulating effect, contribute a third of global methane emissions (Kayranli, Scholz, Mustafa, & Hedmark, 2010). Additionally, wetlands provide significant water purification services, and can capture as much as 80-90% of sediment and 70-90% of nutrients from runoff (Borin, Bonaiti, Santamaria, & Giardini, 2001; Jordan, Stoffer, & Nestlerode, 2011). Furthermore, wetlands are hotspots for nutrient cycling, are important sites for food production, provide fibres and abate floods. As biodiversity hotspots they support a disproportionately high number of species for their area (Dudgeon et al., 2006).

Wetland loss

Despite producing large quantities of highly valuable ecosystem services, we have lost between 64-71% of global wetland extent since the twentieth century (Davidson, 2014). Human activities are the primary cause of wetland loss due to urbanisation, agriculture, peat extraction for fuel and fertilizer, resource extraction (wood, oil, gas, water), and global warming impacts (*e.g.* sea level rise, extreme climatic events, decreased precipitation or increased temperature; Robertson, 2016; Van Asselen, Verburg, Vermaat, & Janse, 2013). Wetlands have highly organic soils and are frequently positioned along floodplains, making them ideal for urban development and agriculture (Tockner et al., 2008). Agricultural conversion of wetlands is the largest cause of wetland degradation (Van Asselen et al., 2013). Population and income growth continues to increase demand for agricultural products and places further pressure on wetland ecosystems (Barral, Rey Benayas, Meli, & Maceira, 2015; Bruinsma, 2009). Concurrently, wetland loss and degradation has diminished the supply of ecosystem services they produce (Yan & Zhang, 2019; Zedler & Kercher, 2005). The opposing trends in the demand and supply of wetland ecosystem services undermines the sustainability of our planet (Zedler & Kercher, 2005).

Freshwater wetlands

A higher proportion of freshwater wetlands than coastal wetlands have been lost (60.8% vs 46.4%, respectively; Davidson (2014)). But freshwater wetlands (herein "wetlands") are particularly important for their water purification-, carbon sequestration-, and flood abatement-ecosystem services. Wetland plant roots increase the heterogeneity of soil properties, creating oxic and anoxic conditions in close proximity. These heterogeneous conditions facilitates the simultaneous activity of aerobic and anaerobic microbial communities, enhancing nutrient cycling (Brune, Frenzel, & Cypionka, 2000; Lamers et al., 2012). Wetlands also receive nutrients from upslope environments and this input of nutrients, together with fast nutrient cycling due to active aerobes and anaerobes makes these systems highly productive (Bodelier & Dedysh, 2013). There are four broad types of wetlands: swamps, bogs, fens, and marshes. Each type is differentiated depending on the landscape, soil, and hydrological characteristics. Swamps are dominated by woody plants, with mineral soils which are highly anoxic and organic. Bogs are spongy peat deposits that are feed predominantly with rainwater, dominated by sphagnum moss, and has acidic water and low nutrient soils. Fens are also peat deposits, but have soils that are relatively nutrient rich, and are connected to a larger watersheds. These conditions lead to less acidic water and a greater diversity of plants in fens than in bogs. Marshes have organic or mineral soils, and typically have emergent macrophytes, occurring along streams and in depressions. They can be hydrologically isolated systems fed by rainwater, or connected to a larger hydrologic scheme by rivers, streams, or springs.

Conversion of wetlands into agroecosystems

Wetland hydrology, soil physiochemical characteristics, soil microbial communities, and plant communities are drastically altered when wetlands are converted to agricultural systems. Drainage reduces the saturation and anoxic conditions of the soil. Additionally, fertiliser use and high stocking rates alter nutrient inputs, while tilling, livestock trampling, and heavy machinery use reduces soil bulk density (Noll, Mobilian, & Craft, 2019). Furthermore, monocrops and pasture plant communities reduce soil habitat heterogeneity, which alters the soil microbiome, and reduces plant, vertebrate, and invertebrate diversity (Moora et al., 2014). These practices create fewer soil microbial habitats and shorten the microbial food web (Bardgett & van der Putten, 2014; Hartman, Richardson, Vilgalys, & Bruland, 2008), leading to changes in the biogeochemical cycling (Sui et al., 2019), soil structure and the rate of erosion (Bever et al., 2010; Koziol & Bever, 2017) of agricultural-wetland sites.

New Zealand context

New Zealand far exceeds the global average of wetland loss, with 90% of pre-European wetlands lost or severely degraded. Currently only 250,000 ha of wetlands remain (Ausseil, Chadderton, Gerbeaux, Theo Stephens, & Leathwick, 2011). The majority of remaining wetlands, which are primarily situated in agricultural or urban dominated landscapes, are highly fragmented, smaller than 10 ha, and in poor condition (Ausseil et al., 2011). New Zealand's fertile lands are dominated by agro-ecosystems: ~15% of land area is used for sheep, ~10% for beef cattle, ~8% for dairy cattle, and ~0.5% for horticulture (StatsNZ, 2021). Almost 70% (348,000 km) of streams run through land used for agricultural production: 45% (227,000 km) of stream length flows through sheep and beef farms and 6% (32,000 km) flows through dairy farms (Daigneault, Eppink, & Lee, 2017). In New Zealand, the sheep, beef, and dairy industries emit 35 Mt $CO_{2equivalent}$ annually, leach 190 kilotons of nitrogen (N), and lose 7.5 kilotons of phosphorus (P) and 136 million tonnes of sediment annually into streams (Daigneault et al., 2017). Eutrophication of waterways, loss of biodiversity, and greenhouse gas emissions are the largest externalities of New Zealand's agricultural industry (Foote, Joy, & Death, 2015).

Restoration

Restoration has gained significant traction recently (Clewell & Aronson, 2013; Martin, 2017; Stavi & Lal, 2015), following studies determining the destabilising effects caused by the unprecedented rate of biodiversity and ecosystem service loss in the 20th and 21st century (Cardinale et al., 2012; Rockström et al., 2009). The Millennium Ecosystem Assessment (Reid et al., 2005) concluded that anthropogenic changes to ecosystems were the fastest in the past 50 years than at any other time in human history. Biodiversity loss and ecosystem degradation increases the risks of abrupt and irreversible changes, and the Stockholm resilience centres' planetary boundary framework has determined that we are far beyond the zone of uncertainty about what this will mean for our planet's stability in future (Steffen, Broadgate, Deutsch, Gaffney, & Ludwig, 2015). Restoration is now a global priority following the 2010 Aichi Convention on Biological Diversity, and several multinational and international programs exist. The United Nations declared 2021-2030 to be the decade of ecological restoration; the New York Declaration on Forests which aims to restore 350 million hectares of forest land by 2030 (UNDP, 2021); and the European Green Deal accompanied by the EU Biodiversity Strategy for 2030 that aims to restore and conserve biodiversity across Europe (European Commission, 2021). In New Zealand, there is widespread recognition of the need to restore wetlands in central and local governments, councils (Myers, Clarkson, Reeves, & Clarkson, 2013), and increasing restoration practice by community groups (Peters, Hamilton, & Eames, 2015), iwi, and private landowners (Schroder, Lang, & Rabotyagov, 2018; Tomscha et al., 2021).

Restoration is the manipulation of successional processes to re-establish a desired ecosystem by accelerating species and substrate change, to achieve desired biodiversity and ecosystem services (Luken, 1990). Restoration is increasingly motivated by the provision of ecosystem services (Alexander, Aronson, Whaley, & Lamb, 2016; Matzek, Wilson, & Kragt, 2019) and the reversal of land degradation (Aradóttir, Petursdottir, Halldorsson, Svavarsdottir, & Arnalds, 2013; Bernhardt et al., 2007), although biodiversity enhancement is still a primary motivation for restoration (Hagger, Dwyer, & Wilson, 2017; Tomscha et al., 2021). Wetland restoration aims to re-establish conditions in soils, plants, and microbes that are responsible for ecosystem service production. It does this by removing the source of problematic disturbance and using techniques to re-establish hydrological, soil, microbial, plant, and animal conditions (Walker, Walker, & Del Moral, 2007). Techniques used can include fencing to exclude livestock, planting, earthworks, removal of invasive/ undesirable plant species, pest removal, and reflooding. The success of restoration efforts can be measured in the change in soil characteristics, and plant and soil microbial communities, and compared to characteristics taken from either unrestored or remnant/ reference wetlands, or both. These changes can be measured over time, measuring the same wetland before and after restoration (Ballantine, Schneider, Groffman, & Lehmann, 2012), however expense of maintaining a long-term study often prevents these types of studies from gaining measurements of a fully or even moderately recovered wetland. Studies can also use a space-for-time method (Ballantine & Schneider, 2009; Dai et al., 2016; Sigua, Coleman, & Albano, 2009) which captures different stages of restoration recovery by measuring multiple sites assumed to be at different stages of development (Damgaard, 2019).

Wetland plant, microbe, and soil characteristics

Plants

Given that wetlands exist in most terrestrial biomes, wetland plants are phylogenetically diverse and exhibit diverse morphologies to adapt to a large range of conditions, the only consistent condition being periodically wet soils. Wetland soils are often anoxic and can contain harmful metabolites (*e.g.*, hydrogen sulfide, organic acids, ammonia and CO_2) (Kinsman-Costello, O'Brien, & Hamilton, 2015; Mitsch & Gosselink, 2015) which plants have to be adapted to also. Nutrient-rich wetlands are highly productive systems and can contain large amounts of plant biomass (Lange et al., 2015). In New Zealand freshwater wetlands are dominated by species such as sedges (*Carex spp.*), rushes (*Juncus spp.*), cattails (*Typhus spp*.), grasses (*Poaceae*), and harakeke (*Phormium tenax*). Freshwater wetland swamp forests are dominated by trees such as kahikatea (*Dacrycarpus dacrydioides*), swamp maire (*Syzygium maire*), pukatea (*Laurelia novae-zelandiae*), ti kouka (*Cordyline australis*), pōkākā (*Elaeocarpus hookerianus*), and occasionally rimu (*Dacrydium cupressinum*) (DOC, 2011). Mosses, lichens, cushion plants, ferns and shrubs are also common New Zealand wetland species.

Soils

Wetland soils undergo periodic and continuous flooding and so are characterised as being saturated for extended periods of time. Saturated conditions leave the bulk of the soil in an anoxic condition, and typically only the rhizosphere has pockets of oxic conditions. With high proportions of water (< 90%), soil material softens so that the bulk density (weight of soil dry per unit volume) is low (typically between 0.07- 0.55 g^{-1} cm^{-3}) and the soil structure is loose (K. R. Reddy, Clark, DeLaune, & Kongchum, 2013). Additionally, wetland soils can contain the highest carbon density of all terrestrial ecosystems (Gorham, 1991). Net primary productivity from upstream and in-situ plant communities often exceeds decomposition rates, and carbon accumulates in anoxic soils (Yu, Huang, Sun, & Sun, 2017). Recalcitrant plant material and microbial residues make stable soil organic matter (Kayranli et al., 2010; Kögel-Knabner, 2017).

The low density, highly saturated, soils slow water movement to maximise the soil: water contact. This maximises nutrient adsorption by capturing excess sediment and nutrients for microbes and plants to cycle and accumulate (Stumpner et al., 2018). Due to the close proximity of anoxic-oxic conditions, wetlands typically have accelerated rates of biogeochemical and nutrient cycles (Noll et al., 2019). However, the chemical properties of soils varies widely from the type of wetland (Brinson, 1993), and changes in chemical reactions caused by anoxia change soil pH and redox potential, among other things (Pezeshki & DeLaune, 2012). For example, in wetlands pH levels can vary between 3.9 to 6.0 (Mayes et al., 2009). A summary of wetland soil and physical characteristics in natural wetlands can be found in Table 1.1.

Table 1.1 Soil physical and chemical characteristics of natural wetland soils (0 - 20 cm), differentiated by wetland type. From K. R. Reddy and DeLaune (2008).

Comparison of Selected Soil Physical and Chemical Properties (0–20 cm) among Wetland Types

Site	BD ($g\ cm^{-3}$)	pH	OM (%)	N ($mg\ g^{-1}$)	P ($mg\ kg^{-1}$)	Ex-Ca ($mg\ kg^{-1}$)	Ex-Mg ($mg\ kg^{-1}$)	Ox-Fe ($mg\ kg^{-1}$)	Ox-Al ($mg\ kg^{-1}$)
Fen (MI)	0.22	6.0	55	22.0	900	8,120	906	4,924	2,295
Pocosin (NC)	0.07	3.9	77	14.0	300	1,033		2,370	814
Bog (MD)	0.11	4.5	68	16.9	1,000	710	477	5,710	6,400
Forested swamp (MD)	0.25	4.5	59	14.1	1,400	706	517	5,410	7,600
Marsh (WI)		6.5	41	17.7		12,730	2,300		
Swamp (NC)	0.55	4.1	17	5.7	800	4,630	499	1,301	2,280

Note: BD = bulk density; OM = organic matter; N = nitrogen; P = phosphorus; Ex-Ca = exchangeable calcium; Ex-Mg = exchangeable magnesium; Ox-Fe = oxalate extractable iron; Ox-Al = oxalate extractable aluminum (summarized by Faulkner and Richardson, 1989).

Wetland soils contain a diversity of micro- and macro- organisms. Most soil biota are in the rhizosphere, where there is adequate oxygen, food, habitat complexity, physical protection and mutualisms with other organisms (Neori & Agami, 2017; Ohtaka et al., 2014). Soil animals include nematodes, enchytraeids, microarthropods and larger insects such as millipedes, earthworms (G. R. Stirling, 2014). In the anoxic layers of soil exist anaerobic microbes (Bodelier & Dedysh, 2013).

Microbes

Soil microbes exist in the anoxic and oxic conditions of wetlands and are the major drivers of biogeochemical cycles of the ecosystem. Wetland soils can contain 10^8 to 10^9 cells/ g soil (Dedysh & Ivanova, 2012; Ishida, Kelly, & Gray, 2006; W. Zhang et al., 2013), however actual numbers are strongly influenced by the characteristics of the wetland soil, and most microbial biomass is within the surface layers of soil (Wright, Ramesh Reddy, & Newman, 2009; Zhen-Yu et al., 2010). Wetlands can contain many different communities of microbes within a small area (Green & Bohannan, 2006), given their responsiveness to plant (Shen, Wang, He, Yu, & Ge, 2021) and soil changes (J. Zhou et al., 2002). For example, both microbial biomass and community composition changes with soil texture (Dale, 1974; Tang et al., 2012), moisture (L. Wang et al., 2019), organic matter (D'Angelo, Karathanasis, Sparks, Ritchey, & Wehr-McChesney, 2005), and nutrients (Golovchenko, Tikhonova, & Zvyagintsev, 2007). Wetland microbial communities include viruses, bacteria, archaea, and fungi (Neori & Agami, 2017).

Bacteria are the best studied microbes in wetland ecosystems (Lv et al., 2014) proteobacteria dominate microbial communities in most wetlands at the phylum level (Ligi et al., 2014; R. M. Peralta, Ahn, & Gillevet, 2013; Sánchez, 2017). The rhizosphere and anoxic bulk soil contain different quantities and types of bacteria and archaea, although both are dominated with species involved with nutrient transformations (Neori & Agami, 2017). Bacteria and archaea contain methanogens, methanotrophs, nitrifiers, and denitrifiers which are intricately involved in nutrient cycling and the production of greenhouse gases (Mojeremane, 2013; Serrano-Silva, Sarria-Guzmán, Dendooven, & Luna-Guido, 2014; L. Wang et al., 2020).

Fungi are only metabolically active within aerobic pockets of the rhizosphere that contain root exudates which allow fungi to feed and grow, as the key decomposer of wetlands (Andersen, Chapman, & Artz, 2013; Z. Xu, Ban, Jiang, Zhang, & Liu, 2016). Mycorrhizal fungi form symbioses with wetland plants (Yutao Wang et al., 2011; Z. Xu et al., 2016), giving plants nutrients and resistance to heavy metals, disease, and waterlogging (Liu et al., 2015; Mohammad & Mittra, 2013; Saha et al., 2016). Most major groups of fungi exist in wetlands, although ascomycetes are the dominant fungal group (Gulis, Su, & Kuehn, 2019).

Secondary succession

Restoration manipulates successional processes to accelerate the establishment of wetland plant and soil microbe communities and ultimately soil conditions. Ecological succession is the change in species composition, structure, and architecture of vegetation through time (Pickett, Cadenasso, & Meiners, 2009), and secondary succession is the recolonization of an area that was disturbed (Horn, 1974). Community succession is one of the foundational ecological theories (Chang & Turner, 2019; Glenn-Lewin, Peet, & Veblen, 1992; Luken, 1990;

Pielou, 1966), and is used as a framework to provide insight into community assembly mechanisms. Community assembly theory states that a community is made of species that can disperse to the site, tolerate the site conditions, and co-occur with existing biota at the site (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012). Therefore, species must pass through three ‘filters’: a dispersal filter, an abiotic filter, and a biotic filter (Belyea & Lancaster, 1999; Dawson et al., 2017; Götzenberger et al., 2012). Within each of these filters there are many mechanisms at play. The dispersal filter includes: dispersal limitation (Makoto & Wilson, 2016; Tilman, 1994), regional species pool effects (Li et al., 2016), and priority effects (Fukami, 2015). The abiotic filter includes: abiotic environmental filtering (Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010), and stochastic processes (Marteinsdóttir, Svavarsdóttir, & Thórhallsdóttir, 2018). Finally, the biotic filter is comprised of inter- and intra-species mutualistic and antagonistic interactions (such as competition, facilitation, herbivory; Connell & Slatyer, 1997; Tilman, 1994) and feedbacks (e.g. soil-plant feedbacks; Bever, 2003).

Successional theory and community assembly theory can inform the development of the relatively new discipline of restoration ecology (Chang & Turner, 2019; Walker, Walker, & Del Moral, 2007), particularly because restoration manipulates successional processes. Restoration aims to accelerate ecosystem recovery by removing the first filter, dispersal, and may also manipulate the third filter, biotic interactions. Further, succession provides an effective framework to examine the progress of a restoration project from a newly restored site that still has many characteristics of the disturbed site (early successional site), towards a site that displays characteristics of the desired ecosystem (late successional site). Although successional studies have found both predictable (Lasky, Uriarte, Boukili, & Chazdon, 2014) and unpredictable patterns (Walker, Walker, & Hobbs, 2007), the mechanisms and general rules can provide insight for restoration and community re-establishment trajectories (Walker, Walker, & Del Moral, 2007). Restoration aims to accelerate successional processes to achieve a later successional ecosystem, and by measuring the rate recovery, we can find the conditions where restoration is most effective. This is particularly useful given the expense and slow nature of restoration. However, we currently have a poor understanding of the factors that alter the rate of secondary succession in the context of wetland restorations.

Plants, soils and microbes as indicators of secondary succession

To assess the efficacy of restoration efforts, plant communities and soil attributes are commonly measured. Multiple soil physical and chemical attributes and plant diversity measurements provides an effective evaluation of wetland conditions (Tiner, 2016). Plants are frequently used as indicators of wetland restoration progress because they reflect current and historic conditions, and respond to disturbance in predictable ways (Matthews, Spyreas, & Endress, 2009). For example, with human disturbance, invasive species predominate, while native diversity reduces, and the size and cover of individual plants reduces (MacDougall, McCann, Gellner, & Turkington, 2013). Soils are also often used to assess restoration progress because measurable physical and chemical characteristics can infer soil ecosystem function (Muñoz-Rojas, 2018). In wetlands, soil functions support key ecosystem services such as carbon sequestration, nutrient cycling, water purification, and flood abatement (Pereira, Bogunovic, Muñoz-Rojas, & Brevik, 2018), and soil measurements can be used as proxies to determine the extent of ecosystem service delivery (Muñoz-Rojas, 2018; Ziter & Turner, 2018).

Soil microbial communities are less commonly measured, despite being key drivers of wetland ecosystem functions (Urakawa & Bernhard, 2017). Microbes are involved in the delivery of most wetland ecosystem services including carbon sequestration, nutrient cycling, water purification, disturbance regulation, and biodegradation of waste (Bodelier & Dedysh, 2013; Jeong & Kim, 2021; Kayranli et al., 2010; Lamers et al., 2012). Microbes are the link between wetland soil physio-chemical and plant indicators and respond rapidly to shifts of environmental conditions (Urakawa & Bernhard, 2017). However, microbial communities have been poorly studied in wetland ecosystems (Jeong & Kim, 2021). Microbes have been used as indicators of eutrophication in the everglades (Wright et al., 2009), because of the rapid growth rates and changes to nutrient loading, pollutants, and redox potential (Sims, Zhang, Gajaraj, Brown, & Hu, 2013; Urakawa & Bernhard, 2017; W. Zhang et al., 2013). But the changes of microbial communities and the implications of these changes for ecosystem function is particularly understudied in wetland restoration (Sims et al., 2013). Microbial community assembly might provide key insights into different rates of restoration success, and improve restoration techniques to sustain and enhance microbial function following restoration (Jeong & Kim, 2021). For example, it is still largely unknown how microbial community structure determines the fate of carbon (C) (Neori & Agami, 2017; Yarwood, 2018).

Elucidation of the microbial response to wetland restoration, may also provide insight to wetland biogeochemical processes.

Interactions among plants, microbes, and soils during wetland succession

During wetland restoration, concurrent successional changes are seen in plants, soils, and microbes, because plant-microbial feedbacks underpin the development of wetland soil physio-chemical characteristics (J. A. Bennett & Klironomos, 2019; Bever, 2003). Wetland plant establishment is a primary aim and initial action of restoration projects. The planting and establishment of wetland species alters microbial habitats and provides niches for wetland microbes, which subsequently support plant growth (Zobel & Öpik, 2014). Over time, these plant-microbial feedbacks alter soil physiochemical characteristics, positively reinforcing a change from a disturbed or degraded state towards wetland conditions (Rogers, Wilton, & Saintilan, 2006; Shen et al., 2021). Therefore replanting degraded agricultural-wetland sites with native wetland species changes the trajectory of the microbial and plant community, and the associated changes in its diversity and biomass (X. Wang et al., 2020).

Plants alter soil properties

Plant communities play a key role in soil formation and nutrient cycles during wetland restoration (van der Bij et al., 2018). Plant biomass is the major storage pool of organic N and P in wetlands (K. R. Reddy & DeLaune, 2008), and by taking up plant-available forms of N and P, plants return wetland soils to historic levels of fertility and reduce nutrient export to waterways (Dørge, 1994). Furthermore, plants drive soil microbial and enzymatic activities that alter nutrient availability (Wardle et al., 2004). Plants produce particulate organic matter (POC) with net primary productivity, which is the primary in-situ carbon source of wetlands (Kayranli et al., 2010). Plants indirectly alter soil density and moisture content because POC develops into SOC, which alters soil structure in a way that causes them to become more absorbent by lowering soil density (K. R. Reddy et al., 2013). Additionally, the root system reduces soil bulk density, encourages sediment accumulation, and alters the water table depth (Crooks, 2002).

Plants influence microbial communities

Plants influence the diversity and abundance of soil microbial communities in the rhizosphere of wetlands directly through root exudation (Philippot, Raaijmakers, Lemanceau, & van der

Putten, 2013). Exudates (root secretions) are made up of compounds such as organic acids, sugars, amino acids, lipids, coumarins, flavonoids, proteins, enzymes, aliphatic and aromatics (Bais, Weir, Perry, Gilroy, & Vivanco, 2006; Berg & Smalla, 2009). The exudates provide microbes with 10-44% of the plants photosynthetically fixed carbon (Bais et al., 2006). The quantity of exudates influences the biomass of microbes, and the plant-species specific composition of exudates influences the community composition of microbes (Berg & Smalla, 2009; Eisenhauer et al., 2010). Increased plant diversity supports increased microbial diversity (Lange et al., 2015), by increasing the type and quantity of root exudates (A. L. Peralta, Muscarella, & Matthews, 2017; Prober et al., 2015; Zak, Holmes, White, Peacock, & Tilman, 2003). The plant community also indirectly influences the soil microbial community by changing soil microhabitats (Eisenhauer et al., 2010; Nilsson, Wardle, & DeLuca, 2008; Zak et al., 2003). Within the rhizosphere plant roots produce areas of aerobic soils that allows the existence of aerobic microbes (Z. Xu et al., 2016). Additionally, plant exudates and debris alter soil structure and pH, changing the physicochemical composition of the microbial habitat (Bever et al., 2010).

Plant-microbe interactions

Microbes and plants interact in a diversity of ways, and these interactions have profound effects on the composition and structure of the entire community (Berg & Smalla, 2009). Microbes breakdown organic compounds and molecules (Romaní, Fischer, Mille-Lindblom, & Tranvik, 2006) to supply plants with P and N (Asmelash, Bekele, & Birhane, 2016). In this way, microbes facilitate plant growth and enhance plant productivity, particularly with mutualistic mycorrhizal fungi (Van Der Heijden et al., 1998). Mutualistic relationships between mycorrhizal fungi and plants are ubiquitous (Van Der Heijden, Martin, Selosse, & Sanders, 2015; Willis, Rodrigues, & Harris, 2013; Zobel & Öpik, 2014). Mycorrhizal fungi and mutualistic bacteria and fungi increase plant immunity to diseases and pathogens by activating plant defences (Ortíz-Castro, Contreras-Cornejo, Macías-Rodríguez, & López-Bucio, 2009), and reduce effects of drought stress (Van Der Heijden, Bardgett, & Van Straalen, 2008). Additionally, fungi can promote seedling establishment, and provide competitive advantages to plant species that form mutualisms (Van Der Heijden et al., 2006). Further, mycorrhizal fungi that can gain more resources from plants can out-compete other microbial species (Janoušková et al., 2013). The impacts of plants - microbial interactions can be seen with changes in ecosystems. For example, invasive plants alter the communities below them, and change the mycorrhizal communities in other plant species adjacent to them through competitive dynamics (Corbin & D'Antonio, 2012). Alternatively, restorations that inoculate plants with mycorrhizal fungi establish plant communities faster than those without inoculation, and have more plant biomass and species diversity (Neuenkamp, Prober, Price, Zobel, & Standish, 2019).

Soil conditions regulate the microbial community.

Microbial communities are sensitive to soil physical characteristics, and respond to changes in physical and chemical conditions in soils (Prober et al., 2015). Microbial communities shift with changes in pH (Fierer & Jackson, 2006), bulk density and moisture (de Sosa et al., 2018), with increased moisture levels leading to increased amounts of microbiologically available organic matter and nutrients (Bai, Deng, Zhu, & Wang, 2004; Sleutel et al., 2008). Soils with high organic matter content typically contain more microbial biomass (K. R. Reddy & DeLaune, 2008).

Plant, soil, and microbial responses to wetland restoration

Studies addressing how plant, soil, and microbial indicators respond to wetland restoration report various rates of recovery (Table 1.2, Moreno-Mateos, Meli, Vara-Rodríguez, & Aronson, 2015). Nevertheless, some general patterns emerge. Firstly, plant indicators tend to recover faster than soil or microbial indicators. This is due to the strong control that restoration planting has on the initial plant community assembly. A 100% increase in plant community metrics within the first 12 years since restoration is not uncommon in restored wetlands (J. Brown & Norris, 2018; Jin et al., 2020; Matthews et al., 2009; Morimoto, Shibata, Shida, & Nakamura, 2017). In contrast, soil physical and chemical characteristics tend to take longer to recover (Ballantine & Schneider, 2009; J. Brown & Norris, 2018). This recovery is variable between studies, with some studies finding soils to show a faster acceleration of soil recovery than others, particularly within the first 12 years of restoration.

Table 1.2 Change of plant, soil, and microbial measurements from unrestored to restored wetlands. Arrow indicates a desirable change, red indicates an undesirable change. Greyed cells indicate no scientific studies were found that measured the indicator in both restored and unrestored wetlands. G^+/G^-= $Gram^+/Gram^-$

Time	**Plant**	**Refence**	**Soil**	**Reference**	**Microbe**	**Reference**
<12	*Richness*	(J. Brown & Norris, 2018; Jin et al., 2020; Matthews et al., 2009; Morimoto et al., 2017)	*SOC*	(Ballantine & Schneider, 2009; S. Xu, Liu, Li, & Tian, 2019)	*Biomass*	(Dai et al., 2016; Shangqi Xu et al., 2017)
				(Dai et al., 2016)		(Z. Ma, Zhang, Xiao, Cui, & Yu, 2017)
				(Gao, Zhang, Lei, & Wang, 2014)		
				(J. Brown & Norris, 2018)		
	Diversity	(Yepsen et al., 2014)	*Bulk density*	(Ballantine & Schneider, 2009)	*Fungi*	(Shangqi Xu et al., 2017)
		(Jin et al., 2020; Morimoto et al., 2017)		(Gao et al., 2014; G.-L. Wu, Liu, Zhang, Chen, & Hu, 2010)		(Z. Ma et al., 2017)
	Evenness	(Jin et al., 2020; Yepsen et al., 2014)	*P*	(Shangqi Xu et al., 2017)	*Bacteria*	(Shangqi Xu et al., 2017)
						(Z. Ma et al., 2017)
	Biomass	(Ballantine et al., 2012)	K_S		*F/B*	(Shiqi Xu et al., 2017) (Z. Ma et al., 2017)
			Moisture	(Gao et al., 2014)	G^+/G^-	(Shiqi Xu et al., 2017)
				(J. Brown & Norris, 2018; Dai et al., 2016)		

Key:

+75%

50 – 74%

25 – 49%

1 – 24%

No change

1 – -24%

-25 – -49%

				pH	=	(Dai et al., 2016; Gao et al., 2014)		
13- 49	*Richness*	↑	(J. Brown & Norris, 2018; Jin et al., 2020)	*SOC*	↑	(Ballantine & Schneider, 2009; S. Xu et al., 2019)	*Biomass*	
					↑	(J. Brown & Norris, 2018)		
	Diversity	↑	(Jin et al., 2020)	*Bulk density*	↓	(Ballantine & Schneider, 2009)	*Fungi*	
					↓	(J. Brown & Norris, 2018)		
	Evenness	↑	(Jin et al., 2020)	*P*			*Bacteria*	
	Biomass			K_S			*F/B*	
				Moisture	↑	(J. Brown & Norris, 2018)	G^+/G^-	
				pH				
50 +	*Richness*			*SOC*	↑	(Ballantine & Schneider, 2009)	*Biomass*	
	Diversity			*Bulk density*	↓	(Ballantine & Schneider, 2009)	*Fungi*	
	Evenness			*P*			*Bacteria*	
	Biomass			K_S			*F/B*	
				Moisture			G^+/G^-	
				pH				

Many studies do not sample restored wetlands long enough for remnant wetland conditions to be attained, and a study by Ballantine and Schneider (2009) found that even after 55 years, restored wetland soils contained 50% less carbon than those of remanent wetlands. This discrepancy likely reflects the variation of contexts that restoration occurs under. Site contexts such as degradation cause, wetland size, type of wetland, dominant plant community, and restoration treatments such as earthworks, drain removal/installation, and application of biochar are likely to alter restoration outcomes (D. Zhou et al., 2020).

Another result of restoration is the production of natural gradients (Y. Ma et al., 2018; McLaughlin & Cohen, 2013; L. Wang et al., 2019). Because topography plays a large role in determining soil conditions in wetlands, and frequent fluctuations in water-levels lead to large differences in soil moisture (Sánchez-Rodríguez, Nie, Hill, Chadwick, & Jones, 2019), a natural gradient occurs in restored wetlands between lowland and upland communities. The hydrology and moisture levels of a wetland controls the biochemical cycle of nutrients and vegetation succession (Weyer, Peiffer, & Lischeid, 2018), and so the moisture gradient that occurs from the edge of the water line to upland areas alters plant and microbial community assembly and soil characteristics (Dawson et al., 2017; Unger, Kennedy, & Muzika, 2009; Shiqi Xu et al., 2017).

While the limited literature available suggests that wetland restoration leads to the recovery of desired plants and soil characteristics, the studies to date have mainly focused on large-scale restoration projects on public land. Less is known about the effectiveness of wetland restoration on private property, which is often smaller-scale, and supported by relatively less funding and expertise. Despite this, most land is in private ownership, and there is a massive potential for restoration of land currently used for agricultural purposes. For example, in New Zealand 259,000 km of stream length flow through private land managed for agricultural productivity (Daigneault et al., 2017). The challenge lies in the fact that restoration projects on private land are much less accessible and harder to identify. Currently no landscape scale monitoring exists to determine what land is restored or not. This means that privately undertaken restoration projects are largely un-monitored, and their effect of ecosystem functions and services are unknown.

Contribution, aims and questions addressed in this thesis

Contribution

Considering the high rate of wetland loss and the huge potential for wetland restoration on private property, I studied whether small-scale private wetland restoration projects produce quantifiable and desirable ecosystem outcomes, and under what conditions these projects were most successful.

Aims and questions

In Chapter 2, I aimed to quantify the outcomes of small-scale private wetland restoration projects. I measured indicators of the plant community, soil physio-chemical characteristics, and microbial community to determine restoration outcomes.

I ask: How does wetland restoration alter: soil physio-chemical characteristics, the soil microbial community, and the plant community?

In Chapter 3, I aimed to explore the variation in indicators of succession during wetland restoration to determine if the variation in plant, soil and microbial data are associated. I also explored causes of this variation.

I ask: How do microbial, plant, and soil characteristics co-vary during wetland restoration?

In addition, I ask: Does restoration change indicators of wetland succession?

Finally, I ask: Are different restoration practices and site contexts influencing wetland outcomes during restoration?

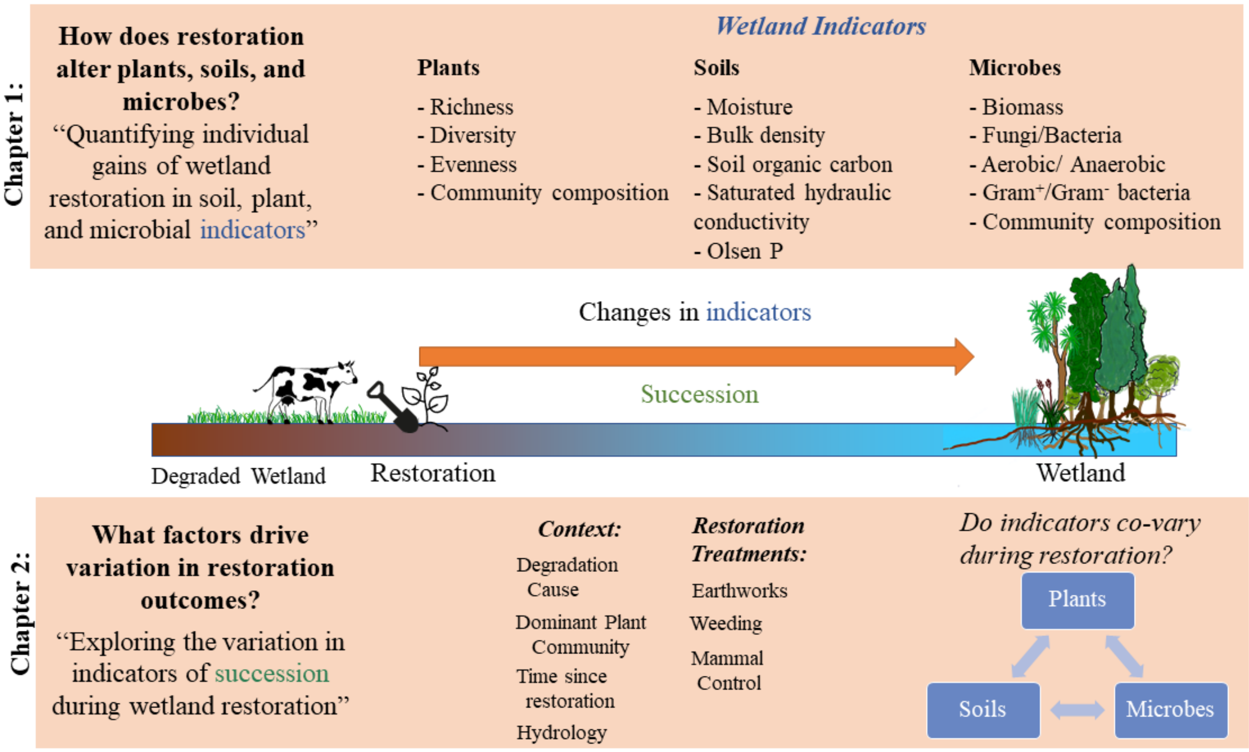

Figure 1.1 Schematic overview of thesis.

Chapter 2 Quantifying individual gains of wetland restoration in soil, plant, and microbial indicators.

Introduction

Given the extensive rate of worldwide wetland loss of > 60% (Davidson, 2014), we have lost large quantities of crucial ecosystem services (Zedler & Kercher, 2005). Wetland loss has reduced the capacity of soils to store carbon (Lane et al., 2016), purify freshwater (Mitsch, Gosselink, Zhang, & Anderson, 2009), and abate floods (Gulbin, Kirilenko, Kharel, & Zhang, 2019), which is undermining the stability of our planet and human societies (Haines-Young & Potschin, 2010; Upadhyay, Singh, & Singh, 2019). Wetland restoration aims to re-establish the unique biology and geology of wetlands to regain a high production of wetland ecosystem services. Restoration on public land has shown progress towards the recovery of wetland biophysical characteristics and increased ecosystem service production (Moreno-Mateos et al., 2015). There is a large capacity to restore on private land: wetland degradation is extensive in lowland environments which are primarily in private ownership and predominantly used for intensive agricultural production (Myers et al., 2013). Some farmers have already restored wetlands (Schroder et al., 2018), but the outcomes of those projects have not been quantified. We need to know if restoration on private property is producing desirable outcomes, as restoration could be a useful tool for increasing the sustainability of our landscapes (Erwin, 2009).

Biophysical changes from wetland restoration

Successful wetland restoration changes the soil, plant, and microbes towards desired characteristics seen in remnant wetlands that have a high production of ecosystem services. Biodiversity enhancement is a primary motivation for restoration (Hagger et al., 2017), and so increases in native plant species richness, diversity, evenness, and habitat heterogeneity is a desired outcome following restoration. The wetland plant community provides habitats for all other wetland biota (Cronk & Fennessy, 2016), and is the major source of organic matter which contributes to carbon sequestration services (Ji et al., 2020). By planting wetland plants that are adapted to wetland conditions, the plant community can more effectively remove nutrients and sediments from the water (Pappalardo, Ibrahim, Cerinato, & Borin, 2017), which influences the development of wetland soils and provides water purification ecosystem services

(K. R. Reddy & DeLaune, 2008). Studies have found that restoration greatly improves plant diversity and evenness (J. Brown & Norris, 2018; Jin et al., 2020; Yepsen et al., 2014), so much so that diversity and plant biomass often overshoots and is larger than what is found in remnant wetlands in the initial stages of establishment due to nutrient dynamics (J. Brown & Norris, 2018). However the plant community composition takes a much longer time to comprised of similar individuals as remnant wetlands (Jin et al., 2020; Matthews et al., 2009).

The desired physio-chemical conditions of wetland soils are typically low bulk density, high organic matter and carbon, high saturated hydraulic conductivity (K_s), and low suspended nutrients (K. R. Reddy & DeLaune, 2008). Organic wetland soils have incredibly low bulk densities, between 0.1- 0.4 g cm^{-3} (K. R. Reddy et al., 2013). Bulk density is associated with the soil's ability to absorb and store water (Fennessy & Wardrop, 2016), while the high soil moisture content of wetland soils is responsible for creating conditions suitable for carbon sequestration (Yin et al., 2019). K_s indicates the speed of water movement across the landscape (Baptestini, Matos, Martinez, Borges, & Matos, 2017). With high K_S, the soil: water contact is maximised which slows water movement across the landscape and helps reduce peak flood heights downstream (Ziter & Turner, 2018). Additionally, high soil: water contact increases the soil's ability to capture excess sediment and nutrients (Weyer et al., 2018). With low suspended nutrients, wetland plants and soils more effectively capture excess nutrients flowing into the wetland, helping purify water downstream (Land et al., 2016; Stumpner et al., 2018). While restoration recovers wetland soil characteristics, there are large disparities in recovery times, and characteristics such as soil organic carbon (SOC) have often not recovered to remnant wetland levels within the timeframes of most studies (Moreno-Mateos, Power, Comín, & Yockteng, 2012). Further, many studies do not assess the recovery of K_s despite its role in water purification and flood abatement services.

Far less has been established about soil microbial community response to wetland restoration (Urakawa & Bernhard, 2017). Soil microbes are the key decomposers in wetlands (Yarwood, 2018), and underpin biogeochemical functions in wetlands (Gutknecht, Goodman, & Balser, 2006), including carbon sequestration (Villa & Bernal, 2018) and nutrient cycling (Chen et al., 2016). The desirable responses to restoration include an increase in microbial biomass, an increase in the proportion of fungal to bacterial biomass (F/B) and aerobic: anaerobic microbes, and a decrease in Gram-positive: Gram- negative bacteria ($Gram^+/Gram^-$; Card & Quideau, 2010). The low bulk density of wetland soils and high SOC content provides ideal conditions for aerobic microbes within the rhizosphere where wetland plants produce “oxic islands”, and for anaerobic microbes within the bulk soil (Neori & Agami, 2017). Increased microbial biomass increases the potential biogeochemical functions of the wetland (Moorhead, Rinkes, Sinsabaugh, & Weintraub, 2013). The community composition of the microbial community determines the functions of the wetland and alters the pathways of biogeochemical cycles (Bridgham, Cadillo-Quiroz, Keller, & Zhuang, 2013). For example, fungi utilise complicated substrates and facilitate accumulation of SOC, while bacteria commonly utilise easily available substrates and are associated with higher rates of SOC turnover (L. Wang et al., 2019). The microbial community composition alters with soil disturbance: Gram-negative bacteria ($Gram^-$) are fast-growing but can exhaust their food supply quickly, while Gram-positive bacteria ($Gram^+$) are slow growing (Zou et al., 2013). Wetland restoration alters community composition (Bossio, Fleck, Scow, & Fujii, 2006), but while some wetland restoration studies have found restoration to increase biomass (Q. Zhang et al., 2016), others have found restoration to decrease total microbial biomass (Moche, Gutknecht, Schulz, Langer, & Rinklebe, 2015; Shiqi Xu et al., 2017). However, moisture has been found to be the controlling factor determining the similarity of restored wetlands to reference wetlands (Card & Quideau, 2010; L. Wang et al., 2019).

Potential of private restoration

While restoration on public land has shown that wetland biophysical characteristics establish following restoration, it remains unknow if biophysical characteristics respond in the same way with wetland restoration on private land. Private restoration is driven by personal preferences and finances, so the extent and form of restoration is varied, especially considering landholders often lack expertise of the best standard of practice for restoration. However, private land in New Zealand, which holds 259,000 stream km and occupies 13 million ha (42.2% of New Zealand), has huge potential for wetland restoration (Daigneault et al., 2017). For example, in the Wairarapa, a region on the North Island of New Zealand, private property contains 75% of all wetlands, and these wetlands are typically small in size (2 - 3 ha) (GWRC, 2003b).

If private restoration successfully establishes plant, microbial, and soil wetland characteristics, then this adds to the mounting evidence towards wetland restoration as a useful tool that increases sustainability in New Zealand’s landscapes (Daigneault et al., 2017; E. J. Dominati, Maseyk, Mackay, & Rendel, 2019). Further, with demonstration that wetland restoration is an effective tool to increase sustainability of farming ecosystems, it may encourage further restoration (P. Brown, Daigneault, & Dawson, 2019). In this chapter, I aim to quantify the outcomes of small-scale private wetland restoration projects. I sampled 18 restored wetlands, and 18 paired unrestored wetlands, on private property in the Wairarapa region. Using a paired sampling design, I was able to compare how restoration changed the plant and microbial communities and soil conditions. I used a Whitaker plot to sample the plant communities and took soil samples which I analysed for soil physio-chemical properties. Additionally, I quantified the biomass and community composition of the microbes in the soil samples using phospholipid fatty acid analysis. I ask: How does wetland restoration alter: the plant community, soil physio-chemical characteristics, and the soil microbial community?

Methods

Study Site

The Wairarapa region is a south-eastern region of North Island flanked by the Rimutaka mountain range to the west and the Pacific Coast to the east. The region is 5938 km^2 and is home to ~45,000 New Zealanders, including Māori Iwi, Ngāti Kahungunu ki Wairarapa and Rangitane o Wairarapa (Figure 2.1). The Wairarapa-Moana Wetlands Park was recently recognised as a Ramsar Wetland of International Importance and is the largest protected wetland complex in the lower North Island. The Wairarapa has lost 98.7% of its pre-colonial wetland extent (Tomscha, Deslippe, de Roiste, Hartley, & Jackson, 2019), exceeding New Zealand's national wetland loss average of 90% (Ausseil et al., 2008) and global wetland loss of 87% (Davidson, 2014). Many wetlands were drained to create pasture, and in the 1960s, the Lower Wairarapa Valley development scheme diverted the Ruamahanga river from its natural course through the valley to prevent floods, further drying soils and wetlands.

Today, 92% of the Wairarapa's land is used for dairy farming, sheep and beef farming, and viticulture (Lewis & Bryant, 2016). Other primary land uses include forestry and conservation. Local stream and river water quality is poor because of the combination of wetland loss and an excess of nutrients from land practices, leading to eutrophication of waterbodies including the super-trophic Lake Wairarapa (GWRC, 2020). Private property holds 75% of existing wetlands, and most of these are smaller than 3 ha in area (GWRC, 2003a). Landowners, farmers, iwi, residents, and community groups are restoring wetlands in the region (Tomscha et al., 2021).

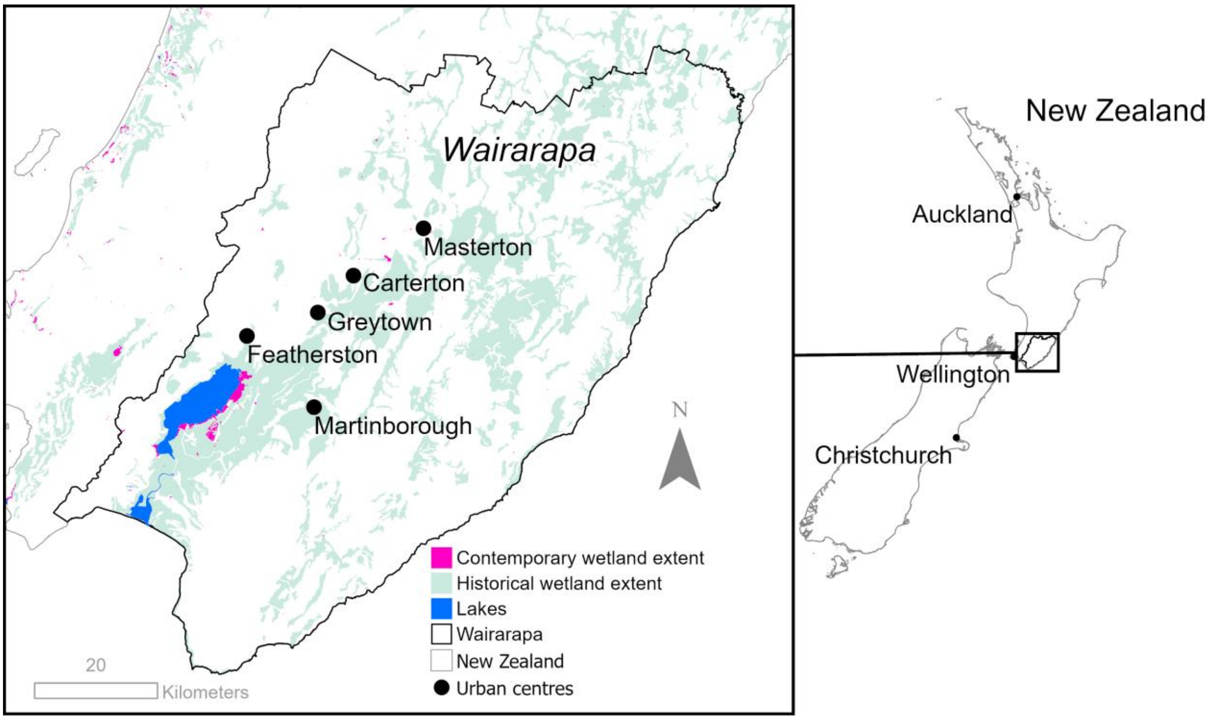

Figure 2.1 Map showing the location of the Wairarapa region in New Zealand and the historical and contemporary wetland extent. Source (Tomscha et al., 2021).

Site Selection:

In 2018, Dr Stephanie Tomscha conducted participatory mapping and survey exercises with 28 private landholders who had undertaken wetland restoration on their property in the Wairarapa region. Landowners were asked to identify wetlands defined as wet paddocks, wet fields, and the terrestrial margins of lakes, ponds, rivers, and streams. Landholders were asked open-ended questions about when and how they had restored their wetland. This resulted in the identification of nine restoration treatments that were applied by the farmers (Table 2.1). The landholders were also asked to map their wetland, to enable calculation of the total wetland area. For this study, I selected wetlands for field sampling that were large enough to hold a 20 m x 20 m standard vegetation plot, and that applied a minimum of one restoration treatment. Eighteen of the 28 restored wetlands met these criteria. Restored wetlands varied in area from 0.4 to 33.7 ha, with a median of 2.5 ha. Wetlands had upstream contributing areas of between 4.17 to 2263.27 ha with a median of 39.24 ha. All restored

Table 2.1: Restoration Treatments Applied to Restored Wetland

Farm	Fencing	Native Plant Species Planting	Exotic Plant Species Planting	Weeding	Herbicide Application	Earthworks	Pond Installation	Drain Installation	Pest Mammal Removal	Total
A	X	X		X	X	X	X	X		7
B	X	X		X					X	4
C	X	X		X					X	4
D	X	X		X	X	X		X	X	7
E	X	X		X	X					4
F	X	X		X	X				X	5
G	X	X	X	X	X	X	X		X	8
H	X	X								2
I	X	X	X	X	X				X	6
J	X	X		X	X	X	X		X	7
K	X	X	X	X	X	X			X	7
L	X	X		X	X	X	X		X	7
M	X	X	X	X		X	X		X	7
N	X	X		X		X				4
O	X	X			X				X	4
P	X	X			X					3
Q	X	X		X						3
R	X	X	X	X		X			X	6
Total	18	18	5	15	11	9	5	2	12	

wetlands were treated with livestock exclusion and planting of native species. Seventeen wetlands were situated on working farms (5 on dairy farms, and 12 on sheep and beef farms). At the time of sampling, the restored wetlands had been restored for between 0.5 - 42 years, with a median of 9 years and an average of 13 years.

As a best approximation of soil conditions and soil microbe and plant communities prior to restoration, we used an unrestored site as a reference condition, allowing for a paired sample design. The unrestored wetland was a baseline to compare the change in soil, plant, and microbial indicator changes that resulted from the application of restoration treatments. Landholders were asked to identify a site that was similar to the restored wetland prior to the application of treatments. Typically, the unrestored sites were boggy paddocks under pastoral land use. For 16 of 18 sites, the unrestored wetland was immediately adjacent to the restored wetland and separated only by a fence. Seventeen of the unrestored wetlands were grazed by stock animals, one unrestored wetland was fallow.

From December 2018 to February 2019, Nicki Papworth, Stephanie Tomscha, and I surveyed plant communities and took soil samples in the 18 restored and 18 unrestored wetlands. We established a 20m x 20m (400 m^2) in each wetland, with one side of the plot running parallel to the water's edge or wettest section of the wetland, and the perpendicular side of the plot running up an elevational gradient (Figure 2.2). Restored and unrestored sites were always sampled on the same day.

Vegetation sampling

We methodically sampled the vegetation within the 400 m^2 plot using a nested Whittaker plot design (Figure 2.2; Stohlgren et al., 1995). We recorded all species present and the percent cover of each species in nested 1 m^2 and 6.25 m^2 quadrats, in 10 m^2 and 20 m^2 quadrats we recorded new species only. All plant species were identified to species and genus. When species identification was not possible, the species family was identified. Percent cover was estimated visually for each tier of the plant canopy, so that total percent cover was often >100% for any one quadrat. I excluded the exotic species in these data to calculate species richness, percent cover, Shannon's diversity, and Peilou's Evenness in the R package "vegan" (Oksanen et al., 2020). I plotted the log-species richness as a function of the log- area to generate species-area curves for each wetland, and calculated the linear best fit of this

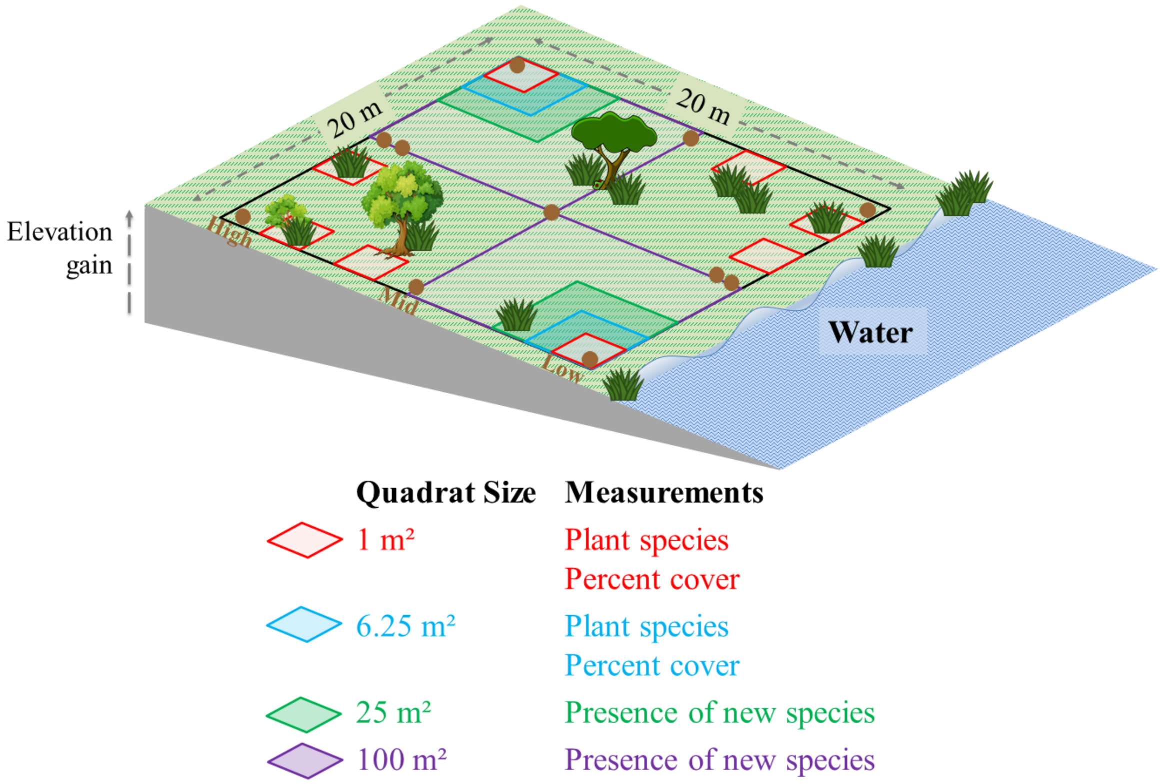

Figure 2.2 Diagram of plot used to sample soil and survey vegetation in restored and unrestored wetlands. Locations of soil cores indicated by 11 brown circles. Coloured boxes indicate the modified Whittaker plot used to sample vegetation for species diversity and species percent cover. Modified from Tomscha et al. (2021)

relationship, generating a species-area curve of combined exotic and native species. I used the slope of the species-area curve (z) as a proxy for the rate of species colonisation in restored and unrestored wetlands.

Soil Sampling

Wetland soils frequently fluctuate between aerobic and anaerobic states, contain high amounts of soil organic matter and SOC, and have a low bulk density. Furthermore, wetland soils are effective at filtering out nutrients, sequestering atmospheric carbon, and flood abatement (Clarkson, Ausseil, & Gerbeaux, 2013). Therefore, 5 metrics were chosen to measure the effect wetland restoration has on soil: SOC, bulk density, soil moisture, Olsen phosphorus (Olsen P), and saturated hydraulic conductivity (K_S).

In each plot, we took eleven soil cores using a 50 mm PCV pipe to a depth of 10 cm. To measure SOC, bulk density, soil moisture, and the microbial community, nine soil cores were taken across 3 parallel transects in the plot at 0 m, 10 m, and 20m, to capture soil characteristics across the topographic profile (Figure 2.2, n = 324). To measure Olsen P, and K_S, two more soil samples were taken at the highest and lowest local elevations of the plot (n = 72). Intact soil cores sealed in plastic bags and kept cool on ice prior during transport to the lab, whereupon they were stored at 4°C.

Laboratory Processing

Soil edaphic characteristics

Soil Moisture and Bulk Density

In each soil sample (n=324), I measured moisture, bulk density, and SOC. The length and radius of every PVC pipe core was measured to calculate the precise volume of each soil sample. Subsamples (~5 g) were weighed, dried by lyophilisation and reweighed to determine soil moisture content. All weights were determined to within ±0.001 g. The lyophilised subsample was then then stored at -20°C and retained for PLFA analysis. The remainder of the sample was oven dried at 105°C overnight, sieved to < 2 mm, and weighed. The mass of sample material >2 mm was determined, and the volume was found using the water displacement method. The volume and mass were subtracted from the total volume and wet weight of the soil in each core. Soil moisture was calculated by subtracting the dry weight of the sum of the main sample and 5 g subsample from the fresh weight of the whole sample. Bulk density was calculated by dividing the sum of the main sample and 5 g subsample dry weights by the total samples volume. All measurements took place between March and August 2019.

Soil organic carbon

SOC is a source or sink of greenhouse gases and is contained within soil organic matter. Soil organic matter (SOM) was used to find SOC. SOM comprises the organic component of soil, including plant, animal, and microbial detritus (Brady, Weil, & Weil, 2008). SOM was determined using the loss on ignition method (Dean, 1974). The dry weight of oven-dried subsamples (~5 g) was measured three times to 0.001 g, and an average weight was recorded. The subsamples were placed in a muffle furnace for four hours at 550°C (Wright et al., 2008). After the samples cooled to room temperate in a desiccator, the ashed weight was measured three times to 0.001 g, and an average weight was recorded. The average ashed weight was removed from the average dried weight to calculate the mass loss of the subsample, which was used to measure the percent soil organic matter (SOM). To estimate SOC, SOM was divided by 1.98 when SOM $\leq$ 10%, and divided by 1.86 when SOM > 10% (Pribyl, 2010).

Phosphorus

Plant available P is a common proxy for the reactive P pool, that is potentially available to flow into waterways in surface runoff (McDowell et al., 2001). I measured Olsen P of wetland soils as this method is the most commonly used measure of plant-available P, and is considered appropriate on a wide range of soil types on New Zealand farms (Drewry, Taylor, Curran-Cournane, Gray, & McDowell, 2013). Olsen P was measured in two soil cores per wetland at the lowest and highest elevations (n = 72). Subsamples of soil (~5 g) were lyophilised, sieved to $\leq$ 2 mm, and sent to Hill's Laboratory Ltd. (Hamilton, New Zealand) for measurement of Olsen P. Olsen P was determined through molybdenum blue colorimetry of bicarbonate extracts (pH 8.5) of the soil samples.

Saturated hydraulic conductivity

K_S, an indicator of flood abatement, is a measurement of the rate water can flow through soil (Ziter & Turner, 2018). Measuring K_S in situ is expensive and often not feasible across large areas. Instead, pedotransfer functions (PTF) are used to estimate K_S. PTFs produce relative estimates of K_S using easily obtainable measurements of soil properties including bulk density, SOM, and particle size distributions. PTFs produce reliable predictions of K_S to ~1.02–1.67 mm hr^{-1} (Tóth et al., 2015), however my samples ranged from 0.41 to 2.36 mm hr^{-1}. But the inclusion of SOC improves the reliability of K_S predictions, with SOC aiding in soil structure and its water-absorption properties (Tóth et al., 2015). Furthermore, I used a pedotransfer function developed for organic topsoil (Equation 1, Wösten, Lilly, Nemes & Le Bas, 1999)

Equation 1

$$\begin{aligned} ln\,(Ks) \;=\; & 7.755 + 0.0352(Silt\,) + 0.93(Topsoil) - 0.967(Bulk\ Density^2) \\ & - 0.000484(Clay^2) - 0.000322\,(Silt^2) + \frac{0.001}{Silt} - \frac{0.0748}{Organic\ Matter} \\ & - 0.01398\ x\ (Bulk\ Density)(Clay) \\ & - 0.1673(Bulk\ Density)(Organic\ Matter) + 0.02986\,(Topsoil)(Clay) \\ & - 0.03305(Topsoil)(Silt) \end{aligned}$$

Implementation of Equation 1 lead to 2 K_S estimates per wetland (72 total), in accordance with the particle size determination. Calculations of K_S used the mean SOC and bulk density values of 3 soil cores averaged across the upper and lower transects of each wetland.

Soil Texture

Soil texture, the proportion of sand, silt, and clay particles in the mineral fraction of soil, determines the soil type and influences bulk density, SOC, K_S, and the microbial community (K. R. Reddy & DeLaune, 2008). Consequently, soil texture influences a variety of ecosystem services. The percent of clay, silt, and sand was determined in samples (n = 72) between March 2019 and December 2019. Subsamples (3 g) were taken from 2 cores at the lowest and highest elevations per plot. They were lyophilised for 48 hours, and then sieved to ≤ 2 mm. To remove organic matter, subsamples were repeatedly placed in H_2O_2 until the reaction ceased. Subsamples taken from transects containing ≤ 10% SOC were placed in 27% H_2O_2, while subsamples taken from transects containing > 10% SOC were placed in 52% H_2O_2. The reaction was catalysed by a 90°C water-bath, and distilled H_2O was added to slow excessive reactions. Once the reaction had ceased, soil samples were rinsed with distilled water, which was then removed by centrifugation and decanting. This was repeated until the waste-water pH was 7. Then samples were lyophilised overnight and disaggregated by an ultrasonic bath for 20 minutes in 0.5% Calgon solution. Samples then were placed in a laser particle sizer (Beckman Coulter LS13320). USDA/ FAO classifications were used to group the particle sizes into sand, silt and clay fractions (FAO, 2006).

2.2.3. Microbial Quantification

Phospholipid fatty acid analysis

Microbes are responsible for decomposition and nutrient cycling in wetlands and contribute to soil structure underpinning the production of a variety of ecosystem services. Phospholipid fatty acid analysis (PLFA) is a sensitive and quantitative method used to characterise living microbial biomass and community structure in environmental samples, albeit with low taxonomic resolution. I characterised PLFA profiles in nine soil samples per wetland, three soil cores at each of high, mid and low elevation transects (n = 324). Soils were subsampled, lyophilised and sieved to < 2 mm, as described above and stored at – 20℃ until processed. SOM increases microbial activity and therefore PLFA concentration (Frostegård, Tunlid, & Bååth, 2011). To ensure that samples would not oversaturate gas chromatograph during lipid analysis 0.75 g of dried soil was measured from samples with ≤10% carbon content, and 0.5g of dried soil was measured from samples with >10% carbon content, as determined by the SOC data. A high-through-put method modified from (Buyer & Sasser, 2012), was applied (Lewe, 2019). Briefly, lipids were extracted from soils using a chloroform:methanol:phosphate-buffer (1:2:0.8, v/v/v) mixture (4.0 ml per sample), containing an internal standard (n = 20 nmol per sample). Samples were sonicated in an ultrasonic bath for 10 minutes and then were rotated end- to- end for 2 hours in the dark. After 10 minutes of centrifugation, the liquid phase was transferred to clean test tubes containing 1.0 ml each of chloroform and water. After 15 minutes of centrifugation, the lower phase containing the lipids was extracted by aspiration and placed into a clean test-tube. Samples were evaporated until dry under a nitrogen concentrator, and then lipids were resuspended in 1.0 ml chloroform. Phospholipids were separated from neutral- and glyco-lipids with chloroform, acetone and a 5:5:1 solution of methanol: chloroform: water through a silica column (50 mg/1 ml, Thermo Fisher, NZ). Liquid was evaporated off under a nitrogen sample concentrator, and then 0.2 ml transesterification reagent was added to each sample and left to sit on a 40°C heat block for 15 minutes. Acetic acid (0.2 ml) was added to neutralise the solution, and then two 0.3 ml volumes of chloroform was added to extract the phospholipids. After each addition of chloroform, the bottom phase was aspirated into a clean vial. The chloroform was evaporated off, and the vials containing phospholipids were sealed and stored at -20°C until analysis. Hexane (70 µl) was added to the sample, immediately prior to analysis in a gas chromatograph with a mass spectrometer (Shimadzu GCMS-QP2010 Plus). Lipid extractions and PLFA analysis occurred between August and November 2020. I characterised 27 lipids (Table 2.2). Fatty acid methyl esters (FAME's) were designated using standard nomenclature (Favre & Powell, 2013). Biomarkers were designated to 6 microbial groups (see Table 2.2 and Willers, Jansen van Rensburg, and Claassens (2015) for more information).

Table 2.2 Fatty acid biomarker designation

Biomarker	FAME name	Reference
Actinomycetes	10Me16:0, 10Me17:0, 10Me18:0	(Francisco, Stone, Creamer, Sousa, & Morais, 2016; Vestal & White, 1989)
Arbuscular mycorrhizal fungi	16:1w5c, 16:1w5t	(Olsson, Bååth, Jakobsen, & Söderström, 1995)
Bacteria	14:0, 15:0, 16:0, 17:0, 18:0	(Zelles, 1997)
Fungi	18:2w6, 18:3w3, 18:1w9c	(Ahlgren, Gustafsson, & Boberg, 1992; Zelles, 1997)
Gram$^-$ bacteria	2OH10:0, 2OH12:0, 3OH12:0, 2OH14:0, 3OH14:0, 16:1w7c, 16:1w7t, 16:1w5t, delta17:0, 2OH16:0, 3OH16:0, 18:1w7c, 18:1w7t, 19:1w9c, delta19:0	(Parker, Smith, Fredrickson, Vestal, & White, 1982; Wilkinson & Ratledge, 1988; Zelles, 1997)
Gram$^+$ bacteria	i15:0, a15:0, i16:0, a16:0, i17:0, a17:0	(Francisco et al., 2016; Vestal & White, 1989)

Statistics

Plant response to restoration

Diversity measures communities to indicate its stability and productivity, and multiple measures of diversity show community attributes, as within plant communities evenness is weakly negatively correlated with richness (Wilsey, Chalcraft, Bowles, & Willig, 2005). Plant diversities response to restoration was measured using four diversity metrics: native plant species richness, Shannon diversity of native plants (H), Peilou's evenness index (J'), and the species-area slope of native plants. Peilou's evenness index is a standardised index of species abundance indicating the rate of species dominance (Hill, 1973). It is on a scale from 0 to 1, with numbers near 0 showing high single-species dominance, while numbers near 1 showing equal abundance of all species (G. Stirling & Wilsey, 2001). Shannon's diversity indicates the effective contribution of the variability in species richness by incorporating both the abundance and evenness (Jost, 2006). A low H value indicates a community that has only a couple of species or only a couple of dominant species, while a high H value indicates a lot of species evenly contributing to the environment. The species-area slope of plants indicates species diversity at multiple scales, and the discovery rate of new species within a given area (Connor & McCoy, 1979). Species richness, Shannon's diversity, and evenness were calculated using the "VEGAN" package (Oksanen et al., 2020) in R studio. To test if restoration changed these diversity metrics, a paired t-test was used. All response variables were checked for normality and homoscedasticity, as described above.

Changes in the plant community composition between unrestored and restored wetlands were assessed using nonmetric multidimensional scaling (NMS) in PC-Ord. In total there were 227 unique plant species sampled, and 171 of these species had abundance data (in the form of percent cover) which is required for NMS. I had many rare species, with 78 species occurring in one plot only (see supplementary material Figure S1). This led to outlier plots and a non-stable NMS solution. Because NMS requires a square matrix, I only included the 36 most common plant species (exotic and native). These species accounted for only 20% and 65% of plant cover in two plots but accounted for > 75% in the remaining 34 plots. A NMS ordination was run in the 'auto-pilot' mode using the method outlined in (Kruskal, 1964) and Mather (1976). 'Auto-pilot' mode performs 250 iterations of random configuration of both real data and randomly generated data. It determines the dimensionality of the solution by minimising stress of the solution. Dissimilarity between samples was measured by Sorensen's distance. Ordination solutions were then plotted on a two-dimensional graph that showed the 2 axes explaining the largest proportion of variance between the samples.

Soil response to restoration

The effect of restoration on SOC, bulk density, moisture, K_S and Olsen P was tested using a linear mixed effects model in R studio (R Core Team, 2020). Distance from waters-edge and restoration state (restored or unrestored) were additive fixed effects, and plot and site were included as random effects, with plot nested within site. Plot included the 36 plots of restored and unrestored plots, while site referred to the farm the wetland was sampled on. By including plot as a random variable, the model interprets that each of the soil samples come from the same wetland plot, and not from independent wetlands. Further by including site as a random effect, variation introduced by differing baselines at each farm was accounted for. I used boxplots and histograms to confirm the absence of outliers and data normality. I confirmed the homoscedasticity of the data by inspecting plot of residuals versus fitted values. In addition, I used a Non-Constant Error Variance test in the “car” package (Fox & Weisberg, 2019) to confirm the homoscedasticity of the data. Where necessary I used log-transformations of data to meet the assumptions of the linear model. The “lmer” function in the package ‘lme4’ (Bates, Maechler, Bolker, & Walker, 2015) was used to model the data, and an ANOVA with a type 3 Wald chi-square test from the package “car” was used to partition the variance associated with the fixed effects.

To test restorations overall effect on the soil, a Principal Component Analysis (PCA) was performed on all measured soil physical and chemical characteristics. This (and all other) multivariate analyses were performed in PC-Ord (McCune & Mefford, 2018). A PCA plots the data in multidimensional space to find the ‘line of best fit’ that has the smallest sum of squared distances. This forms principal components, or eigenvectors, which are linear combinations of variables. Each eigenvector has an associated eigenvalue that explains the proportion of the total variation explained by the principal component. Synthetic variables (principal components) that represent the greatest proportion of variance in the data are then displayed in 2-dimensions. To achieve the requirements of a PCA, I expanded the 72 measurements of Olsen P, K_S, and the soil texture classes datasets to 324. The high and low transect samples were averaged in each plot to find a mid-transect estimation, and the replicates along each transect were given the same value. Soil characteristics were log transformed to meet the assumption of normality. A correlation cross products matrix was used, and Rnd-Lambda was used to test the significance of eigenvalues.

To test the statistical significance between soil characteristics in restored and unrestored wetlands, multiple response permutation procedure (MRPP) was used. MRPP non-parametrically tests the hypothesis that two or more groups are the same. I applied MRPP to examine the effect restoration and site on the chance-corrected within group agreement (A). MRPP reports A as a measure of within-group homogeneity compared to that expected by chance; A varies between 0 and 1, with 0 corresponding to within-group heterogeneity equal to or larger than that expected by chance, and 1 corresponding to identical members within each given group (McCune, Grace, & Urban, 2002).

Microbial response to restoration

To assess how the microbial community responded to restoration, changes in biomass and proportional abundances were assessed between restored and unrestored wetlands (Table 2.3). Microbial biomass measurements were all measured in FA/ g dried soil and included total biomass; total bacterial biomass; total fungal biomass; arbuscular mycorrhizal fungi (AMF); actinomycetes; $Gram^-$ bacteria; $Gram^+$ bacteria; other fungi lipids; other bacterial lipids. The proportional abundances of microbial groups were used to assess the differences in the functional microbial community composition. Three ratios were calculated: fungi: bacteria (F/B), Gram-positive bacteria: Gram-negative bacteria ($Gram^+/Gram^-$), and aerobic microbes: anaerobic microbes. The F/B ratio indicates soil conditions, with fungi preferring low bulk density and organic rich soils, and bacteria favouring wet soils (Q. Zhang et al., 2016). $Gram^+/Gram^-$ ratio indicates the tolerance and stability of the soil community (Zou et al., 2013), and can be used to indicate the relative C availability for bacterial communities (Fanin et al., 2019). $Gram^+$ bacteria are slow growing and use carbon sources from recalcitrant SOM, while $Gram^-$ bacteria are fast-growing and use relatively liable carbon sources that allows them to be competitive and respond quickly to favourable environmental conditions (Fanin et al., 2019). Finally, the aerobic: anaerobic microbe ratio indicates soil aeration. Soils that have a high ratio of aerobic microbes have favourable conditions for microbial communities to grow in, while soils with a low ratio have low amounts of oxygen caused either by permanent soil saturation or high bulk density.

Microbial biomass measurements and proportional community responses to restoration were tested using a linear mixed effects model. Restoration state and distance from water's edge were additive fixed effects, and plot was nested within site identity and included as random variables in the model. Assumptions were checked for in the same fashion as the soil response linear models (see page 30 for more details). To examine potential effects of restoration on the microbial community composition, a PCA was run on the 37 PLFA lipid biomarkers in PC-ord. A correlation cross products matrix was used, and Rnd-Lambda was used to test the significance of eigenvalues. MRPP analysis was employed to test if restored wetlands had a significantly different lipid composition to unrestored wetlands. Additionally, I used an indicator species analysis to identify lipids associated with restoration treatments. I used the IndVal method (Dufrêne & Legendre, 1997), which combines the relative abundance of a lipid in each treatment (specificity) with its relative frequency of occurrence (fidelity) in that treatment. Indicator values vary between zero and 100%, with 100% representing perfect indication of a lipid for the treatment.

Table 2.3 Response factors used to test microbial community response using a linear mixed effects model

	Response Factors	*Indicative of*	*Reference*
Microbial biomass (FA/ g dried soil)	Total biomass	Potential microbial activity	(Moorhead et al., 2013)
	Total bacterial biomass	Control methanogenesis and other wetland biogeochemical cycles	(Andersen et al., 2013)
	Total fungal biomass	Soil health, greater carbon use efficiency	(Six, Frey, Thiet, & Batten, 2006)
	AMF	Low soil fertility	(Gutknecht et al., 2006; Wetzel & Valk, 1996)
	$Gram^-$ bacteria	Exists in aerobic conditions. Fast growing and competitive, so responds to disturbance quickly. Derives carbon from liable sources.	(Fanin et al., 2019)
	$Gram^+$ bacteria	Exists in anaerobic conditions. Slow growing, taking carbon from recalcitrant sources.	(Fanin et al., 2019)
Community composition	F/B	Soil conditions; carbon sequestration potential	(Waring, Averill, & Hawkes, 2013)
	$Gram^+$ / $Gram^-$ bacteria	Stability of microbial community Carbon availability	(Fanin, Hättenschwiler, & Fromin, 2014)
	Aerobic: anaerobic microbes	Soil aeration/ saturation	(Gutknecht et al., 2006)

Results

How do plant communities respond to wetland restoration?

Native plant species richness

Restored wetlands harboured significantly more native biodiversity than unrestored wetlands ($\chi^2_{(17)} = 6.254$, $p<0.001$), containing on average 15.1 native species, although there was a large amount of variability, with restored wetlands containing between 3 and 39 native plant species (Figure 2.3). Unrestored wetlands had an average of 2.1 native plant species, contained up to 6 native species. Four unrestored plots contained no native species.

Native plant diversity

Restoration increased the native plant community diversity at the local wetland level. It increased Shannon's diversity (H) in all but 2 wetlands, with restored wetlands having an average H of 1.13, and unrestored wetlands having an average H of 0.25 (Figure 2.3). A paired t-test showed that restoration increased Shannon's diversity by 0.65 ($t_{(17)}= 4.40$, $p<0.001$). Peilou's evenness index (J') also significantly increased with restoration ($t_{(17)}= 2.78$, $p=0.012$). The unrestored plots had an average J' of 0.27, and the plots that contained native species had a J' of between 0.05 and 0.88, while restored plots had values between 0.11 and 0.91, with an average of 0.57.

Plant species area relationship

All restored wetlands accumulated more species within less area than their paired unrestored wetland. Restored wetlands had a significantly steeper species area curve ($t_{(17)} = -9.09$, $p<0.001$, Figure 2.3) and had species-area curve slopes between 0.19 and 0.40, and unrestored wetlands had species-area curve slopes of between 0.08 and 0.22 (Figure 2.4).

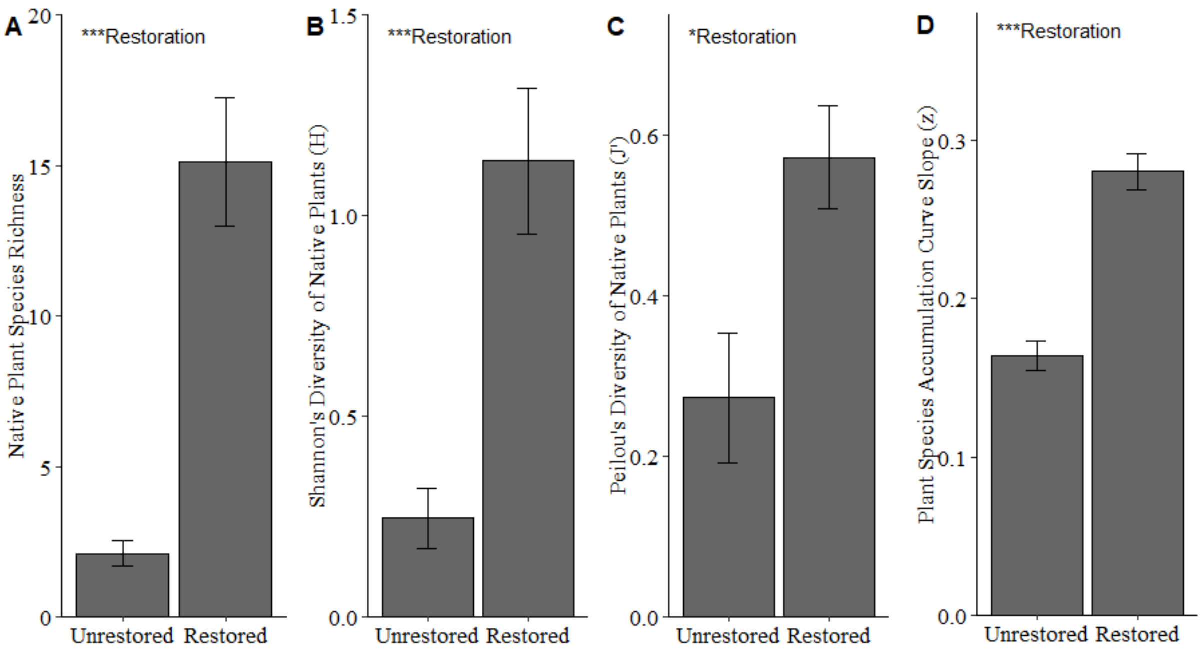

*Figure 2.3 Mean plant species diversity metrics measured in unrestored plots compared to restored plots, ± SE bars. A= Native species richness, B= Shannon's diversity of native plants, C= Peilou's evenness index of native plants, D= Plant species accumulation of native and exotic plants. Asterisks indicating significance in linear mixed effects models: * p<0.05, **p<0.01 ***p<0.001*

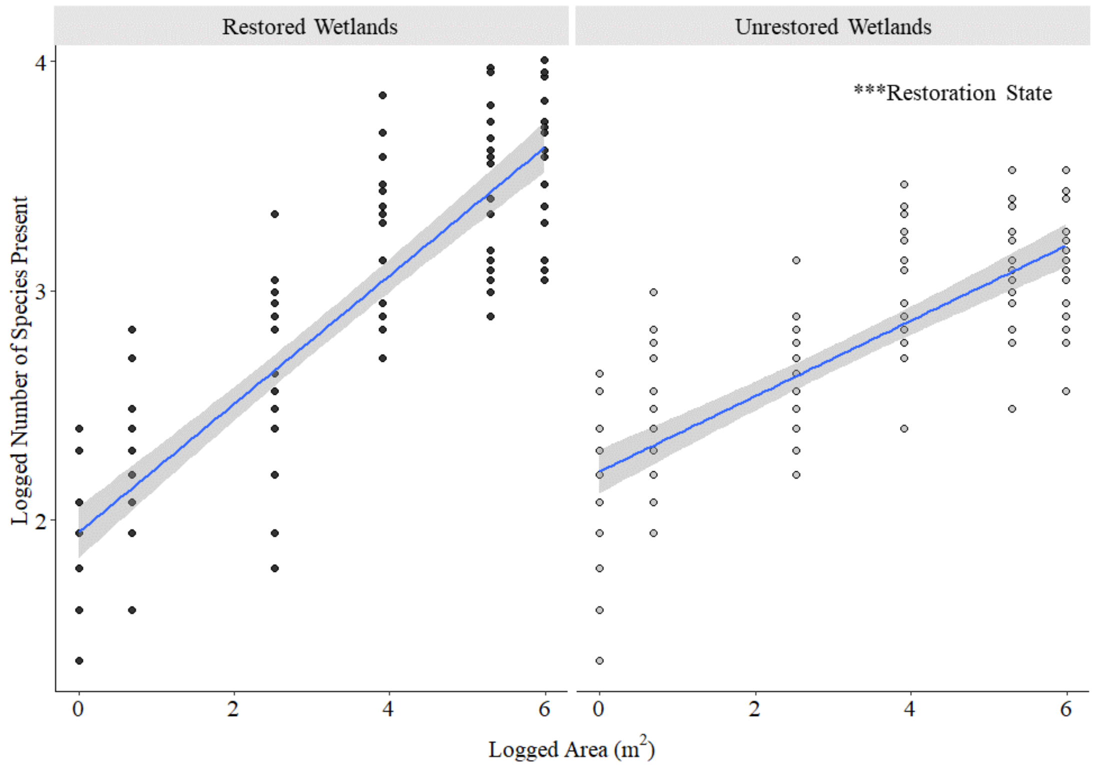

Figure 2.4 Species area relationship of native and exotic plants in restored and unrestored wetlands, fitted with a linear trend line and 95% confidence intervals.

Plant community composition

Restoration also increased diversity of plants at the landscape level, in particular by increasing the variation in the composition of wetland plant communities. NMS ordination of the 36 plots by all plant species present described 72.5% of the variance in the plant community across samples and revealed a clear clustering of samples according to the restoration state (Figure 2.5). This clustering occurred across 2 significant axes, the first axis accounting for 51.6% of the variation, and the second axis accounting for 20.9% of the variation. MRPP found a significant difference between the two communities (A= 0.125, $p<0.001$).

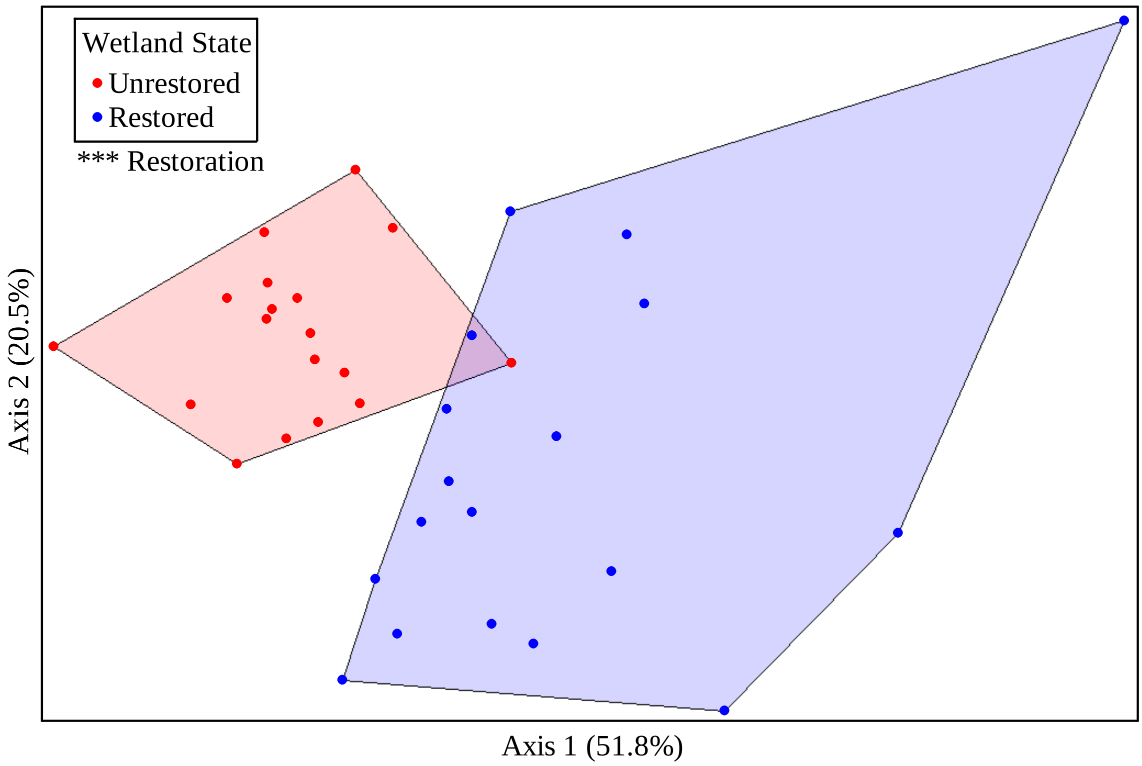

Figure 2.5 NMS graph of all plant species in ordination space by wetland state (restored or unrestored).

How do soil physio-chemical characteristics respond to wetland restoration?

The soils were predominantly silty-loam and silty soils, containing largely silt particle sizes (Figure 2.6). Wetlands did not show much variation in clay content (0.7- 10.8%) but were variable in silt and sand contents (23.3 – 72.9%, 14.4 – 41.7% respectively). Restoration treatments had no effect on soil texture.

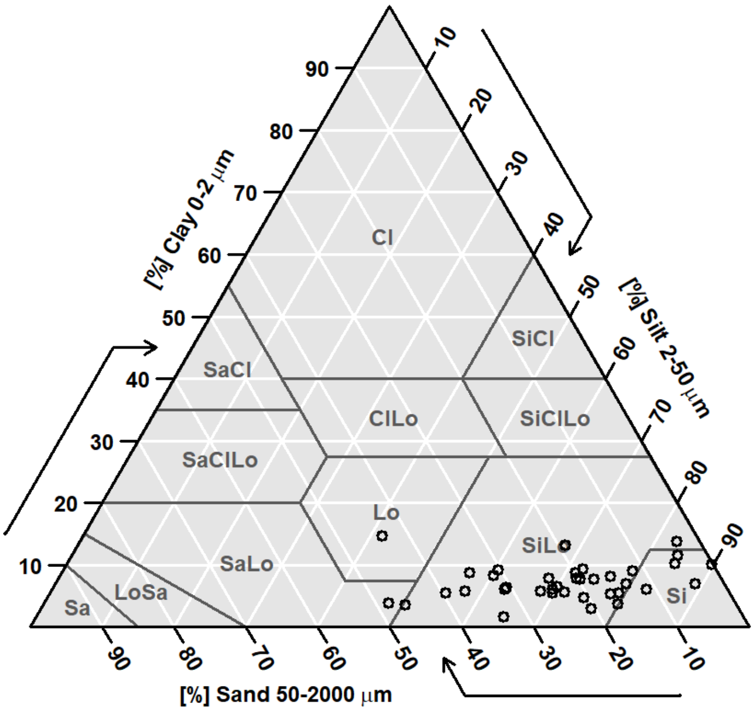

Figure 2.6 Soil texture for each wetland plotted on a soil texture triangle according to the USDA classifications. Each point shows the average texture of the 36 plots.

Soil Water Content

Soils were predominantly very wet with unrestored wetland soils containing an average water content of 92.48%, and restored wetland soils containing an average water content of 203.6% (Figure 2.7a). Despite sampling soils from November to February, I sampled the paired restored and unrestored soils on the same day, giving me confidence to compare between restoration treatments. Soil moisture increased with restoration proportionally by 93.1% ± 16.1 ($t_{(89)} = 5.63$, $p < 0.001$) and with proximity to water ($t_{(84)} = 3.01$, $p= 0.004$). The effect of restoration on soil water content was different according to the soils by proximity to water, with soils by the waters edge being very saturated, while soils further upland were drier compared to the unrestored soils ($t_{(72)} = 3.88$, $p < 0.001$, Figure 2.7b).

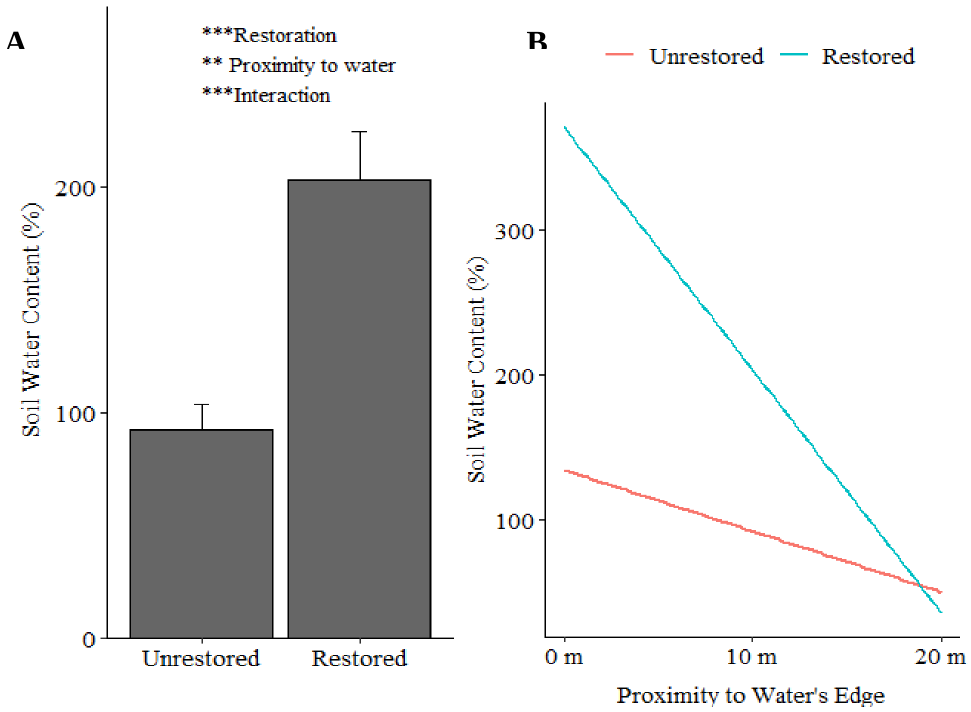

*Figure 2.7 Soil Water Content (%) in restored and unrestored wetlands. A) Mean Soil Water Content in unrestored wetlands compared to restored wetlands fitted with standard error bars. Asterisks indicating significance in linear mixed effects models: **p < 0.01, ***p < 0.001. B) Linear fit of soil water content across a gradient of proximity to water and separated by restoration state.*

Bulk Density

Unrestored soils were more compact with an average bulk density of 0.8 g^{-1} cm^3, while restored soils were less dense with an average bulk density of 0.61 g^{-1} cm^3 (Figure 2.8a). Samples varied greatly, having bulk densities between 0.06 g^{-1} cm^3 and 1.49 g/cm^3. Restoration decreased bulk density by 0.19 ± 0.05 g^{-1} cm^3 ($t_{(80)} = -5.51$, $p< 0.001$) as did proximity to water ($t_{(72)} = 4.07$, $p< 0.001$). Proximity to water changed the effect of restoration on bulk density ($t_{(72)} = 2.00$, $p< 0.001$, Figure 2.8b).

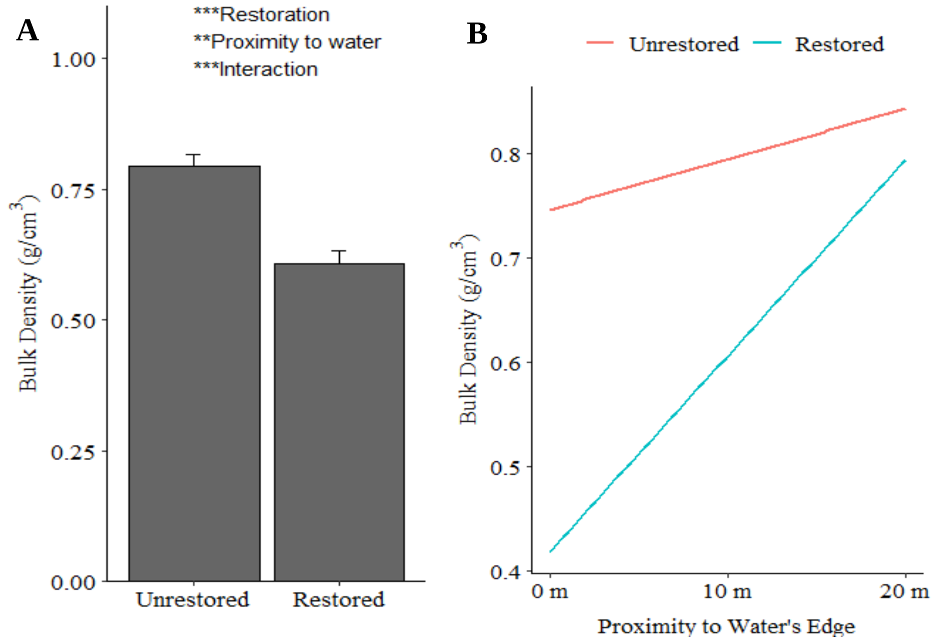

*Figure 2.8 Bulk Density's response to restoration. A) Average bulk density in unrestored and restored wetlands fitted with standard error bars. Asterisks indicate significance in linear mixed effects models: **p < 0.01, *** p < 0.001. B) Linear fit of bulk density across a gradient of proximity to water and separated by restoration state.*

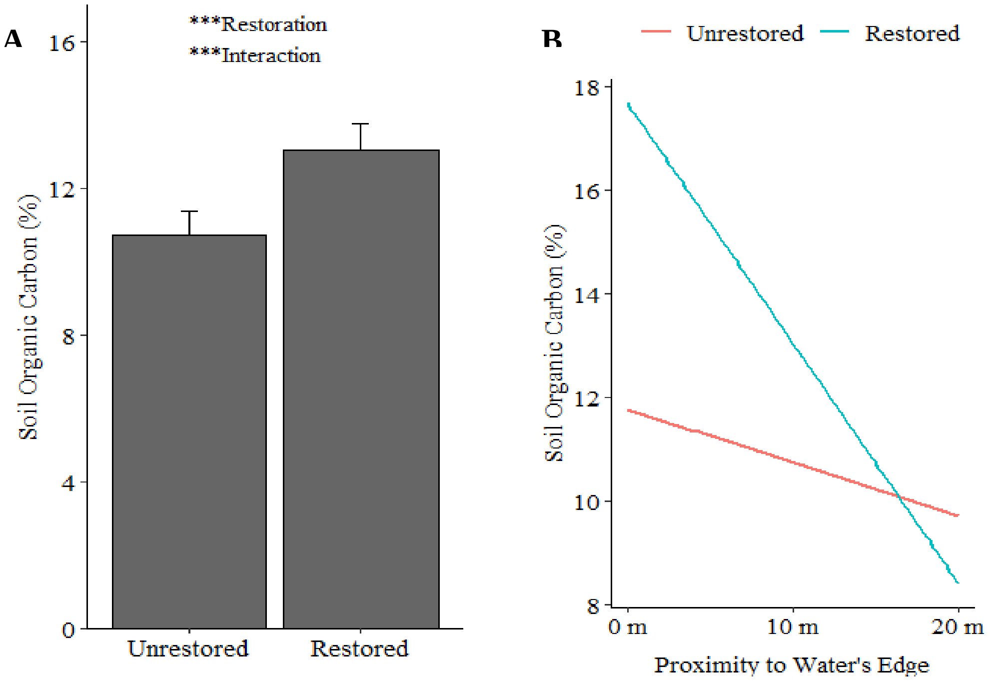

*Figure 2.9 Soil organic carbon (%) in restored and unrestored wetlands. A) Mean SOC in unrestored wetlands compared to restored wetlands fitted with standard error bars. Asterisks indicating significance in linear mixed effects models: *** p<0.001. B) Linear fit of organic carbon across a gradient of proximity to water, and separated by restoration state*

Soil organic Carbon

All wetlands were highly organic, and plots contained between 4.2% and 31.9% SOC. Restored wetlands had an average SOC of 13.1% and unrestored wetlands had an average SOC of 10.75% (Figure 2.9a). Restoration increased SOC in wetland soils by 19.7% ± 10.0 ($t_{(84)} = 4.14$, $p < 0.0001$). The effect of restoration on SOC changed depending on the soils proximity to water ($t_{(72)} = -3.66$, $p = 0.0005$, Figure 2.9b).

Phosphorus

Olsen P varied greatly by site and showed more variability in the restored wetlands than in the unrestored wetlands. Restored wetland soils contained between 6 and 62.5 ug P cm^3 dry soil, and unrestored wetland soils contained between 11 and 51.5 ug P cm^3 dry soil (Figure 2.10a). The linear mixed effects model showed that Olsen P decreased with restoration proportionally by 22.95% ± 13 ($\chi^2_{(1)} = 4.36$, $p = 0.036$). Proximity to water did not affect Olsen P quantities ($\chi^2_{(1)} = 0.030$, $p = 0.862$).

Saturated hydraulic conductivity

Restored wetlands, on average, had a higher capacity to attenuate floods and hold water compared to unrestored wetlands, with an average K_S of 1.24 mm hr^{-1} in restored wetlands and 0.97mm hr^{-1} in unrestored wetlands (Figure 2.10b). K_S ranged from 0.41 to 2.36 mm hr^{-1}; however, pedofunction-derived K_S is reliable from ~1.02- 1.67mm hr^{-1} (RMSE) (Tóth et al. 2015). Although my samples had K_S values on either side of this range, my inclusion of organic matter in the pedofunction helps to reduce this uncertainty. Furthermore, because my paired study design compares soils in restored and unrestored wetlands with similar site characteristics, I have high confidence in the restoration comparison. The linear mixed effects model showed that restoration increased a wetland soil's K_S proportionally by 27.3% ± 11% ($\chi^2_{(1)} = 5.58$, $p = 0.018$). Proximity to water had no effect ($\chi^2_{(1)} = 2.87$, $p = 0.090$).

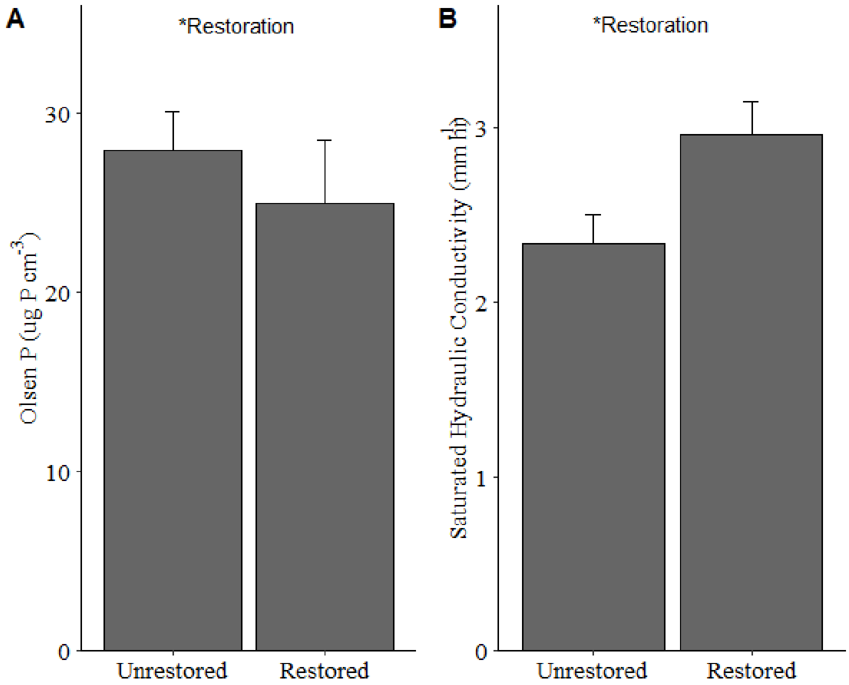

*Figure 2.10 Response of unrestored wetlands compared to restored wetlands fitted with standard error bars. Asterisks indicate significance in linear mixed effects models: * p < 0.05.*

*Table 2.4 Change in soil physio-chemical characteristics in response to restoration (restored or unrestored) and proximity to water (0 - 20m) according to linear mixed effects models. (SOC= soil organic carbon, K_S= Saturated hydraulic conductivity). ^proportional change. n.s.= not significant; * p <0.05; ** p < 0.01; *** p < 0.001.*

Soil Characteristic	**Response to restoration**	**Restoration significance**	**Proximity to water significance**	**Interaction significance**
*Soil Moisture^*	93.1% ± 16.1%	***	**	***
Bulk Density	0.19 ± 0.05 g/ cm^3	***	**	***
*SOC^*	19.7 % ± 10.0	***	n.s.	***
*Phosphorus^*	22.95% ± 13%	*	n.s.	NA
Silt		n.s.	n.s.	NA
*Sand^*		n.s.	***	NA
Clay		n.s.	n.s.	NA
*K_S^*	27.3% ± 11%	*	n.s.	NA

What is the effect of wetland restoration on soil characteristics?

Soil properties significantly changed between restored and unrestored wetlands (F_1= 43.229, p=0.0002, Figure 2.11B) and were significantly different depending on the site sampled (F_{17}= 122.46, p= 0.0002, Figure 2.12). A Principal Components Analysis (PCA) of all measured soil properties extracted two significant factors (Table 2.5). Forty-one percent of the variation in edaphic properties of the samples was explained by PC1. Soil organic carbon (r = 0.91,), bulk density (r = -0.93), soil water content (r = 0.88) and % silt (r = -0.67) all contributed strongly to the formation of PC1. Soil samples that scored high on PC1 had high in SOC and water content but low bulk density and silt content (Figure 2.11a). PCA2 explained a soil texture gradient among samples and accounted for an additional 25% of the variation of edaphic properties in the samples. Percent sand (r = -0.89), % silt (r = 0.59), and K_S (r = -0.55) all weighed heavily in forming PCA2.

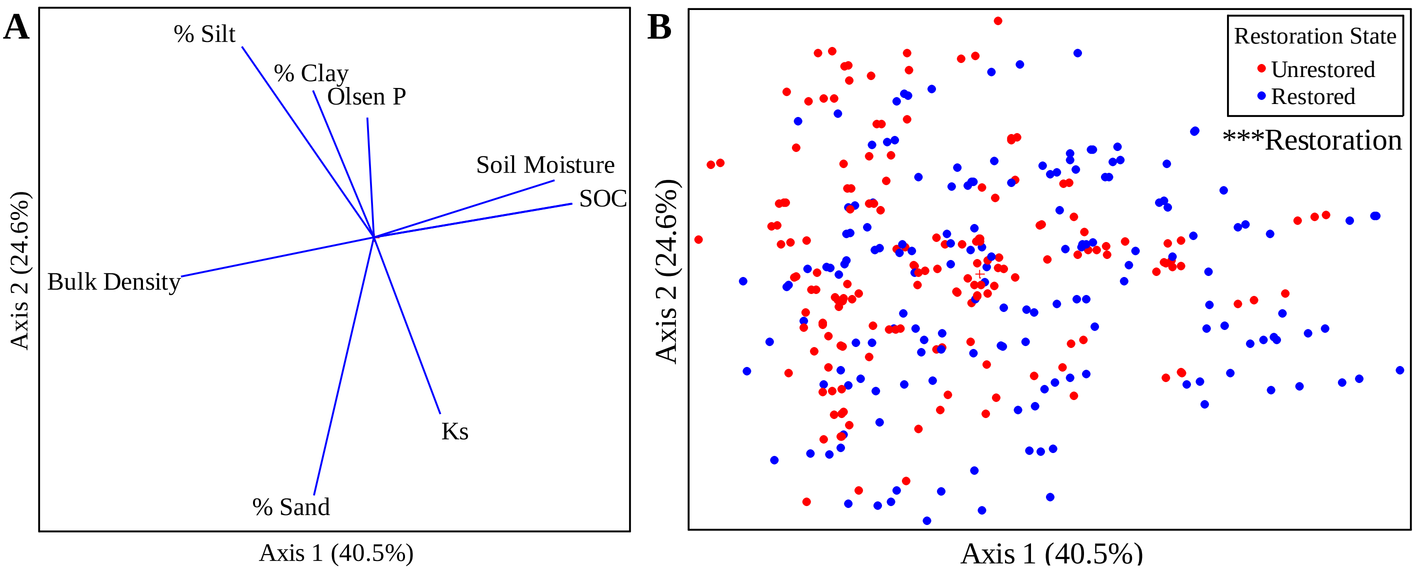

Figure 2.11 Principal Components Analysis of soil physio-chemical characteristics, A) illustration of the correlation of the individual soil properties within the two significant PCA factors. B) Ranking of soil samples on PCA factors 1 and 2, separated by wetland state (restored or unrestored).

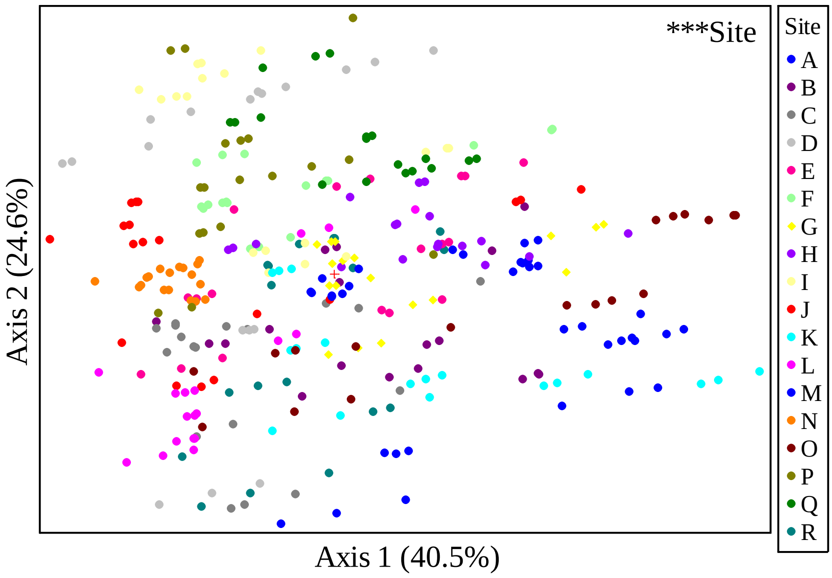

Figure 2.12 Principal Components Analysis of soil samples in soil physio-chemical characteristic space. Samples are colour coded by site (farm) Samples from a common site cluster closely together, reflecting their similar soil characteristics.

Table 2.5 Factor loadings of soil physiochemical variables as derived from the Principal Components Analysis.

Variable	**Factor 1 (40.5%)**		**Factor 2 (24.6 %)**	
	r	*r-squared*	*r*	*r-squared*
Soil Organic Carbon	0.910	0.827	0.178	0.032
Bulk Density	-0.932	0.869	-0.212	0.045
Saturated Hydraulic Conductivity	0.400	0.160	-0.550	0.303
% Clay	-0.321	0.103	0.473	0.225
% Silt	-0.670	0.449	0.592	0.350
% Sand	-0.225	0.051	-0.887	0.787
Olsen P	-0.077	0.006	0.392	0.153
Soil Water Content	0.881	0.775	0.273	0.074
Age	0.255	0.065	-0.235	0.055
Upstream Area	-0.078	0.006	0.200	0.040

How do microbial communities respond to wetland restoration?

Microbial Biomass

Microbial biomass increased with restoration at 11 of 18 farms but was extremely variable, with samples containing between 10.3 and 707.3 FA's/g soil, and plot level averages between 91.3 and 481.1 FA's/g soil. Given this huge site-level variability, average microbial biomass was similar in restored (237.5 FA/g) and unrestored wetlands (231.8 FA/g, Figure 2.13a). Nevertheless, the linear mixed effects model showed that restoration increased microbial biomass ($t_{(90)}= 2.66$, $p= 0.009$) by 24.5 ± 0.6 FA/g soil. In restored wetlands, the effect of restoration changed according to proximity to water ($t_{(70)}= -2.34$, $p= 0.022$, Figure 2.13a). This increase in biomass was driven by an increase in the amount of fungal biomass, which significantly increased with restoration by 8.4 ± 5.0 FA's/g soil ($t_{(186.3)}= 3.73$, $p= 0.0003$, Figure 2.13c). In contrast, total bacterial biomass did not change between restored and unrestored wetlands, nor with changing proximity to water (Figure 2.13d). The increase in fungal microbial biomass saw an increase in the ratio of fungal to bacterial biomass in restored wetlands ($t_{(90.4)}= 3.30$, $p= 0.001$), although this effect again depended on the proximity to water in restored wetlands but not in unrestored wetlands ($t_{(70.6)}= -2.43$, $p= 0.018$, Figure 2.13b).

Aerobic: anaerobic FA's

Restoration increased the proportion of aerobic microbes compared to anaerobic microbes in 15 of 18 wetlands (Figure 2.13e). A linear mixed effects model showed an increase of 0.237 ± 0.06 more aerobic FA's/g soil in restored wetlands compared to anaerobic FA/g soil ($t_{(87.6)}= 3.99$, $p< 0.001$). This effect was changed depending on proximity to water in restored wetlands ($t_{(66.7)}= -2.23$, $p= 0.029$, Figure 2.13e)

$Gram^{+}$/ $Gram^{-}$

The proportion of $Gram^{+}$ to $Gram^{-}$ bacteria did not change with restoration.

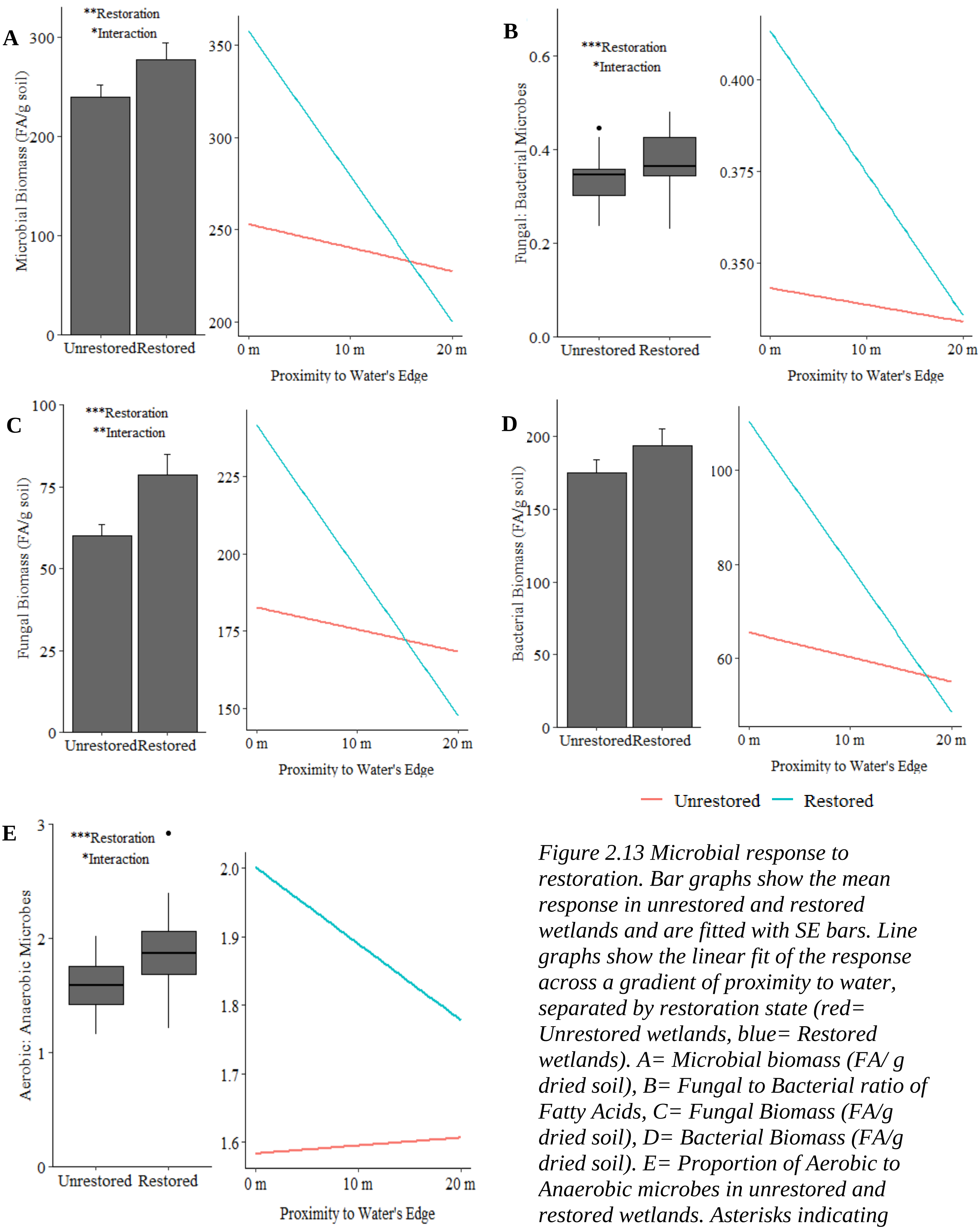

*Figure 2.13 Microbial response to restoration. Bar graphs show the mean response in unrestored and restored wetlands and are fitted with SE bars. Line graphs show the linear fit of the response across a gradient of proximity to water, separated by restoration state (red= Unrestored wetlands, blue= Restored wetlands). A= Microbial biomass (FA/ g dried soil), B= Fungal to Bacterial ratio of Fatty Acids, C= Fungal Biomass (FA/g dried soil), D= Bacterial Biomass (FA/g dried soil). E= Proportion of Aerobic to Anaerobic microbes in unrestored and restored wetlands. Asterisks indicating significance in linear mixed effects models: * p<0.05, **p<0.01 ***p<0.001.*

*Table 2.6 Change in microbial indicators in response to restoration (restored or unrestored) and proximity to water (0m- 20m) according to linear mixed effects models. ^proportional change. Asterisks indicating significance in linear mixed effects models: . ≤ 0.1, * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001.*

	Microbe Indicator	Response to restoration	Restoration Significance	Proximity to water Significance	Interaction significance
Quantity of FA' s	*Total Microbial Biomass^*	24.5% ± 0.6	**	n.s.	*
	Total Fungal Biomass	8.4 ± 5.0	***	n.s.	**
	Total Bacterial Biomass		.	n.s.	.
	Actinomycetes (%)		n.s.	n.s.	n.s.
	*AMF^*	18.4% ± 13.7	**	n.s.	**
	Gram$^+$ bacteria		n.s.	n.s.	n.s.
	Gram$^-$ bacteria		n.s.	n.s.	n.s.
	*General bacterial FA^*	10.7% ± 8.4	**	n.s.	*
	*General fungal FA^*	4.57% ± 11.4	.	n.s.	.
Proportions of microbial groups	*F/B^*	278.5% ± 274.4	***	n.s.	*
	Aerobic: anaerobic microbes	0.247 ± 0.060	***	n.s.	*
	Gram$^+$/Gram$^-$ bacteria		n.s.	n.s.	n.s.

Does the microbial community shift with restoration?

Across all wetlands, the composition of microbial PLFAs did not change markedly with restoration treatment, (A = 0.001, p = 0.17, Figure 2.14) but was significantly affected by the farm sampled (A= 0.153, p < 0.001). A PCA of microbial lipid data revealed two significant axes and explained a total of 71.6% of the variance of FA composition of the soil samples (Supplementary material's: Table S1). A large proportion (67%) of the variance was explained by PC1, although there were no FA's or other variables that significantly separated samples across this axis or the second. Instead, the ordination highlighted the divergence of

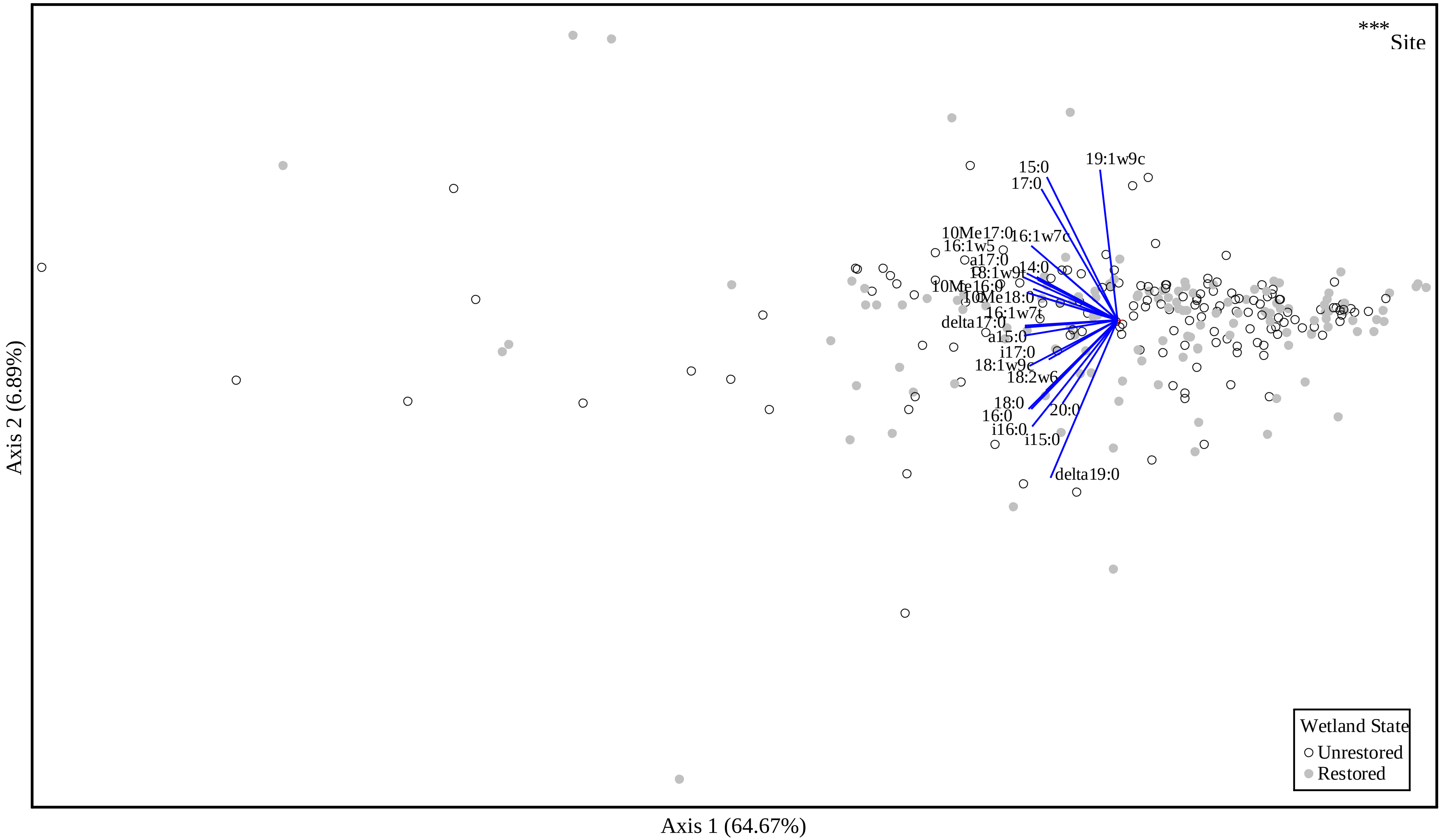

*Figure 2.14 Principal Components Analysis of soil PLFA biomarkers. Samples separated by wetland state (restored or unrestored). Asterix denotes significance level of MRPP analysis: *** ≤ 0.001.*

the FA profiles of soil samples from a few farms, again reflecting the heterogeneity of biotic responses to wetland restoration. Five PLFA's were indicators for unrestored wetlands, three of which were $Gram^+$ bacteria: i17:0, i16:0, and a17:0 (indicator value (IV) = 53.8, $p = 0.009$; IV = 54.0, $p = 0.014$; IV = 52.6, $p = 0.014$, respectively), and two of which were Actinobacteria: 10Me17:0 and 10Me18:0 (IV= 46.6, $p < 0.001$; IV = 54.5, $p < 0.001$ respectively).

Discussion

Wetland restoration enhanced desirable soil properties, and increased plant diversity and microbial biomass. Restored wetlands had greater variation in plant, microbial, and soil characteristics at both landscape and plot-level scales compared to unrestored wetlands. By using a paired sampling design and quantifying changes in plant communities, soil microbial communities, and soil physical characteristics, I found wetland restoration on private land was effective in initiating the reestablishment of wetland conditions. In particular, restoration led to soils becoming wetter, less dense, and richer in organic matter, and these changes were generally compounded in close proximity to the water's edge. The microbial community increased in biomass and changed community composition with an increase in the ratio of fungal to bacterial microbes and reduced ratio of anaerobic to aerobic microbes. The strongest effect of restoration was seen within the plant community, which increased by an average of 13 new native plant species and increased in overall in community diversity, evenness, and species accumulation.

Restoration enhances biodiversity and habitat heterogeneity.

Plant communities consistently responded with the largest desirable change with wetland restoration, with richness, diversity, evenness, and z each significantly increasing. Native plant biodiversity was enhanced, as evidenced by restored wetlands containing 13 more native species than unrestored wetlands. This response has been directly influenced by the planting of native and exotic species, which greatly accelerates the process of colonisation and re-establishment of native wetland communities, causing the plant community to recover faster than microbial and soil characteristics (J. Brown & Norris, 2018; Meli, Benayas, Balvanera, & Martínez Ramos, 2014). This increase in native plant diversity is encouraging, especially considering New Zealand lowland farms contains only 1.4% of native diversity that the land once contained (E. Dominati, Mackay, Bouma, & Green, 2016). Furthermore, diverse wetland plant communities show increased productivity, so large amounts of excess nutrients and atmospheric carbon are captured through plant growth (Brisson, Rodriguez, Martin, & Proulx, 2020).

Additionally, restoration increased plant diversity, and therefore habitat heterogeneity at both local and landscape levels. Restored wetlands had a larger z, showing a greater plant diversity at multiple scales within the plot compared to unrestored wetlands. Furthermore, restoration increased habitat heterogeneity across the landscape, with restored wetland plant communities showing a wide variation in composition. Habitat heterogeneity is a beneficial outcome from restoration because it increases connectivity (Graham & Quinn, 2020), diversity across multiple trophic levels (Pollock, Naiman, & Hanley, 1998; Stein, Gerstner, & Kreft, 2014), and increases ecosystem function (Lamers et al., 2012; Larkin, Bruland, & Zedler, 2016). Additionally, increased habitat heterogeneity reduces ecosystem service trade-offs to diversify the number of services a landscape produces (Rodríguez et al., 2006). For example, ecosystem service trade-offs that can be seen at a single wetland, such as the negative association between carbon sequestration flood-abatement (Jessop et al., 2015), become complimentary with increased landscape spatial complexity (Laterra, Orúe, & Booman, 2012).

Soil characteristics are developing slowly following restoration.

While restoration changed soils to be more characteristic of wetlands, the changes were variable and less distinct compared to the change seen in the plant community, and site sampled was the greatest determinant for what soil conditions you could expect to see. As soil processes occur over longer timeframes, these patterns are commonly found within restoration literature (Besasie & Buckley, 2012; J. Brown & Norris, 2018; Bruland, Richardson, & Management, 2006; Sigua et al., 2009; Q. Zhang et al., 2016). For example, soil texture changes over far longer timescales than restoration studies measure, yet it strongly influences soil density, SOC, moisture, nutrient holding capacity, and K_S (Schimel et al., 1994; Telles et al., 2003). Additionally, wetland restoration studies have found SOC accumulation following restoration is slow, requiring 15 - 300 years to reach SOC levels in remnant wetlands (see for syntheses: Yu et al. (2017) & Moreno-Mateos et al. (2012)). Although soil characteristics were still developing towards remnant wetland conditions, I found that private restoration is effective in producing changes in changes in soils towards the desired remnant conditions outcomes.

While restoration increased soil moisture, bulk density, and SOC, these changes were highly variable within each plot, and displayed a gradient of response in restored wetlands that was determined by the soil's proximity to water. In restored wetlands, soils sampled nearest to the waterbody were wetter, less dense, and contained more SOC. However soils in the transect furthest away from the water displayed characteristics that were similar to upland soils, being drier, denser, and containing less SOC. This pattern is likely driven by tree and vegetation respiration, as trees have a larger capacity to respire, and have greater root depth, drying out the soils. SOC storage is increased in saturated soils, as shown by PCA (Figure 2.11), as saturated soils tend to have lower bulk densities, and have more biogeochemical cycling processes occurring at the oxic/anoxic interface (Lamers et al., 2012). A hydrological gradient across the wetland produces different soil properties that are adept at produce different ecosystem services (Richards, Moggridge, Maltby, & Warren, 2018; L. Wang et al., 2019). For example, as shown here, soils contained the highest amounts of carbon near the waters edge, suggesting wetlands created for the purpose of sequestering carbon should focus on restoring soils that will stay highly saturated. However, soils further upland that are less saturated can support a greater amount of diversity (Odum, Finn, & Franz, 1979) and can act as buffers between nutrient rich agricultural soils and waterways (Mayer, Reynolds Jr., McCutchen, & Canfield, 2007).

Olsen P

Restoration reduced Olsen P, although it was variable within plots and between sites, as seen in other wetland restoration studies (Verhoeven, Whigham, van Logtestijn, & O'Neill, 2001; Yu et al., 2017). Olsen P levels are heavily influenced by wetland size which considerably varied (0.4 - 33.7 ha), and differences in nutrient loading, which was not measured here but was likely very variable between sites (Land et al., 2016). Despite this, the reduction in soil Olsen P suggests that P was up taken by plant biomass, because P sticks to sediment and is not readily washed away within the water-column (unless attached to clay particles; Wang & Mitscha, 2000). Although anecdotal, I observed during site visits, restored wetlands had significantly more biomass than unrestored wetlands. Planting during restoration causes plant-soil feedbacks to reduce P leeching into waterways, which reduces downstream eutrophication (D. Xu et al., 2005). Because restored wetlands have a greater capacity to hold P in plant biomass than unrestored wetlands as demonstrated by a decrease in soil Olsen P, it shows that restored wetlands are better at purifying water, a key ecosystem service. This is a highly desired outcome for landholders, particularly given the history of farming practices reducing water quality (Maseyk, Dominati, White, & Mackay, 2017).

Ks

Restoration increased K_S, although there was a large variability in recovery between plots. K_S is strongly influenced by vegetation and soil characteristics such as SOM (Ebel & Martin, 2017). Increased plant diversity following restoration plantings increases the type of root systems binding soil together, and reduces soil erosion during heavy rainfall (Ford, Garbutt, Ladd, Malarkey, & Skov, 2016). Additionally, I found bulk density (which is incorporated into the K_S pedo-transfer function) to decrease following restoration, likely because fencing reduces compaction by livestock and machinery. With reduced bulk density, the soil-water repellency reduces (Doerr, Shakesby, & Walsh, 2000). Furthermore, SOC (also incorporated into the K_S pedo-transfer) is effective at absorbing water (Libohova et al., 2018) . Therefore, fencing and planting during restoration effectively increased the soils capacity to hold and store water by increasing SOC and root system diversity, and reduced bulk density, as seen by the increase in K_S following restoration. This means surface water flow is reduced in restored wetlands and peak flood heights are reduced downstream from restored wetlands, increasing another key ecosystem service: flood abatement (Ziter & Turner, 2018).

Increased fungal biomass indicates improved soil conditions

No restored wetlands had yet reached remnant soil conditions, as demonstrated by fungal biomass increasing with restoration and with proximity to water. Fungi almost exclusively use aerobic respiration, requiring oxygen to live. However, remnant wetland soils are anaerobic and contain a far higher proportion of bacterial to fungal biomass (Cao, Wang, Chen, Wang, & Liu, 2017; Ligi et al., 2014). In fact, unrestored wetlands under agricultural management have been found to contain three times the amount of fungal biomass to remnant wetlands (Shangqi Xu et al., 2017). Long term, restored wetlands had the lowest fungi to bacterial ratio, while wetlands which were only flooded for short periods had higher ratios (Moche et al., 2015). The increase in the F/B ratio therefore indicates two things. The first that unrestored soils are less suited for fungal growth due to compaction and SOC depletion from farm activities (Oehl, Laczko, Oberholzer, Jansa, & Egli, 2017). Second, while soil conditions have become more organic and less dense, they are still aerobic, meaning that the increase in fungal biomass indicates the partial development of wetland soil characteristics. This is supported by the increased ratio of aerobic to anaerobic microbes in restored soils comparative to unrestored soils, which shows that soils are experiencing less disturbance but are still not reaching anaerobic conditions of wetland soils (Gutknecht et al., 2006).

Microbial community change alters carbon sequestration potential.

Restoration changed the microbial community composition, which altered carbon cycling and enhanced the carbon sequestration potential of restored wetlands. I did not find a significant effect of restoration on the PLFA community composition by MRPP, because variability caused by the site soil conditions overwhelmed the effect of restoration (Bossio et al., 2006; Shiqi Xu et al., 2017; Q. Zhang et al., 2016). However, I found an increase in microbial biomass following restoration, which was driven by an increase in fungi and AMF biomass. This impacts the carbon sequestration potential of restored wetlands in three ways: (1) by enhancing primary productivity, (2) by directly up taking nutrients from organic pools and leaving behind C-rich substrate, and (3) by increasing potential biogeochemical cycling.

AMF and fungi enhance primary productivity, which has knock on effects for POC production (Morris et al., 2019). AMF form obligate relationships with 80% of vascular plants to help facilitate plant growth, change plant community competitive dynamics, and are involved in soil stability and nutrient cycling (Lee, Eo, Ka, & Eom, 2013). Although unable to persist in anaerobic soil in the long-term (Wirsel, 2004), AMF frequently inhabit wetland rhizosphere soils, where oxygen is concentrated (Cooke & Lefor, 1998). AMF aid in plant community succession and diversity (Daleo et al., 2008; Weishampel & Bedford, 2006), and increase primary productivity (Van Der Heijden et al., 2006). In this way, fungi and AMF increase SOC, by increasing leaf litter production to become recalcitrant in anoxic soils (Orwin, Kirschbaum, St John, & Dickie, 2011). Additionally, indicator species analysis found five lipids associated with Gram^{+} and actinomycete bacteria that were specific to unrestored wetlands. Gram^{+} and actinomycete bacteria are slow growing and rely on recalcitrant carbon and are outcompeted by fast-growing Gram^{-} bacteria that rely on liable carbon sources such as leaf-litter (Fanin et al., 2019). It is therefore likely that unrestored wetlands have more recalcitrant carbon sources, while increased leaf litter production means that restored wetlands have more liable carbon sources (Fanin et al., 2019).

Although it was initially thought at the bulk of SOC was from leaf litter, studies show that 50 - 70% of SOC could be derived from mycorrhizal fungi and roots (Clemmensen et al., 2013). SOC is determined by the rate of plant litter production and rate of decomposition (De Deyn, Cornelissen, & Bardgett, 2008). Fungi are effective at processing more complex carbohydrate chains such as those seen in leaf litter, allowing them to decompose organic matter more effectively than bacteria (Weise et al., 2016). While decomposition reduces the carbon storage potential of wetlands by reducing the amount of organic matter to become recalcitrant, Orwin et al. (2011) show that in nutrient-limited conditions the direct uptake of nutrients by fungi from organic pools leave carbon-rich, nutrient-poor substrates behind. Finally, an increase in biomass increases the potential biogeochemical cycling that could be occurring. Therefore, with improved soil conditions following restoration, an increase in abundance of microbial biomass, particularly fungi and AMF, enhances the conditions for carbon sequestration, a key wetland ecosystem service, by increasing primary productivity and directly up taking nutrients from organic pools, leaving behind C-rich substrate.

Conclusions

Wetland restoration occurred under a large variation of conditions including degration context (dairy, sheep and beef, and fallow), wetland size (0.4 - 33.7 ha), upstream contributing area (4 - 2263 ha), time since restoration (0.5 - 42 years ago), and number of restoration techniques used (2 – 8). Despite the variability of restoration context at each site, restoration was still effective at changing plant, soil, and microbial characteristics towards conditions seen in remnant wetlands. Specifically, private wetland restoration added ~13 native plant species, increased microbial biomass by 25 FA/ g soil, and increased fungal and AMF presence in microbial communities. Additionally, restoration increased soil moisture, increased SOC by 20%, reduced bulk density by 0.19 g/cm^3 and Olsen P by 23% and increased K_S by 27%. These biophysical changes enhanced ecosystem service production in multiple ways. First, an increase in plant diversity and heterogeneity helps reduce ecosystem service trade-offs, and increases biodiversity habitat. Second, a change in microbial community composition enhanced the carbon sequestration potential of the wetland by enhancing primary productivity, and increasing mycorrhizal derived SOC. Third, with increases in plant diversity and biomass help remove plant available P from soils to reduce downstream eutrophication. Finally, by reducing compaction and increasing root system diversity, restored wetlands have a higher K_S, allowing them to abate floods more effectively. However, changes in the soil microbial and physio-chemical characteristics were variable at the plot and landscape level, reflecting the contextual variability of private restoration projects and the slow development of wetland soil characteristics. My quantification of changes in soils, plants, and microbes show that restoration on private property re-establishes wetland conditions that enhance ecosystem service production including carbon sequestration, water purification, flood abatement, and biodiversity habitat. This demonstrates that wetland restoration is an effective tool that can be used to increase the sustainability of New Zealand's landscapes.

Chapter 3 Exploring the variation in indicators of succession during wetland restoration

Introduction

Restoration ecology aims to accelerate successional processes.

Restoration ecology aims to re-establish desired ecosystem attributes by manipulating successional processes in a way that accelerates species and substrate change, and leads to desired biodiversity and ecosystem services delivery (Luken, 1990). Succession is a community-level change in species composition and associated substrate changes over time (Walker, Walker, & Del Moral, 2007). The first stage of succession involves the successful arrival and recruitment of plants to a disturbed site. Restoration projects involve the removal of disturbance and the deliberate sowing of seed or planting of plants, sometimes after site preparation (Benayas, Newton, Diaz, & Bullock, 2009). During natural succession, plant establishment relies on the local seed bank and dispersal of seed from nearby source populations (Horn, 1974). However, local seed banks are often depleted in disturbed sites and high-intensive agricultural landscapes may have heavily reduced source populations (Morimoto et al., 2017). These conditions are prevalent within the Wairarapa region where 98% of wetlands have been removed (Ausseil et al., 2008) and agriculture is a dominant land use. Planting during restoration reduces the reliance on seed banks and dispersal and reduces competitive dynamics between seedlings and the established un-desirable plant community (Porensky, Perryman, Williamson, Madsen, & Leger, 2018). Furthermore, restoration planting directly manipulates the plant community by only introducing desired plant species, not unwanted pest species. Changes in the plant community alters soil physio-chemical characteristics and soil microbial communities.

Planting influences soil and microbial succession

Changes in the plant community directly influence the soil microbial community by changing substrate availability through altered plant root exudates (Broeckling, Broz, Bergelson, Manter, & Vivanco, 2008). Exudates are the primary food source for microbes in the rhizosphere (Philippot et al., 2013) and the quantity and type of exudate production is plant species specific (Eisenhauer et al., 2017), which in turn influences the biomass and community composition of microbes (Berg & Smalla, 2009; Eisenhauer et al., 2010). The plant community also indirectly influences the soil microbial community by changing the soil physical and chemical properties (J. A. Bennett & Klironomos, 2019). Plant communities play a key role in soil formation and nutrient cycles during wetland restoration (van der Bij et al., 2018). Through root exudation, plants drive soil microbe enzymatic activities that alter nutrient availability (Wardle et al., 2004). By taking up plant-available N and P, plants restore the typically nutrient poor conditions of wetland soils, becoming the major storage pool of organic nutrients in wetlands (K. R. Reddy & DeLaune, 2008). Furthermore, plants are the primary in-situ source of carbon in wetlands, and soil carbon content alters soil density and moisture content (Yarwood, 2018). Additionally, the root system reduces soil bulk density, encourages sediment accumulation, and alters the water table depth (Crooks, 2002). Plants facilitate microbes as the key decomposers of the trophic web by providing energy and changing soil conditions. Microbial communities facilitate nutrient cycles, breaking down compounds and molecules (Romaní et al., 2006) to supply plants with P and N (Asmelash et al., 2016). Microbes facilitate plant growth and are responsible for many of the biogeochemical processes occurring in wetland soils (Andersen et al., 2013). Additionally, because microbial communities are sensitive to soil physical characteristics, feedbacks arise between soil conditions and soil microbes (Chaparro, Sheflin, Manter, & Vivanco, 2012).

Plants, microbes, and soils as indicators of succession

It is important to measure the success of restoration to see under what conditions restoration effectively accelerates successional processes. Succession cannot be measured directly, so instead measurable ecological indicators infer changes in the structure and function of a recovering wetland (Sims et al., 2013). Indicators often used include soil physiochemical measurements (Muñoz-Rojas, 2018), plant species (Dufrêne & Legendre, 1997), plant community indices (Matthews et al., 2009), and macroinvertebrate communities (Al-Zankana, Matheson, & Harper, 2020). Although not extensively used, microbial communities also indicate ecosystem system change (Sims et al., 2013; Urakawa & Bernhard, 2017). Soil, plant and microbial indicators can provide information on the rate of recovery of biodiversity, wetland function, and ecosystem service production (Table 3.1). Plants, soils, and microbes follow (relatively) predictable patterns following restoration (Figure 3.1), so measuring these indicators gives a snap shot of the recovery stage of a restored wetland.

Table 3.1 Wetland indicators expected to increase with restoration, and the rationale of their use.

	Indicator	Description/ Rationale
Soil	*Soil organic carbon*	Indicates general soil quality. Natural wetlands have the highest density storage of carbon per unit area of any ecosystem (Yarwood, 2018).
	Bulk Density	Indicates soil condition and is inversely related to SOC accumulation. Influences K_S, soil moisture conditions, and water purification (Moreno-Mateos et al., 2012).
	Soil moisture content	Indicates saturation and strongly influences microbial biomass (L. Wang et al., 2019).
	Saturated Hydraulic Conductivity	Indicative of potential infiltration rates. Soils with higher K_S better attenuate runoff and floods (Ziter & Turner, 2018).
	Olsen P	Plant available P. Indicates P likely to be lost in surface runoff affecting downstream water quality (McDowell, Sharpley, Brookes, & Poulton, 2001).
Plant	*Diversity*	Shannon's diversity of native vascular plants. Increased diversity suggests greater habitat heterogeneity.
	# Guilds	Number of plant guilds present, indicating the functional variation of plant diversity.
	Slope of species accumulation curve	Indicates species richness at multiple scales, and the rate of encounter of new species within a given area.
	Grass: Non-grass species	This ratio alludes to vegetation with high vs. low biomass turnover rate.
Microbe	*Microbial Biomass*	Indicates the absolute biomass of soil microbes. Microbes drive many wetland ecosystem services (Van Der Heijden et al., 2008) and higher biomass can indicate higher nutrient cycling potential.
	Fungi: Bacteria	The functional makeup of the microbial community. Fungi utilise complicated substrates and facilitate accumulation of SOC. Bacteria commonly utilise easily available substrates and are associated with higher rates of SOC turnover (L. Wang et al., 2019)
	Aerobic: Anaerobic microbes	Aerobic microbes require soils with sufficient pore space for oxygenation and, their abundance is inversely related to soil compaction/ bulk density.
	Gram$^+$/Gram$^-$ bacteria	Shows the tolerance and stability of the microbial community. Gram$^+$ bacteria withstand changing soil conditions, while Gram$^-$ bacteria are more sensitive to environmental degradation (Zou et al., 2013).

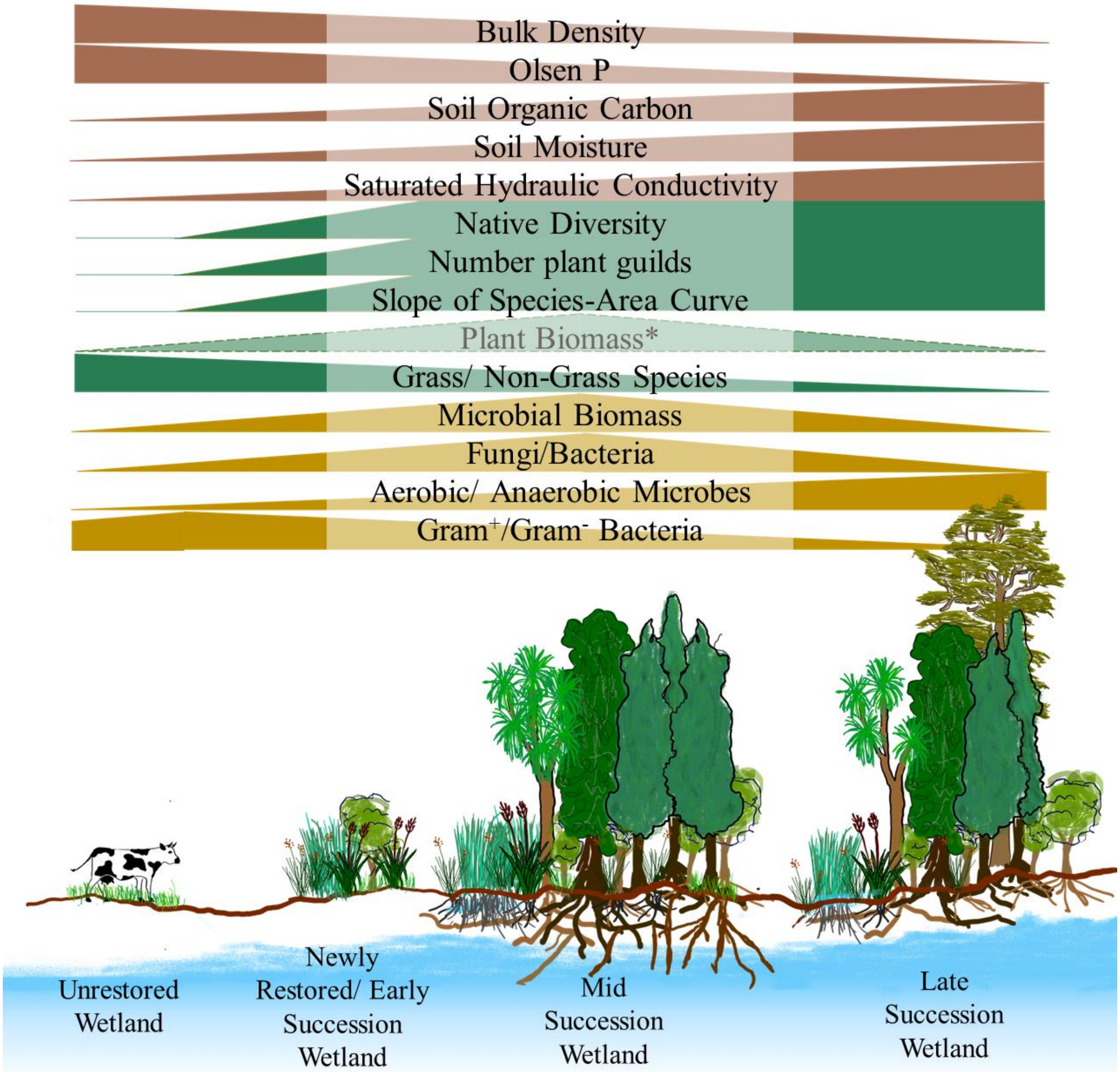

*Figure 3.1 Successional changes seen in wetland indicators during wetland recovery from a degraded wetland to a late succession wetland. *indicator not used in this study.*

Successional rates change depending on site context

The rate of recovery following restoration is influenced by the wider site context restoration is occurring within. Despite secondary succession during restoration being a temporal process, site context is frequently a more important determinant of the speed of recovery (Hobbs & Cramer, 2008). For example, across multiple wetland restoration projects, site context was more important than time since restoration in predicting biodiversity and ecosystem service recovery (Meli et al., 2014). At global scales, climate and soil type explain an order of magnitude of variation in the rate of succession (Yu et al., 2017). At local scales, larger wetlands recover faster than small wetlands (<100 ha, Moreno-Mateos, Meli, Vara-Rodríguez,

& Aronson, 2015), and the upstream area and hydrological context (connected vs isolated) also alter recovery rates (Moreno-Mateos et al., 2012). Additionally, the cause and severity of degradation changes recovery time: when considering multiple types of ecosystem restorations, ecosystems degraded by agriculture are second only to multiple degradation causes in having the longest recovery time (H. P. Jones & Schmitz, 2009).

Restoration is expensive and time consuming, consequently, it is important to determine what conditions lead to the most effective use of resources. In chapter 2, I found a large variation in indicators of restoration outcomes across restored wetlands, particularly in regard to soil physical and microbial characteristics. Each restored wetland I sampled differed in a variety of ways; with different causes of degradation and times since restoration (0.5 to 42 years) as well as large differences in upstream watershed area (4 - 2263 ha), wetland size (0.4 to 33.7 ha), dominant plant community (woody *vs.* herbaceous), and the number of restoration treatments applied (2 – 8). In this chapter, I explore the relationships among variation in plant, soil and microbial datasets. Additionally, I test causes of this variation. I use measurements of plant, microbial, and soil characteristics as indicators of wetland succession. I employ Procrustes analysis to look at the association of variation in the spatial distribution of plants, microbes, and soil characteristics to see if successional processes of these attributes are concurrent within wetlands. I then use hierarchical cluster analysis to determine which wetlands are undergoing succession of attributes at similar rates. Taken together, these analyses provide insight to the conditions that accelerate successional processes in restored wetlands. I ask the following questions: 1) How do microbial, plant, and soil characteristics co-vary during wetland restoration? 2) How do indicators of wetland succession respond to restoration? 3) Are different restoration practices and site contexts influencing wetland outcomes during restoration?

Methods

How do microbial, plant, and soil characteristics co-vary during wetland restoration?

For site description and data collection methods please see chapter 2. I used Procrustes analysis to test if the shape of the variation in plant, microbial, and soil properties were similar. Procrustes analysis tests the matrix association to see if the spatial distribution of variation is related (Peres-Neto & Jackson, 2001). Ordinations of data matrices are scaled and rotated to find an optimal superimposition to maximise their fit. By rotating the matrices, the sum of squared residuals between the matrices are maximised to produce the resultant statistics, m^2 (Siqueira, Bini, Roque, & Cottenie, 2012). The level of community congruence, or the strength of the ordinations match, is shown with the r statistic, the square-root of $1-m^2$.

I compared the variation in the plant community to soil characteristics and to the microbial community using a pairwise comparison. To compare the soil and microbe matrices to the plant matrices, only the two soil samples taken within two 1m x 1m vegetation plots were considered (Figure 3.2), resulting in a sample size of 68. The soil characteristics matrix contained SOC, bulk density, moisture, K_S, % sand, % silt, % clay, and Olsen P measurements, and was ordinated using a PCA. Only the first 2 PCA axes were significant, explaining 62.1% of the variation in the matrix. The microbe matrix, containing the relative proportions of PLFA biomarkers, was ordinated with a PCA, of which the first 2 axes were significant and explained 72.2% of the variation within the matrix. The plant matrix was reduced to the 68 most common plant species to obtain a square matrix. The NMS explained only 12.8% of variation in the data in 2 significant axes.

For the pairwise comparison of the soil characteristics and microbial matrices, all soil samples (n = 324) were considered. A PCA was run on both larger sets, and the soil characteristics PCA explained 64.6% of variation across 2 significant axes, while the microbe characteristics PCA explained 67% of variance across 2 significant axes.

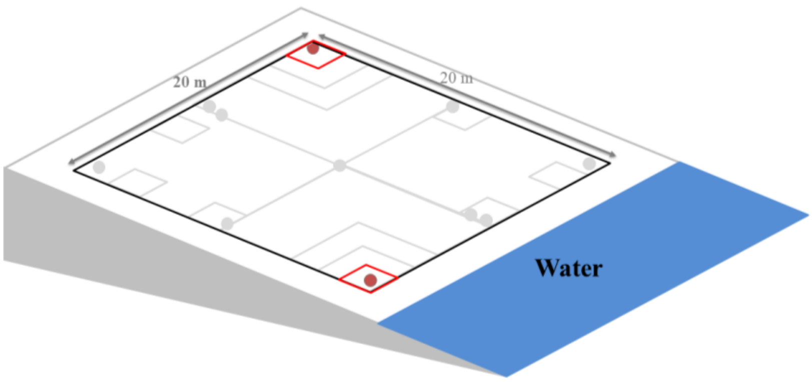

Figure 3.2 Plot diagram showing the relevant soil samples and vegetation plots used for Procrustes analysis, highlighted in red.

Pearson’s correlation analysis was used to determine the relationship between individual variables to find what variables co-varied between the data matrices. Because a species matrix could not be used in a correlation analysis, microbial indicators were used. The microbial indicators included microbial biomass, fungal biomass, bacterial biomass, and the ratios of F/B, aerobic: anaerobic, and $Gram^{+}/Gram^{-}$.

How do indicators of wetland succession respond to restoration?

How do indicators of wetland succession respond to restoration?

To assess the effect of restoration on wetland succession, I monitored 13 indicators of wetland succession, focusing on measurements of soil, microbe, and plant characteristics. These indicators were used to determine which sites were recovering faster after restoration. The indicators included five soil characteristics, four microbial indicators, and four plant indicators (see Table 3.1). To give each indicator equal weighting, soil, plant, and microbial indicators were normalised from between 0 and 1, with 0 reflecting the earliest successional stage of the 36 wetlands, and 1 reflecting the most advanced successional stage of the 36 wetlands. To ensure that all indicators would increase from 0 to 1 with succession, the inverse of soil bulk density, Olsen P, and grass: non-grass species were used.

I then used a two-way cluster analysis to explore how the 36 wetlands clustered according to their production of the 13 normalised wetland indicators. This analysis revealed whether restored wetlands clustered separately from unrestored wetlands, while simultaneously showing what clusters of indicators were particularly important in affecting this separation. Hierarchical clustering sequentially merges objects and groups of objects to agglomerate them according to their similarity. A dissimilarity matrix is calculated of squared elements, and an algorithm then preforms clustering cycles of n-1 loops until wetlands are joined based on their similarity to other wetlands' indicators (McCune et al., 2002). The clustering is then displayed on a dendogram. A two-way hierarchical cluster analysis simultaneously classifies sample units (wetlands) and response variables (indicators) to display clusters of variables and clusters of wetlands simultaneously (Gauch & Whittaker, 1981). I preformed the cluster analysis in PC-Ord, using Ward's method and Sorensen's distance as the distance measure. The dendogram of wetlands revealed a clear separation of clusters. The statistical significance of the perceived clustering was tested using MRPP with Sorensen's distance.

Are different restoration practices and site contexts changing succession outcomes during wetland restoration?

To explore how site context and restoration treatments influences indicators of wetland succession, a second two-way cluster analysis was performed on the restored wetlands (n=18) according to the 13 indicators. Ward's method, using Sorenson's distance as the distance measure, was used for the cluster analysis. This established clusters of wetlands which were at similar successional stages. There were 2 distinct clusters of later successional wetlands and early succession wetlands, and one outlier-wetland. To test if these were statistically significant clusters, I added the 3 clusters as a categorical factor in the subsequent MRPP analyse measured with Sorenson's distance. All analyses were carried out in PC-ord.

I made a table to visually assess what site variables appeared to be involved in the difference between early and late succession wetlands. A PCA was used to test for the effects of continuous variables (time since restoration and upstream catchment area) on wetland succession indicators. MRPP with Sorenson's distance was used to determine if discrete variables (wetland hydrology, dominant plant community, and earthworks) could explain differences between clusters.

Results

How do microbial, plant, and soil characteristics co-vary during wetland restoration?

Microbial communities and soil characteristics were strongly associated and showed very similar patterns of spatial variation ($m12^2 = 0.80$, $r^2 = 0.44$, $p = 0.001$). Soil conditions explained 44% of variation in the composition of microbial communities. In contrast, plant communities were not significantly associated with microbial communities ($m12^2 = 0.93$, $r^2 = 0.26$, $p = 0.103$) nor with the soil conditions ($m12^2 = 0.93$, $r^2 = 0.27$, $p = 0.181$). Restoration did not alter the association between soil and microbial properties ($t_{275} = 0.25$, $p = 0.804$), which remained strong in both restored and unrestored wetlands.

Of the measured soil characteristics, soil moisture showed the strongest correlations with microbial indicators, being significantly correlated with all but one microbial indicator ($Gram^+$/ $Gram^-$). Soil moisture was strongly correlated to fungal biomass and moderately correlated to microbial biomass, bacterial biomass, and F/B. Soil organic carbon was positively correlated with all microbial indicators, except $Gram^+$/ $Gram^-$ ratios with which it was weakly negatively correlated (Table 3.2). Conversely, bulk density was negatively correlated to all microbial indicators except $Gram^+$/ $Gram^-$ ratios with which it was positively correlated. Fungal biomass was more highly correlated with the measured soil variables than bacterial biomass was with measured soil variables. SOC and bulk density, rather than moisture, were more highly correlated with the aerobic: anaerobic content and $Gram^+/Gram^-$ ratios. K_S was weakly correlated with all microbial indicators except $Gram^+/Gram^-$. Olsen P was not correlated with any microbial indicators.

Table 3.2 Pearson's co-relation between soil characteristics and microbial indicators. SOC= soil organic carbon, BD= bulk density, SM= soil moisture, K_S= Saturated hydraulic conductivity.

Microbial indicator	**SOC**	**BD**	**SM**	**K_S**	**Olsen P**
Total biomass	0.56 ***	-0.56 ***	0.64 ***	0.08 **	NS
Bacterial biomass	0.54 ***	-0.54 ***	0.57 ***	0.07 *	NS
Fungal biomass	0.57 ***	-0.58 ***	0.75 ***	0.10 ***	NS
Fungi/ Bacteria	0.28 ***	-0.41 ***	0.55 ***	0.12 ***	NS
Aerobic: Anaerobic	0.42 ***	-0.42 ***	0.36 ***	0.13 ***	NS
$Gram^+$/ $Gram^-$	-0.24 ***	0.24 ***	NS	NS	NS

Significance levels= *p<0.05, **p<0.01, *** p<0.001

How do indicators of wetland succession respond to restoration?

I found that indicators of wetland succession were generally more advanced in restored relative to unrestored wetlands. Of the 13 indicators of wetland succession measured, between 7 and 12 indicators (mean = 10) increased in restored wetlands (Figure 3.3). Concurrently, an average of 3 indicators decreased at each site, with a range of between 1 and 6 decreasing. When assessing the magnitude of change in these indicators, there was no restored wetland that stood apart as more advanced in its recovery compared to the others (Figure 3.4). The response of indicators of wetland succession to restoration varied widely, and all restored wetlands had both one indicator that was in the bottom 25% range of values sampled and one indicator in the top 25%. Unrestored wetlands had less variability in

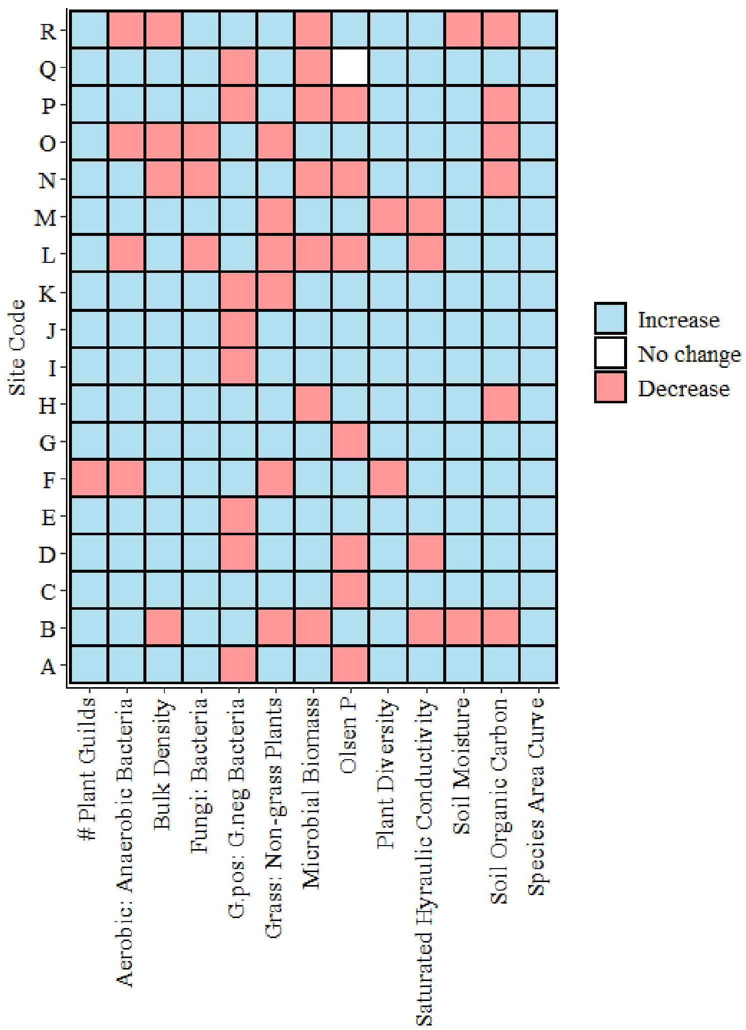

Figure 3.3 Change in wetland indicators because of restoration. Blue tiles indicate an increase in the indicator, white indicates the indicator did not change, and red indicates the indicator decrease with restoration.

indicators, with 7 of the 18 unrestored wetlands having no indicators in the top 25% range (Figure 3.4). All unrestored wetlands had at least one indicator in the bottom 25%.

While broadly, indicator values increased with restoration, there was a lot of variance in the response of each indicator and in the response of each site to restoration. The only indicator that increased with restoration at all sites was z. All other indicators decreased with restoration in at least 1 site. Plant indicators showed the biggest magnitude of change, with plant guilds, z, and plant diversity showing the largest increases with restoration (Figure 3.4). Of the soil indicators, bulk density was most responsive to restoration, and of the microbial indicators, the ratio of aerobic: anaerobic bacteria were the most responsive to restoration. SOC, bulk density, moisture, and microbial biomass all changed at similar magnitudes with restoration.

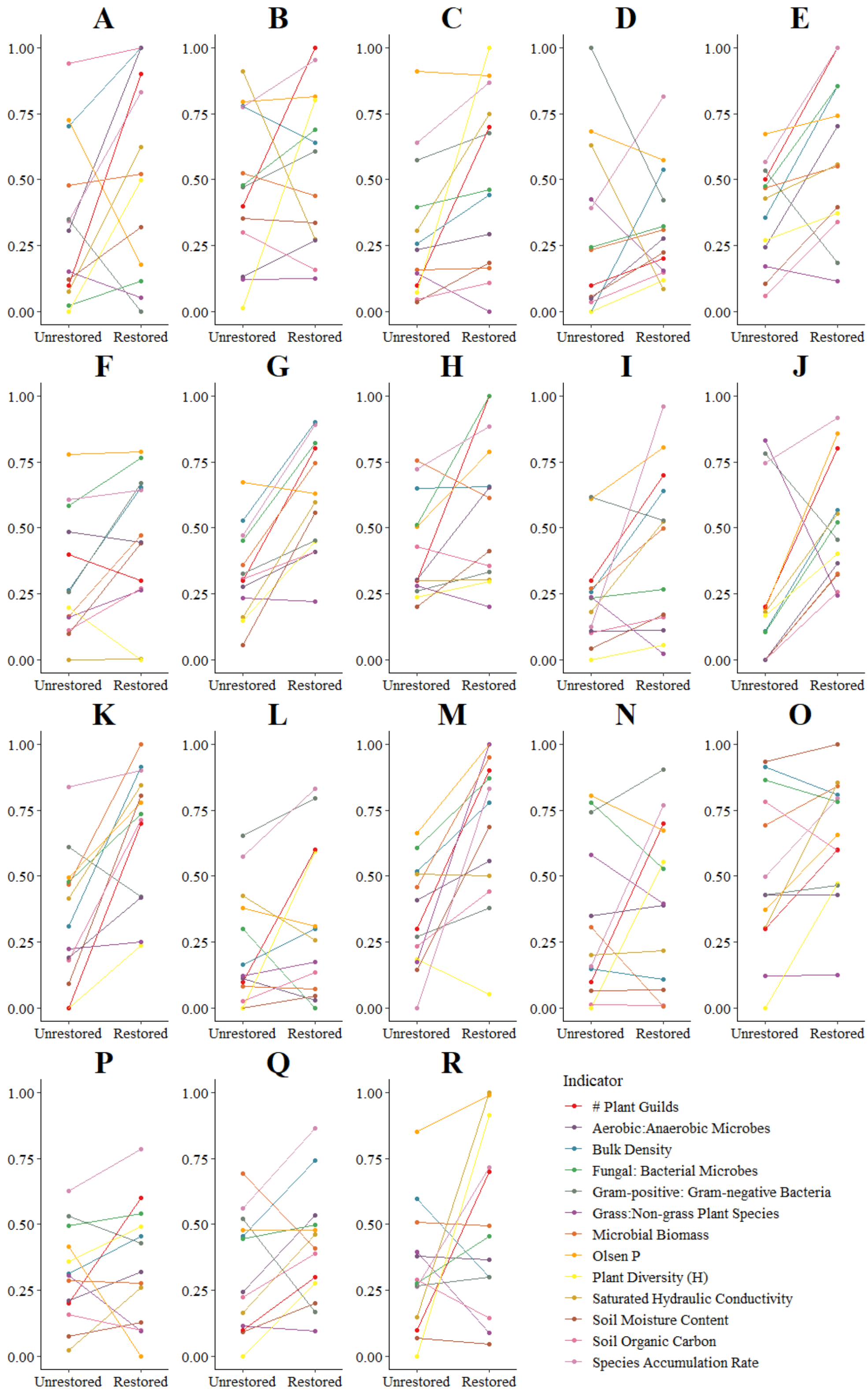

Figure 3.4 Scaled change of succession indicators at each site. Each succession indicator is scaled between 0-1, and inversed where required so that 1 shows more advanced succession.

Cluster analysis found two distinct groups of wetlands (A= 0.15, $p < 0.001$, Figure 3.5), the first comprising of predominantly restored wetlands with high indicator values showing they were further along in successional processes. The second group was predominantly unrestored wetlands with lower indicator values showing they were still in early successional stages. In the first cluster, wetlands had more diverse plant communities, and soils that were SOC and moisture rich, low in bulk density, high in K_S and microbial biomass, with higher proportions of fungi compared to bacteria and aerobic to anaerobic microbes (Figure 3.5). In the second cluster wetlands had soils that were characterised as denser, less organic, and drier, with reduced microbial biomass, a higher proportion of anaerobic bacteria to aerobic bacteria, and reduced plant diversity.

At sites at B, H, and O, the unrestored wetlands were more like restored wetlands and were in the first cluster. These unrestored wetlands could be characterised as having low-density soils. The unrestored wetland at site O had particularly wet, organic rich soils, while the unrestored wetland at site B had soils that were high in K_S. Both O and B unrestored wetlands were fed with an underground spring. The unrestored wetland at site H was high in microbial biomass and z, which were characteristics seen in restored wetlands more than in unrestored wetlands.

There were five restored wetlands that were more like unrestored wetlands, all of which had soils that were inorganic, dense, relatively dry, and low in microbial biomass. All these restored wetlands only had the indicators z and/or a high $Gram^+/Gram^-$ that were in the top quartile of indicator ranges, other than at site F which had the F/B proportion and Olsen P in the top quartile only (Figure 3.4). At sites L, P, N, the restored wetlands had been restored ≤ 6 years ago. At sites D and F, the plant communities were dominated by pasture species.

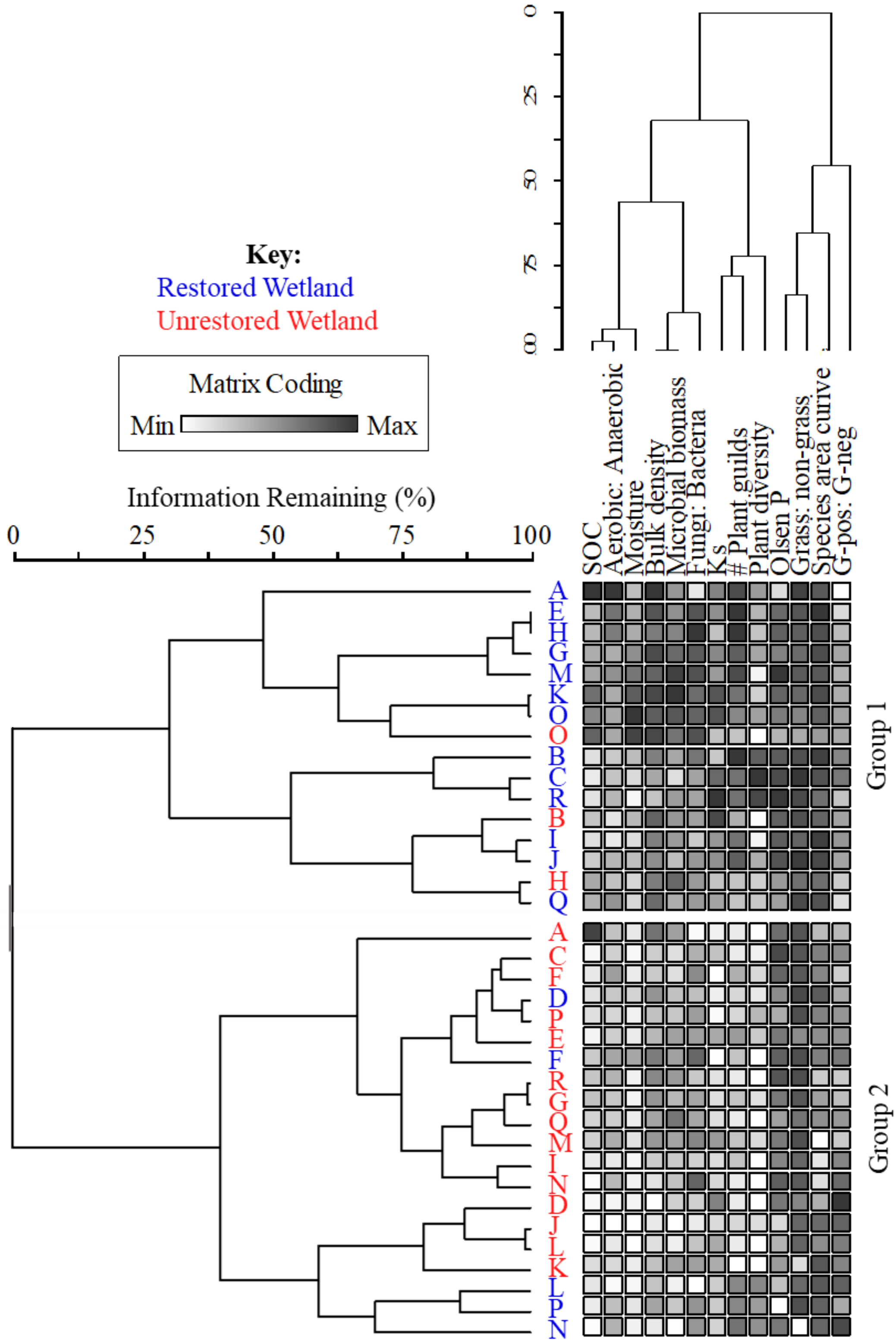

Figure 3.5 Two-way cluster analysis of restored and unrestored wetlands clustered according to their wetland succession indicators.

Are different restoration practices and site contexts changing indicators of wetland succession during restoration?

When considering only the restored wetlands, two broad groups separate based on the measurement of wetland succession indicators ($A = 0.16$, $p < 0.001$, Figure 3.6). Group one are early successional wetlands, and group two is later successional wetlands. As established in chapter 2, no wetland had reached soil or microbial characteristics of remnant wetlands, and so group 2 is referred to as *later* succession wetlands in reference that they are further along the successional process than the early succession wetlands but are still recovering. The first group of wetlands was characterised by having comparatively low indicator values. These soils were denser, drier, less organic and contained less microbial biomass (Table 3.3). They also had a lower proportion of aerobic: anaerobic microbes and F/B compared to the second group of wetlands. The second group consisted of late succession wetlands and were characterised as having high levels of most wetland indicators (Table 3.3).

Cluster analysis found one wetland that was not similar to either group, and thus, this wetland formed group 3. This wetland at site A was an old kahikatea wetland stand that was particularly dry due to drainage being near the location sampled. This wetland had very different characteristics compared to the other wetlands, having soils that were extremely high in SOC (plot level average of 31.9%), bulk density, and microbial biomass. However, its

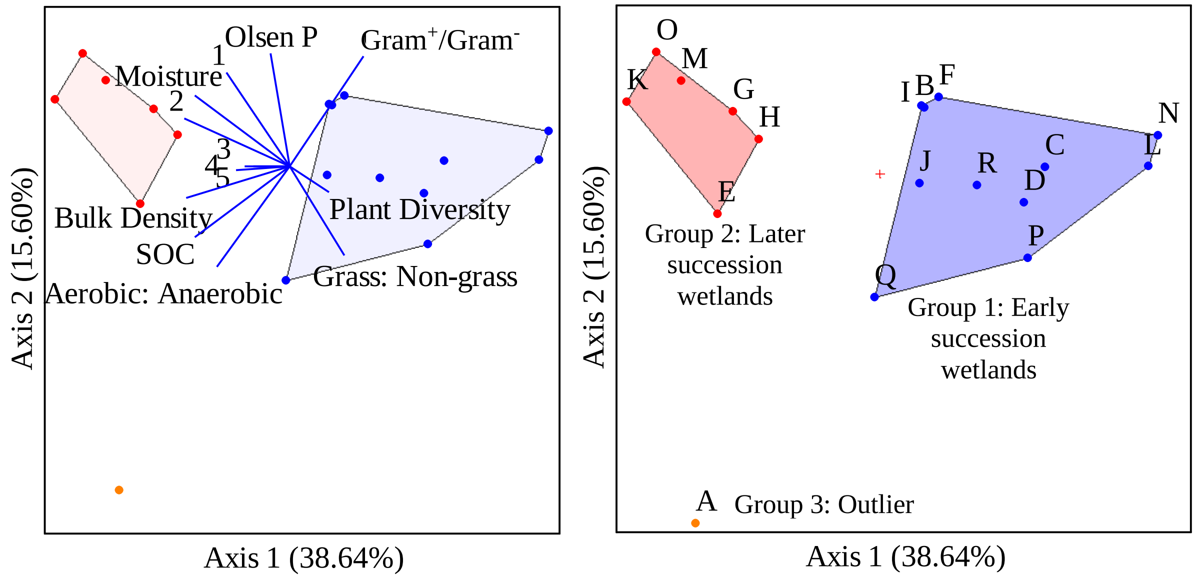

Figure 3.6 PCA of groups of restored wetlands as separated by cluster analysis. 1= Fungi/ bacteria; 2= Soil moisture; 3= # Guilds; 4= K_S; 5= Species Accumulation.

Table 3.3 Factor loadings of wetland succession indicators as derived from Principal Components Analysis. Number's in bold indicate significance.

Variable	Factor 1 (38.7%)		Factor 2 (15.6%)	
	r	*r-squared*	*r*	*r-squared*
Soil Organic Carbon	**-0.828**	0.686	-0.394	0.155
Bulk Density	**-0.907**	0.822	-0.176	0.031
Soil Moisture	**-0.831**	0.690	0.392	0.154
Saturated Hydraulic Conductivity	-0.472	0.223	-0.020	0.000
Olsen P	-0.170	0.029	0.627	0.393
Plant Diversity	0.341	0.116	-0.142	0.020
# Plant Guilds	-0.396	0.157	0.003	0.000
Species area slope	-0.320	0.103	-0.001	0.000
Grass: Non-Grass Species	0.474	0.224	-0.495	0.245
Microbial Biomass	**-0.919**	0.845	0.266	0.071
$Gram^+/Gram^-$	**0.647**	0.418	**0.611**	0.373
Aerobic: Anaerobic	**-0.638**	0.407	**-0.561**	0.314
F/B	**-0.551**	0.304	**0.522**	0.272
Time since restoration	-0.126	0.016	-0.382	0.146
Upstream catchment area	-0.068	0.005	0.255	0.065

microbial communities were very different with a low F/B and $Gram^+/Gram^-$ ratio that was not seen in other wetlands high in SOC and bulk density.

Time since restoration did not explain the variation in succussion indicators (A= -0.001, t= 0.581, p=0.459), with wetlands in group 1 restored between 1 and 32 years ago, and wetlands in group 2 restored between 0.5 years and 42 years ago. Therefore, site context and restoration techniques played a key role in determining wetland succession indicators (Figure 3.7). In particular, I found that wetland hydrology was a significant driver of variation in indicators of wetland succession (A= 0.068, t= -3.414, p=0.009). Wetlands with connected hydrology's were associated with later successional indicators, and were ranked high on PCA axis 2, so showed particularly high measurements of F/B, and low measurements of $Gram^+/Gram^-$ and Olsen P (Figure 3.8). All the late successional wetlands in group 2 have connected hydrology's, while the early successional wetlands in group 1 had a mixture of connected and isolated hydrology's

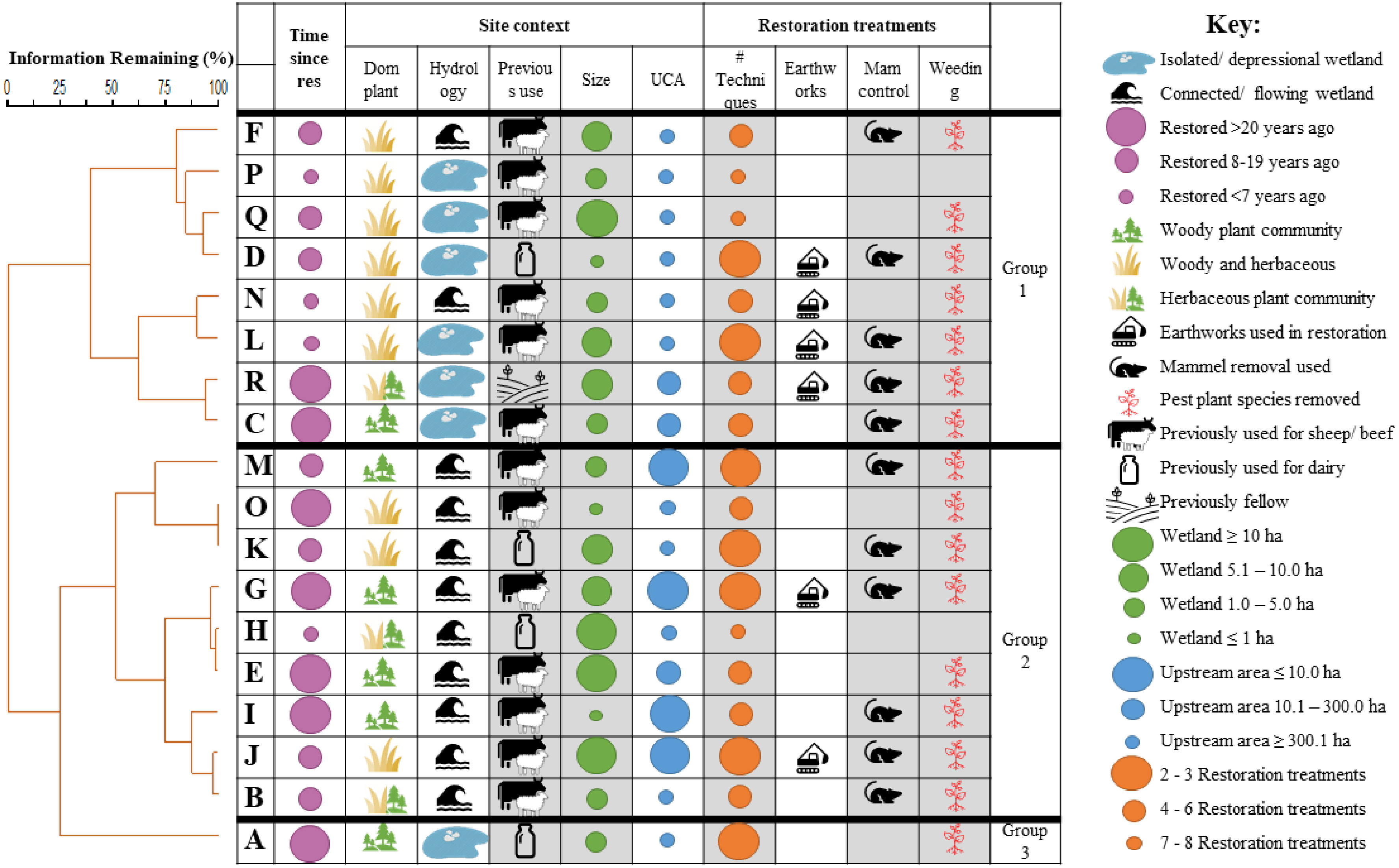

Figure 3.7 Cluster analysis of 18 restored wetlands (labelled A-R), separated into 3 significantly different groups (A= 0.16, p <0.001). Greyed columns indicate visual assessment found no consistent effect and so were not considered for further analyses.

Earthworks altered succession indicators (A = 0.055, t= -2.62, p = 0.021, Figure 3.9). Half of the wetlands in group 2 were restored using earthworks. Wetlands restored using earthworks ranked high on PCA axis 1, so had lower amounts of SOC, moisture, and microbial biomass in their soils, of which were generally denser. Their soils contained higher ratios of Gram$^+$/Gram$^-$ bacteria and more anaerobic bacteria.

Visual inspection of Figure 3.7 showed that previous land-use, wetland size, number of restoration techniques used, mammal control restoration technique, and weeding restoration technique had no consistent effect on restoration succession indicators. Additionally, MRPP showed that dominant vegetation did not play a significant role in clustering wetlands (A= 0.006, t= -0.345, p=0.287), although the vegetation communities in group 1 were predominantly herbaceous, while group 2's the dominant vegetation communities were a mixture of woody, herbaceous, and woody/herbaceous. Upstream catchment area did not weigh into either significant principal component axes, so also did not explain the variation seen in succession indicators. Nevertheless, it is noteworthy that four of nine later successional wetlands had large upstream contributing areas, and it is likely that a sample size of 18 wetlands was not enough to see the effects of this variable.

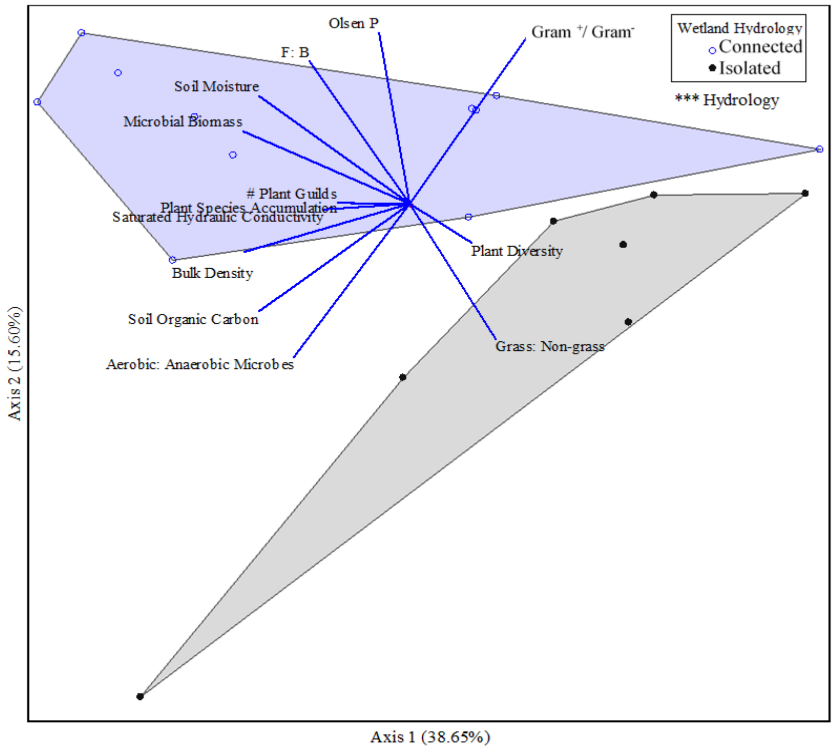

Figure 3.8 PCA of the clustering of restored wetlands based on wetland indicators and separated by the hydrology of the wetland.

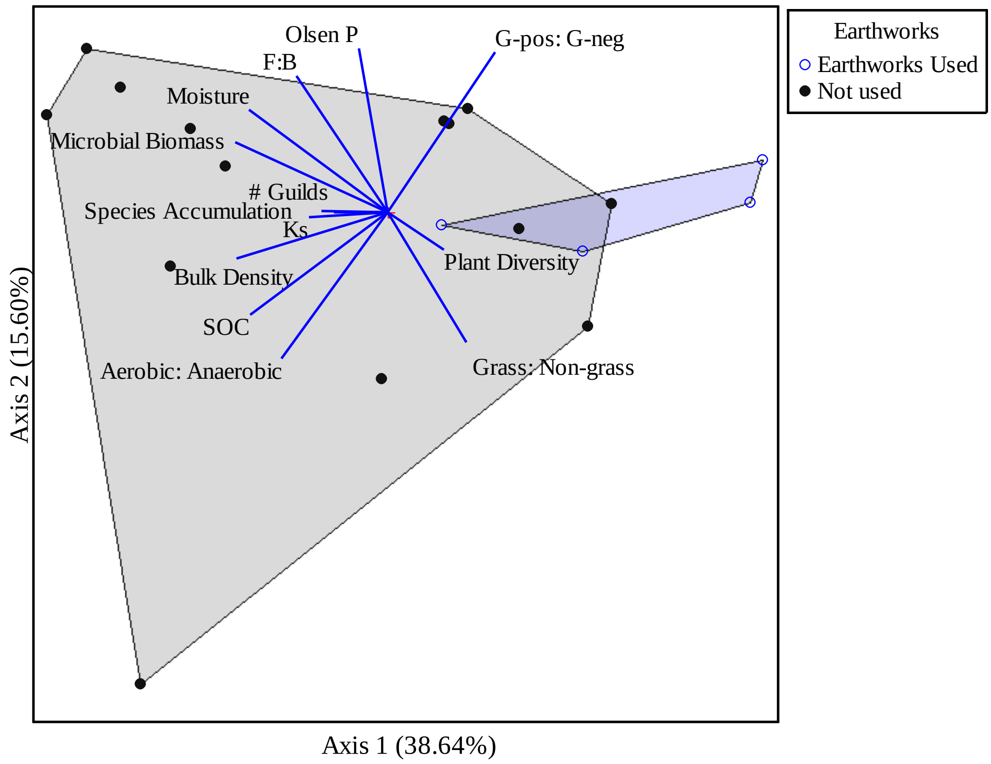

Figure 3.9 PCA of restored wetlands according to their wetland characteristics, separated by if earthworks had been used during restoration.

Discussion

Here, I explored the causes of variation in indicators of succession during wetland restoration. I found that while restoration accelerated successional processes in plant, microbe, and soil characteristics, there was high variability in wetland recovery. Procrustes analysis revealed a lack of congruence in the recovery of plant, microbial, and soils physiochemical indicators of succession. The plant community succeeded faster than the microbial community and soil characteristics. Most of the variation in microbial indicators was dependant on the soil characteristics, and wetlands that had wet, low density, highly organic soils contained more microbial biomass, particularly fungal biomass. The variation in soil development separated restored wetlands into two groups of early and later succession wetlands, as found by cluster analysis. MRPP and visual inspection of site contextual variables showed that the difference in recovery was not explained by time since restoration, but by wetland hydrology, supporting the findings that site context significantly alters rates of succession (Meli et al., 2014).

Plant and soil lag time

Restoration accelerated the rate of succession, causing indicators to diverge in unrestored and restored wetlands, contributing to evidence that active restoration accelerates the process of biodiversity recovery (Pezzati, Verones, Curran, Baustert, & Hellweg, 2018). Restoration had the biggest and most consistent effect on the plant community, increasing species richness in all wetlands, and species diversity in 16 wetlands, which is in line with previous studies (Berkowitz, 2019; J. Brown & Norris, 2018). However, the outcomes of soil and microbial characteristics were frequently more varied and displayed smaller changes with restoration. As found within the Procrustes analysis, the plant community displayed different patterns of variation compared to soil and microbial responses. Although there was so much beta diversity in restored wetlands that the ordination of the plant community in Procrustes analysis explained only 12% of the variation in plant community composition. Nevertheless, a lag between the response of plant communities and soil indicators of recovery has been reported in other restoration studies (Ballantine & Schneider, 2009; Moreno-Mateos et al., 2015). Plant biomass tends to take longer to recover than plant diversity (J. Brown & Norris, 2018), so litter production for SOC accumulation is reduced until after plant establishment. SOC development is a crucial part of soil formation and microbial habitat (Chapman, Cadillo-Quiroz, Childers, Turetsky, & Waldrop, 2017; Yarwood, 2018).

There is a lack of research addressing microbial changes in response to restoration, despite their sensitivity as indicators to environmental changes (Urakawa & Bernhard, 2017) and their role in wetland biogeochemical cycling (Lamers et al., 2012; Y. Ma et al., 2018; Yarwood, 2018). Instead studies have focused on examining restoration recovery using plant and soil measurements (Sims et al., 2013). I found that 40% of variation in microbes could be explained by soil conditions, confirming microbial sensitivity to the soil environment (M. Wang et al., 2019; X. Zhang et al., 2020). However, changes in proportions of microbial communities give insight into biogeochemical functions (Gutknecht et al., 2006), for example altering the fate of carbon (Yarwood, 2018). Identifying microbial community responses aids in understanding changes of ecosystem function throughout restoration (Card & Quideau, 2010). I found that microbial biomass, particularly fungal biomass, responded to restoration in a similar fashion to SOC, soil moisture, and bulk density. However microbial communities were not responsive to Olsen P, as also found by L. Wang et al. (2019). Wetland studies have shown mixed results between P and wetland species, despite AM fungi association with plant P uptake in uplands.

For example, Stevens, Spender, and Peterson (2002) found AMF colonisation levels to reduce with increased P in inundated wetland soil, but Xie, Weng, Cai, Dong, and Yan (2014) found AMF colonisation levels to increase until soils contained 60 mg kg^{-1} of P, after which it decreased. These contrasting results highlight the need for further research to understand microbial community linkages to P cycling under wetland restoration conditions.

Context dependence of restoration

Site context and restoration practices significantly altered successional recovery, despite succession being a temporal process. Despite the 18 wetlands being situated within the same climatic landscape, I found a wetland restored within 6 months of sampling to display later succession characteristics than a wetland restored 32 years ago. Additionally, degradation cause (initial use), had no consistent effect on recovery rates. Therefore, as a result of these wetlands being restored by landowners, there was huge variability of site context and restoration effort, which had a big impact on successive processes. Meta-analyses addressing differences in successional rates with restoration do not concur what contextual variables and restoration practices have the biggest influence in controlling recovery. While Meli et al. (2014) found cause of degradation to be the most important factor determining recovery, (followed by restoration action, experimental design, and ecosystem type), Ballantine and Schneider (2009) found hydrologic connectivity to alter recovery, which was supported by Moreno-Mateos et al. (2012) who found wetland size and hydrologic connectivity to be of most importance. Despite only assessing the recovery of 18 wetlands that showed magnitudes of variability in site context and restoration treatments, I found that hydrologic connectivity was crucial for determining if a wetland was in early or later successional stages. Given the small sample size, I did not see the effects of other contextual variables emerge, although they are also likely to play a role.

I found hydrologically connected wetlands to display higher soil and microbial succession indicators than geographically isolated wetlands, supporting findings by Moreno-Mateos et al. (2012), but contesting findings by (Yu et al., 2017). All geographically isolated, depressional wetlands that were rainwater fed were still in early successional stages, while wetlands connected to a larger hydrological network via streams were more likely to go through successional processes at a faster rate. This finding is contradictory to Yu et al. (2017) and Ballantine and Schneider (2009) who found faster soil recovery in isolated water systems. They hypothesized that it was due to the rapid recovery of plant biomass. While I did not examine plant biomass recovery, my results may be explained by increased input in hydrologically open systems of sediment, organic matter, seeds, and rhizomes (Anderson, Mitsch, & Nairn, 2005). Additionally, connected wetlands are fed by a larger hydrological network that catches rainwater from a larger catchment area than the local wetland, and so is more likely to stay wet for longer periods of time. This allows longer periods of wetland biogeochemical functions to develop and prevents carbon cycling allowed by aerobic conditions. Geographically isolated wetlands are minimally connected to larger hydrological systems so have minimal external source inputs (Ballantine & Schneider, 2009).

Additionally, the use of earthworks was proportionally more predominant in geographically isolated wetlands, providing another explanation for why connected wetlands recovered faster. Half of the isolated wetlands were created using earthworks to form duck ponds, while only three of eleven connected wetlands had earthworks used during restoration. Wetlands restored with earthworks had denser soils containing reduced SOC, moisture, and microbial biomass (Figure 3.9). Heavy machinery used in earthworks during restoration compacts the earth, increasing bulk density, hindering root growth, and slowing the downward distribution of SOC (Ballantine et al., 2012). Furthermore earthworks commonly removes the rhizosphere, which contains high microbial biomass and SOC (Larson et al., 2020). While earthworks helps increase the height of the water table, it initially slows the rate of succession because of the disturbance it creates (J. Brown & Norris, 2018).

Conclusions

The lack of congruence in the recovery of plant, microbial, and soils physiochemical indicators of succession suggests that the plant community succeeded faster than the microbial community and soil characteristics. Variation in soil and microbial properties separated restored wetlands into two groups of early and later succession wetlands, which was independent of the number of years since restoration began at the sites but corresponded to elements of wetland hydrology. Soil and microbial characteristics in hydrologically connected wetlands recovered more quickly following restoration than hydrologically isolated wetlands. There is a lack of consensus about what factors are the most important in influencing wetland recovery. Nevertheless, recovery of privately restored wetlands is heavily influenced by site context and restoration practices, and I provide evidence that hydrology may be playing a key role. This finding is promising because although this study only looked at actively restored wetlands, my findings provide insight to the potential for positive but unintended outcomes of the passive riparian restoration policy that is about to be implemented on private land in New Zealand (P. G.-G. Reddy, 2020), which will reduce disturbance around streams, wetlands, and rivers on private land.

Chapter 4 Thesis synthesis, strengths, limitations, and future directions

Consequences of worldwide wetland loss are already seen in freshwater eutrophication rates (Finlayson et al., 2019), biodiversity loss (Tickner et al., 2020), and greenhouse gas emissions (Tan et al., 2020). Additionally, global warming is predicted to cause further wetland loss (Van Asselen et al., 2013). While wetland restoration is occurring, it is not at pace with wetland loss (Robertson, Ausseil, Rance, Betts, & Pomeroy, 2019; Stavi & Lal, 2015). Further, because most lowland areas are held on private property, we need to quantify the outcomes of wetland restoration on private land to ascertain its net effects. Evidence-based assessment of the impacts of private restoration has potential to establish its utility to increase the sustainability of agroecosystems. For example, despite wetlands containing the most carbon-rich soils of all ecosystems, they are not recognised in the New Zealand emissions trading scheme. Additionally, new legislation mandates 3 m buffers around waterways and wetlands on farms to help reduce eutrophication of waterways (P. G.-G. Reddy, 2020), but with further investment in planting, multiple ecosystem services have the potential to be produced. Because wetland restoration reduces the area of land in production, it comes at a direct economic cost to the landholder. Therefore, it is important that we determine what benefits are gained from restoration. Further, demonstration of practice is the most effective way to disseminate practices within the farming community (P. Brown et al., 2019). Through quantification of the physiochemical and biological outcomes of restoration treatment for soil, microbial and plant components of ecosystems, I demonstrate the multiple benefits of wetland restoration.

Aim of thesis

In this thesis, I aimed to quantify the outcomes of small-scale private wetland restoration projects. Specifically, I looked at how the plant community, soil physiochemical characteristics, and the soil microbial community changed with restoration of private land. I focused on soil, microbial and plant responses because together, they interact to produce the majority of wetland ecosystem services. In my second chapter I asked: How does wetland restoration alter the plant community, soil physio-chemical characteristics, and the soil microbial community? Next, I explored the relationships among variation in plant, soil, and microbial datasets, because wetland ecosystem re-establishment following restoration occurs as a consequence of feedbacks between them. Further, because private restoration occurs in a vast array of biophysical contexts which alter plant, soil, and microbial relationships, I examined the causes of this variation. Specifically, in my third chapter I asked: 1) How do microbial, plant, and soil characteristics co-vary during wetland restoration? 2) How do indicators of wetland succession respond to restoration? 3) Are different restoration practices and site contexts influencing wetland outcomes during restoration?

Wetland restoration on private land was effective in initiating the re-establishment of desirable wetland soil properties and increased plant diversity and microbial biomass. Specifically, private wetland restoration increased soil moisture by 93%, SOC by 20%, and K_S by 27%, and reduced bulk density by 0.19 g^{-1} cm^3 and Olsen P by 23%. Additionally, restoration added ~13 native plant species, increased microbial biomass by 25%, and increased the abundance of total fungi and AMF in microbial communities. The strongest effects of restoration was seen in the plant community, while soils and microbes took longer to respond to restoration and varied in outcomes within and between plots. This reflects the contextual variability of outcomes in private restoration projects. Specifically, a strong effect of restoration was to increase the variation in plant, microbial, and soil characteristics within and between restored plots compared with unrestored wetlands. Within plots, the response of restored wetland soils and microbial communities depended upon a hydrological gradient from the water's edge to upland areas. Restored wetlands also increased plot-level heterogeneity, with high beta diversity of plant community composition among restored wetlands.

Time since restoration did not explain the high variability in wetland recovery as shown by variability of plant, soil, and microbe outcomes. There was a lack of congruence in the recovery of plant, microbial, and soils physiochemical indicators of succession, presumably because planting effectively accelerated succession, and led to the largest changes in indicators of wetland succession. Most of the variation in microbial indicators were dependant on the soil characteristics, and wetlands that had wet, low density, highly organic soils contained more microbial biomass, particularly fungal biomass. Cluster analysis showed that the variation in soil development separated restored wetlands into two groups of early and later succession wetlands, which was independent of the number of years since restoration. Despite only having a sample set of 18 wetlands, my data suggest that wetland hydrology altered wetland recovery; a connected hydrological regime accelerated successional processes so that connected wetlands showed later successional indicators while isolated wetlands displayed early succession characteristics. This helps us to understand where we should restore wetlands to enable the recovery of biodiversity and ecosystems services.

Synthesis

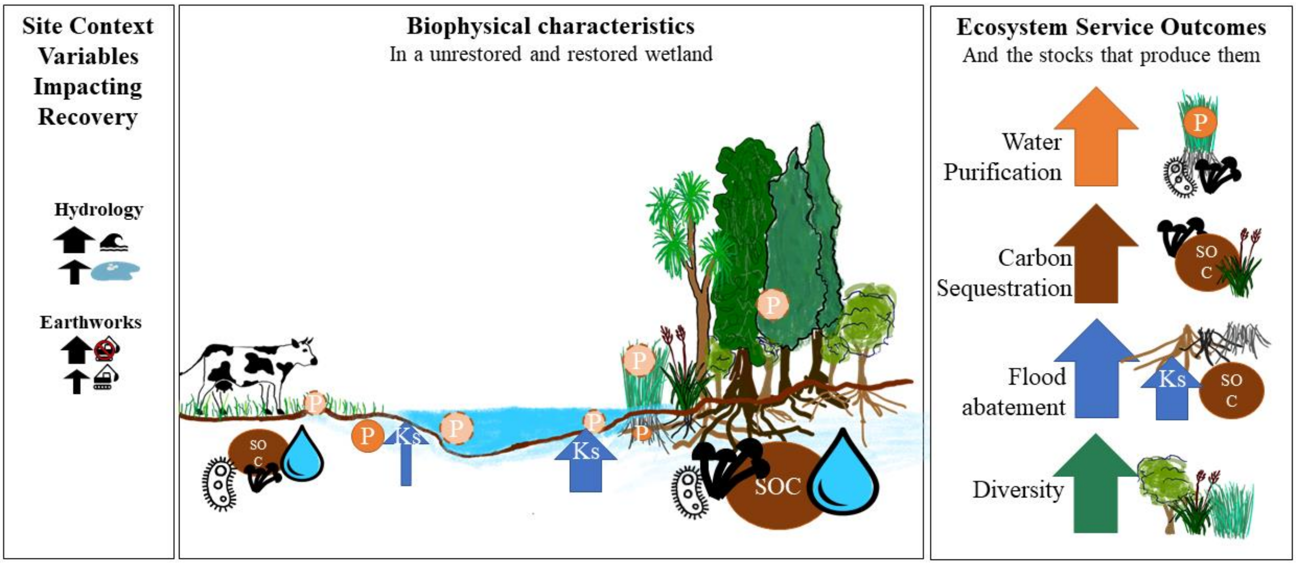

Figure 4.1 Diagrammatic overview of thesis findings. Size of the symbols suggests the size of the stocks of biophysiochemical characteristics that contribute to ecosystem service outcomes. All stocks shown are measured in this study except for plant and water phosphorus, as denoted by stippled symbols.

Restoration increased the spatial variability of soil, microbial and plant properties, resulting in increased habitat heterogeneity within and across restored wetland sites. Humans have drastically modified the natural environment to increase homogeneity of landscapes dominated by a few cash-crop species (Buhk et al., 2017; Olden, Poff, Douglas, Douglas, & Fausch, 2004). Wetland restoration should aim to recover plot to farm scale variation because:

- Wetlands are naturally heterogeneous due to hydrological gradients and natural disturbance with flooding (Ward, 1998).
- Landscape variability increases diversity and resistance of plant and animal communities to disease and disaster (Isbell et al., 2015).
- Habitat heterogeneity increases the number of ecosystem services produced (Richards et al., 2018) and increases niche space available to other biota, fostering a greater biodiversity at the plot to farm scales (Shi, Ma, Wang, Zhao, & He, 2010).

I found that restoration increased the variation of microbes and soils at the plot level as well as the variation of plant communities and indicators of succession across sites.

Wetlands are naturally heterogenous because of periodic flooding.

Due to the dynamic nature of wetlands, they show a lot of habitat heterogeneity along hydrological gradients (Bolpagni & Piotti, 2016). For example, I found the effect of restoration on both microbial communities and soil physical characteristics to change with the distance from the water's edge. In the upland areas of restored wetlands, the soils were even drier than the soils in unrestored wetlands, likely due to the presence of trees with relatively high leaf surface area that transpire greater volumes of water and consequently reduce soil moisture (Soylu, Kucharik, & Loheide, 2014). However, near the water's edge, restored wetland soils were saturated many times more than those of unrestored wetlands, and microbial biomass, community composition, and other physiochemical characteristics followed the same pattern of increasing near the water's edge. Additionally, z always increased with restoration, showing plant diversity increased across spatial scales. While planting directly increases plant diversity, wetlands are naturally biodiverse systems because they experience frequent disturbance by flooding (Dawson et al., 2017). Disturbance mediates heterogeneity in plant species composition by providing new areas for seedling establishment (Petraitis, Latham, & Niesenbaum, 1989), and sites with high disturbance tend to have higher plant diversity (Pollock et al., 1998). Furthermore, there was a temporal mismatch between the recovery of plant and soil communities during restoration, likely because of planting. This mismatch has implications for ecosystem service delivery, as plant communities contribute to ecosystem services in different ways than microbial communities and soil physical characteristics, which adds to the heterogeneity of functions (Richards et al., 2018).

Diversity increases ecosystem resilience.

Diversity increases the sustainability of landscapes. Habitat heterogeneity increases spatial refugia which allows for the existence of weaker competitors and increases diversity in a multitude of ways including through genetic, population, biogeochemical, and physiological processes (Larkin et al., 2016). Diversity on multiple scales increases resistance to diseases and disturbance, therefore contributing to the persistence of entire ecosystems (J. Wu & Loucks, 1995) and increasing stability of local communities (Levin, 2000). I found the unrestored wetlands clustered together in the NMS, while the restored wetlands had a vastly different composition of plant communities. This suggests an increase in farm-scale heterogeneity through wetland restoration. Additionally, with increased ecosystem heterogeneity, the types of ecosystem services produced also increases (Richards et al., 2018). Ecosystem service trade-offs are seen because the specific biophysical conditions required for the provision of one service is different for the provision of another (E. M. Bennett, Peterson, & Gordon, 2009; Rodríguez et al., 2006). For example, I found that no restored wetland increased in all wetland restoration indicators. Often restored wetlands would increase in two out of three soil characteristics that can be used as ecosystem service proxies: SOC (carbon sequestration), Olsen P (downstream water quality), and K_S (flood abatement). Other than z, there was no indicator of succession that increased in every wetland. Instead, all restored wetlands had both one indicator that was in the bottom 25% range of values sampled and one indicator in the top 25%.

My thesis demonstrates that wetland restoration on private property is effective at altering plant, soil, and microbial characteristics towards desirable wetland characteristics, despite restoration occurring in a vast array of conditions. My results show that wetland restoration on private land increased the spatial and temporal heterogeneity of outcomes within and across plots, and that the responsive indicators changed depending on the restoration project due to site context. Taken together, my data suggests that private wetland restoration increases the types and amounts of wetland ecosystem services and increases diversity at multiple scales, these patterns are associated with increased ecosystem stability and resilience (Carrick & Forsythe, 2020; Tilman, Wedin, & Knops, 1996; Van Der Heijden et al., 1998). Finally, I present evidence that restoration context strongly impacts the recovery of wetland restoration indicators as well as evidence that indicates the importance of hydrological flow in determining post-restoration wetland recovery times. Therefore, I conclude that private wetland restoration is an effective tool to increase the sustainability and stability of agricultural landscapes, but further work needs to be done to address the relative importance of contextual variables altering recovery times.

Strengths and limitations

By taking measurements of wetlands that were restored on working farms at the farmer's own prerogative, my study reflects the reality of what is happening on the ground and the real-world variation in private restoration projects. Using an experimental system where I could control for site context, variation in restoration treatments and planting, my data would likely show greater effects of restoration treatments. However, despite the huge variability in restoration and site context, I still found positive and significant changes in indicators of wetland succession, which provides strong evidence that private restoration is effective at producing desirable ecological outcomes.

Furthermore, by measuring the plant and soil microbial communities and five soil physio-chemical characteristics, my thesis produced an integrative understanding of how restoration is changing biophysiochemical characteristics. Wetlands are biogeochemical hotspots of many processes, and through measuring these multiple biophysiochemical characteristics, I provide a detailed assessment of how ecosystems change with wetland restoration. Soils, plants, and microbes all interact together through feedbacks to alter the outcomes, but frequently, only soils and plants are measured in wetland restoration studies (Sims et al., 2013). By also measuring microbes, I provide insight to soil successional and decomposition processes with restoration.

Finally, I link soil physiochemical characteristics and microbial communities to ecosystem function and consequent ecosystem services. Ecosystem services are increasingly being recognised by policy makers and markets (Villa & Bernal, 2018), so by linking changes seen in biophysical characteristics from wetland restoration to ecosystem function and ecosystem services, I demonstrate that investing in restoration has practical and beneficial outcomes further than restoring the ecosystem for its own intrinsic value. This demonstrates why wetland restoration is worth the investment and should be further incorporated into policy (Finlayson et al., 2019).

A significant limitation of my study is that I only sampled 18 wetlands. This meant I had the statistical power to detect changes in biophysical characteristics, but I lacked the power to resolve where restoration was having the greatest effect. For example, my dataset was too small to determine the effects of different restoration treatments, or site contexts, such as the initial plant community or degradation cause. Restoration treatments are known to have a large impact on restoration outcomes (Liang et al., 2017; Zhao et al., 2016), and while I saw the impacts of earthworks as a restoration treatment, I was not able to measure how recovery times were influenced by the other treatments, such as weeding, herbicide application, pond installation, drain installation, and pest mammal removal. Additionally, while I was able to establish that site context overwhelmed successional recovery processes so that time since restoration was not an effective predictor of a wetlands state of recovery, I was not able to look at the proportional effects of the contextual variables (wetland size, degradation cause, upstream area, hydraulic connectivity, number of restoration treatments used, dominant plant community), although my data suggest that the hydrological regime might have a role in recovery times.

Another limitation of my study was the sampling time of wetlands from December 2018 to early February 2019. This long period of sampling meant that I sampled wetlands across the summer months, meaning that my data will include variability naturally caused by season and the drying soil conditions that result from reduced rainfall and longer, hotter days in summer. Water levels drop during summer months, meaning areas that would have previously been saturated become aerobic. This was partially accounted for by keeping the plot consistently by the water's edge, but it also means that the water-table drops for the vegetation further up the plot, and with a reduced water table, soil moisture reduces, and the dominance of aerobic microbial communities can increase, to alter the biogeochemical pathways of nutrient and carbon cycling. Additionally, drought-stress changes the plant and microbial community composition and biophysical processes (Ploughe et al., 2019; Sun et al., 2020; Yanfen Wang et al., 2014). While I accounted for some of this variation in the paired plot design, it is likely that restorations effect may vary across different seasons (C. N. Jones, Scott, Guth, Hester, & Hession, 2015). However, unfortunately it was necessary because each wetland took a day to take measurements of, and co-ordinating with landholders reduced the days available we could sample.

Future work

Systematic research teasing out the impacts of site context is lacking in a wetland restoration context, and so future work should aim to determine under what contexts and treatments restoration is most effective. Restoration is expensive and time consuming but urgently needed to regain the critical wetland habitats and ecosystem services. Current information is variable about how context impacts restoration recovery, despite many studies reporting incomplete recovery of biophysical indicators after half a century (Ballantine & Schneider, 2009; Land et al., 2016). A few meta-analyses have tried to determine the relative impacts of site contextual variables such as time since restoration, hydrological regime, landscape position, wetland size, elevation and latitude; however, they have found contrasting results (Meli et al., 2014; Moreno-

Mateos et al., 2012; Pezzati et al., 2018; Yu et al., 2017). For example, my research points towards the importance of isolated *vs*. connected hydrological regimes as an important factor affecting wetland recovery, but meta-analyses report contrasting results of the impact of hydrological regimes on recovery times (Moreno-Mateos et al., 2015; Yu et al., 2017). Additionally, very few studies measure the recovery of multiple restored wetlands. Restoration practitioners could gain a lot of information from grassland restoration studies that utilise large experimental designs to systematically find effective restoration protocols (for example see: "The Jena Experiment" 2021). This large-scale approach may help determine the effect of connected *vs.* isolated hydrology and the effect of wetland size, the dominant plant community, and restoration treatments so that restoration can be more effective and deliver larger quantities of ecosystem services faster.

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Supplementary materials

Supplementary material A:

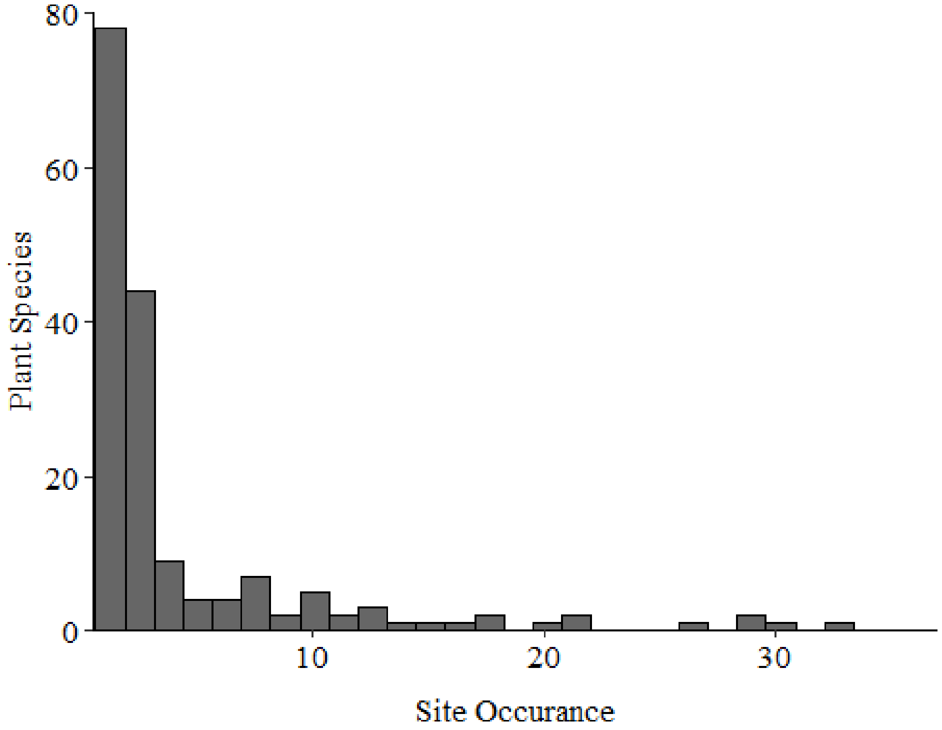


Figure S1 Histogram showing the site occurrences of the 171 plant species found in the 36 vegetation plots which had percent cover data

Supplementary material B:

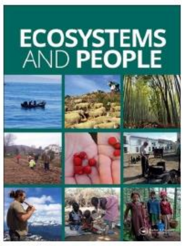
Table S1 Factor loadings of PLFA biomarkers derived from PCA. X1 and X2 were axis co-ordinates from the principal component's analysis run on the soil characteristics.

Variable	**Factor 1 (64.67%)**		**Factor 2 (6.89%)**	
	r	*r-squared*	*r*	*r-squared*
10Me16:0	-0.221	0.049	0.080	0.006
10Me17:0	-0.160	0.025	0.139	0.019
10Me18:0	-0.190	0.036	0.056	0.003
14:0	-0.209	0.044	0.105	0.011
15:0	-0.184	0.034	0.375	0.141
16:0	-0.233	0.054	-0.232	0.054
16:1w5	-0.237	0.056	0.123	0.015
16:1w7c	-0.226	0.051	0.195	0.038
16:1w7t	-0.238	0.057	0.073	0.005

17:0	-0.200	0.040	0.342	0.117
18:0	-0.188	0.035	-0.186	0.034
18:1w9c	-0.230	0.053	-0.119	0.014
18:1w9t	-0.211	0.045	0.113	0.013
18:2w6	-0.179	0.032	-0.104	0.011
19:1w9c	-0.047	0.002	0.394	0.155
20:0	-0.143	0.020	-0.218	0.047
a15:0	-0.243	0.059	-0.013	0.000
a17:0	-0.246	0.060	0.112	0.013
delta17:0	-0.241	0.058	-0.020	0.000
delta19:0	-0.174	0.030	-0.413	0.170
i15:0	-0.223	0.050	-0.277	0.077
i16:0	-0.224	0.050	-0.232	0.054
i17:0	-0.243	0.059	-0.042	0.002
Age	-0.014	0.000	0.004	0.042
Upstream area	-0.018	0.000	-0.014	0.079
X1	-0.412	0.169	-0.335	0.004
X2	-0.116	0.014	-0.096	0.160

Supplementary material C:

Publication “Multiple methods confirm wetland restoration improves ecosystem services” in Ecosystems and People. As a co-author, I was involved extensively in the data collection and analysis of the measured ecosystem service changes, and I also contributed to the writing.



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Multiple methods confirm wetland restoration improves ecosystem services

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ABSTRACT

Global wetland loss has reduced biodiversity and ecosystem services. These declines have inspired many landholders to restore wetlands, but the success of these efforts remains unclear, in part, because quantifying ecosystem services requires diverse methods. Here, we blend participatory mapping and surveys, field measurements and high-resolution models to track ecosystem services from restored wetlands on private land. We ask: 1) What ecosystem services do people perceive from restored wetlands? 2) What modelled/field measured ecosystem services were enhanced through restoration? and 3) How do field measured, modelled and perceived ecosystem services in restored wetlands interact? Participating landholders mapped their restoration project and shared their perceptions of ecosystem services. Next, we modelled ecosystem service changes using the Land Use Capability Indicator (LUCI) model and contrasted these to field measured ecosystem services for each wetland. Landholders perceived ~6.5 services from their restored wetlands. For modelled services, restoration significantly enhanced nitrogen and phosphorous retention. For field-measured services, restoration increased soil organic carbon by ~20%, soil permeability to water by ~27% and native plant species richness by ~15 species, while reducing plant-available phosphorous by ~23%. Correlating across methods revealed that reduced plant-available phosphorus and site age and size were associated with more perceived services, whereas an increase in plant species richness was not a good proxy for gains in measured, modelled or perceived services. Based on the diverse ecosystem services gained, demonstrated by multiple methods, we contend that private wetland restoration can be successful as well as leveraged to meet multiple management and policy objectives.

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Introduction

Momentum for wetland restoration is growing, in part, because the consequences of wetland loss for ecosystem services are increasingly apparent. Since 1900, global estimates of wetland drainage range from 64% to 71%. This drainage has resulted in losses of many ecosystem services, the benefits people gain from ecosystems (Ausseil et al. 2008; Tomscha et al. 2019), usually in exchange for agricultural productivity. Relative to their area, wetlands are disproportionately important for ecosystem services (Barbier et al. 1997). Wetlands store carbon, trap sediment and retain excess nutrients (thus promoting better freshwater quality), and attenuate floods (Clarkson et al. 2013). To regain the diverse ecosystem services from wetlands, restoration and reconstruction will be key.

While efforts to restore wetlands are widespread (Peters et al. 2015), providing evidence of the ecosystem services regained from wetland restoration remains challenging. The restoration research community has long grappled with how to define and measure wetland restoration success (Ruiz-Jaen and Aide 2005). Approaches have included measuring species diversity, vegetation structure and ecological processes (Ruiz-Jaen and Aide 2005). Although frameworks are developing, no globally applicable methods exist to assess wetland ecosystem services via modelling and/or field measurement (Janse et al. 2019). Tracking restoration gains may encourage more landowners to participate in wetland restoration, underscored by the growing market of wetland mitigation banking (Palmer and Filoso 2009). Additionally, systematic assessment of progress could enable restoration policy to be target towards landscape contexts providing the most favourable outcomes. Finally, evidence of gains in ecosystem services may inspire more government, industry and philanthropic support for what might otherwise be perceived as a costly endeavour.

Ecosystem services are notoriously difficult to measure, because they represent the dynamic flow of benefits from ecosystems to people (Haines-Young and Potschin 2010). To fully represent this

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Supplemental data for this article can be accessed here.

social-ecological system, both biophysical and social components of ecosystem services should be measured (Reyers et al. 2013). Furthermore, ecosystem services are often produced and received at different spatial and temporal scales (Holland et al. 2011; Bagstad et al. 2013), and they may be highly variable across space and time (Rau et al. 2018). These attributes mean ecosystem services are difficult to measure in the field. Often, direct measurements are not sensible or even possible. Nonetheless, field-measured indicators are key for estimates of service gains from restoration projects, and a range of biophysical indicators have been developed to facilitate field measurements (Sutherland et al. 2016b; Ziter and Turner 2018). For example, soil organic carbon is an indicator of soil carbon storage, while saturated hydraulic conductivity is an indicator of flood mitigation (Ziter and Turner 2018). Multiple methods, including social science, can complement field measurements to capture the range of ecosystem services gained through restoration. Interviews and surveys may be particularly useful for asking about temporally dynamic process in difficult to access sites. For example, asking people how often and where they hunt is more feasible than waiting for observations of hunters on private land.

Another challenge in studying restored wetlands is identifying their locations. For example, in New Zealand, no centralized database or maps of restored wetlands exist, partly because many wetlands are located on private land (GWRC 2003), where management decisions are considered confidential. Furthermore, wetlands are often small and therefore difficult to map (Gallant 2015). Consequently, costly high resolution, multispectral imagery is often required to adequately map wetlands. High-resolution data also facilitate the detection of soil moisture (Maxa and Bolstad 2009; Adam et al. 2010). Even when wetlands can be detected, distinguishing restored versus intact wetlands may not be feasible if their spectral signatures are indistinguishable. In addition, land-use history and some restoration treatments, such as predator control and fencing, are not visible in satellite imagery. One solution to the problem of locating restored wetlands is participatory mapping; where researchers ask local people to identify restored wetlands and describe associated management activities. This approach is easily paired with surveys and interviews to capture the intangible ecosystem services from wetland restoration.

To estimate ecosystem service delivery over large areas, modelling is necessary. However, heterogeneity in small-scale ecosystem processes is generally unresolved by models that run at the watershed or sub-watershed scale. Modelling changes in ecosystem services due to small restored wetlands is therefore challenging (Tomscha et al. 2019). The Land Use Capability Indicator (LUCI), an extension of Polyscape, is one of the few tools that models multiple ecosystem service indicators at high spatial resolutions (<5 m; Jackson et al. 2013). LUCI is designed to answer questions about land and water restoration, making it ideal for analysis of wetland ecosystem services. The framework can incorporate minute variations in topography and diverse approaches to land management which can affect patterns of nutrient flow at the farm scale (White et al. 2015). For example, LUCI was used to examine which farms would provide the greatest gains in ecosystem services if receiving agricultural subsidies in Wales (Sharps et al. 2017). Importantly, one challenge in robustly estimating ecosystem service gains from wetlands is that the landscape context of each wetland is an essential input. Nutrient exports from upstream areas may change the magnitude of nutrient retention provided by a restored wetland (Trepel and Palmeri 2002). Thus, a spatially explicit model that accounts for upstream contributing areas, such as LUCI, is critical for accurate estimates of ecosystem service delivery.

Here, we use a blend of in-person surveys, geospatial modelling, field measurements and participatory mapping to identify changes in ecosystem services through wetland restoration. Drawing on the strengths of each approach, we ask three main questions: 1) What ecosystem services do people perceive from restored wetlands? 2) What modelled/measured ecosystem services were enhanced through restoration? 3) How do field measured, modelled and perceived ecosystem services in restored wetlands interact? Using multiple methods to estimate ecosystem service gains from restoration, we create a more comprehensive picture of the social-ecological system that responds to wetland restoration.

Methods

Study site

This study was conducted in the Wairarapa region, the southern part of the North Island, New Zealand. The Wairarapa is bounded by the Remutaka mountain range and the Pacific Coast (Figure 1). The 5938 km^2 region is home to ~45,000 inhabitants, including Māori iwi (tribes) Ngāti Kahungunu ki Wairarapa and Rangitane o Wairarapa. Primary land uses in the region include dairy and beef cattle and sheep farming, viticulture, forestry and conservation. Wetland area in the Wairarapa has declined 98.7% from its pre-colonial extent, exceeding global loss averages of 71% and the New Zealand loss average of 90% (Ausseil et al. 2008). Of the existing wetlands, 75% are located on private property, and the majority do not exceed 3 ha (GWRC 2003). Influxes of phosphorus and nitrogen have led to eutrophication of waterbodies (Conley et al. 2009), including Lake Wairarapa, the largest lake in the region, which is now classified as

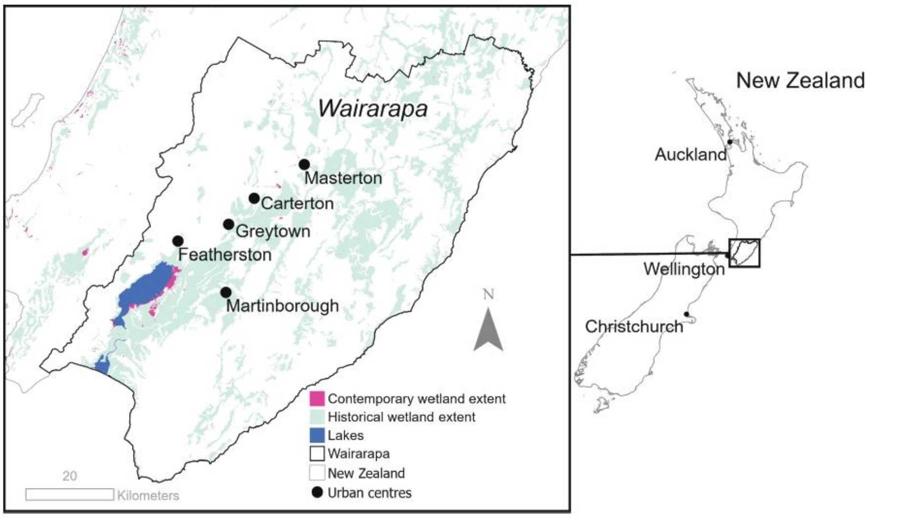

Figure 1. Extent of contemporary and historical wetlands in Wairarapa, New Zealand.

supertrophic (GWRC 2012). Within the region, landholders, farmers, iwi and community groups are restoring wetlands on private and public property, often with the goal of improving water quality.

Measuring ecosystem services using multiple methods

We assessed ecosystem services using multiple approaches; participatory mapping and interviews, modelling, and field and lab-based measurements (Figure 2). Each method addressed different ecosystem services and produced different data structures (e.g. binary, continuous). First, we conducted a participatory mapping and survey exercise with private landholders who had restored a wetland on their property, including questions about their use and values for their restored wetland. The resulting maps of restored wetlands were then used to calculate the upstream contributing area for each wetland. Next, we used LUCI to estimate changes in ecosystem services resulting from restoration. Finally, we conducted field surveys of plant diversity and characterised soil properties in restored wetlands, and

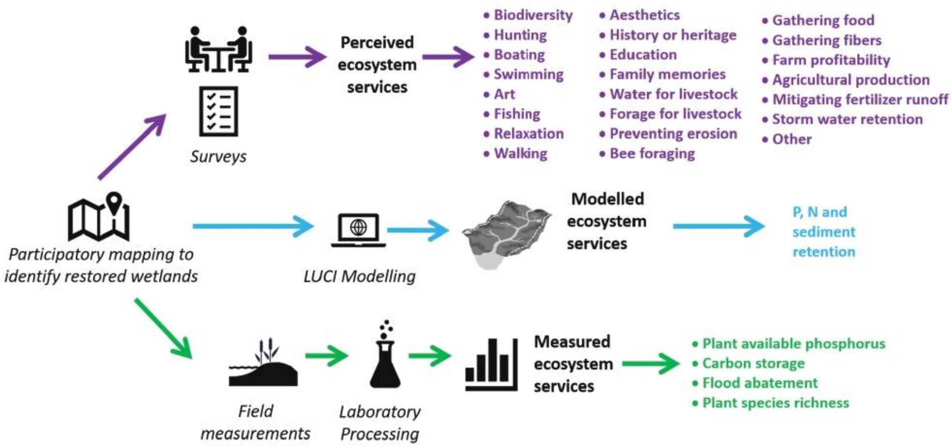

Figure 2. Overview of methodological approach. Participatory mapping informed surveys of perceived ecosystem services and facilitated field measurements and watershed modelling. Ecosystem services measured by each approach were different as shown by different coloured text.

adjacent unrestored land, to estimate differences in ecosystem services achieved through restoration.

Participatory mapping, surveys and site selection

We recruited landholders in the Wairarapa with wetlands – defined as wet paddocks, wet fields and the terrestrial margins of lakes, streams, rivers or ponds – on their property. We sent flyers advertising our research to all registered farms in the Ruamahanga Basin and received eight direct responses. We also contacted local restoration groups, the regional council and others through our research networks. In total, we interviewed 28 landholders. Twenty-five of these landholders had restored one or more wetland on their property, while the remaining three were interested in doing so but had not yet applied restoration treatments.

Participatory mapping and surveys were completed using Maptionaire, an online map-based survey tool. All mapping and surveys were completed in person by S. Tomscha from June – October 2018. Participants elected to input data independently using a laptop or to be guided in data input by the researcher. The mapping captured the size and location of one restored wetland on each property. Where more than one wetland had been restored, participants selected either their largest or most important restoration project.

We then asked the landholders a series of structured and semi-structured questions related to their values and restoration practices. For example, we asked: Which of the following are uses of the wetland on your property? (see Appendix 1 for survey details). Landholders identified ecosystem services from a list of 22 services, resulting in binary data for 22 ecosystem services per site. The 22 ecosystem services available in the list were selected through an iterative process of input from practice interviews with restoration practitioners and Wairarapa residents.

Next, we selected locations for field sampling and modelling work from among the 28 wetlands. Each site met the following criteria: 1) the property must have a wetland that has received a restoration treatment, and 2) the wetland must exceed 20 × 20 m in size (to allow standard vegetation monitoring). Eight sites did not meet these criteria, and a further two were unable to provide site access. Thus, fieldwork modelling, and the evaluation of landholders' perceptions, was conducted on 18 sites.

For modelling and fieldwork, we applied a paired sampling design, whereby restored wetlands were contrasted to a locally similar, unrestored site (for fieldwork) or to a baseline agricultural condition (for modelling). For fieldwork, locally similar unrestored sites were often located immediately adjacent to the restored wetlands, separated only by a fence (16/18 farms). In all cases, farmers identified a location as similar as possible to their restored wetland site prior to the application of restoration treatments (i.e. similar elevation, slope, aspect, soils, vegetation, etc.).

LUCI modelling

LUCI is a spatial modelling tool that can be used to create maps and measures of ecosystem service provision (Sharps et al. 2017; Trodahl et al. 2017). We used LUCI to quantify ecosystem service changes from wetland restoration, producing a 5 m modelled output. We determined the upstream contributing watershed area for each wetland site, including the wetland polygon itself. Within this watershed, we generated quantitative estimates for three soil-hydrological processes: sediment export, nitrogen exported and phosphorus exported; first under restored conditions and secondly under 'no restoration' (i.e. pasture conditions). Calculating the difference between these two scenarios allowed us to estimate the amount of sediment, N and P retained per annum, due to the restoration of the wetland.

Input data

Seven map-layers were obtained from publicly available databases and used as inputs to LUCI, with minor alterations (Table 1). To generate multiple sets of land cover data, we created two edited land cover files by overlaying restoration site maps with the LCBD (New Zealand Land Cover Database) data. In the first, restored sites were classed as either 'Indigenous Forest' (swamp) or 'Herbaceous Wetland Vegetation' (fen) depending on their terrain. In the second, we assumed a 'no-restoration' scenario and manually reclassified all sites as 'High Producing Exotic Grassland', the LCBD category which best corresponded to pasture.

Nutrient exports (N and P)

Nutrient losses were calculated using a modified 'export coefficient' approach, where nutrient load inputs are calculated based on soil, climate, topography and land management (Trodahl et al. 2017). Here, total accumulated nutrient exports were calculated by including contributions from runoff at nearby higher elevation sites and accounting for reductions in load where nutrients are routed through mitigating features such as forests and wetlands (Trodahl et al. 2017; Taylor et al. 2018). Here, the model outputs for each watershed were focused on one grid cell of the Digital Elevation Model (DEM); the water-flow exit point of the wetland polygon. The change in nutrient exports at the watershed outflow point, which was measured as the difference between restored wetland and pastureland cover conditions, provided a measure of the nutrient mass retained annually as a result of the restoration projects.

Table 1. Descriptions of data sources and manual processing used to prepare inputs for the LUCI services model. Data processing steps and input descriptions adapted from Tomscha et al. (2019).

Input	Source	Description
Digital elevation model (DEM)	LINZ 2013	Raster layer based on a LiDAR point cloud data of 1 m resolution resampled to a 5 m resolution
Land cover	New Zealand Land Cover Database v4.1 (Landcare Research 2015a)	10 m resolution LCBD contains 33 named land classes derived from satellite imagery (SPOT-5). The layer was manually edited to produce a hypothetical 'no-restoration' or 'restoration' condition, using restoration site polygons from participatory mapping
Restoration site polygon and upstream contributing area	Participatory mapping	LUCI's baseline tool uses the DEM to calculate the upstream contributing area for each wetland site, based on surface flows
Soils	New Zealand Fundamental Soils Layer (Landcare Research 2015b)	Derived from New Zealand Soil Classifications, resolution varies based on origin of soil maps. Across New Zealand, there are 15 soil orders, which are divided into 73 major soil groups with 35 of these groups found in the Wairarapa.
Rainfall	NIWA 2018	0.5-km raster of average precipitation in mm/yr from 1972–2013
Evapotranspiration	(NIWA 2018)	Potential evapotranspiration (PE) data edited to represent actual evaporation (AE) using the average rainfall from 1972–2013 and PE as a onetime calculation with the following equation: If (rainfall-PE)/rainfall >0.5:AE = PE Else: AE = rainfall * 0.5
Rivers and streams	(NIWA 2018)	Derived from New Zealand's River Environmental Classification

Erosion/sediment retention

A quantitative measure of how sediment retention responded to wetland restoration was obtained using LUCI's implementation of the RUSLE (Revised Universal Soil Loss Equation) algorithm. The algorithm calculates the flow and volume of sediment export in tons km^{-2} yr^{-1} according to soil, land cover, topographical and management characteristics (Benavidez et al. 2018). To convert sediment loss to soil retention, loss values in tons yr^{-1} for pastureland cover were subtracted from those calculated for restored wetlands.

Field-measurements of ecosystem services

Restored wetlands varied in size (0.4 to 33.7 ha with a median of 2.5 ha). Time since restoration treatments were first applied ranged from 6 months and 42 years prior to sampling (median = 9). All restored wetlands were fenced and planted with native or exotic species. However, the combination of additional restoration treatments applied to each wetland varied. These treatments included invasive plant species removal (herbicide or physical removal), pest removal (trapping, baiting, hunting), earthworks, pond creation and/or drain blockage or installation. Of the 'unrestored' wetland sites (i.e. paddocks) used for comparison, seventeen were used for grazing livestock, while one lay fallow.

Fieldwork was conducted in summer between December 2018 and early February 2019. Within each restored and unrestored wetland pair, we established a 400 m^2 (20 m × 20 m) plot for the sampling of plants and soils (Figure 3; 36 plots total). Plots were oriented so that one edge ran parallel to the waterbody, while the perpendicular edge followed the increasing elevational gradient of the wetland. If no surface water was visible, plots were oriented parallel to the lowest elevation locally. Within each of the 18 restored and 18 unrestored paired plots, we recorded vascular plants to species. When complete identification was not possible, vascular plants were recorded either to genus or family, noting their status as native or non-native. We also recorded the number of bryophytes species present, but these were not identified to species. The total number of native vascular species sampled per plot was used as a measure of native species richness.

Soils were sampled by coring with a 5 cm PVC pipe to a depth of 10 cm along three parallel transects at, 0 m, 10 m and 20 m within the plot. Nine cores were taken to measure soil organic carbon (SOC) for each plot, totalling

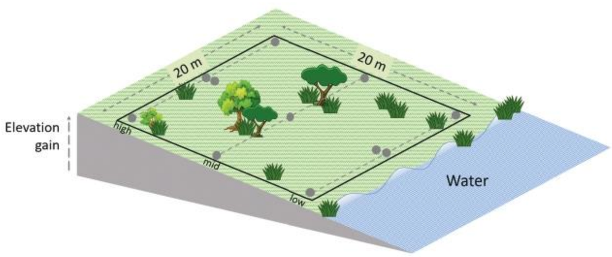

Figure 3. Diagram of plot used to sample soil and vegetation in restored and unrestored wetlands. Locations of soil cores are denoted by 11 grey circles.

324 across all wetlands (Figure 3). Two further soil samples were collected at the highest and lowest elevations of each plot and used for determination of soil Olsen P (P) and saturated hydraulic conductivity (K_s). Cores were placed on ice before refrigeration at 4°C. Laboratory analysis took place between March and August 2019.

Laboratory processing

Soil organic carbon (SOC)

We measured soil organic matter (SOM) content using the loss on ignition method (Dean 1974). Samples were dried at 105°C in an oven overnight and sieved to <2 mm. The volume of all material over 2 mm was recorded and subtracted from the total volume of the core. The <2 mm fraction was then weighed to allow for calculations of soil bulk density. Subsamples (5 g) were taken from the <2 mm fraction and placed in a muffle furnace for 4 hours at 550°C, cooled and reweighed (Wright et al. 2008). The mass loss of the soil sample was taken as a measure of SOM. We estimated SOC by dividing SOM by 1.98 when SOC was between 1% and 10%, and by 1.86 when SOC was and >10% (Pribyl 2010).

Phosphorous

Plant-available phosphorous, measured here as Olsen P, is an indicator of phosphorous likely to be lost in surface runoff (McDowell et al. 2001). For Olsen P analysis, soil samples were lyophilised for 48 hours, mechanically crushed and sieved to 2 mm. Coarse roots and other large organic material were discarded, and the volume of lithogenic material over 2 mm was measured. Olsen P was determined on 5 g subsamples by bicarbonate extraction (pH 8.5) and measured with a Molybdenum Blue colorimeter by Hills Laboratory Ltd. (Hamilton, New Zealand).

Saturated hydraulic conductivity

Measuring saturated hydraulic conductivity (K_s) over large areas can be expensive and impracticable. Estimations of K_s from empirical relationships (such as pedotransfer functions) regressed against easily obtainable lab measurements, however, offer an acceptable level of insight. To estimate soil K_s we used bulk density, particle size measurements and soil organic carbon (Equation 1). The high organic matter content in these soils, required use of a pedotransfer function developed for organic topsoils (Wösten et al. 1999).

$$\begin{aligned} \ln(Ks) = {} & 7.75 + 0.0352(Silt) + 0.93(Topsoil) \\ & - 0.967(Bulk\ Density^2) - 0.000484(Clay^2) \\ & - 0.000322(Silt^2) + \frac{0.001}{Silt} - \frac{0.0748}{Organic\ Matter} \\ & - 0.643In(Silt) - 0.01398x(Bulk\ Density)(Clay) \\ & - 0.1673(Bulk\ Density)(Organic\ Matter \\ & + 0.02986(Topsoil)(Clay) \\ & - 0.03305(Topsoil)(Clay) \end{aligned} \tag{1}$$

To find bulk density and soil organic matter measurements, the results from the loss on ignition method were averaged for each lower and upper transects of each plot, from the cores used for SOC measurements. For particle size analysis, 3 g subsamples were taken from the two cores at high and low elevations in the plot. These subsamples were lyophilised for 48 hours and then sieved to 2 mm. First, we removed organic material by chemical digestion with H_2O_2. Samples taken from transects containing <10% organic material were digested in 27% H_2O_2 until the reaction ceased. Samples taken from transects containing >10% organic material were digested in 52% H_2O_2 until the reaction ceased. The samples were then neutralised and lyophilised. Particles were disaggregated in 0.5% calgon solution in an ultrasonicator for 20 minutes. We determined the size of the sand, silt and clay fractions of subsamples using a laser particle sizer (Beckman Coulter LS13320), following USDA/FAO classifications (FAO 2006).

Statistical analyses

1) What ecosystem services do people perceive from restored wetlands?

To characterize the co-occurrence of perceived ecosystem services from restored wetlands, we calculated a Gower's distance matrix between sites based on the number of perceived ecosystem services they shared divided by the total number of services assessed (here 22) (Gower 1971, McCune et al. 2002). The co-occurrence patterns were then visualised in two dimensions using non-metric multidimensional scaling (NMS) ordination based on Gower's distance. NMS was run using PC-ORD version 7.08 (McCune and Mefford 2018) in the 'auto-pilot' mode, which performed 500 iterations (250 runs each of real and randomized data) with random starting configurations and assessed dimensionality by minimizing stress.

We then applied Ward's method of hierarchical cluster analysis of the distance matrix to examine how perceived ecosystem services co-occurred on sites. This identified four distinct clusters of 'perceived ecosystem services', which we coded as a categorical factor in subsequent analyses. The statistical significance of the perceived ecosystem services clusters was assessed by calculating chance-corrected within-group agreement (A) using non-parametric Multiple Response Permutation Procedure (MRPP; Zimmerman and Goetz 1985) with Euclidean distance in PC-ORD. The chance-corrected within-group agreement (A) is a measure of within-group homogeneity compared with that expected by chance, where A = 1 corresponds to identical members within each given group (maximum effect of categorical factor), and where $A \leq 0$ corresponds to within-group heterogeneity equal to or larger than that expected by chance (no effect of categorical factor (McCune et al. 2002)).

2) *What modelled/measured ecosystem services were enhanced through restoration?*

We standardised modelled estimates of phosphorus, nitrogen and sediment retention by the area of each restored wetland, and significant differences between restored and unrestored wetlands were determine via paired *t*-test. Data were log transformed so that they met the assumption of normality.

We tested field-measured differences in restored versus unrestored wetlands using either paired *t*-tests (for native plant species richness) or linear mixed-effects models (for all soil variables), because the latter had within-plot replication of samples. In the SOC, Olsen P and Ks models, distance from water's edge and restoration state (restored vs. unrestored) were additive fixed effects. Site identity and plot nested within site were included as random variables affecting the intercept only. Plots of residuals vs. fitted values were inspected visually for normality and homoscedasticity, and a non-constant error variance test from the car package was used to check homoscedasticity among levels of categorical variables (Fox and Weisberg 2019). We applied ANOVA with a type 3 Wald chi-square test to partition the variance associated with fixed factors. To test if restoration had a significant effect on native species richness, a paired *t*-test was used. All response variables were non-normal and were therefore log-transformed to conform to the assumptions of the linear mixed-effects models and *t*-test. All analyses were conducted in R studio (R Core Team 2019), using the package lme4 for linear mixed-effects models (Bates et al. 2015).

3) *How do field measured, modelled and perceived ecosystem services in restored wetlands interact?*

To understand how measured, modelled and perceived ecosystem services of restored wetlands interact, first, we visualised how sites clustered according to the perceived ecosystem services that landholders held for their restored wetlands. To this end, we transformed the initial matrix so that it contained 18 sites x 22 perceived values. We then calculated a Gower's distance between sites based on the number of perceived ecosystem services shared divided by the total number of perceived ecosystem services assessed (here 22) (Gower 1971, McCune et al. 2002). Next, we used NMS ordination to visualize sites in 'perceived ecosystem service space'. This step resulted in a high proportion of variance explained by the first two ordination axes. Then, we calculated Pearson correlations among each of the individual modelled and measured ecosystem services and the significant ordination axes of perceived ecosystem services. We also calculated Pearson correlations among the significant ordination axes of perceived ecosystem services and the number of years since restoration began, restoration site size, upstream contributing areas, the ratio of restored area to upstream contributing area and the total count of perceived ecosystem services at each site. We visualized the significant relationships among measured or modelled ecosystem services and the ordination axes of perceived ecosystem services as joint-plots, which were overlaid on the NMS in PC-ORD. The angle and length of the joint-plots lines describe the direction and strength of these correlations.

Results

1) What ecosystem services do people perceive from restored wetlands?

Landholders used their restored wetlands in different ways and had a variety of perspectives on the ecosystem services they provided. Of the 22 possible ecosystem services of their restored wetlands (Figure 4), landholders perceived a median of 6.5 (IQR = 5.25–9.75). The maximum number of ecosystem services perceived was 21, while the minimum number was two (Figure 5). The most commonly cited ecosystem service of wetland restoration was wildlife habitat or biodiversity, and the second most commonly identified ecosystem services was aesthetics or beauty. No landholders reported gathering fibres as an ecosystem service.

The NMS ordination revealed that 88% of the variation in landholder-perceived ecosystem services of restored wetlands could be described by two NMS axes (Figure 5). Moreover, we found statistical support by MRPP for four significant clusters of ecosystem services ($A = 0.222$, $p \ll 0.001$) (Figure 5). The majority (77%) of variation in landholder-perceived ecosystem services for wetlands encompassed the transition from very tangible, mostly provisioning services which clustered high on NMS axis 1 to abstract/intangible ecosystem services for aesthetics, relaxation, history and habitat for wildlife ranked low on axis 1. While axis 2 accounted for only 11% of the variation in landowner-perceived ecosystem services it helped to differentiate two additional ecosystem service clusters. The third cluster, which ranked low on axis 2 includes ecosystem services that are potentially more individually enjoyed (e.g. family, photography and space for bee foraging) versus the final cluster of ecosystem services which provide collective services, potentially for those residing off the landowner's property (e.g. sediment and nutrient retention, education and hiking).

2) What modelled/measured ecosystem services were enhanced through restoration?

Modelled gains in ecosystem services

The difference between the amount of nitrogen, phosphorous or sediment exported in restored versus unrestored wetlands can be interpreted as the amount retained per annum through restoration. Upstream contributing

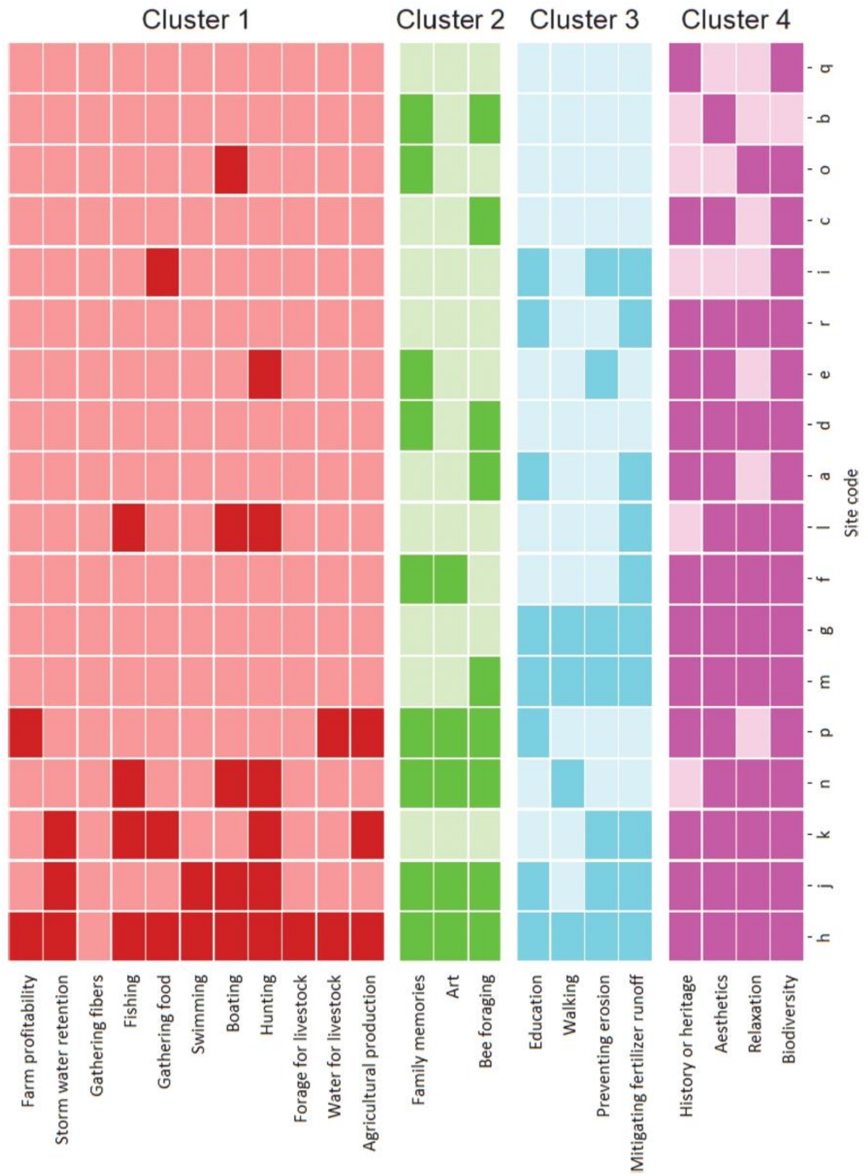

Figure 4. Perceived ecosystem services from restored wetlands. Dark colours show services perceived by landholders, whereas light colours represent those services not perceived. Sites are ordered based on the number of perceived ecosystem services.

areas of the restored wetlands varied considerably (4.2 ha to 2263.3 ha) (Table 2); therefore, we standardized our ecosystem service data by restored area to increase comparability across sites. Consistent gains in modelled ecosystem service were found with all sites benefiting from restoration for all three indicators.

Nitrogen retention

Biophysical models implemented in LUCI indicated lower total nitrogen exports in restored wetlands (Figure 6). Restored wetlands exported a mean of 148 ± 43 kg N ha^{-1} yr^{-1}, while unrestored wetlands exported a mean of 166 ± 48 kg N ha^{-1} yr^{-1}, and this

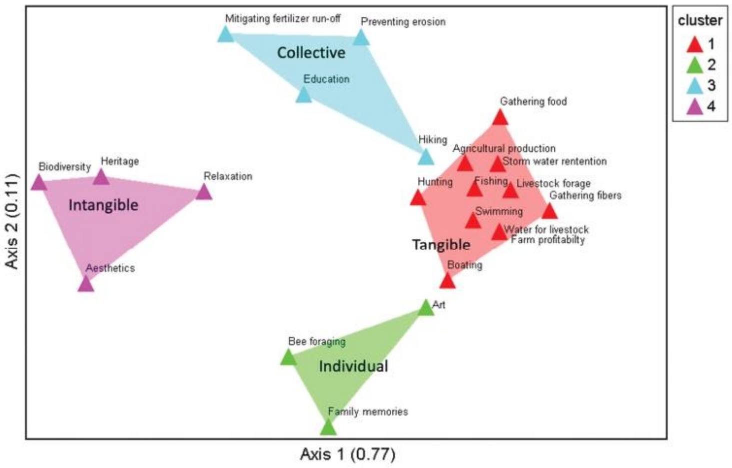

Figure 5. NMS ordination of the perceived ecosystem services of restored wetlands on private land reveals that these ecosystem services formed four distinct clusters of co-occurrences.

Table 2. Upstream contributing area, restored area, their ratios and the number of years restored for each site. Sites are listed from lowest upstream contributing area to highest.

Site code	Upstream contributing area (ha)	Restored area (ha)	Ratio of restored area to upstream contributing area	Years restored
a	4.2	1.5	0.356	4
r	7.9	3.5	0.442	13
o	9.4	0.5	0.049	32
m	14.1	1.8	0.128	29
p	18.1	1.3	0.072	17
l	27.2	4.4	0.164	10
i	27.7	0.4	0.015	8
b	29.0	1.7	0.058	42
g	36.8	8.5	0.231	0
q	41.7	11.4	0.274	3
e	63.5	15.2	0.239	16
d	110.0	0.4	0.004	23
f	126.1	6.4	0.051	1
c	281.5	2.4	0.009	15
k	453.5	2.6	0.006	6
n	551.3	2.4	0.004	8
h	1165.2	11.8	0.010	4
j	2263.3	33.7	0.015	5

difference was statistically significant ($t_{(17)} = -4.15$, $p < 0.001$).

Phosphorus retention

Likewise, restored wetlands were associated with lower phosphorus exports than unrestored wetlands (Figure 6). Restored wetlands exported a mean of 711 ± 268 g P ha^{-1} yr^{-1} compared to a mean of 1347 ± 366 g P ha^{-1} yr^{-1} exported from unrestored wetlands, and this difference was statistically significant ($t_{(17)} = -5.79$, $p < 0.001$).

Sediment retention

Wetland restoration led to a small difference in modelled sediment exports (Figure 6). Restored wetlands exported a mean of 771 ± 468 t ha^{-1} yr^{-1}, whereas unrestored wetlands exported a mean of 775 ± 468 t ha^{-1} yr^{-1} (paired $t_{(17)} = -2.06$, $p = 0.055$).

Gains from field measurements

Soil organic carbon (SOC)

All soils we measured were highly organic, with plot-level averages between 4.2% and 31.9% SOC. Soils in restored wetlands averaged 13.1% SOC, while soils in unrestored wetlands had an average of 10.75% SOC (Figure 7). Restoration increased the proportion of soil organic carbon by 20.0% ± 10% ($\chi2_{(1)} = 3.89$, $p = 0.049$). SOC was higher when soils were sampled close to water ($\chi^2_{(1)} = 66.09$, $p < 0.001$). Soil organic carbon for restored wetlands was higher than unrestored wetlands in 12 of 18 wetlands (Figure 8).

Phosphorus

Olsen P, an indicator of downstream water quality, varied greatly by site. Soils in restored wetlands contained between 6 and 62.5 μg P cm-3 dry soil, with an average of 25 μg P cm-3 dry soil. Unrestored wetlands contained between 11 and 51.5 μg P cm-3 dry soil of Olsen P, with an average of 28 mg/L (Figure 7). Overall, the linear mixed effect model showed that restoration decreased Olsen P, by 22.95% ± 13% ($\chi^2_{(1)} = 4.36$, $p = 0.036$). Distance from water did not affect Olsen P quantities ($\chi^2_{(1)} = 0.030$, $p = 0.862$). Olsen P was higher in restored wetlands than in unrestored wetlands for 10 of 18 sites and had no effect at one site (Figure 8).

Saturated hydraulic conductivity

Saturated hydraulic conductivity, an indicator of flood mitigation, ranged from 0.41 to 2.36 mm hr^{-1} in restored and unrestored wetlands with lower

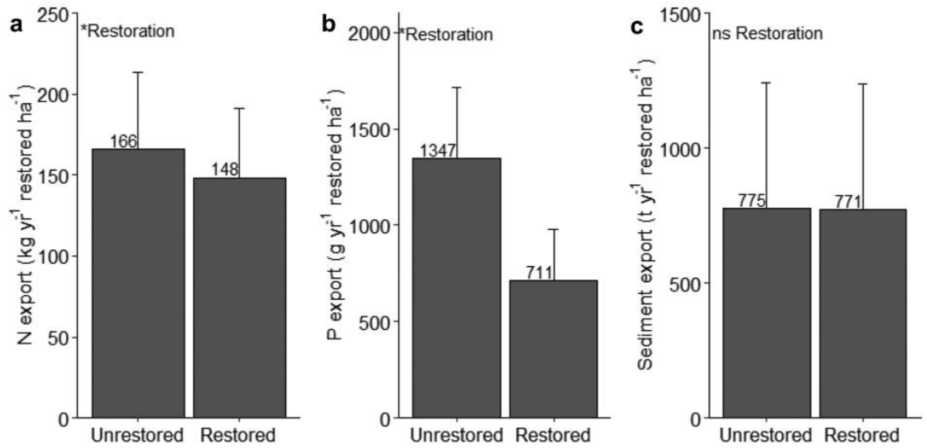

Figure 6. Modelled (LUCI) estimates for N, P and sediment exports in unrestored versus restored wetlands. (a) N exports, (b) P exports and (c) sediment exports. Bars indicate means ±SEM. Asterisks indicate significance difference in paired *t*-test of unrestored versus restored wetlands as follows: ns = not significant, $^{*}p < 0.05$.

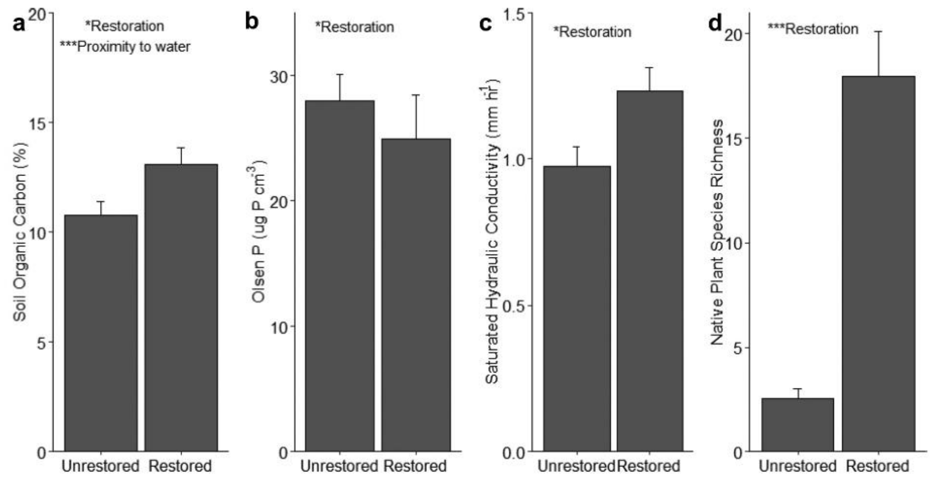

Figure 7. Mean ecosystem service indicators measured in unrestored plots compared to restored plots, ± standard error bars. A = Soil Organic Carbon, B = Plant-available phosphorous, C = Saturated Hydraulic Conductivity, D = Native Plant Species Richness. Asterisks indicate significance in models as follows: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

values having a lower capacity to attenuate floods. Pedofunction-derived saturated hydraulic conductivity is reliable to ~1.02–1.67 mm hr^{-1} (RMSE) (Tóth et al. 2015). As such, the relative uncertainty of each Ks value is as much as 100%; however, inclusion of organic matter tends to decrease RMSE. This means that between site comparisons in Ks are tentative; however, we have high confidence in the restoration comparison because of the similar soil characteristics between restored and unrestored wetlands within each site. The average K_s of restored wetlands was 1.239 mm hr^{-1}, whilst unrestored wetlands average K_s was 0.97 mm hr^{-1} (Figure 7). The linear mixed model showed that restoration increased a wetland soil's saturated hydrologic conductivity by 27.3% ± 11% ($\chi^2_{(1)} = 5.58$, $p = 0.018$). Distance from water did not significantly change soil Ks ($\chi^2_{(1)} = 2.87$, $p = 0.090$). Restoration improved K_s relative to paired unrestored wetlands for 14 of 18 wetlands (Figure 8).

Native plant species richness

Restoration had a significant effect on species richness ($t_{(17)} = -8.72$, $p < 0.0001$), with restored plots having a mean richness of 17.9 species, and

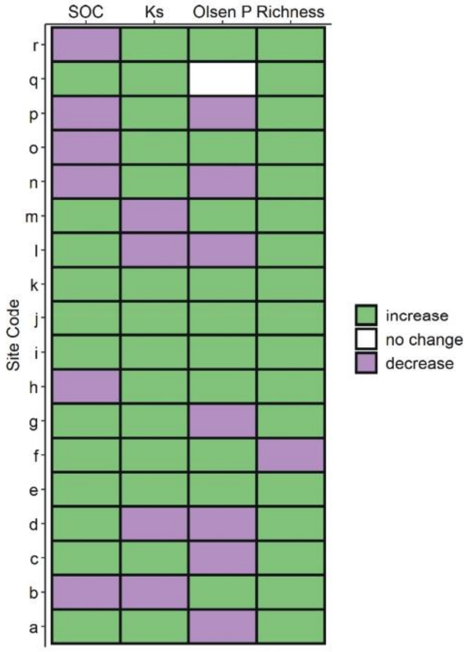

Figure 8. Changes in ecosystem services indicators from restoration. Green tiles indicate this ecosystem service increased following restoration at this site, while light purple tiles indicate that this ecosystem service decreased. White tiles mean this ecosystem service remained neutral. Soil organic carbon (SOC), saturated hydraulic conductivity (Ks) and Olsen P were variable by site, where as plant species richness increased at all but one site.

unrestored plots having a mean richness of 2.6 species (Figure 7). In one case, the restored wetland plot contained 37 more native plant species than the unrestored plot. Restoration increased the native plant richness in 17 of 18 wetlands (Figure 8).

Total gains in measured ecosystem service indicators

Of the four ecosystem service indicators measured in the field (SOC, K_s, Olsen P and native plant species richness), wetland restoration increased at least two ecosystem services indicators for all sites, and restoration never resulted in a net loss in ecosystem services. For four of 18 sites, all four ecosystem services increased. A further nine sites showed a net gain in three of the four measured ecosystem services. Five sites were net neutral, showing gains in two ecosystem services and losses in two others (Figure 8).

3) How do field measured, modelled and perceived ecosystem services in restored wetlands interact?

The NMS ordination of the perceived ecosystem services by site showed that 79.2% of the variation in the data could be captured in two axes (Figure 9). Axis 1, which explained more than 60% of variability in perceived ecosystem services was strongly driven by the total number of perceived ecosystem services at each site, as revealed by the very strong Pearson correlation between axis 1 and the count of perceived ecosystem services ($r = 0.972$, $p \ll 0.001$). We also found a weaker correlation between the number of years that a site had been restored and axis 1, although this was only statistically significant at $P < 0.1$ ($r = 0.403$, $p = 0.097$). Correlating the measured and modelled ecosystem services with Axis 1 of landowner-perceived services revealed that it was significantly correlated with the change in plant-available P due to restoration (Table 3, Figure 9). We also found Axis 1 was significantly correlated with upstream contributing area and restored area (Table 3). Axis 2 generally corresponds to the split between cluster 2 and cluster 3 services; with landowners of sites p and n reporting all three of the cluster 2 ecosystem services, while sites i and k reported none of the three ecosystem services in cluster 2, but two or more of the ecosystem services in cluster 3. In fact, field measurements of SOC were significantly correlated to axis 2, along which sites rich in collective ecosystem services (e.g. sediment and nutrient retention and education and hiking) separate from sites rich in individually experienced benefits. The association between SOC and cluster 3 values is germane as soil C storage is a benefit that is collectively enjoyed, even if it may be not always be perceived by landowners engaged in wetland restoration.

Discussion

Wetland restoration enhanced ecosystem services on private land as demonstrated by field measurements, modelling and landowners' perceptions. Our approach quantified both the scope and magnitude of ecosystem service gains, using multiple methods to gain a holistic perspective of restoration outcomes. Although the median size of the restored wetlands was only 2.5 ha, all restored wetlands increased overall biodiversity or ecosystem services, which shows promise for landholders interested in small restoration projects. Nonetheless, as restored wetland size and their upstream areas increased, landholders identified a higher number of perceived services. These associations suggest that landholders who perceive more wetland services are inspired to restore larger wetlands. The strong positive correlation between perceived ecosystem services and upstream contributing areas suggests landholders may be aware of how landscape position affects the ecosystem services provided by their wetlands. From a biophysical perspective, these perceptions are supported by the significantly negative correlation between plant-available P and wetland size, which suggests that larger restored wetlands may be more important for improving water quality.

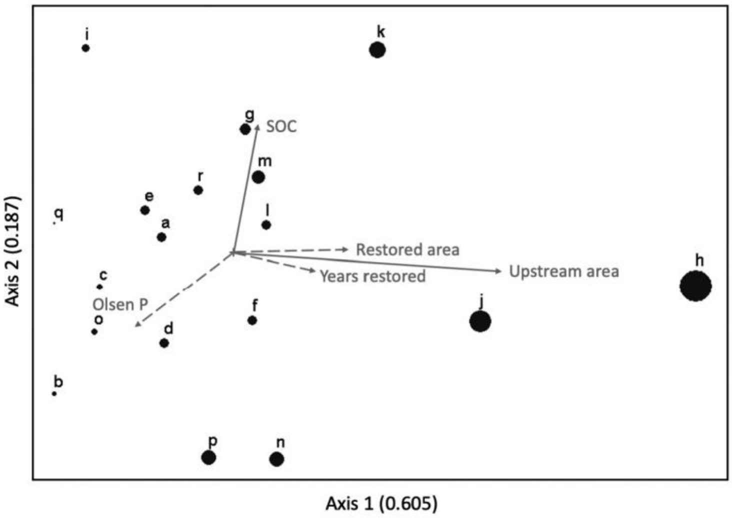

Figure 9. NMS ordination of sites in 'perceived ecosystem service' space. Axis 1 represents 60.5% of variability in perceived ecosystem services, while axis 2 shows 18.7% of this variation. Symbol size indicates the total count of perceived values per site. Significant correlations among axis one and two and measured and modelled ecosystem services indictors overlaid onto the ordination as vectors, dashed lines indicate $P < 0.1$, solid lines indicate $P < 0.05$.

Landholders differed primarily by the total number of ecosystem services they perceived, rather than by their perception of individual or clusters of ecosystem services. These shared perceptions suggest broad commonalities among landholders engaged in wetland restoration. The most commonly perceived ecosystem service was biodiversity (17/18 landholders) followed by aesthetics (15/18 landholders). The perception of wetlands as beautiful signals landholder opinions of wetlands have shifted, as historically, many farmers perceived wetlands as unattractive wastelands (Nassauer 2004). In contrast, no landholders perceived gathering fibres as a service from their wetlands, suggesting privately restored wetlands are not providing this service. In New Zealand, harakeke (*Phormium tenax*) is a wetland plant traditionally used by Māori for weaving. People who would gather these fibres may not have access to these privately held wetlands, which underscores that public restoration projects are still key for maintaining this important cultural resource.

Ecosystem services often co-occur in clusters, sometimes called bundles. Typically, these clusters are defined across diverse land uses and stakeholders (e.g. Raudsepp-Hearne et al. 2010; Queiroz et al. 2015). Our approach is unique in that we clustered ecosystem services from one ecosystem (restored wetlands), among a narrow group of stakeholders (landholders with restored wetlands). Within this narrow group of landholders, perceived services separated into four clusters: tangible, intangible, collective and individual ecosystem services. While there are justifiably numerous frameworks to categorize ecosystem services (e.g. MA 2005; Costanza 2008), our results give insight into how current classifications align with clustered perceptions of ecosystem services. For example, our clusters showed recreational services were more tightly tied with provisioning services, rather than to broader cultural ecosystem services, despite them being generally categorized as cultural (MA 2005). In contrast, collective vs. individualistic services reflected the degree to which these ecosystem services are used exclusively by landholders, aligning well with ecosystem service excludability categorizations (Costanza 2008). Discerning clustered patterns among socio-cultural preferences for ecosystem services can facilitate better management for their holistic provision (Martín-López et al. 2012; Mouchet et al. 2014).

Ecosystem service interactions are often measured using correlations (e.g. Raudsepp-Hearne et al. 2010). However, assessments of interactions across measurement methods are rare (Mouchet et al. 2014). By assessing these relationships, we found interactions among perceived and measured services, as well as among perceived services and site attributes. Site attributes, such as the upstream contributing area, the area of wetland restored and restoration age are relatively easy to measure and all correlated with the major axis of variation in perceived services (axis 1). Likewise, the

Table 3. Pearson correlation among the first two ordination axes of perceived values from the NDS shown in Figure 9 and measured and modelled ecosystem services in this study, significant correlations at $P < 0.1$ are underlined, significant correlations at $P < 0.05$ are in bold type. Asterisks indicate significance in models as follows: *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < .0001$.

		Perceived			Measured				Modelled			Site attributes		
		Axis 1	Axis 2	# Perceived	Δ Richness	Δ SOC	Δ P	Δ Ks	Δ N	Δ Sediment	Δ P	Years restored	Upstream contributing area (ha)	Restored area (ha)
Perceived	Axis 2	0												
	# perceived	**0.972******	0.074											
Measured	Δ Richness	−0.081	−0.186	−0.072										
	Δ SOC	0.218	**−0.505***	0.149	−0.226									
	Δ P	−0.416	0.297	−0.341	−0.153	−0.257								
	Δ Ks	−0.041	−0.27	−0.022	0.349	−0.168	−0.069							
Modelled	Δ N	0.177	−0.297	0.119	−0.328	0.217	−0.308	−0.133						
	Δ Sediment	−0.104	0.244	−0.073	−0.118	0.009	−0.042	−0.063	0.347					
	Δ P	−0.112	−0.277	−0.135	−0.279	−0.011	0.025	−0.087	**0.790******	0.12				
Site attributes	Years restored	0.403	0.212	0.381	0.141	−0.04	0.052	−0.377	−0.024	0.003	−0.225			
	Upstream contributing area (ha)	**0.729*****	0.169	**0.699****	0.099	0.229	**−0.590****	0.029	0.08	0.051	−0.322	0.166		
	Restored area	**0.480***	0.018	0.419	0.004	0.345	**−0.534***	0.09	0.143	−0.158	−0.294	−0.048	**0.804******	
	Ratio (restored/upstream)	−0.275	−0.299	−0.328	0.066	−0.112	0.318	0.436	0.075	−0.221	0.173	−0.376	−0.384	−0.001

change in plant-available P with restoration was correlated to axis 1. These associations, together with the shared perceptions of landholders engaged in wetland restoration, suggest that people may prioritise the restoration of wetlands with large contributing areas. Over time, as trees replace pasture plant species, these restored wetlands support greater plant biomass, which enables greater uptake of phosphorus (Chapin et al. 2011). However, because our analysis of ecosystem service interactions is based on correlation, we cannot determine causality. In contrast to the suggestion that large wetlands and/or large wetland contributing area sizes are explicitly prioritised, it is possible that as landholders become increasingly aware of the ecosystem services their wetlands provide over time they become motivated to restore greater wetland areas. Most probably, some combination is true. We contend that perceived ecosystem services from wetlands, which are shaped by landscape context, evolve as the cultural context and biophysical ecosystem services of restored wetlands develop over time.

Relationships among biodiversity and ecosystem services in a restored wetland context

Native plant species richness increased in all but one of the restored wetlands. However, richness was not significantly correlated with any other measured or modelled service, nor was it correlated with perceived services. A lack of correlation among biodiversity and ecosystem services has been found in a variety of other systems, and relationships among biodiversity and ecosystem services remain complex and unclear (Ricketts et al. 2016). Furthermore, understanding these relationships is challenging, in part, because diverse methods are used to measure both biodiversity and ecosystem services (Harrison et al. 2014). Relationships among biodiversity vary widely depending on the biodiversity metrics and ecosystem services considered. Using spatial correlations, many studies have associated modelled ecosystem service to maps of species counts (Watson et al. 2020), but equally, biodiversity proxies, such as functional diversity and/or stand age, may also be correlated with ecosystem service delivery (Harrison et al. 2014). Our study represents a highly localized example of data collection for ecosystem services and biodiversity, e.g. measurements were taken in the same location, and thus have the benefit of not being subject to spurious correlations which may result when data are pooled across large spatial areas. While native plant species richness was uncorrelated to other service gains accrued through restoration in our study, its nearly universal increase suggests that wetland restoration on private land will, at a minimum, be effective in promoting biodiversity. All but one landholder perceived this to be true of their restored wetland.

Site differences may obscure interactions among modelled, measured and perceived ecosystem services

Apart from a strong positive correlation among modelled P and N retention, modelled and measured services were not significantly correlated. This lack of correlations suggests that none of these measurements are good proxies for one another, nor can we expect their changes to occur in tandem. Furthermore, despite the associations among perceived services with measured services and restoration age, we did not find an association between restoration age and measured or modelled services, contrasting results from other studies which highlight stand age as important for ecosystem services (Sutherland et al. 2016a). This lack of correlation may be because restoration age is not equivalent to stand age or successional stage in our study. The initial conditions of our wetlands varied among sites, as did the range of management techniques applied to achieve restoration. Some sites were initially degraded wetlands, while others were pastures. Furthermore, some restoration techniques are more disruptive, such as earthworks, while others are less intrusive, such as fencing. Exploring these patterns across wetlands with more similar initial conditions and more standardised array of management regimes may elucidate some of these contrasting patterns.

Leveraging multi-method approaches for future benefit

Multi-method approaches can be leveraged to create better ecosystem service models. Ecosystem service models are faster and cheaper than field measurements. Similarly, rapid assessments of ecosystem services are popular for extrapolating site-level gains in ecosystem services from restoration, including economic gains (Peh et al. 2014; McInnes and Everard 2017). However, rapid assessments and models rely on quantitative ecosystem service estimates that are already published or qualitative assessments from stakeholders or experts. Nonetheless, models are parameterized based on field measurements, and their accuracy depends on the availability and quality of these field measurement data. By collecting primary data through field measurements, our work facilitates the adoption of better models. For example, accurate flood mitigation modelling is hampered by a lack of soil saturated hydraulic conductivity measurements (Ebel and Martin 2017), and our saturated hydraulic conductivity data, which includes high-resolution measurement of its variability across small wetlands may be used to supplement flood models. Similarly, spatially explicit carbon models are often based on national or global scale soil tables, but our work now provides better estimates of mean SOC, as well as the spatial variability of these quantities. Furthermore, Olsen P is used as an input to many spatially explicit phosphorus models, but measurements of Olsen P in wetland-specific sites are rare. Future work could leverage our measured data to improve ecosystem service models.

Meeting needs for the greater good on private land

Acknowledging multiple ecosystem service gains from wetland restoration can illuminate interlinkages that bolster the role of wetlands in currently disparate policy objectives. For example, soils from restored wetlands may be leveraged to mitigate greenhouse gasses. In New Zealand, only afforestation has been recognised under the emissions trading scheme. Consequently, landholders are not credited for the carbon gains in restored wetland soils. Concurrently, we demonstrated that by restoring wetlands, N and P are less likely to leach into nearby lakes and streams, resulting in improved water quality downstream. Finally, we add to evidence that wetland restoration increased soil permeability, and thus, the capacity to abate floods (Ameli and Creed 2019), indicating that wetland restoration may provide a promising alternative to engineered flood protection. Taken together, wetland restoration may reduce land-atmosphere carbon emissions, improve freshwater quality and provide a promising and cost-effective alternative to engineered solutions for flooding mitigation. Despite the solutions wetlands can provide, current policies overlook wetland restoration as a key tool. Elevating the role of wetlands in policy is especially urgent as the current scale of wetland restoration does not match the magnitude of their continued loss in New Zealand (Robertson et al. 2019).

Conclusion

Wetland restoration on private land provided significant gains in SOC, native plant species richness and saturated hydraulic conductivity, and also achieved desirable declines in plant-available P. Restoration also led to significant gains in N and P retention and minor gains in sediment retention. Additionally, landowners perceived their restored wetlands to provide a median of six ecosystem services, which in some cases, were correlated with measured gains in services. Using multiple methods allowed us to capture a wide range of ecosystem services and how they interacted, providing comprehensive and quantitative estimates of the gains received when wetlands are restored on private lands. The overwhelming evidence of significant gains in multiple ecosystem services from wetland restoration upholds a need for continued restoration efforts. Harnessing the potential of wetland restoration may be key for meeting a range of policy objectives in New Zealand and globally.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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