

## REVIEW ARTICLE

### Microbial ecology research in New Zealand

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**Abstract:** There are very few, if any, ecosystems that are not profoundly influenced by the activity of microbial communities. Microorganisms, encompassing domains *Bacteria* and *Archaea* as well as microscopic members of the *Eukarya* such as protozoa, yeasts and many other fungi, are tremendously abundant and contribute significantly to the major biogeochemical processes. In the last decade, technological advances in DNA sequencing have afforded ecologists the ability to study microbial communities at hitherto unseen resolution, with the capacity to address increasingly complex ecological questions. Here we review a selection of microbial ecology research being undertaken in New Zealand and Antarctica, from animal- and plant-hosted ecosystems, freshwater and marine habitats, and agricultural and geothermal environments. We have highlighted the broad range of high-quality and diverse microbial ecology research being conducted by New Zealand researchers and observe that much of this work underpins the greater biosecurity, ecosystem services, health and conservation efforts being undertaken in this country and globally. We conclude the review by offering some ideas for future directions in microbial ecology and, in particular, argue the importance of integrating microbiology with general ecological research.

**Keywords:** animal hosts; Antarctica; aquatic microbial ecology; archaea; bacteria; fungi; geothermal; protozoa; terrestrial microbiology

## Introduction

*'This is truly the "age of bacteria" – as it was in the beginning, is now and ever shall be'.* So said the noted paleontologist and evolutionary biologist, Stephen Jay Gould (Gould 1994), in recognition of the integral role of microorganisms in global ecology. Microorganisms, defined here in practical terms as any organism not visible to the naked eye, include all *Archaea*, *Bacteria* and microscopic members of the *Eukarya* such as unicellular algae, protozoa, and some fungi. Collectively, these organisms contain as much cellular carbon as all plants on earth (Whitman et al. 1998), and there are 100 million times more bacteria in our oceans ( $13 \times 10^{28}$ ) than there are stars in the visible universe (Copley 2002; Anon. 2011). Microorganisms drive all the major biogeochemical cycles on earth and have profound influences on all other organisms (and indeed their habitats) due to their varied roles as pathogens, symbionts, biological nutrient transformers, decomposers, and primary food sources. There are practically no environments on earth that are free from the influence of microorganisms: from the deep biosphere to the troposphere (D'Hondt et al. 2004; DeLeon-Rodriguez et al. 2013), from the most heavily polluted to the most pristine environments (Gutierrez et al. 2013; Shtarkman et al. 2013), microorganisms play an important role in ecosystem function.

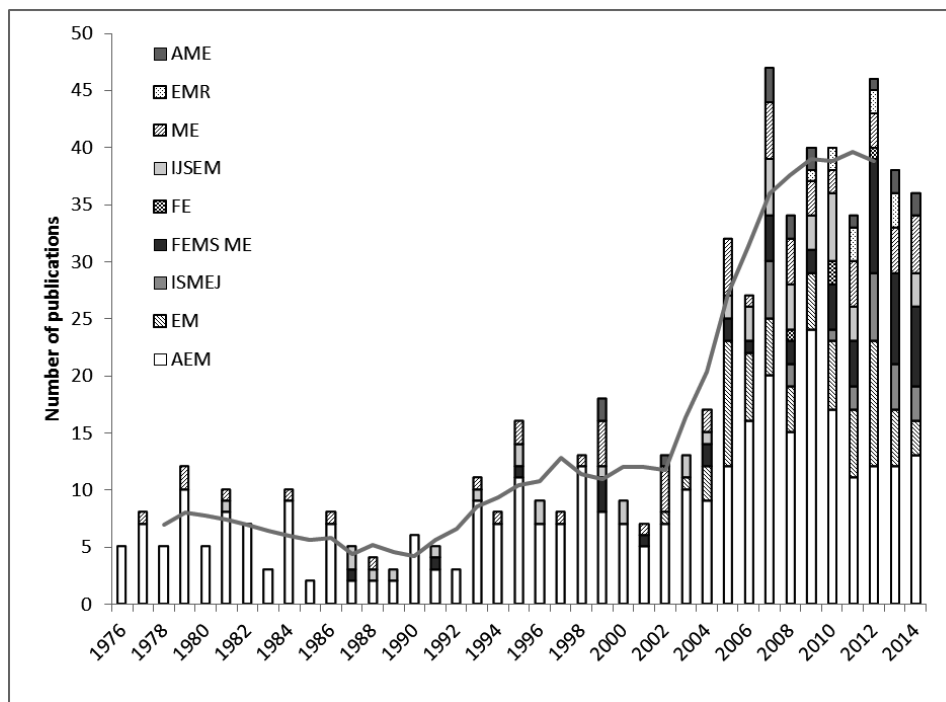
The discipline of microbial ecology in New Zealand (NZ) has a long and rich history. Indeed, the first significant international gathering of microbial ecologists (1st International Symposium in Microbial Ecology – ISME1) took place at the University of Otago, Dunedin in 1977 (Tiedje 1999). Activity in microbial ecology has continued in earnest locally, with

greater publication outputs in recent years (Fig. 1) reflecting the increasing numbers of NZ researchers drawn to this field. The purpose of this review is to highlight ongoing microbiology research in NZ and Antarctica and its contribution to ecology.

## Geothermal microbiology

New Zealand is blessed with a significant number of geothermal features arising from our position on the western boundary of the Pacific tectonic plate, within the 'Ring of Fire'. Microorganisms, particularly bacteria and archaea, thrive in these environments despite the challenging conditions they encounter. Possibly the first thermophilic microorganism to be formally described from NZ was the moderate thermophile '*Bacillus flavothermus*' (now *Anoxybacillus flavithermus*), which was cultivated from the Wairakei geothermal field in 1982 (Heinen et al. 1982). However, the microbiology of NZ geothermal systems has been actively investigated by researchers since the mid-1970s, primarily through the pioneering efforts of Hugh Morgan and Roy Daniel at the University of Waikato (Hickey et al. 1979; Daniel et al. 1982; Jansen et al. 1982). Although much of the early geothermal microbiology research focused on the description of thermostable enzymes (Bragger et al. 1989; Patchett et al. 1991), isolation of novel thermophilic strains (Hudson et al. 1989a; Niederberger et al. 2006), and the application of lignocellulose-degrading thermophilic microorganisms to biofuel production (Reynolds et al. 1986; Bergquist et al. 1999), these studies significantly contributed to global ecological understanding of geothermal ecosystems.

We describe a number of examples from geothermal



**Figure 1.** Peer-reviewed publications relating to environmental and microbial ecology studies by NZ researchers 1976-2014. Data were generated via searching the database 'Scopus' for country affiliation in the following journals: Aquatic Microbial Ecology (AME), Environmental Microbiology Reports (EMR), Microbial Ecology (ME), International Journal of Systematic and Evolutionary Microbiology (IJSEM), Fungal Ecology (FE), FEMS Microbiology Ecology (FEMS ME), The ISME Journal (ISMEJ), Environmental Microbiology (EM) and Applied & Environmental Microbiology (AEM). Grey line represents a five-year floating average.

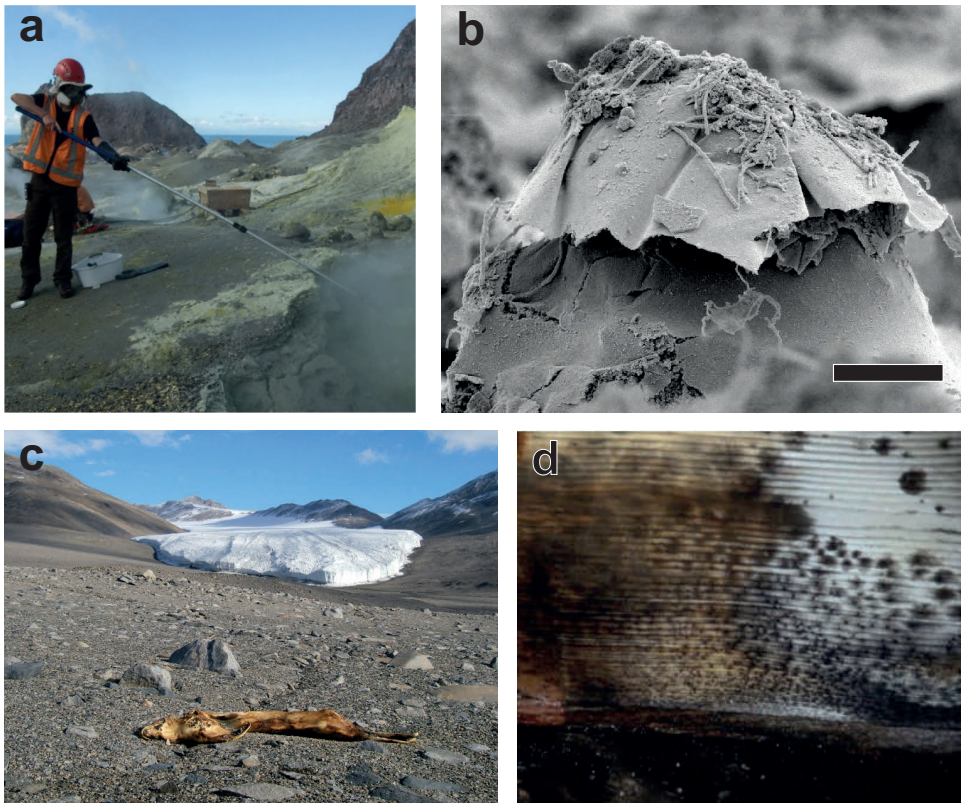
ecosystems to highlight the diversity and uniqueness of the microbial inhabitants and associated environments. The first example is from multiple hydrothermal vent sites at the Brothers volcano, a submarine volcano in the Kermadec Arc. Two studies (Stott et al. 2008b; Takai et al. 2009) indicated that phase separation of the hydrothermal gases had a significant influence on the selection and diversity of the microorganisms present. Stott et al. (2008b) found that more than one-third of the microbial phylotypes detected were from candidate phyla (for which no cultivated representatives existed) and only 1% of detected phylotypes could be identified down to genus or species level. In a second example, a similar level of phylotype uniqueness was described at Tramway Ridge on the flank of Mt Erebus at Ross Island in Antarctica (Soo et al. 2009). The composition of the resident microbial communities was strongly correlated with local physicochemical gradients, and included phylotypes distantly related to candidate phylum OP10 and *Chloroflexi*, as well as several examples of undescribed phylotypes from the archaeal phylum *Crenarchaeota* (Soo et al. 2009; Herbold et al. 2014). A third example is White Island, a subaerial volcano off the Bay of Plenty coast, which contains extensive geothermal features characterised by strongly acidic sulphate springs and fumaroles. An acidic stream at White Island contained a diverse microbial community, including a moderately thermophilic strain of the algal rhodophyte, *Cyanidium caldarium*, capable of growth at a remarkable pH 0.2 (Donachie et al. 2002).

The fourth example, Champagne Pool at Waiotapu, Waikato, is perhaps the most widely recognised geothermal feature in NZ, as well as the most extensively studied. The spring is particularly well known for its bright orange subaqueous sediments, white subaerial silica sinter rim and carbon dioxide (CO<sub>2</sub>)-saturated water body. It has elevated concentrations of arsenic and antimony, along with methane (CH<sub>4</sub>), hydrogen sulphide (H<sub>2</sub>S) and CO<sub>2</sub>, a moderately acidic pH of 5.5, and a temperature of 75°C, which makes it a challenging environment, even for microbial life. A number of studies have investigated the microbial communities within

Champagne Pool, focusing in particular on the strategies employed to deal with the elevated concentrations of arsenic. For example, the bacterium *Venenivibrio stagnispumantis*, which was enriched and isolated from Champagne Pool, displayed no growth inhibition in the presence of 8 mM and 20 mM arsenite and arsenate species, respectively (Hetzer et al. 2008). It is postulated that the resident microbial strains can restrict the toxic effect of arsenite species at Champagne Pool via the formation of methylated and/or thioarsenic anions (Hug et al. 2014). The microbial influence on the formation of white silica sinters on the periphery of Champagne Pool has also been reported (Mountain et al. 2003; Handley et al. 2005). Electron microscopic examination of these (and other geothermal) silica sinters showed that the internal sinter structures are made up of laminated, silica-encapsulated microbial cells. The vertical growth of these structures is a result of meniscus formation of silica-saturated spring water nucleated by resident microbial biofilms (Fig. 2). A genomic analysis of *A. flavithermus* further highlighted the mechanism for microbial contribution to silica nucleation and led to speculation about the contribution of thermophilic microorganisms to the formation of subaqueous and subaerial sinters (Saw et al. 2008) in geothermal systems such as Champagne Pool.

The isolation and characterisation of novel microbial strains plays an important role in piecing together the ecology of microbial communities and contributions to geochemical cycles. This is no different in extreme environments, where NZ researchers have played a substantial role in expanding our understanding of the metabolic capabilities and diversity of these systems. Novel isolates feature strongly in the literature, including several cases where type strains of novel phyla, classes and genera have been described. Of particular note was the isolation and description of *Fervidobacterium nodosum* (Patel et al. 1985). At the time of isolation, molecular techniques were not widely used and taxonomy was instead based primarily on physiological and morphological characteristics. As a result, the taxonomic placement of *F. nodosum* was uncertain and it now appears that Patel and colleagues were





**Figure 2.** (a) Sampling a hot spring at Whakaari, White Island. (b) Scanning electron micrograph (SEM) image of a single silica sinter spicule and microbial cells from Champagne Pool, Waikato (scale bar = 10  $\mu\text{m}$ ). The silica sinters at the margin are a result of the encapsulation of microorganisms by silica deposition via wave and capillary action. (c) A mummified seal carcass at the base of Adams glacier, Meirs Valley, Antarctica. (d) Fungal mould on a crate in Cape Evans hut kitchen, Antarctica. Photos/images courtesy of Steve Sherburn (a), Kim Handley (b), Ian McDonald (c), and Roberta Farrell (d).

the first to isolate and describe a representative of the phylum *Thermotogae*. Similarly, Stott and colleagues isolated a number of new strains by enrichment from geothermal soils using oligotrophic media, including the first representative (*Chthonomonas calidirosea*) of candidate phylum OP10 (renamed *Armatimonadetes*) (Stott et al. 2008a). Subsequent phenotypic and genomic characterisation revealed that this strain is an aerobic saccharolytic scavenger that occupies a very narrow ecological niche defined particularly by its obligate requirement for isoleucine supplementation and narrow pH growth range (Lee et al. 2011; Lee et al. 2014). Other extremophilic microorganisms from NZ ecosystems, notable because they either represented first descriptions (at the time of publication) of high-level taxonomic rankings or had unusual phenotypic characteristics compared to phylogenetically related microbes, include *Pyrinomonas methylaliphatogenes* (Crowe et al. 2014), *Thermonema lapsum* (Hudson et al. 1989b), *Limisphaera ngatamarikiensis* (Anders et al. 2015), *Thermoflavifilum aggregans* (Anders et al. 2014), and *Spirochaeta thermophila* (Aksenova et al. 1992).

The characterisation of a number of NZ microbial isolates has substantially changed our understanding of microbial metabolic capabilities and ecology. The alkaliphilic (alkaline-loving) *Caldalkalibacillus* strain TA2.A1 (Peddie et al. 1999; Olsson et al. 2003; Kalamorz et al. 2011) was isolated from an alkaline thermal bore at Mount Te Aroha, Waikato. Before study of this microbe, it was considered thermodynamically impossible for microorganisms to grow in heated, highly alkaline environments because of the need to retain protons to drive endothermic reactions in proton-deficient alkaline conditions. Research has now demonstrated that strain TA2.A1 is able to capture and utilise protons as coupling ions by linking the importation of sucrose to the sodium gradient, thus retaining the electrochemical gradient needed to drive a protonmotive force. Similarly, the isolation and description

of the thermophilic and acidophilic methanotroph ( $\text{CH}_4$ -oxidising) *Methylacidiphilum infernorum* from Hell's Gate/Tikitere, Rotorua (Dunfield et al. 2007; Op den Camp et al. 2009) challenged long-held paradigms of methanotrophy. The methanotrophic lifestyle is highly specialised and was thought to be restricted to neutral or slightly acidic environments and to two families of phylum *Proteobacteria*. This strain not only deviated from the neutrophilic methanotroph phenotype, but it also assimilated carbon non-conventionally via the Calvin-Benson Cycle, and was phylogenetically placed outside the traditional proteobacterial families, in the phylum *Verrucomicrobia* (Sharp et al. 2012).

## Microbial ecology in the Antarctic

Procuring a living in Antarctica is difficult and requires specialised adaptations to deal with the extreme climatic and nutritional challenges. Environmental conditions such as desiccation, low nutrient availability, high UVB levels, variations in light regimes, and steep temperature gradients all restrict species richness (Cary et al. 2010). Yet remarkably, microbial communities appear to have adapted to, and thrive in, these conditions. Indeed, studies over the last 60 years have demonstrated that polar microbial communities are highly diverse and have unexpected prevalence in even the most extreme of Antarctic environments. We direct the reader interested in this subject to a recently published book that reviews terrestrial microbiology research in Antarctica, including sizeable contributions from NZ authors (Cowan 2014).

The soils of the Antarctic Dry Valleys are among the more extreme global environments and were originally considered to be 'sterile'—devoid of all life (Horowitz et al. 1972). However, modern molecular detection techniques and next-generation

sequencing (NGS) have shown that these soils accommodate a wide diversity of microbial populations (Smith et al. 2006; Lee et al. 2012). These organisms have adapted to the high salinities, low moisture contents, and steep physicochemical gradients (soil temperature variations range from  $-60^{\circ}\text{C}$  to  $27^{\circ}\text{C}$ , with daily temperature changes sometimes in excess of  $20^{\circ}\text{C}$ ) that prevail in these environments (Cary et al. 2010). However, a lack of available energy inputs is probably the most challenging aspect for microbial survival. Exogenous inputs of organic matter are limited to phototrophs (algae, cyanobacteria, moss – there are no vascular plants), sediments from former waterways, and marine macroorganisms, such as seal and penguin, that contribute faeces (Banks et al. 2009) and carcasses (Tiao et al. 2012) (Fig. 2).

Despite such adversity, a wide diversity of bacteria has been identified in the Dry Valley environments, along with archaea and eukaryotic algae and fungi (Pointing et al. 2009). Most photoautotrophic biomass is concentrated in cryptic rocky refugia, where cyanobacteria and other taxa exploit marginal advantages in microenvironments on surfaces of exposed and porous rocks (Pointing et al. 2009). Cyanobacteria are a major source of C-fixation into the valley ecosystems, particularly on the peripheries of lakes and ponds and, to a lesser extent, soil (Wood et al. 2008a, b; Pointing et al. 2009; Cowan et al. 2010; Niederberger et al. 2012). Soil communities dominated by members of at least 14 bacterial phyla have been identified, including commonly identified *Bacteroidetes*, *Proteobacteria* and *Actinobacteria*, as well as *Deinococcus-Thermus*, *Chloroflexi* and the candidate phyla OP10, OP11 and TM7 (Lee et al. 2012). Fungal diversity is strikingly restricted, with only seven phylotypes associated with the *Helicodendron* and *Zalerion* genera detected (Rao et al. 2013). The archaeal diversity of the Dry Valleys has been found to be non-existent or limited to the low-temperature *Crenarchaeota* (Pointing et al. 2009; Ayton et al. 2010).

Many of the Dry Valley research programmes have focused on determining the main environmental drivers of diversity within these soils. For example, organic carbon and soluble salts were found to be key drivers in the soils and rocky substrates in McKelvey Valley (Pointing et al. 2009). A broad inter-valley physicochemical and bacterial diversity survey of maritime valleys of the McMurdo Dry Valleys indicated that elevated salt content, lead, and low moisture content were the primary drivers defining bacterial (including cyanobacterial) community compositions (Lee et al. 2012). The latest research suggests that microbial communities within these valleys are highly localised, strongly defined by their individual physicochemical environments, and are likely to be endemic (Barrett et al. 2006; Cary et al. 2010; Lee et al. 2012; Yung et al. 2014). Metagenomic approaches to investigate functional diversity have revealed the presence in Dry Valley microbial communities of a unique pool of genes associated with organic hydrocarbon and lignin-like degradation (Chan et al. 2013).

An interesting component of microbiological research in Antarctica, spearheaded by NZ researchers, has centered on the need for low-cost and low-tech remediation of hydrocarbons derived from anthropogenic activities (Aislabie et al. 2000, 2004, 2012; Baraniecki et al. 2002; Saul et al. 2005). Hydrocarbon spills and associated microbial communities at scientific research stations and drilling operations, such as the Scott and McMurdo Stations, and the surrounding Ross Island region, have been studied extensively (Aislabie et al. 2000, 2004; Bej et al. 2000; Saul et al. 2005). Bioremediation strategies are limited to *in situ* technologies by practicalities

associated with the remoteness of the location, the removal of contaminated soil, and Antarctic Treaty restrictions on the importation of foreign remediative organisms. As in the Dry Valleys, low and fluctuating temperatures and low nutrient availability (particularly N and P) appear to restrict microbial hydrocarbon degradation to the summer months. Laboratory tests demonstrated that rates of hydrocarbon mineralisation were significantly increased by amendments of N and P via fertiliser (Aislabie et al. 2000). Interestingly, while some genera of bacteria, such as *Sphingomonas*, *Pseudomonas*, *Acinetobacter* and *Rhodococcus*, as well as the fungus *Phialophora*, are enriched in contaminated soils, the overall microbial richness decreases (Aislabie et al. 2004; Saul et al. 2005).

An arguably more unusual aspect of microbial ecology research in the Antarctic is the study of fungi that inhabit historical dwellings on Ross Island (Duncan et al. 2006, 2008, 2010; Farrell et al. 2011; Arenz et al. 2014). Huts used by Shackleton's and Scott's expeditions are of high historic value and are visited regularly by tourists, scientists and conservators (Duncan et al. 2010). However, the huts and their contents are vulnerable to fungal contamination and degradation, facilitated by the comparatively higher ambient temperatures in the huts, particularly in the summer months (Fig. 2). A diverse array of fungi, including *Cadophora*, *Pseudodeurotium*, *Cladosporium*, *Geomyces*, *Hormonema*, *Rhodotorula*, and *Fusarium* spp., inhabit the interiors and exteriors of these huts (Duncan et al. 2008; Farrell et al. 2011). In particular, the cellulolytic soft rot fungus *Cadophora* was highly prevalent on the exterior of two historic huts, although its presence is considered endemic and not due to human contamination (Blanchette et al. 2004). The key drivers for fungal proliferation in Antarctica are soil carbon and nitrogen content. Hence, the introduction of exogenous C and N sources (e.g. huts) selects for cold-adapted and thus presumably indigenous fungal strains (Arenz et al. 2011; Farrell et al. 2011). Overlapping fungal species diversity is observed in both non-impacted Ross Island environs and in the historical huts, suggesting that indigenous fungal strains are the primary colonisers of the huts (Farrell et al. 2011). Further, fungal biomass did not vary significantly during seasons, suggesting visitors to the huts (primarily during summer) do not significantly contribute fungal contamination (Duncan et al. 2010). Partially due to these research efforts, conservation works have reduced fungal blooms and spores, which should restrict the degradation of the huts and associated artifacts.

Sea ice in the Antarctic is an important habitat and covers an area almost twice the size of Australia at its winter maximum (Maas et al. 2012). The microorganisms present in sea ice contribute significantly to primary and secondary production in the Southern Ocean. However, like other polar systems, it is under threat from changes in global climate, and it is unclear how the microorganisms inhabiting sea ice will respond to these changes. New Zealand researchers have been examining microbial community diversity and function within sea ice (Koh et al. 2010, 2011; Maas et al. 2012) to develop a baseline from which to monitor any future impacts. Recent research has shown that perturbations in temperature will not significantly affect the ability of phytoplankton to survive overwintering or provide inocula for blooms (Martin et al. 2012), but there is evidence of a lag in the response time of bacterial communities to rapid temperature, salinity and/or light changes (Martin et al. 2011).



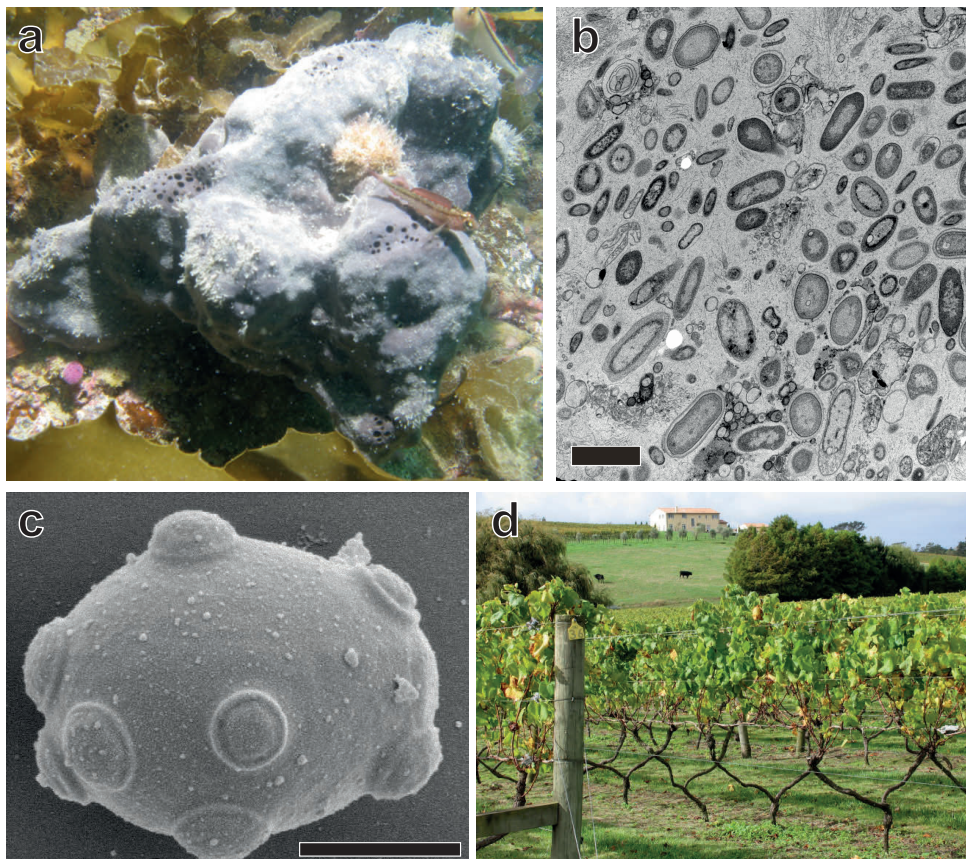
## Aquatic microbial ecology

With >15 000 km of coastline and the world's sixth-largest exclusive economic zone, the islands of NZ are tightly linked to the state of our oceans. Given that a single millilitre of seawater contains  $10^5$ – $10^7$  bacterial cells, with 10 times that many viruses, as well as a plethora of microalgae, archaea and protozoa, it is hardly surprising that marine microorganisms are vital contributors to global processes (Arrigo 2005). Among the most significant players in the global carbon cycle are the unicellular microalgae (phytoplankton), and much of the NZ-based research into marine planktonic microbiology has focussed on these taxa (Boyd et al. 2000, 2012). The role of phytoplankton and pelagic bacteria in the biogeochemical cycling of iron has been particularly well studied, due to the limiting nature of this trace metal in much of the world's oceans, and a high-profile hypothesis from the 1980s that iron enrichment could enhance phytoplankton growth on a massive scale, ultimately leading to increased carbon sequestration in the ocean and amelioration of global climate change (Martin et al. 1988; Martin 1990; Boyd et al. 2010). Through their involvement in chemical, biological and large-scale iron fertilisation experiments, NZ-based researchers have played an integral role in elucidating the drivers of iron cycling in the Southern Ocean (Boyd et al. 2000; Tagliabue et al. 2014). The interplay between viruses and bacteria during a spring phytoplankton bloom within NZ waters has also been studied (Matteson et al. 2012), as have the microbial communities associated with sinking particles, or marine snow (LeClerc et al. 2014).

Any animal inhabiting the marine realm is immersed in a literal sea of microbes, including potential mutualists,

pathogens and even sources of food. One marine taxon of particular note for its interactions with microorganisms is that of the filter-feeding sponges (phylum Porifera), which often harbour diverse and abundant communities of microbes that comprise up to 35% of total 'sponge' volume and contribute to many aspects of sponge biology, including nutrition and chemical defence (Taylor et al. 2007; Hentschel et al. 2012). The degree of host specificity (i.e. the extent to which microbial symbionts associate with only a few (= specialist) or many (= generalist) host species) was recently determined for a number of NZ sponges within the context of a large global study of sponge symbiont biogeography (Schmitt et al. 2012). The common NZ sponge *Ecionemia (Ancorina) alata* (Fig. 3), for example, contains dense microbial communities that are similar to those of other sponges at coarse phylogenetic levels (e.g. phylum), but exhibit considerable host specificity at finer (e.g. genus/species) levels (Kamke et al. 2010; Schmitt et al. 2012). Another NZ sponge, *Mycale hentscheli*, produces the potent anti-cancer agent peloruside A (West et al. 2000), and structural similarities between this compound and metabolites of known microbial origin have prompted considerable microbiological research into this sponge species (Webb et al. 2002; Anderson et al. 2010). Other marine animals to have received attention from microbiologists in NZ include echinoderms (Lawrence et al. 2010), the tetrodotoxin-producing sea slug *Pleurobranchaea maculata* (Wood et al. 2012; Chau et al. 2013), and herbivorous fishes, which utilise gut bacteria in the digestion of algae (Moran et al. 2005; Clements et al. 2007).

Early studies on the microbiology of NZ fresh waters focused on the detection of potentially pathogenic species, with human gut-associated bacteria such as *Escherichia coli* and other so-called 'faecal coliforms', as well as human-



**Figure 3.** (a) Marine sponge *Ecionemia (Ancorina) alata* from the New Zealand coast. (b) Marine sponges often harbour dense and diverse communities of microorganisms, as seen in this transmission electron micrograph (scale bar = 2  $\mu$ m). (c) The yeast *Saccharomyces cerevisiae* (scale bar = 2  $\mu$ m) invariably dominates by the end of a wine ferment, even in wild ferments where no additional microorganisms are intentionally added. (d) Vineyard in west Auckland. Winemakers often employ spontaneous (wild) ferments in order to produce wine. Photos/images courtesy of Mike Taylor (a), Susanne Schmitt (b), and Mat Goddard (c, d).

derived enteroviruses, often targeted as indicators of ecosystem contamination (Duncan et al. 1981; Lewis et al. 1986, 1992). More recently, such studies of one or a few target species have been extended to encompass entire microbial assemblages, with the development of novel proxies for aquatic ecosystem health (Lear et al. 2009, 2011; Washington et al. 2013). Methods to measure stream health based on microbial community composition and/or function compare favourably with more traditional indicators based on macroinvertebrate communities, responding differently to catchment conditions and offering a complementary, or even alternative, approach to those in current use (Lear et al. 2011; Dopheide et al. in press). By focusing on the relatively immobile microbes living within biofilms (multi-species assemblages found on virtually all aquatic surfaces), these approaches can provide an integrated measure of the recent environmental conditions at a specific site. The same principle has been applied to evaluate the effects of stormwater-derived metals (Ancion et al. 2014) and the ionophore monensin (Winkworth et al. 2014) on the health of receiving streams.

Engineered aquatic systems have also been the subject of microbiological scrutiny. Biological wastewater treatment, for example, represents one of the world's largest biotechnology industries, with annual expenditure of \$727 million in NZ alone (Anon. 2013b). The breakdown of municipal wastes, which are typically rich in carbon, nitrogen and phosphorus, is achieved by microbial action in a variety of treatment plant configurations. One system of increasing popularity, due to its high efficiency and small footprint, is the moving bed biofilm reactor (MBBR), exemplified by two full-scale treatment plants in the Wellington area. Recent molecular studies revealed distinct and predictable changes during the development of MBBR biofilms (Biswas et al. 2014a, b), with the emergence of a bacterial community that allows both aerobic and anaerobic nutrient breakdown to occur simultaneously. Microalgae are also used in wastewater treatment, with recent investigations into the effects of carbon addition (Sutherland et al. 2014b, 2015a), mixing frequency (Sutherland et al. 2014a), and light provision (Sutherland et al. 2015b) on microalgal productivity and nutrient removal. High-rate algal ponds have come under renewed scrutiny due to their potential for combining nutrient removal with biofuel production. Microbial fuel cell technology also allows energy generation, converting chemical energy to electrical energy via the microbial metabolism of various substrates including wastewater (Rabaey et al. 2005). Microbial fuel cells can be driven by the activities of a single microorganism or, as in the case of a recent NZ study, use a mixed community of microalgae and cyanobacteria (Commault et al. 2014).

New Zealand's aquatic systems have provided fertile testing grounds for evaluating ecological theory. Much of the existing theory surrounding, for example biogeographic patterns and latitudinal gradients in diversity, was developed for macroorganisms (plants and animals), but there remains a lack of clarity about the extent to which those principles apply to microbes (Barberan et al. 2014). A recent study of bacterial communities growing on biofilms in 244 streams across NZ found that catchment land use had the largest effect on richness and community structure, both latitude and geographic distance between samples had a significant effect, and elevation had less of an effect (Lear et al. 2013). Other research has used aquatic microcosms (Lear et al. 2013) and alpine ponds (Lear et al. 2014) to study the role of immigration and fine-scale biogeographic patterns, respectively, in determining microbial community structure.

## Microbial communities associated with animal hosts

Animals provide a diverse array of habitats for microorganisms to colonise, and virtually all animals form symbiotic relationships with one or more microbial species (in this article we use the most liberal possible definition of the term 'symbiosis', i.e. the living together of dissimilar organisms). There are compelling reasons to study host-associated microbes in NZ, whose fauna was described by Jared Diamond as 'the nearest approach to life on another planet' (Gibbs 2006, p. 7). New Zealand has evolved a distinct and highly unusual fauna and flora, with high levels of endemism among insects and other taxa (Gibbs 2006).

Many insects form close nutritional mutualisms with microbes which can, rather simplistically, be split into two main categories. Firstly, sap-sucking insects such as aphids and psyllids rely heavily on intracellular bacterial symbionts to provide the essential amino acids and/or vitamins that cannot be derived from their carbon-rich diet. While the related scale insects have received less attention from a microbiological perspective, recent work has provided insights into the diversity and evolution of bacterial symbionts in the scale insect family Coelostomidiidae (Dhami et al. 2012, 2013), whose members are mostly endemic to NZ. The coelostomidiid scales are of considerable ecological importance and provide a dramatic example of how microbial symbionts can influence the food web of an entire ecosystem. Scale insects feed exclusively on plant phloem sap, which is extremely rich in carbohydrate (sugar) but deficient in essential amino acids. Excess sugar is excreted by the immobile feeding stage as honeydew. In the beech forests of the Nelson Lakes, scale insects of the genus *Ultracoelostoma* excrete honeydew in quantities up to a staggering 4500 kg / hectare / year (Beggs et al. 2005), providing food for diverse species including microorganisms, invertebrates, reptiles and birds (Beggs et al. 2006). The survival of scale insects on their nutritionally unbalanced diet is directly due to the presence of bacterial symbionts, which essentially function as amino acid factories to provide the nitrogen necessary for the insect to synthesise, among other things, proteins and nucleic acids. Scale insects, aphids and other insects on a highly specialised diet typically contain only a low diversity (two to seven species) of bacterial symbionts.

A second, quite different type of nutritional symbiosis between insects and microorganisms is the high-diversity symbiosis exemplified by the termite gut. Termites contain hundreds of bacterial and archaeal species within their hindguts, with many also harbouring dense populations of flagellated protozoa (Brune et al. 2006). The protozoa, which play an integral role in the breakdown of recalcitrant dietary components such as lignin and cellulose, comprise up to half the fresh weight of the termite and enable the insect to thrive on a diet of wood or soil. New Zealand has three species of native termite which, while on the radar of the forestry industry, do not share the notoriety of their overseas counterparts as destroyers of wooden structures such as homes. Somewhat analogous to the situation for aphids and scale insects, the termite's woody diet is rich in carbon but poorer in nitrogen, so bacterial symbionts capable of fixing atmospheric nitrogen (a useful trait which eukaryotes do not possess) are often key components of the termite microbiota (Brune et al. 2006). The diversity of nitrogen-fixing bacteria was determined for the NZ termite *Stolotermes ruficeps* by sequencing the gene which encodes for the nitrogenase enzyme, *nifH* (Reid et al. 2009),



and the authors suggested that wood-dwelling termites could represent a significant source of nitrogen in temperate forests. The ability to study microbial activity *in situ* by targeting such 'functional genes' highlights a key weapon in the arsenal of today's microbial ecologists, enabling an understanding of cellular metabolism even for the vast majority of bacteria that have thus far resisted cultivation in the laboratory.

The kākāpō (*Strigops habroptilus*) is an iconic NZ species; once among the most abundant of our native birds it was almost wiped out following the introduction of mammalian predators such as stoats. Thanks to intensive conservation efforts, kākāpō now number c. 125 individuals, a significant improvement over the c. 60 individuals existing some two decades ago. While much is known about kākāpō genetics, ecology and nutrition, until recently virtually nothing was known about the microbiology of these unique birds. This is surprising, since gut microbes are likely to contribute to kākāpō health by aiding in digestion and preventing establishment of pathogenic microorganisms. A recent study employed sequencing of the bacterial 16S rRNA genes to describe bacterial community composition along the kākāpō gastrointestinal tract (Waite et al. 2012), while subsequent research has built upon these baseline data by examining the impacts of human interaction (e.g. hand-rearing, antibiotic usage) on the bacterial communities resident within the kakapo gut (Waite et al. 2014). Such an approach will hopefully aid in kākāpō conservation and management and should be equally applicable for the conservation of any endangered species.

Nowhere is the contribution of symbiotic microorganisms to host nutrition more apparent than in the guts of commercially important ruminants such as cattle and sheep, which house in their rumen (fore-stomach) dense and diverse communities of bacteria, archaea, protozoa and fungi (Jeyanathan et al. 2011; Kittelmann et al. 2013). Within the rumen, ingested food – typically cellulose-rich grass – is broken down by microbial fermentation into substances such as volatile fatty acids, which are more readily assimilated by the host animal. Methanogenic (CH<sub>4</sub>-generating) archaea within the rumen have gained particular notoriety due to the emission of CH<sub>4</sub> from farmed ruminants. Given the importance of ruminants to NZ's agriculture sector, it is hardly surprising that intensive research efforts are underway in this country to investigate ways of reducing CH<sub>4</sub> emissions. Any CH<sub>4</sub> mitigation strategy should aim to target traits that are conserved across all rumen methanogens, ensuring that all methanogens are affected with no unaffected species left to fill the vacated niche (Attwood et al. 2011). Equally important is that other (non-CH<sub>4</sub>-producing) rumen microbes remain unaffected so that they maintain their normal roles in digestion. Clearly, development of such strategies requires detailed knowledge of the physiology and diversity of rumen methanogens, which is now being provided via the genome sequencing of *Methanobrevibacter ruminantium* and other rumen-derived methanogens (Leahy et al. 2010; Attwood et al. 2011). Potential CH<sub>4</sub> mitigation strategies resulting from this work include inhibition of methanogen-specific enzymes or the development of an anti-methanogen vaccine (Attwood et al. 2011; Buddle et al. 2011).

The microbial ecology of the human gut is a rapidly expanding field worldwide, driven by a new appreciation for the importance of gut microbes to human health, and facilitated by massive improvements in DNA sequencing technology (Qin et al. 2010). Research in this country has been spearheaded by Gerald Tannock at the University of Otago, who has worked for over 40 years on the ecology of gastrointestinal bacteria

(Tannock et al. 1974; Roach et al. 1977). Much of this work has focused on the gut symbiont *Lactobacillus reuteri*, which exists in many vertebrates and, like several other members of this genus, is also used as a human probiotic. Comparative analyses of the genome sequences of different *L. reuteri* strains have shed light on the mechanisms responsible for the specialisation of these strains to different vertebrate hosts (Frese et al. 2011) while another recent study used a number of complementary approaches to examine the interactions of *L. reuteri* with another, related bacterium (Tannock et al. 2012). *L. reuteri* and *L. johnsonii* co-exist in the fore-stomach of mice (often used as an experimental proxy for the human gut), despite the niche exclusion principle predicting that this should not happen due to both species being able to utilise the two main food sources present – glucose and maltose. However, analysis of gene expression in these bacteria, coupled with *in vivo* and *in vitro* experimentation, revealed that resource partitioning was occurring, with one species growing more rapidly on glucose while the other preferentially used maltose (Tannock et al. 2012). Nutritional influences on the gut microbiota of juvenile rodents (Young et al. 2012) and humans (Thum et al. 2012) have more generally been a subject of interest among NZ researchers, while other aspects of the human microbiome to have come under research attention include the oral microbiota (Rasiah et al. 2005; Filoche et al. 2010; Burton et al. 2011, 2013) and bacteria of the sinus cavities (Biswas et al. 2015).

## Microbial ecology of terrestrial ecosystems

Soils are of vital ecological importance due to the myriad ecosystem services that they provide (Aislabie et al. 2013). At the most basic level, soils provide the physical substrata for terrestrial animal (including human) life, as well as a growth medium for plants. They also buffer water flows, represent sites for decomposition and the liberation of nutrients, and play a key role in regulation of greenhouse gas emissions. Microbes living in the soil are intimately associated with all of these functions (Aislabie et al. 2013). Elucidating the role of microorganisms in soil is thus an important research objective and, unsurprisingly, soil microbiology is a dynamic field internationally (East 2013; Fierer et al. 2013). New Zealand itself has a productive history regarding the study of soil microbes including, but not limited to, investigations into carbon and nitrogen cycling (Singh et al. 2007; Di et al. 2009, 2010; Das et al. 2012; Hamonts et al. 2013; Morales et al. 2013, 2015), interactions between above- and below-ground communities (Wardle et al. 2004, 2005), influence of land management practices (Condrón et al. 2012; Simpson et al. 2012; Wakelin et al. 2012; Adair et al. 2013) and carriage of (potentially pathogenic) bacteria through soil (McLeod et al. 2008; Aislabie et al. 2011).

Agriculture is the mainstay of the NZ economy, with dairy farming alone contributing a quarter of NZ's export income. Timber, wine, kiwifruit and wool are among our other significant export products, with all relying to some degree on the provision of a healthy soil environment. Ensuring the sustainability of soils in an agriculture-intensive country such as NZ demands a sound understanding of the long-term effects of agricultural practices, including on microbial communities (Adair et al. 2013). Long-term field trials offer exemplary insights due to the experimenter's ability to manipulate parameters in a controlled, replicated manner. Two such trials, at Lincoln University (Adair et al. 2013) and outside Hamilton

(Wardle et al. 1999), examined changes in soil communities relative to agricultural practices such as herbicide usage, mowing, mulching and addition of nitrogenous fertiliser. Nitrogen is critical to all life, and the dynamics of its addition to, and loss from, agricultural soils is a topic of considerable interest to microbiologists. Ammonia-derived fertilisers such as ammonium nitrate and urea are frequently added to pastoral soils to increase productivity, yet naturally-occurring nitrifying microorganisms can oxidise this ammonium to nitrite and subsequently nitrate. This is significant because nitrate is far more mobile within soils than ammonium, and is thus prone to leaching into groundwaters (Spalding et al. 1993; Aislabie et al. 2013). A nitrification inhibitor has been applied to NZ soils in an effort to minimise this nitrate leaching (Guo et al. 2014). In grazed grasslands, the majority of ingested nitrogen can be returned to the soil via urine from grazing livestock, with levels of nitrogen under a dairy cow urine patch reaching as high as 1000 kg per hectare (Di et al. 2009). The importance of urine as a nitrogen input, potentially affecting microbial communities in soil, is reflected in the large numbers of publications on this topic from NZ researchers (e.g. Orwin et al. 2010; Bertram et al. 2012; Dai et al. 2013; Guo et al. 2014). A second major pathway for nitrogen loss from pastoral land relates to the release of nitrous oxide ( $N_2O$ ), a potent greenhouse gas with a global warming potential c. 300 times that of  $CO_2$  (Solomon et al. 2007). Denitrification is the microbially mediated reduction of nitrate to nitrogen gas ( $N_2$ ). However, 'incomplete denitrification', as carried out by many denitrifiers, yields  $N_2O$  as the final product, and this represents a substantial source of greenhouse gas emissions from NZ pastures (Aislabie et al. 2013; Saggart et al. 2013). The effects of  $N_2O$  emissions from NZ soils have been researched for several decades and continue to receive considerable attention (Sherlock et al. 1983; Carran et al. 1995; de Klein et al. 2001; Hamonts et al. 2013; Kelliher et al. 2014).

Among the more aesthetically and gastronomically pleasing consequences of microbial activity is the production of wine. This country has a proud heritage of winemaking, with annual wine exports in excess of \$NZD 1.2 billion (Anon. 2013a). The yeast *Saccharomyces cerevisiae* has been used by humans to make alcoholic beverages for literally thousands of years (Cavaliere et al. 2003), with this organism frequently added to grape juice by winemakers in order to drive a ferment to completion (Fig. 3). Recent NZ research has provided novel insights into the biogeography (Gayevskiy et al. 2012) and modes of dispersal (Goddard et al. 2010; Palanca et al. 2013) of *S. cerevisiae* and other yeasts, as well as the mechanisms by which *S. cerevisiae* comes to dominate a ferment even when it is rare to begin with and is not specifically added (Goddard 2008).

A less desirable outcome of microbial interactions with fruit involves the well-publicised outbreak of the kiwifruit canker pathogen, *Pseudomonas syringae* pv. *actinidiae* (Psa; Vanneste 2013). In a multi-institution collaboration that examined the genomes of more than 30 Psa isolates, a number of distinct clades were identified, and it was suggested that a diverse global source population exists, from which multiple transmission events have led to separate Psa outbreaks (McCann et al. 2013). Although control measures for Psa remain limited at best, genome analyses have identified candidate genes as potential targets for resistance breeding programs.

Molecular techniques have also provided valuable insights into the microbiology of the NZ grass grub *Costelytra zealandica*, with studies of both its natural microbial

community (Zhang et al. 2008), and of bacterial strains that could act as biological control agents for this agricultural pest (Hurst et al. 2002; Hurst et al. 2007). The protein structure of a key insecticidal toxin produced by *Yersinia entomophaga* was recently described (Landsberg et al. 2011), leading to new insights into the mode of action of this and related toxins of bacterial origin (Busby et al. 2013).

Non-agricultural ecosystems have also been the subject of intense study among NZ's microbial ecologists. Much of this work has explored the interactions between above- and below-ground ecosystem components, which were traditionally examined separately, but warrant being considered together due to the inextricable links between the two (Wardle et al. 2004). Plants supply the organic carbon upon which soil decomposers depend, while the latter both break down dead plant matter and profoundly influence the cycling of nutrients within the soil (in turn affecting plant growth). Root-associated microorganisms can also have both positive and deleterious effects on the coupling between plant and decomposer communities (Wardle et al. 2004). Still more complexity is added by herbivores operating both above ground (foliar) and below ground (root), potentially affecting soil microorganisms and processes by a variety of mechanisms (Bardgett et al. 2003). The enduring importance of plants to soil processes was demonstrated in a 'removal experiment' carried out in Te Urewera National Park, which compared soil properties (including nutrient composition and microbial community structure) in adjacent areas, some of which had been subjected to selective logging of rimu (*Dacrydium cupressinum*) some 40 years earlier (Wardle et al. 2008). Even after this period of time the stumps of removed rimu trees elicited measurable effects on certain soil and microbial community characteristics. Concerns over such long-term ecological consequences are among the many worrying aspects surrounding the current spread of kauri dieback disease. This disease, caused by the oomycete (water mould) *Phytophthora* 'taxon Agathis', poses an existential threat to kauri (*Agathis australis*), an iconic NZ species. Effective management of kauri dieback requires an improved understanding of its etiology, with current research efforts including field surveys of potential kauri pathogens (Waipara et al. 2013) and glasshouse trials to establish pathogenicity (Horner et al. 2014).

With NZ holding the dubious distinction of being among the world's most heavily invaded ecosystems (Allen et al. 2006), it is fitting that the impact of invasive species on the composition and activities of microbial communities has received considerable research attention in this country. In a series of studies on nine NZ islands invaded by rats and a further nine rat-free islands, Fukami and colleagues showed that these introduced mammals, via their predation on seabirds, led to diminished soil fertility due to reduced nutrient deposition by birds (Fukami et al. 2006). While active microbial biomass was largely unaffected in the seabird study, subsequent experiments identified changes in fungal community structure, but not wood decomposition rates, on invaded vs rat-free islands (Peay et al. 2013). The presence of introduced rodents, as well as invasive wasps, also influenced how decomposer communities responded to the addition of honeydew in the aforementioned beech forest system at Nelson Lakes (Wardle et al. 2010). The influence of browsers such as deer, goats and possums has also been investigated within NZ forests, and while these did not seem to have a consistent effect on the activities of soil microbial communities (Wardle et al. 2001), they may facilitate the spread of invasive trees



and associated ectomycorrhizal fungi (Wood et al. 2015). The ecology of mycorrhizal associations has more generally been an area of considerable research activity within NZ (Powell 1976; Clayton et al. 1984; Johnston 2010; Orwin et al. 2011), with their role in shaping plant communities recently highlighted by Dickie and co-workers (Bever et al. 2010; Klironomos et al. 2011). It is estimated that as much as 57% of observed variation in plant community composition could be explained by mycorrhizal symbioses (Klironomos et al. 2011). Lack of mycorrhizal inoculum has been investigated as a potential constraining factor for the spread of iconic NZ tree species such as beech (*Nothofagus* spp.), kānuka (*Kunzea* spp.) and mānuka (Dickie et al. 2012a; Davis et al. 2013).

Ecological theory holds that assembly history, which describes the order and timing of species arrival, can have a profound effect on community structure. A series of elegant experiments in NZ with wood-decomposing fungi revealed the impact of assembly history on not only community composition, but also wider ecosystem functioning (Fukami et al. 2010). Such effects were just as substantial at the level of communities and ecosystems as they were at the level of individual species, as demonstrated by a field experiment in the South Island beech forest (Dickie et al. 2012b). Similarly important impacts were demonstrated using a laboratory-based microbial model, whereby both the order and timing of bacterial introduction significantly influenced subsequent diversification (Fukami et al. 2007). The use of microbial model systems to address evolutionary and ecological questions, as exemplified by the research of Paul Rainey and co-workers (Rainey et al. 1998; Fukami et al. 2007; Beaumont et al. 2009), has represented an important step towards unifying microbial ecology and the ecology of 'macro' organisms (Jessup et al. 2004; Prosser et al. 2007; Barberan et al. 2014).

## Synthesis & future directions

In this review we have attempted to convey the vibrant nature of microbial ecology research conducted in NZ, both today and over the preceding decades. Dramatic improvements in DNA sequencing technologies, coupled with the unique attributes of our natural environment (e.g. geothermal ecosystems, endemic 'host' animals), make this a particularly exciting time for microbial ecology in NZ. The 'democratisation' of science enabled by reduced sequencing costs, coupled with the increasing ease of global collaboration, ensures that even modestly-funded laboratories in a small country such as NZ can continue to compete effectively on the international stage. While we are reluctant to be too prescriptive here, we share below some brief thoughts on what we believe are profitable areas for future research focus.

NGS technologies offer fantastic potential to obtain previously hidden insights into the ecology of microbial communities via the use of metatranscriptomic and metaproteomic approaches (Morales et al. 2011); these techniques define the gene expression and protein production, respectively, within communities and thus can be used to assess the immediate community responses to ecosystem variation. Future research efforts will no doubt increasingly lean on these '-omics' techniques to gain new insights into the ecology of microbial communities across all the research areas described in this review. We highlight in particular the use of NGS in human/animal/plant microbiome ecology as an area that is currently receiving, and will continue to receive,

intense global interest (Cho et al. 2012; McFall-Ngai et al. 2013; Berg et al. 2014). Nevertheless, we equally caution that there is a risk that over-reliance on such approaches can lead to a loss of appreciation for – and subsequent lack of training in – 'traditional' techniques such as bacterial cultivation, and microbial physiological and chemotaxonomic characterisation. Undoubtedly a crucial role remains for experiments that seek to cultivate, or at least enrich for, the microbes in question, as such endeavours can yield invaluable information about novel metabolisms and provide important ground-truthing for omics-derived hypotheses. A case in point is the recent description of persistence-level hydrogen utilisation by the obligate aerobe, *Mycobacterium smegmatis* (a non-pathogenic relative of *M. tuberculosis*). Genomic screening of *M. smegmatis* identified a number of hydrogenases (enzymes that can both oxidise and reduce molecular hydrogen), with unknown metabolic roles. Hydrogenases are generally considered highly sensitive to oxygen, so the maintenance of these enzymes by an aerobe was counter-intuitive. Subsequent physiological characterisation has not only demonstrated that mycobacterial strains can use sub-tropospheric concentrations of hydrogen for persistence (Greening et al. 2014a), but also that hydrogenase usage in soils is widespread and possibly a ubiquitous strategy employed by soil microorganisms (Greening et al. 2014b).

New Zealand is undeniably celebrated for its unique fauna and flora. But are our microorganisms equally unique? Does NZ simply harbour the same microorganisms as found overseas, or does there exist a NZ- (or perhaps Gondwana)-specific microbiota? Biogeography is a major subdiscipline within contemporary microbial ecology (Hanson et al. 2012), and NZ researchers are very active in this area. For example, the ongoing 1000 Springs Project ([www.1000springs.org.nz](http://www.1000springs.org.nz)) coordinated by Stott, Cary and collaborators seeks to describe the microbial inhabitants of 1000 hot spring samples from NZ and determine whether these organisms mirror those in hot springs overseas (e.g. in USA, Japan, Iceland). In a very different context, Goddard and co-workers have traced the origins of wine yeasts isolated in NZ, in some cases back to oak barrels sourced from France (Goddard et al. 2010). Other strains appeared to have a more local origin. The bacterial symbionts of moss bugs (Hemiptera), Gondwanan relicts still found in Australia, South America, and NZ have also been studied and their phylogenies compared between these regions (Kuechler et al. 2013). Given the remarkable dispersal abilities of microorganisms, particularly via aeolian currents (Yamaguchi et al. 2012; Herbold et al. 2014), it is likely that the NZ microbiota will represent a mix of cosmopolitan and endemic species. Further research in this area is warranted.

Finally, considering the ubiquity of microbes and their influence on global biogeochemical cycles, there is little doubt that future ecological research will (need to) increasingly investigate the role and influence of microorganisms in climate change. Research here is already well underway, with groups investigating the mitigation of greenhouse gas production in ruminants (CH<sub>4</sub>) and in soils (CH<sub>4</sub> and N<sub>2</sub>O), as well as the mycorrhizal influence on carbon capture above- and below-ground. We have no doubt that the emphasis on microorganisms and their role in climate modulation will increase as global steps increase to combat climate change.

We recognise that many, if not most, readers of this journal are not specialist microbial ecologists, with their research focusing more on the activities of macro-organisms such as plants and animals. It thus seems fitting to conclude this review article by returning to the first sentence in the introduction,

'This is truly the "age of bacteria" - as it was in the beginning, is now and ever shall be', a quote from Stephen Jay Gould, which we believe encompasses all that we have written above; that is, microorganisms play an essential role in all ecosystems. We encourage investigators in all ecology-based research to consider the integration of microbial ecology into their ecological studies. Microbial ecology can benefit enormously from the integration of ecological theory that was developed largely from plant and animal ecology, while microorganisms are simply too important to omit when considering the ecology of NZ environments.

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