

special issue: 

Feathers to Fur

The ecological transformation of Aotearoa/New Zealand

Causes and consequences of changes to New Zealand's fungal biota

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Published online: 6 October 2009

Abstract: This paper briefly reviews advances in knowledge of the non-lichenised fungi of New Zealand over the past 25 years. Since 1980, the number of species recorded from New Zealand has doubled, and molecular techniques have revolutionised studies on fungal phylogeny and our understanding of fungal distribution, biology and origins. The origins of New Zealand's fungi are diverse; a few appear to be ancient, whereas many have arrived in geologically more recent times following trans-oceanic dispersal. Some of these more recent arrivals have evolved subsequently to form local endemic species, while others may be part of larger populations maintained through regular, trans-oceanic gene flow. Although questions remain about which fungi truly are indigenous and which are exotic, about one-third of the fungi recorded from New Zealand are likely to have been introduced since human settlement. While most exotic species are confined to human-modified habitats, there are some exceptions. These include species with potential to have significant impacts at the landscape scale. Examples from saprobic, pathogenic, endophytic and ectomycorrhizal fungi are used to discuss the factors driving the distribution and dispersal of New Zealand's fungi at both global and local scales, the impact that historical changes to New Zealand's vascular plant and animal biota have had on indigenous fungi, and the broader ecological impact of some of the exotic fungal species that have become naturalised in native habitats. The kinds of fungi present in New Zealand, and the factors driving the distribution and behaviour of those fungi, are constantly changing. These changes have occurred over a wide scale, in both time and space, which means New Zealand's indigenous fungi evolved in response to ecological pressures very different from those found in New Zealand today.

Keywords: non-lichenised fungi; phylogeny; biogeography; origins; indigenous; endemic

Introduction

This paper briefly reviews advances in knowledge of the non-lichenised fungi of New Zealand over the past 25 years. It focuses on our understanding of the origins of New Zealand's fungal biota, the changes to that biota at both geological and human time scales, and the ecological impacts of those changes. Galloway (2007) provided a recent review and comprehensive treatment of New Zealand's lichenised fungi.

The number of species of fungi reported from New Zealand in the literature approximately doubled over the past 25 years, with 6300 species being reported to date (data from Anon. 2001–2007). This represents about one-quarter of the 22 000 species of fungi estimated to occur in New Zealand (Buchanan et al. 2004). Complementing this increase in knowledge at the alpha-taxonomic level have been huge advances in molecular technologies. These are having a profound impact on our understanding of fungal relationships (Blackwell et al. 2006) and are providing, for the first time, reliable methods for tracking the occurrence of fungi through time and across ecosystems (e.g. Carbone & Kohn 2004; Dickie & FitzJohn 2007).

This review focuses strongly on plant-associated fungi,

but fungi form pathogenic and mutualistic relationships with animals as well, especially cold-blooded animals (Casadevall 2005). Leschen (2000) reviewed the impact of feeding preference (mycophagy versus predation) on beetle phylogeny. These relationships are often highly species-specific and the questions raised below for New Zealand's plant-associated fungi with respect to the loss and gain of hosts or potential hosts are just as relevant to the arthropod-associated fungi. The insect-pathogenic Laboulbeniomycetes are barely investigated for New Zealand, but are currently subject to research by Alex Weir, Monica Hughes and others, and show high levels of endemism at both species and generic levels (Hughes 2007). A decline in frog populations has been associated with the chytrid *Batrachochytrium dendrobatidis* (e.g. Bell et al. 2004). The chytrid is assumed to be a recent introduction. The epidemiology of the frog disease caused by this fungus remains poorly understood in natural ecosystems, as do the origins and spread of the New Zealand populations of this fungus. Other fungal groups barely considered in this review are the non-Laboulbeniomycete insect pathogens, fungi of veterinary and medical importance, and the poorly studied marine and freshwater fungi.

Origin of New Zealand's fungi

New Zealand's geological and cultural history has resulted in New Zealand's biota comprising several different components:

- ancient lineages derived from the supercontinent Gondwana;
- geologically more recent introductions following natural trans-oceanic dispersal, sometimes with subsequent evolution of local endemics;
- deliberate or accidental introduction of new organisms following human settlement.

Molecular studies have shown that New Zealand's fungi reflect these diverse influences as much as other, better studied, groups of organisms (e.g. Gibbs 2006; Tennyson 2010).

Ancient taxa from Gondwana

Observations of geographic distribution have in the past been used to speculate that some of New Zealand's fungi may be ancient, the present day distribution across the Southern Hemisphere being traced back to the breakup of Gondwana. Examples include the ectomycorrhizal, *Nothofagus*-associated mushrooms *Rozites* (Bougher et al. 1994), the *Nothofagus* pathogen *Cyttaria* (Korf 1983; Buchanan et al. 2004), the discomycete genus *Bivallum*, found only on Podocarpaceae and Southern Hemisphere Cupressaceae (Johnston 1997), and the order Coryneliales, leaf pathogens of *Podocarpus*. Species-level observations invoking the same explanation (e.g. Horak 1983) probably represent examples of long-distance dispersal, because species in geographically isolated populations are unlikely to remain morphologically and genetically identical for many tens of millions of years.

Recent molecular studies challenge some of the observation-based hypotheses. For example, a molecular phylogeny of the *Nothofagus* pathogen *Cyttaria* has shown that the New Zealand species arrived here following trans-oceanic dispersal from Australia, with subsequent local species radiation (K. Peterson, pers. comm; Johnston & Peterson 2006). This explanation is congruent with the *Nothofagus* phylogeny in Knapp et al. (2005), where the only New Zealand host of *Cyttaria*, *N. menziesii*, is hypothesised to have arrived following long-distance dispersal less than 30 million years ago, long after the opening of the Tasman Sea. *Rozites*, cited as another example of an ancient Southern Hemisphere, *Nothofagus*-associated genus (Bougher et al. 1994), has been shown subsequently to be polyphyletic, with no clear relationship between Australasian and South American species (Peintner et al. 2002).

Coetzee et al. (2003) invoked ancient geological vicariance events to explain geographic relationships among Southern Hemisphere *Armillaria* species. *Armillaria* forms three broad geographic clades, one African, one predominantly Northern Hemisphere and one Southern Hemisphere (Coetzee et al. 2000, 2001, 2003; Pérez-Sierra et al. 2004). Within the Southern Hemisphere clade are two lineages, each containing species from Australia, New Zealand and South America, and the area cladograms of the species in each clade are congruent with the currently accepted geological breakup of Gondwana – (NZ (AU, SA)). However, the genetic divergence between taxa from the three regions differs markedly between the clades, suggesting a different timing of divergence events in each clade. Hence different explanations are required for geographic relationships within each clade.

One of the real problems for timing divergence within fungal phylogenies, based almost invariably on molecular data

derived from modern day taxa, is a lack of independent evidence for the ages of lineages. Fungal fossils are rare, and interpreting the relationship between these fossils and modern taxa is problematic (Taylor & Berbee 2006). One approach possible with host-specialised groups of fungi is to calibrate the fungal phylogeny using ages estimated from the host phylogeny. An as yet unpublished study of the discomycete genus *Torrendiella* in New Zealand (Fig. 1) provides an example. *Torrendiella* is highly diverse in New Zealand, all known species being restricted to a single host species, genus or family. The New Zealand and Australian *Torrendiella* spp. comprise a series of lineages, host-specialised at the level of host family or genus. Within these lineages there is often further specialisation at lower taxonomic levels. One of the *Torrendiella* clades comprises three species, each restricted to a single species of *Metrosideros*. The three *Metrosideros* hosts are closely related and, based on data provided by Wright et al. (2000), they diverged about 30 million years ago, implying that the fungi associated with each of them can be no older than this. Using this calibration across the *Torrendiella* tree dates the *Nothofagus* clade at about 80 million years old, of sufficient age to postulate that the ancestors of the present-day New Zealand and South American species in that clade were present in Gondwana prior to the separation of New Zealand.

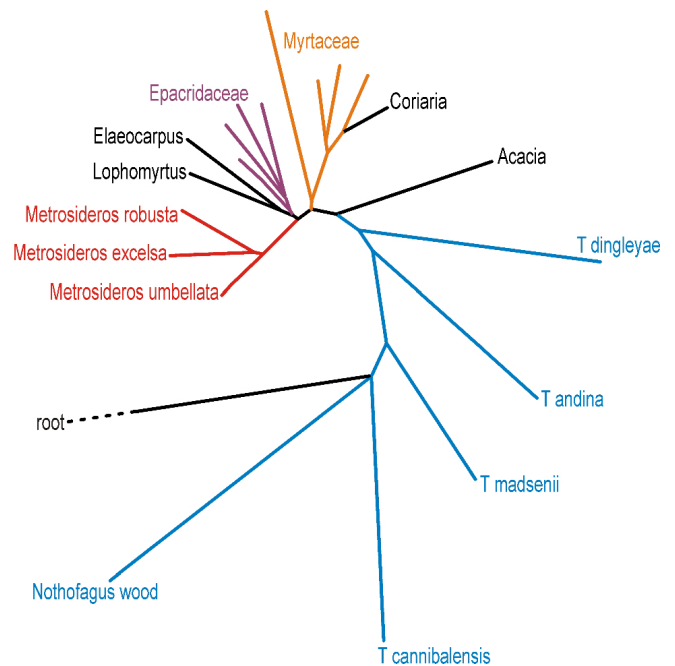


Figure 1. Phylogeny of *Torrendiella* species from New Zealand, Australia, and South America, based on a PAUP neighbour-joining analysis of ITS, rDNA LSU, calmodulin, and chitin synthase genes (unpubl. data). Each branch on the tree represents a morphologically and genetically distinct species. Most of the species are undescribed, and in these cases the taxa are labelled with the name of their specialised host plant rather than the fungus. All species in the blue clade are specialised to *Nothofagus* in New Zealand and Argentina, the orange clade to Myrtaceae in New Zealand and Australia, the pink clade Epacridaceae in New Zealand and Australia, and the red clade to *Metrosideros* in New Zealand. One of the species in the Epacridaceae clade occurs in both New Zealand and Australia, the single *Elaeocarpus*-specialised species occurs in both New Zealand and Australia, while all other species are known from only one region (the *Acacia*-inhabiting species has been introduced to New Zealand along with exotic *Acacia* species). Several of the New Zealand species in the Epacridaceae clade are each specialised to a single species of *Dracophyllum*. Sequence divergence amongst the 5 species in the *Nothofagus* clade is 7–12 % between pairs of species; in the *Metrosideros* clade is 2–3 % between pairs of species; 0.9–1.5% between isolates of the *Coriaria*-inhabiting species and its sister Myrtaceae-inhabiting species.

Introduction through natural trans-oceanic dispersal

Although there may be examples of Gondwanic breakup vicariance amongst some lineages of New Zealand's fungi, the large majority of New Zealand's native fungi almost certainly arrived in geologically more recent times, following trans-oceanic dispersal. There are many examples of the co-occurrence of genetically and morphologically identical or similar fungi between New Zealand and other regions, especially eastern Australia and tropical Asia. Some of the published examples include the discomycetes *Cookeina* (Weinstein et al. 2002) and *Leotia* (Zhong & Pfister 2004), the earthballs *Pisolithus* (Moyersoen et al. 2003), and the mushroom *Pleurotopsis* (Hughes et al. 1998), where New Zealand and Australian individuals are identical for the genes sequenced. Moncalvo & Buchanan (2008) reported a similar pattern across the Southern Hemisphere, with genetically identical populations of *Ganoderma australe* in New Zealand, Australia, and southern South America. An intriguing question is whether the fungi sampled in these studies represent individuals in single panmictic populations maintained through regular, trans-oceanic gene flow. To address this question requires more intensive sampling within each geographic region using methods aimed at distinguishing differences within populations rather than between species (e.g. Carbone & Kohn 2004). There are few, mostly preliminary, studies on population structure and gene flow between natural fungal populations within New Zealand or between New Zealand and other regions (e.g. Jin et al. 2001; Geml et al. 2005; Laursen et al. 2005), although Moncalvo & Buchanan (2008) invoke trans-oceanic gene flow as an explanation for some of the geographic patterns observed in their *Ganoderma* study.

Whether or not the biology and anatomy of fungi can be used to predict their potential to disperse remains unknown. Moncalvo & Buchanan (2008) noted that *Ganoderma* spores, aerially dispersed and with thick, melanised walls, appear to be ideally adapted to long-distance dispersal. However, Hosaka et al. (2008) also invoke long-distance dispersal to explain distribution patterns in their study of ectomycorrhizal hypogeous fungi, a group that appear intuitively to be unsuited biologically and anatomically to long-distance dispersal.

There are examples where dispersal is infrequent enough to allow for subsequent genetic divergence. The mushroom genus *Lentimula* includes American and Asian lineages, and within the Asian lineage the New Zealand endemic *L. novae-zelandiae* is estimated to have diverged about 8 million years ago from its tropical Asian ancestor, presumably following long-distance dispersal to New Zealand (Hibbett et al. 1995; Hibbett 2001). *Galerina patagonica*, a small mushroom widespread through the Australasian subantarctic and adjacent mainlands, has many genetically identical, geographically widespread populations. However, minor genetic divergence in one clade appears to show geographic structure between Auckland, Campbell and Macquarie Islands (Laursen et al. 2005). *Panellus stypticus*, a mushroom distributed widely through both the Northern and Southern Hemispheres, has distinct northern and southern clades, and the New Zealand and Australian populations are also genetically distinct (Jin et al. 2001). No estimate was made of the timing of the Australasian population divergences. Whether there is any mechanism maintaining the genetic distinctness of these populations of saprobic mushrooms, beyond the rarity of chance dispersal events, is not known. A better understanding of the factors driving evolution of fungal species in natural ecosystems awaits studies with a sampling intensity matching that applied to some of the major plant pathogens (e.g. Zhan & McDonald 2004).

The mobility of fungi must limit their potential for vicariant speciation through geographic isolation. In some instances mating compatibility is retained for long periods following isolation (e.g. Petersen & Bermudes 1992), so in theory at least the potential for successful, rare episodes of gene flow is retained. Host-specialisation is common amongst New Zealand's indigenous fungi (McKenzie et al. 2004), and using *Torreodiella* as a model (Fig. 1), Johnston & Gamundí (2002) speculated that the interruption of gene flow through host specialisation rather than geographic isolation may be one of the major evolutionary drivers for New Zealand's native fungi. In other regions, Johannesson & Stenlid (2003) and Dusabenyagasani et al. (2002) have invoked host specialisation rather than geographic distance to explain genetic structure within *Heterobasidion annosum* sensu lato and *Gremmeniella* spp. respectively.

Deliberate or accidental introduction of new organisms following human colonisation

About one-third of New Zealand's non-lichenised fungal species are exotic (data from Anon. 2001–2007). Mycology in New Zealand has traditionally had a strong focus on fungi that cause diseases of cultivated plants (McKenzie 1983). Most of our economically important cultivated plants are exotic, and most of the fungi associated with them are also exotic. This has resulted in the exotic fungi of New Zealand being the group best understood in terms of occurrence and distribution. Despite this, the number of exotic species reported from New Zealand is still steadily increasing; about 25% of the fungi first reported from New Zealand since 2000 are exotic. This increase is due to both the (mainly accidental) introduction of new fungi, as well as the recent discovery and reporting of fungi present here for many years. Rust fungi are amongst the most commonly recognised new introductions, regularly found in New Zealand shortly after becoming established in Australia (McKenzie 1998). A recent example is *Puccinia myrsiphylli*, a rust self-introduced from Australia after its introduction there as a biological control for its host *Asparagus asparagoides* (Anon. 2006). Few exotic amenity plants in New Zealand have been systematically surveyed for fungi. Many unrecorded fungi may be present. Cooper (2005) provided an example, with numerous new records of exotic fungi following an intensive survey of microfungi associated with the exotic tree *Quercus ilex*. Most exotic fungi are found in association with exotic plants and animals in human habitats, with few becoming naturalised in native ecosystems (Fig. 2).

One question basic to a discussion on exotic fungi and their impacts, is how decisions are made about whether fungi are exotic or not. Typically, these decisions have been based on observations of the ecology of the fungus. Fungi restricted to exotic plants, for example those causing diseases of corn or Pinaceae, are assumed to be exotic. Similarly, fungi restricted to native plants are assumed to be native. Similar criteria have been applied to saprobic fungi restricted to human habitats, such as mushrooms known only from pasture or only from wood-chip mulches. These have been assumed to be exotic. Almost invariably the putative exotic fungi are known from the same kinds of habitats in other parts of the world. A few fungi have been described as new from New Zealand that are specific to exotic plants, and again these are assumed to be exotic, still awaiting discovery in their native range (e.g. McKenzie 1998).

In some cases the exotic/indigenous decision is not straightforward, especially with species of wood-rotting or

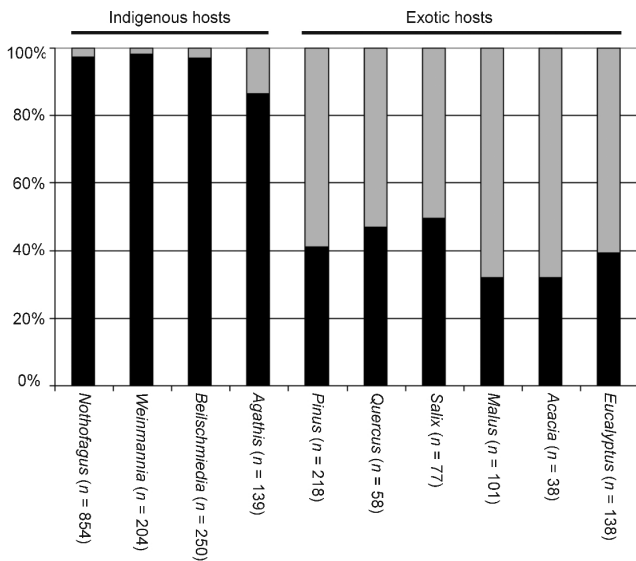


Figure 2. The proportion of indigenous (black) and exotic (grey) non-lichenised fungi on a range of tree hosts in New Zealand, both indigenous (*Nothofagus*, *Weinmannia*, *Beilschmiedia*, *Agathis*) and exotic (*Pinus*, *Quercus*, *Salix*, *Malus*, *Acacia*, *Eucalyptus*). Data from NZFungi (Anon. 2001–2007).

litter-inhabiting fungi known from both human and natural habitats, and with some plant pathogens which have a broad host range. To confirm the exotic/indigenous status of these fungi requires detailed, population level genetic studies aimed to address this question specifically. The question is important for biosecurity as well as understanding the ecology of, and threats to, native ecosystems. Specific examples include *Phytophthora cinnamomi*, a root pathogen assumed to be introduced (Newhook & Podger 1972), but with a very wide distribution in native ecosystems, and *Cryptosporiopsis actinidiae*, initially described from fruit rots from commercial kiwifruit orchards, but later found to be widespread and common as a leaf endophyte in native forests and perhaps a native fungus (Johnston et al. 2005). *Schizopora radula*, a paint splash wood-rotting fungus first collected in New Zealand from native forests in 1927 and at least now widespread in native forests, is also found on rotting wood in human landscapes and has New Zealand isolates genetically identical to some from Australia and Canada (Paulus et al. 2000). It could perhaps have been introduced from the Northern Hemisphere and subsequently become naturalised in native forests. Orlovich & Cairney (2004) raised the possibility that *Pisolithus* may have been introduced by humans along with *Eucalyptus*, despite it never being associated with this genus of trees in New Zealand and Moyersoen et al. (2003) concluding it was an example of natural long-distance dispersal from Australia to New Zealand. It is completely unexplored whether or not populations of fungi common in orchards and crops in genera such as *Botryosphaeria*, *Phomopsis* and *Colletotrichum* have arisen from native populations which have moved from natural to human landscapes, or have been introduced from other parts of the world by humans.

Confusion over the origin of a fungus can also arise if old, Northern Hemisphere names are mistakenly used to refer to collections from New Zealand. Examples include names used by early authors for the wood-rotting polypore (Buchanan & Ryvardeen 2000) and corticioid fungi (Paulus et al. 2007) and for the ectomycorrhizal *Amanita* species (Ridley 1991). Molecular studies are also revealing situations where local taxa have been inappropriately regarded as part of large, variable,

geographically widespread species. For example, the powdery mildews on *Weinmannia* and *Aristotelia*, originally described from New Zealand as *Erysiphe carpophila* and *E. densa* respectively, were placed in synonymy with a very broadly defined *E. polygoni* by Pennycook (1989), but recent DNA sequencing (*E. carpophila*, Genbank deposition DQ005440; *E. densa*, DQ005439) confirms they are distinct species native to New Zealand.

Molecular studies have the power to determine pathways through which plant pathogens have been introduced to New Zealand, potentially important for predicting biosecurity risks. Examples include the pine needle endophyte *Lophodermium pinastri*, a fungus shown by Johnston et al. (2003b) to comprise genetically distinct European and North American clades, with all the New Zealand isolates sampled matching those from North America. *Amanita muscaria* is widespread throughout the Northern Hemisphere, has been introduced to New Zealand and is present here under trees from both North America and Europe. Oda et al. (2004) and Geml et al. (2006) included a single New Zealand isolate in studies with a broad sample from the Northern Hemisphere. Strong genetic and geographic structure was revealed across the Northern Hemisphere, but the New Zealand isolate could not be linked with certainty to any of the northern populations sampled. Although the *Amanita* studies demonstrate the power of the method, more intensive sampling is needed to determine whether there have been multiple introductions of this fungus to New Zealand, and to determine the origin(s) of those introduced populations.

New Zealand collections of the insect pathogens *Beauveria* have been compared genetically with those from other parts of the world (Reay et al. 2007). Rehner & Buckley (2005) demonstrated cryptic genetic variation within the morphologically defined, cosmopolitan species *Beauveria bassiana*, variation that appeared to be at least partly geographically defined, but they included no New Zealand isolates in their study. New Zealand isolates of this fungus collected from South Island beech forests were genetically diverse, matching isolates from three separate clades from other parts of the world. One of the New Zealand isolates belongs in a clade with specimens primarily from northern Asia, another in a clade with specimens primarily from Europe, and the third in a clade with specimens primarily from North America (Reay et al. 2007). It is not known whether the geographic structure shown by Rehner & Buckley (2005) will break down with more intensive geographic sampling, or whether these results suggest *B. bassiana* is exotic in New Zealand, its occurrence here resulting from several independent introductions from different parts of the world.

Impact of exotic fungi on natural ecosystems

The impact on indigenous ecosystems of exotic naturalised fungi is often limited (e.g. McKenzie 1998), but in some cases potentially significant. A speculative discussion on these possible landscape-scale impacts is presented below for mycorrhizal, saprobic and plant pathogenic fungi associated with native plants.

Mycorrhizal fungi

The importance of mycorrhizal fungi to the health and nutrition of plants means that changes to mycorrhizal fungal communities have potential to create an impact at the landscape scale. The exotic ectomycorrhizal mushroom *Amanita muscaria* is widespread in New Zealand in association with a range of exotic trees, but has become naturalised in *Nothofagus*

forests at several sites (Stevenson 1958; Johnston et al. 1998; Bagley & Orlovich 2004). The sites at which *A. muscaria* is becoming naturalised appear to be increasing (Johnston et al. 1998; unpubl. data) and are often clustered, suggesting that initial establishment at a site could perhaps be followed by localised spread. Persistent at sites where it has become invasive, this fungus has potential to disrupt the diversity of the natural fungal communities of *Nothofagus* forests (Bagley & Orlovich 2004), which in turn may impact on the other parts of the biota normally associated with those fungi. The competitive ability of the individual *Nothofagus* trees infected by the fungus could be affected. Individual *Nothofagus* trees are infected by a phylogenetically diverse set of mycorrhizal fungi, and this phylogenetic diversity is likely to reflect also a broad physiological diversity (Read 1991). If the presence or absence of *A. muscaria* affects the diversity of fungi found on an individual tree, this then has the potential to change the physiological tolerance of that tree. Another potential impact could be *A. muscaria* acting as a kind of 'Trojan horse', facilitating invasion of beech forests by exotic ectomycorrhizal tree species usually excluded by their inability to utilise native ectomycorrhizal fungal partners. Bagley & Orlovich (2004) investigated population structure of *A. muscaria* at one urban site in New Zealand, important basic information to understand the behaviour of the fungus, but there have been no studies as yet on its impact on invaded ecosystems. Such studies will need to target below-ground ectomycorrhizal diversity; such diversity is sometimes poorly correlated with the above-ground diversity assessed using fruit body observations (e.g. Gardes & Bruns 1996).

Another example of potential impact on native ecosystems is the role that exotic species of the ectomycorrhizal fungi *Suillus* and *Rhizopogon* have on the invasion of native grasslands by weedy pines (Dickie et al. 2007). *Suillus* and *Rhizopogon* appear to have spores with the ability to persist in the soil for long periods, allowing inoculum to build up to levels sufficient for the establishment of seedlings across the landscape, independent of existing ectomycorrhizal trees. It is widely observed that the seedlings of obligately ectomycorrhizal plants establish successfully only within the established root zones of existing mycorrhizal trees, a biology that has been implicated in the slow spread of *Nothofagus* in New Zealand since the last glaciation (Baylis 1980). *Nothofagus* is unable to utilise the exotic *Suillus* and *Rhizopogon*; these fungi form mycorrhizal partnerships with Pinaceae alone. The distribution and physiology of the potential mycorrhizal associates of *Nothofagus* and *Pinus* appear to be driving the different abilities of these trees to expand their range in New Zealand.

Ericoid mycorrhizal fungi have the ability to extract nutrients directly from organic materials in low pH, waterlogged and often cold soils, making their ericaceous mycorrhizal partners very competitive in heathlands (Read 1991, 1996). Most mycorrhizal fungi of ericaceous plants from both the Northern and Southern Hemispheres are members of the Helotiales, but within the order the Australian epacridaceous mycorrhizas are phylogenetically distinct from those on Northern Hemisphere Ericaceae (Berch et al. 2002; McLean et al. 1999), and the same is likely to be true of New Zealand's native ericoid mycorrhizal species. In the central North Island, native heath communities have been invaded by *Calluna vulgaris* (heather), deliberately introduced from the Northern Hemisphere in the early 1920s. Assuming the invasive *Calluna* plants are associated with exotic mycorrhizal fungi and the native epacrids with indigenous mycorrhizal fungi,

then understanding the biological differences and interactions between the two groups of fungi will help understand patterns of invasion of this weed. For example, competition between, and comparative physiological abilities of, the native and exotic mycorrhizal fungi may in part control the susceptibility to invasion of native heath communities at particular sites. Also, invasion by *Calluna* may change the mycorrhizal inoculum potential of the soil, impacting on the ability of native epacrids to re-establish following weed control. Apart from the fact that morphologically and functionally typical ericoid mycorrhizas are present on the roots of native epacrids in New Zealand (Brook 1952; Morrison 1957; McNabb 1961), nothing is known about the ecology, diversity, identity or distribution of these fungi in New Zealand.

Saprobic fungi

The NZFungi database records a number of saprobic, putatively exotic fungi from native plants, but the only one well-characterised in terms of its exotic status and its naturalisation in indigenous ecosystems is the orange-pore fungus *Favolaschia calocera*. Field observations suggest this fungus was first introduced to New Zealand in the 1950s and it is now widespread in forests through the warmer parts of New Zealand (Johnston et al. 1998, 2006). Genetic studies confirmed its exotic status (Johnston et al. 2006). The abundance of fruiting bodies of *F. calocera* at some sites suggests it may be displacing native saprobic fungi normally found at those sites, although again the possible lack of correlation between fruit body production and hyphal abundance needs to be kept in mind (e.g. Gardes & Bruns 1996; Allmér et al. 2006). The ability of *F. calocera* to produce the anti-fungal strobilurans (Nicholas et al. 1997) provides a possible mechanism through which it might displace other fungi. However, laboratory tests using agar and sawdust substrates suggest it has poor competitive ability, being displaced by a range of native wood-rotting fungal species (Johnston et al. 2006). *Favolaschia calocera* is unusual amongst basidiomycetes in being homothallic, able to form fertile fruiting bodies from a single basidiospore. This may in part explain its weedy biology; it is able to colonise a substrate rapidly and produce spores, but unable to defend that substrate against invasion from other species of fungi. However, the competitive ability of *F. calocera* has not been tested in natural situations, and it may be able to displace groups of fungi that are yet untested. Other unpredictable impacts of *F. calocera* are possible. For example, Dickie et al. (2007) showed that the history of species colonisation has an impact on fungal community structure; they suggested that the addition of the early-colonising *F. calocera* to the forests could alter the fungal community that might otherwise develop.

Favolaschia calocera has a high profile as a naturalised, exotic fungus because its brightly-coloured, distinctive fruiting bodies are easily seen and identified in the forest. The presence and impact of other naturalised saprobic fungi is perhaps being overlooked because of the more cryptic appearance of their fruiting bodies.

Plant pathogenic fungi

Of the exotic plant-pathogenic fungi naturalised in New Zealand native ecosystems, it is the *Phytophthora* species which have most potential to cause landscape-scale impacts. Diseases caused by *Phytophthora* spp. have the ability to kill large trees rapidly, and internationally have resulted in changes to plant community composition over a large scale in many regions. Examples include Dieback in Australia caused by

P. cinnamomi (e.g. Grant & Barrett 2003), and Sudden Oak Death in North America and Europe caused by *P. ramorum* (e.g. Brasier et al. 2004).

An emerging issue in New Zealand is Collar Rot disease of kauri (*Agathis australis*), caused by an as yet unidentified, putatively exotic *Phytophthora* sp. This fungus attacks the vascular system of kauri trees, causing bleeding lesions near the base of the trunk. It can ringbark and kill trees, both large and small. Known from several sites, infected areas tend to be restricted in size (from 1 ha to about 10 ha), but a large proportion of trees within those sites will be infected (Beever et al. 2007). As this disease spreads, it has the potential to seriously threaten kauri forest communities at a landscape scale.

Phytophthora cinnamomi is widespread through New Zealand, in both native and human ecosystems. Limited genetic studies support its putative introduction by humans (Beever et al. 2007), but it could have been introduced by the first Polynesian settlers (Newhook & Podger 1972), so potentially present in New Zealand for around 800 years (Wilmhurst & Higham 2004). *Phytophthora cinnamomi* infects a wide range of New Zealand plants, kills a proportion of fine roots, but causes little visible disease unless infected plants are under additional environmental stress. Johnston et al. (2003a) discussed the impact of *P. cinnamomi* on regeneration of kauri and *Nothofagus* seedlings, speculating that the addition of the fungus to these forest ecosystems could have altered the long-term regeneration dynamic of these forests. *Nothofagus* has been expanding more slowly than other forest types in New Zealand, and it remains out of balance with the environment since the last glaciation (Leathwick 1998). Most seedlings establish within the root zone of existing trees, which allows seedlings to become rapidly infected by mycorrhizal fungi. This need for rapid development of mycorrhizas has been attributed to the inability of seedlings to otherwise survive in New Zealand's low phosphorus soils (Wardle 1980). However, field and shade house observations by Johnston et al. (2003a) suggested that the need for rapid mycorrhizal development may relate to protection against disease caused by *P. cinnamomi*, rather than nutrient capture. If this is the case, then perhaps the natural spread of *Nothofagus* has slowed following the introduction of *P. cinnamomi* to New Zealand by humans.

Phytophthora cinnamomi is widespread in kauri forests. Horner (1984) showed it reduced seedling establishment at those sites particularly suited to disease development. Sites on which kauri seedlings establish preferentially (high light, high temperatures and potentially prone to drought) are also those that favour infection by the fungus and the development of disease. The extreme age of mature kauri trees and the cohort regeneration model of kauri forests (Ogden et al. 1987) mean the visual impact of the introduction of this fungus on kauri forest dynamics will be subtle at human time scales, but the fungus could lead to long term changes in natural regeneration patterns of these forests (Johnston et al. 2003a).

Impact on fungi of changes to associated biota

Since its split from Gondwana about 80 million years ago, New Zealand has had a continuous history of turnover in plant species through loss by extinction and gain by introduction as a result of long-distance dispersal. Many fungi evolve to become host-specialised, so those specialised to a host lineage which becomes extinct must inevitably also become extinct. This raises an interesting dilemma in relation to some of New Zealand's putative ancient fungi. For example, the phylogenetically isolated (Vellinga 2004)

New Zealand endemic and monotypic *Notholepiota areolata* is an ectomycorrhizal species restricted to the roots of *Kunzea ericoides* and *Leptospermum scoparium*, two geologically recent introductions to New Zealand (Harris et al. 1992). Its biology and geographic distribution suggest this *Notholepiota* species might have evolved in association with a now extinct member of the New Zealand *Leptospermum*-like Myrtaceae (Fleming 1979) and is present today only because it was able to successfully switch hosts within the family over evolutionary time (note that no other extant New Zealand native Myrtaceae is ectomycorrhizal). Another example of this dilemma is provided by the putatively ancient *Nothofagus*-specialised *Torreodiella* spp. discussed above in the section on ancient fungi. The history of the genus *Nothofagus* in New Zealand has apparently been continuous, but individual species, and whole subgenera, have undergone a series of extinctions followed by reintroduction through long-distance dispersal (Knapp et al. 2005). How the putatively ancient *Nothofagus*-specialised fungi have managed to survive despite the extinction of the hosts with which they must have originally evolved has not been explored. A feature of New Zealand's *Nothofagus*-associated fungi is their extreme diversity (McKenzie et al. 2000). Many of these fungi are confined to *Nothofagus* and how this diversity has been maintained in the light of ongoing extinction of the hosts is unknown.

Although few of New Zealand's exotic fungi have become naturalised in native habitats, a significant proportion of fungi associated with exotic plants are native (Fig. 2). Just as the extinction of hosts has provided an ongoing threat to New Zealand's fungi, the introduction of new plants has provided new evolutionary opportunities. Because host specialisation is a major driver of fungal evolution, the introduction of these new plants provides novel evolutionary opportunities for those fungi able to take advantage of them. One recent overseas example has been the adaptation of the South American rust *Puccinia psidii* to *Eucalyptus* in plantations in Brazil. Originally reported on *Eucalyptus* in Brazil in 1912, the first serious disease outbreak was in 1973, in a plantation established using South African seed of *Eucalyptus grandis* (Coutinho et al. 1998). In New Zealand, few indigenous fungi have had significant economic impact in human-modified ecosystems. Exceptions include the mushroom *Armillaria*, pathogenic to kiwifruit vines (Horner 1992) and pine seedlings (Gadgil 2005), and the corticioid fungus *Gloeocystidiellum sacratum*, a root and stem pathogen of introduced conifers and other trees (Dingley 1969, as *Peniophora sacrata*).

The potential for native fungi to take advantage of the new opportunities provided by new plants will not be confined to human time scales; it is likely to have been occurring regularly over geological time and is very relevant to understanding the evolution of New Zealand's natural plant communities. The geologically recent host switch within a Myrtaceae-specialised clade of *Torreodiella* to *Coriaria*, a plant genus first established in New Zealand less than 10 million years ago (Yokoyama et al. 2000), provides an example for a plant which was not introduced by humans (Fig. 1).

The influence that New Zealand's pre-human, bird-dominated animal biota had on the evolution of some distinctive features of New Zealand's plants has been long debated (e.g. McGlone & Webb 1981; Lee et al. 2010; McGlone et al. 2010; cf Gibbs 2010). New Zealand-specific adaptations in one group of New Zealand's fungi also may have been due to birds. The hypogeous basidiomycetes, with the spore-producing part of the fruiting body remaining enclosed, rely on animal

vectors for spore dispersal. In most parts of the world the vectors are small mammals and generally the fruiting bodies of these fungi are rather dull in colour, attracting their vectors through smell. In New Zealand, the hypogeous fruiting bodies are often bright, in colours known to attract birds, perhaps New Zealand's major pre-human vectors of these fungi (Beever 1999). The loss of much of New Zealand's ground-bird biota will have had a major impact on the ecology of these fungi, by disrupting their natural patterns of dispersal. Although there is evidence that introduced mammals eat fungi at some sites (Cowan 1989; Sweetapple 2003), little is known about the kinds of fungi targeted. If they include the hypogeous fungi previously dispersed by birds, it is not known whether these fungi, having evolved to attract birds, are able to attract mammals in sufficient numbers to provide effective spore dispersal.

Discussion

The kinds of fungi present in New Zealand, and the factors driving the distribution and behaviour of those fungi, are constantly changing. These changes have occurred over a wide scale, in both time and space, which means New Zealand's indigenous fungi have mostly evolved in response to ecological pressures very different from those found in New Zealand today. For example, New Zealand's *Nothofagus*-associated fungi evolved largely in response to a *Nothofagus* diversity dominated by the subgenus *Brassopora* (McGlone et al. 1996) that is now extinct from New Zealand. Recent human-mediated additions to New Zealand's fungal biota have potential to cause impacts at the landscape scale, with the addition of new diseases and changes to patterns of regeneration in New Zealand's forests. Additions to New Zealand's plant biota, on both human and geological timescales, have provided new opportunities for New Zealand's indigenous fungi to evolve in novel directions.

Knowledge of the occurrence and behaviour of New Zealand's fungi is increasing, driven in part by technological advances. Molecular technologies are now essential research tools, even for basic alpha-taxonomic studies on fungi. For the first time in the history of mycological research such technologies provide the ability to develop reliable phylogenies, address questions about the ages and origins of fungal lineages, and determine the exotic/indigenous status of fungal species. The subsequent increase in knowledge is revealing a complex set of relationships with respect to both the origins and geographic relationships of New Zealand's indigenous fungi. For example, New Zealand species of the wood-rotting fungus *Hypochnicium* each have a sister relationship with a phylogenetically diverse range of Northern Hemisphere species (Paulus et al. 2007). In contrast, the species of *Armillaria*, another wood-rotting fungus, group mostly into distinct Northern and Southern Hemisphere clades (Coetzee et al. 2001), but even in this genus there is a single Australasian species in the Northern Hemisphere clade, suggesting a single, geologically recent long-distance dispersal event from the north to the south. *Chlorociboria*, a genus of wood-inhabiting ascomycetes, is morphologically and genetically highly diverse in New Zealand, but has two Northern Hemisphere species in terminal clades, suggesting, in this case, rare, geologically recent dispersal events from the south to the north (Johnston & Park 2005).

Some of New Zealand's fungi are special in terms of understanding fungal relationships on a global scale because they represent members of exclusively southern lineages or basal Southern Hemisphere lineages of geographically widespread clades. Examples include: the *Chlorociboria* plus *Cyttaria* clade basal to the Erysiphales (Wang et al. 2006), itself an order with basal southern genera (Takamatsu et al. 2005); basal lineages amongst the Gomphales and Hysterangiales that are often southern (Hosaka et al. 2006); the New Zealand endemic *Flammulina stratosa* that is basal in the genus (Hughes et al. 1999); and the Southern Hemisphere genus *Austropaxillus* that is one of the basal clades of the Boletales (Binder & Hibbett 2006). Similarly, the Southern Hemisphere genus *Chlorovibrissea*, plus southern species of the genus *Vibrissea*, are genetically distant from Northern Hemisphere species of *Vibrissea* (Wang et al. 2006). Ensuring more robust phylogenies through sampling genetic diversity not represented by taxa from the Northern Hemisphere also has the benefit of increasing knowledge of New Zealand's fungal diversity. Over the last 25 years approximately 40% of the fungal species described as new from New Zealand have been described by overseas-based authors (data from Anon. 2001–2007). Continuing strong international collaboration is important to maintain progress in discovering and describing the approximately 15 000 species of as yet unknown species of New Zealand fungi.

Acknowledgements

The ideas and themes developed in this review have resulted from discussion with many colleagues from within Landcare Research and elsewhere. Kris Peterson (Farlow Herbarium, Harvard University) kindly provided access to unpublished data on *Cyttaria* phylogeny from her PhD thesis. I thank Duckchul Park (Landcare Research) for the *Torreodiella* sequencing and for providing sequences for specimens of *E. carpophila* and *E. densa*. Preparation of this paper was supported by the New Zealand Foundation for Research, Science and Technology through the Defining New Zealand's Land Biota OBI (Outcome-based Investment). The Department of Conservation and Landcare Research supported the publication of this special issue.

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