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Naturalised plants transform the composition and function of the New Zealand flora

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Abstract The New Zealand flora has a high proportion of endemic species but has been invaded by almost the same number of non-native plant species. To support management of invasive plant species, we provide an updated inventory of New Zealand's naturalised flora and compare it with the native flora to identify key taxonomic and functional distinctions. We also assess how the naturalised flora may impact ecosystem processes differently than the native flora using functional traits related to plant resource use strategy. The 1798 species in the naturalised flora currently comprise 43.9% of the total number of vascular plant species, and add 67 plant families and 649 genera to the total vascular flora. The naturalised flora has a greater proportion of herbaceous species and annual species than the native flora, which could influence ecosystem processes such as decomposition and nutrient cycling. Naturalised trees have higher leaf nitrogen concentration for a given leaf area than native trees, which could increase rates of nutrient cycling in invaded forest ecosystems. A greater number of naturalised species are present in larger, more northerly, and more populated regions of New Zealand. Our results demonstrate both taxonomic and functional

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differences between the native and naturalised flora of New Zealand that can be used to guide management of naturalised plants, including the 314 species currently managed as environmental weeds, from the local to national scale.

Keywords Exotic species · Functional traits · Indigenous plant species · Naturalised plant species · Plant growth forms · Regional distribution

Introduction

New Zealand is an isolated archipelago ranked among the world's top 25 biodiversity hotspots (Myers et al. 2000) because of high endemism (e.g., 83% of reptiles, 99% of millipedes, 100% of conifers, 85% of angiosperms; Lee, Lee 2015) but it is also "ravaged by biological invasions" (Simberloff 2009). The effects of invasive non-native mammals in New Zealand are well documented, and introduced mammals are the focus of national initiatives to reduce or even eradicate some species (Owens 2017; Peltzer et al. 2019). However, a contemporary nationwide management strategy for non-native plants has lagged behind that developed for mammals, despite legislative efforts (reviewed in Hulme 2020) to control the high levels of plant invasions (Gatehouse 2008; Williams and West 2000) that continue to increase through ongoing naturalisation (i.e. establishment of self-sustaining wild populations of introduced non-native species, Blackburn et al. 2011; Howell 2019; Williams and Cameron 2006). Here, we update a previous inventory of the naturalised flora of New Zealand (Howell and Sawyer 2006) and compare it with the native flora to identify key taxonomic and functional distinctions. Our aim is to support management of naturalised plants at local and national scales by summarising our current knowledge of naturalised species traits and distribution at the scale of the whole flora (Blackburn et al. 2014; Nunez-Mir et al. 2019).

The native flora is highly endemic at the species level but very few genera and no plant families are endemic to New Zealand. The ca. 2000 km of ocean that has separated New Zealand from the nearest continent (Australia) for at least 50 million years has acted more as a selective filter than a barrier to immigration (McGlone et al. 2001), and the extant flora is surprisingly young, mostly arriving after the Oligocene (Heenan and McGlone 2019). The flora is also functionally distinct compared to other temperate, continental areas, a consequence of its isolation and highly oceanic climatic regime (McGlone 2006). Prior to human settlement, dense evergreen podocarp-angiosperm forests dominated lowland to subalpine landscapes. Few native species are deciduous or summer-green (McGlone et al. 2004) and many native tree species are small-statured (McGlone et al. 2010). Mammalian browsers and grazers were completely absent prior to European arrival (Atkinson 2006), their place taken by birds which, lacking teeth and prehensile tongues, may exert quite different pressures on the vegetation (Antonelli et al. 2010; Wilson and Lee 2012). These and other differences have resulted in a flora lacking species with trait combinations that are common in other similar temperate environments; such apparently unoccupied ecological spaces have been described as 'functional gaps' (Blonder 2016; Dansereau 1964; Lee 1998).

The introduction of non-native plant species to New Zealand by humans broke down biogeographic barriers and filled apparent functional gaps in the flora. When Māori arrived in New Zealand (ca. 1280 AD; Wilmshurst et al. 2008), approximately 90% of the archipelago was forested (McGlone 1983) and open habitats were confined to the alpine and other areas where disturbance, climate or soils precluded dominance by trees. Fire frequency and severity increased significantly with human settlement, transforming large areas of closed canopy forest ecosystems to open, seral vegetation (McGlone 1983; McWethy et al. 2010). Colonisation by Europeans from the 1770s onwards accelerated deforestation. Fire regimes were intensified, wetlands were drained, and most suitable soils were given over to pastoral agriculture. Both pastoralism and forestry were initially based on native grasses and trees but quickly transitioned to a near complete dependence on non-native species. More than half of New Zealand's land area is now comprised of a range of ecosystems dominated by non-native plants (Hulme 2020; Thomson 1922; Walker and Bellingham 2011).

Non-native plant species were introduced to New Zealand deliberately for agriculture, forestry and horticulture (Gatehouse 2008; Smith et al. 2000; Thomson 1922; Williams and Cameron 2006), with accidental introductions accompanying many of these sources (e.g. as seed contaminants). Deliberately introduced species were selected for their ornamental novelty or to fill functions or services not provided sufficiently by native species (see Castro-Díez et al. 2019 for a global treatment of this trend; Hulme 2020). Māori introduced perhaps a dozen plant species from the Pacific (Horrocks 2004; Leach 2005; Williams and Cameron 2006), while Europeans introduced >25,000 species from all regions of the world (Crosby 2004; Diez et al. 2008, 2009; Fridley and Sax 2014; Gatehouse 2008; Howell 2019). Deliberately introduced species were often selected for their ability to thrive under the prevailing climatic conditions, ease of establishment, rapid growth, and high fecundity, and unintentionally introduced species include cosmopolitan invaders with rapid growth and high fecundity (e.g., *Jacobaea vulgaris, Erigeron sumatrensis*). It is thus unsurprising that ca. 10% of plant species introduced to New Zealand have naturalised (i.e. established wild populations; Williams and Cameron 2006), though anthropogenic drivers such as source selection and introduction effort can be much stronger than biological characteristics of species for determining rates of naturalisation and invasion (McGregor et al. 2012).

Naturalisation of introduced plants in New Zealand was already apparent in the first half of the nineteenth century (Darwin 1859; Kirk 1870), and the rate of naturalisation has increased since (Atkinson and Cameron 1993; Gatehouse 2008), particularly from the mid-twentieth century (Hulme 2020). Naturalised plants now dominate much of New Zealand's urban and rural landscapes. Auckland, the country's largest city, has been described as the "world's weediest city" (cf. Esler 1988). Naturalised plants readily invade habitats subject to disturbance, such as abandoned agricultural land (Mason et al. 2016), riverbeds, and dunes (Brummer et al. 2016; Hilton et al. 2005), but are also a concern for public conservation land, with over 300 'environmental weeds' actively managed due to their known or expected environmental impacts (Howell 2008).

Many naturalised plants in New Zealand are likely to be distinct from native species, even within similar taxonomic or functional groups, due to different biogeographic origins, and thus evolutionary selection pressures, as well as anthropogenic selection for certain traits as described above. Such trait differences could result in naturalised species having substantial environmental and economic impacts. For example, naturalised grasses and herbs are often faster-growing and shorter-lived, with lower tissue density and higher foliar nitrogen (N) concentrations than native species (Craine and Lee 2003; Kichenin et al. 2013; Peltzer et al. 2009), with consequences for grassland community dynamics (Gross et al. 2013). Additionally, several naturalised woody species have traits linked to pyrogenicity such as serotiny, thick bark, the ability to sprout vigorously, and high litter (fuel) accumulation (Wyse et al. 2018), traits which few species in the native flora possess because natural fires were rare in New Zealand prior to human colonisation (Perry et al. 2015). Greater understanding of functional differences between the native and naturalised flora should better enable land managers to prioritise management efforts based on likely impacts (e.g. faster nutrient cycling and litter decomposition associated with higher foliar N).

Here, we provide an updated inventory of naturalised plant species in New Zealand and explore differences between the native and naturalised floras and the features of environmental weeds in three key areas: taxonomic composition, growth forms and life history, and a case study of functional differences in tree leaf N. We also document the distribution of naturalised plants and environmental weeds across the political regions of New Zealand.

Methods

We compiled a list of vascular plant species occurring outside cultivation in the New Zealand political region (including the Chatham, Kermadec, and New Zealand Subantarctic Islands) as of July 2020 using checklists of the seed plant (Schönberger et al. 2020a) and fern and lycophyte floras (Schönberger et al. 2020b), as well as updates to the online database from which these checklists were drawn (Allan Herbarium 2000). We extracted species classified as 'native' ("occurs naturally in the region") or 'naturalised' ("accidentally or deliberately introduced into the region" and "has self-maintaining populations in the wild") from these checklists, excluding cultivars, hybrids with both parental taxa in the wild non-native flora, and taxonomic treatments below the level of species (Online Resource 1). We further classified 314 of the 1798 naturalised plant species as 'environmental weeds' sensu Howell (2008), defined here as naturalised species either managed in at least one weed control programme, or expected to have negative impacts on at least one site, on public land administered for conservation (Online Resource 1). Environmental weeds thus exclude many species classified as urban and agricultural weeds. Our list of environmental weeds differs from the 328 species presented in Howell (2008) as a result of taxonomic changes and our exclusion of native species, cultivars, and 'casual' non-native species (i.e. a species "accidentally or deliberately introduced into the region" that "occurs only occasionally in the wild…or only in the vicinity of cultivated/captive parents"; Blackburn et al. 2011; Schönberger et al. 2020a, b).

Taxonomic composition

We classified all vascular species into four taxonomic groups: dicotyledonous angiosperms ('dicots'), monocotyledonous angiosperms ('monocots'), gymnosperms, and ferns and lycophytes ('ferns and allies'; Online Resource 2). We calculated the number of species per taxonomic group, family, and genus, and the number of families and genera per taxonomic group, for the native and naturalised floras, as well as for the subset of naturalised species classified as environmental weeds. Because many families and genera are unique to either the native or naturalised flora, we used a two-tiered approach to compare the taxonomic composition of the native to the naturalised flora. First, we tested whether the Jaccard similarity between native and naturalised families present in New Zealand, and between native and naturalised genera present in New Zealand, was lower than expected using the bootstrap method (based on 1000 iterations; see Table 1 for calculated expectations) in the *jaccard* package (Chung et al. 2018) in R version 4.0.2 (R Development Core Team 2020). We conducted these tests for the whole floras and within each taxonomic group. Second, we used Chi-square tests for independence with a simulated p value (based on 2000 iterations) in R to compare the family and generic composition (i.e. species distribution among families and species distribution among genera) of the native to the naturalised flora for the whole floras and within each taxonomic group.

Plant growth forms and life histories

We compared growth form and life history composition of the native and naturalised floras to identify functional gaps in the native flora that may have been filled by naturalised species. We assigned each species a growth form and life history category using descriptions from published floras and online resources (see references in Brandt et al. 2020a, b), recognising six growth form categories (tree, including tree ferns; shrub; subshrub; herb, including ferns and lycophytes; caespitose; and climber, including vines and lianas; see Online Resource 3 for definitions). Species described as having multiple growth forms were classified in the category of largest size or longevity (e.g., a species described as "tree or shrub" was classified as a "tree"). We conducted two-sample proportion tests in R to compare the proportions of woody species (trees and shrubs), herbaceous species (herbs and caespitose), and climbers in the native vs. naturalised floras and for natives vs. environmental weeds.

We classified species into three life history categories (annual only, perennial only, and other, which comprised a variety of life histories including biennial and species whose lifespan ranged from annual to perennial). We conducted two-sample proportion tests in R to compare the proportions of annual and perennial species in the native and naturalised floras, and the proportions of perennial species in the native flora vs. environmental weeds.

Functional differences: case study of tree leaf N

We compared leaf N-use strategy between native and naturalised trees based on tree leaf N content and specific leaf area (SLA). We extracted leaf N and SLA data for angiosperm and gymnosperm tree species from the TRY online database (Kattge et al. 2020) supplemented with primary data collected in New Zealand, resulting in data for both traits for a total of 108 native and 73 naturalised tree species (see references in Online Resource 4; Brandt and Richardson 2020). We excluded data for N-fixing trees (3 native and 7 naturalised species) from our analysis as they were often outliers with high leaf N. We focused this case study on trees to minimise differences in other confounding variables that could differ between native and naturalised species (e.g. life history), and

Table 1 Comparisons of the taxonomic composition of the native and naturalised vascular floras in New Zealand

	Jaccard similarity			Chi-square	
	Expectation	$J_{centred}$	*P*	χ^2	*P*
Comparison of families					
Whole flora	0.53	− 0.14	**0.001**	1351.9	**< 0.001**
Dicots	0.55	− 0.12	**0.001**	859.2	**< 0.001**
Monocots	0.46	− 0.20	**0.003**	305.4	**< 0.001**
Gymnosperms	0.52	− 0.12	0.50	40.5	**< 0.001**
Ferns and allies	0.45	− 0.05	0.18	71.5	**< 0.001**
Comparison of genera					
Whole flora	0.34	− 0.24	**0.001**	3166.2	**< 0.001**
Dicots	0.31	− 0.20	**0.001**	2185.4	**< 0.001**
Monocots	0.35	− 0.26	**0.001**	748.5	**< 0.001**
Gymnosperms	0.33	− 0.33	**0.004**	49.0	**< 0.001**
Ferns and allies	0.26	− 0.12	**0.001**	132.5	**< 0.001**

Similarities in presence of families and genera (determined using a Jaccard similarity test), and distributions of species across families and genera (determined using a Chi-square test for independence), were compared across the whole flora and within each of four taxonomic groups: dicotyledonous angiosperms ("Dicots"), monocotyledonous angiosperms ("Monocots"), gymnosperms, and ferns and lycophytes ("Ferns and allies")

P-values < 0.05 are given in bold

because data on these traits were available for a good proportion of both native (45.9%) and naturalised species (33.8%) present in New Zealand. Similar analyses for New Zealand ferns and grasses were precluded by limited data availability. We could obtain leaf N and SLA for 97 native ferns (48.3%) and 101 naturalised grasses (40.4%), but only 6 naturalised ferns (24.0%) and 15 native grasses (7.8%).

We calculated mean leaf N content per unit leaf area (leaf N_{area}; g m^{-2}) as a measure of resource-use strategy (i.e. photosynthetic capacity per unit leaf area), which distinguishes species having a more conservative resource use strategy, characterised by low leaf N concentration and low leaf turnover, from species having a high resource use strategy, characterised by high leaf N concentration and more rapid turnover of leaves (Wright et al. 2004). We compared tree leaf N_{area} between native and naturalised species, and between deciduous species and evergreen species using a linear mixed effects model with the *lme4* R package (Bates et al. 2015), after confirming normality of the response variable distribution. Native status was treated as a fixed effect and genus nested within family and taxonomic group (i.e. dicot, monocot, gymnosperm) as a random effect to account for phylogenetic relatedness among species. The significance of the fixed effect was tested by comparing a full model to a null model with only the random effect based on maximum likelihood (Bates et al. 2015).

Distribution of naturalised plant species

We determined the presence of naturalised species and environmental weeds within each of the 16 mainland political regions across New Zealand (i.e. excluding offshore islands; Stats NZ 2019) using the R packages *rgbif* (Chamberlain and Boettiger 2017) and *sf* (Pebesma 2018), and all available records from the Global Biodiversity Information Facility (GBIF). We downloaded all reliably georeferenced records from GBIF that were listed as being in New Zealand and that matched a naturalised species name in our list (Schönberger et al. 2020a; Schönberger et al. 2020b) with >95% confidence (Etherington and Brandt 2020). We calculated the total number of naturalised species and environmental weeds that occurred within each political region, and the number of regions in which each naturalised species and environmental weed occurred.

Results

Taxonomic composition

As of 2020, naturalised plant species comprised 43.9% of New Zealand's vascular plant flora (Fig. 1, Online Resource 5). The naturalised flora was more taxonomically diverse (150 families and 759 genera) than the native flora (145 families and 426 genera), with 67 families and 649 genera unique to the naturalised flora (Online Resource 5). The native and naturalised floras were less similar to each other with respect to family and generic composition than expected by chance ($P = 0.001$ for each Jaccard test of whole flora comparisons; Table 1), with only 83 of 212 families and 110 of 1075 genera shared between the floras (Online Resource 5, Online Resource 6). The native and naturalised floras were also less similar than expected by chance in family and generic composition of dicots and monocots ($P \leq 0.003$ for each Jaccard test within a taxonomic group) and in generic composition of gymnosperms ($P = 0.004$) and ferns and allies ($P = 0.001$; Table 1).

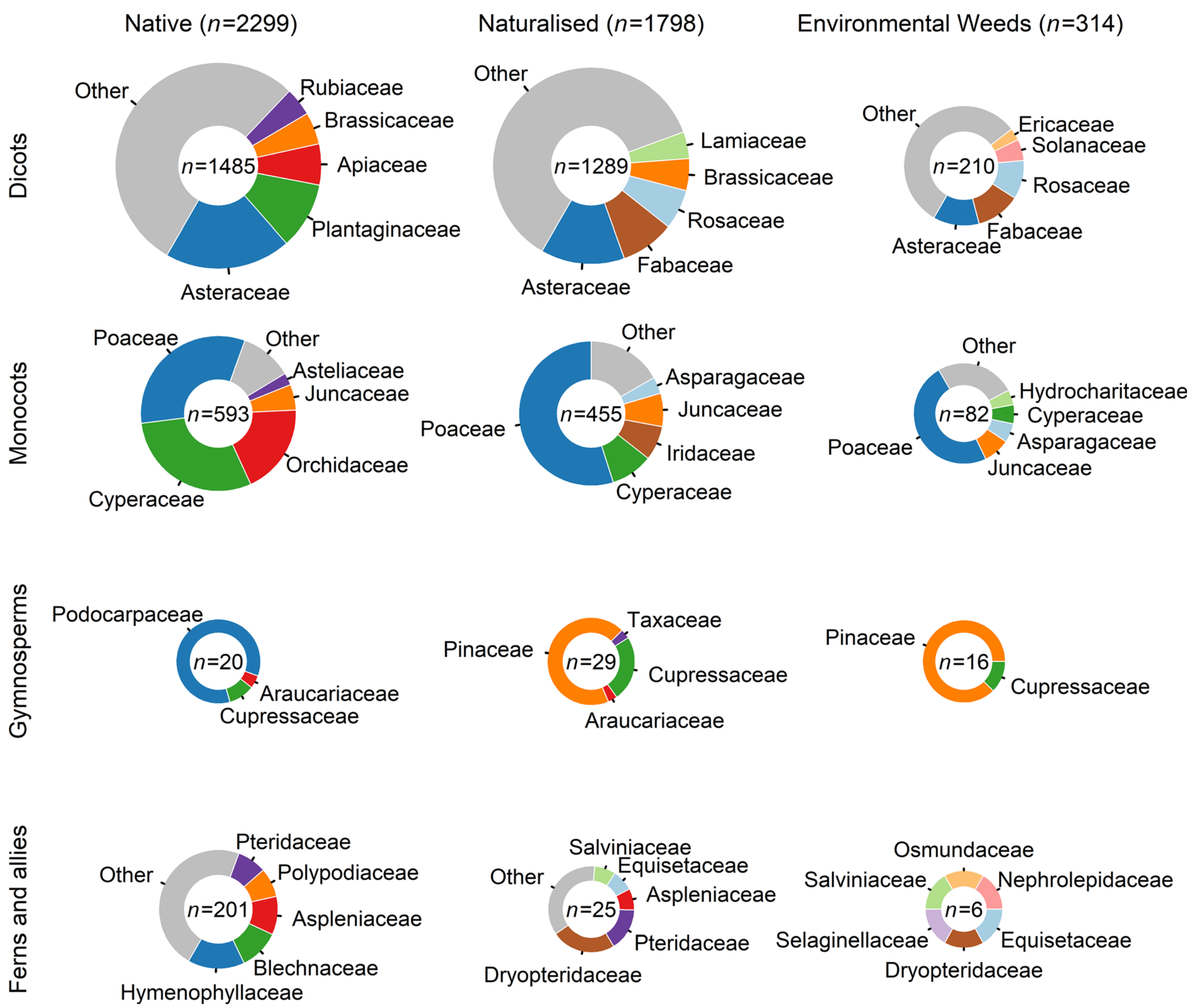

Fig. 1 The five most species-rich families of native, naturalised, and environmentally weedy vascular plants in New Zealand in four taxonomic groups: dicotyledonous angiosperms ("Dicots"), monocotyledonous angiosperms ("Monocots"), gymnosperms, and ferns and lycophytes ("Ferns and allies"). The remaining species in each group are combined into "Other" families. Fewer than five families of gymnosperms occur in New Zealand and six families of ferns and lycophytes are represented by environmental weeds

Asteraceae was the most species-rich dicot family and Poaceae the most species-rich monocot family in both the native and naturalised floras (Fig. 1). Nevertheless, the species richness of families and genera differed between the native and naturalised floras as a whole and within each of the four taxonomic groups ($P < 0.001$ from Chi-square tests of independence; Table 1, Fig. 1, Online Resource 6).

Plant growth forms and life histories

The native and naturalised floras were both predominantly herbaceous although the naturalised flora had a significantly higher proportion of herbaceous species (74.0%) than the native flora (65.6%, $P < 0.001$; Table 2, Fig. 2a). In contrast, the native flora had a significantly higher proportion of woody species (26.2%) than the naturalised flora (22.4%, $P = 0.005$), but the two floras did not differ in the proportion of climbers (2.3% native and 2.2% naturalised, $P = 0.93$; Table 2, Fig. 2a). The subset of 314 environmental weeds had a lower proportion of herbaceous species (46.8%) and a higher proportion of both woody species (46.2%) and climbers (6.1%) than the native or naturalised flora ($P < 0.001$; Table 2, Fig. 2a).

The naturalised flora comprised a much higher proportion of obligate annual species than the native flora (21.8% vs. 1.5% respectively, $P < 0.001$) and a lower proportion of obligate perennial species (68.1% vs. 95.6% respectively, $P < 0.001$; Table 2, Fig. 2b). However, the proportion of obligate perennial species did not differ between the native flora and subset of the naturalised flora considered environmental weeds (95.2%, $P = 0.90$; Table 2, Fig. 2b).

Functional differences: case study of tree leaf N

Naturalised tree species had 49% greater leaf N_{area} than native species ($P < 0.001$) regardless of their leaf habit (i.e. deciduous, evergreen; Fig. 3), suggesting that naturalised tree species tend to have a potentially greater photosynthetic capacity per unit leaf area than native counterparts.

Distribution of naturalised plant species

Of the 1798 naturalised species (314 environmental weeds) on our list, we obtained reliable georeferenced records within mainland New Zealand for exact or closely-matched species names from GBIF for 1759 species (311 weeds; GBIF.org 2020). More naturalised species occurred in larger, more northerly, and more populated regions, with Auckland and Canterbury having the greatest numbers (Fig. 4a). The distribution of environmental weeds followed a similar pattern to the naturalised species, but the differences between regions were not as notable, with Northland, Auckland, Waikato, Bay of Plenty, Manawatū-Whanganui, Wellington, and Canterbury having the greatest numbers (Fig. 4b). Many naturalised species appear localised, with 61% occurring in eight or fewer of New Zealand's 16 political regions (Fig. 5). In contrast, many environmental weeds were widespread, with 77% occurring in eight or more political regions (Fig. 5).

Table 2 Two-sample proportion tests comparing growth forms and life history of the native vs. naturalised floras of New Zealand, and the native flora vs. naturalised species considered environmental weeds

	Native vs. naturalised			Native vs. environmental weeds		
	χ^2	df	*P*	χ^2	df	*P*
Growth forms						
Herbaceous	33.0	1	**< 0.001**	41.4	1	**< 0.001**
Woody	7.8	1	**0.005**	53.1	1	**< 0.001**
Climbers	0.009	1	0.93	13.6	1	**< 0.001**
Life histories						
Annual only	445.1	1	**< 0.001**	N/A	N/A	N/A
Perennial only	549.7	1	**< 0.001**	0.02	1	0.90

Fewer than five environmental weeds were obligate annuals, thus a proportion test could not be used for that comparison

P-values < 0.05 are given in bold

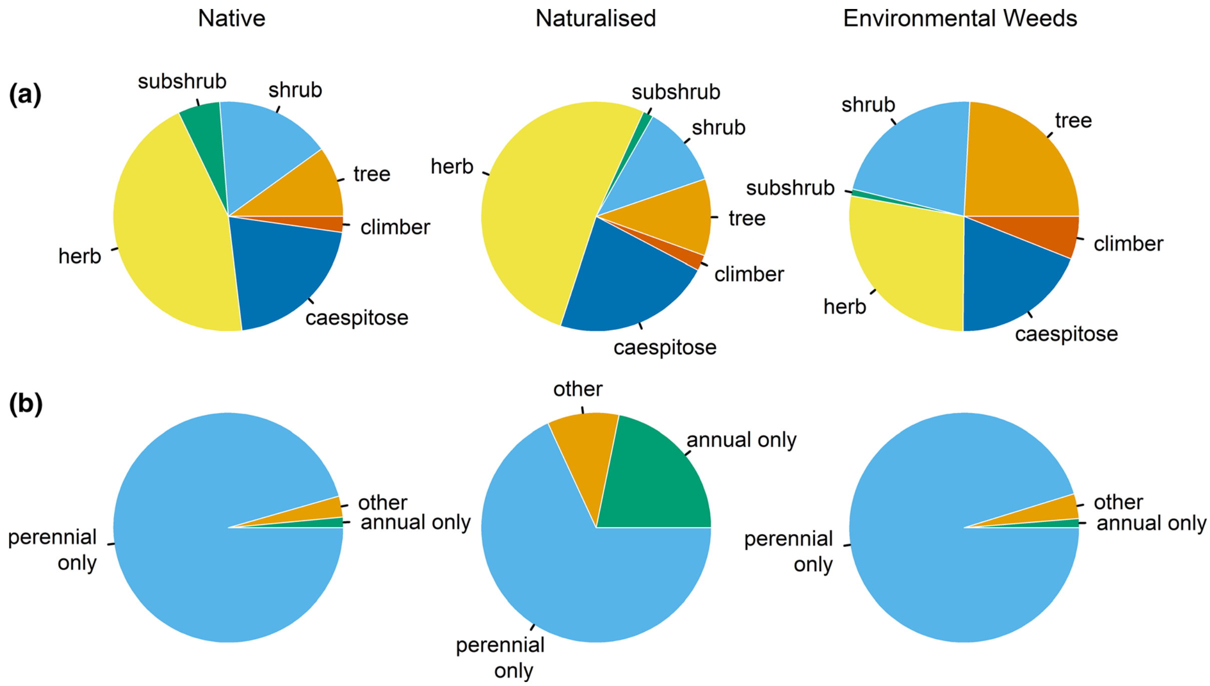

Fig. 2 (**a**) Growth-form and (**b**) life-history composition of the native (2299 species), naturalised (1798 species), and environmentally weedy (314 species) vascular plants in New Zealand

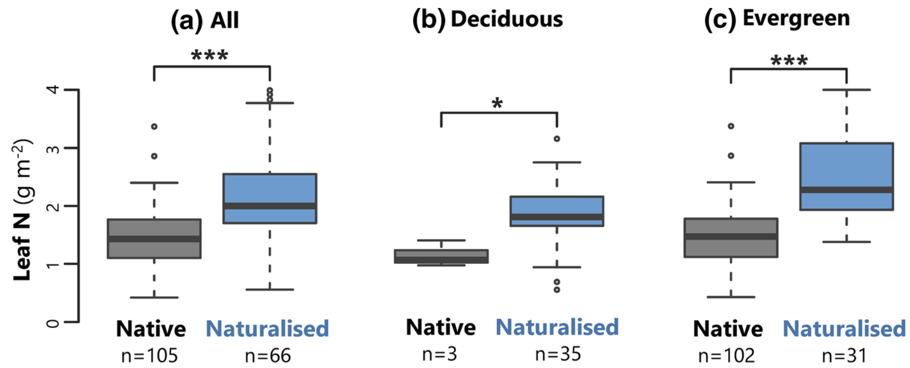

Fig. 3 Leaf nitrogen content per unit leaf area of trees that are native to and naturalised in New Zealand. Significance of the difference between native and naturalised species was tested using a mixed effects model with native status as a fixed effect and genus nested within family and taxonomic group as random effects. $^*P < 0.05$, $^{***}P < 0.001$

Discussion

This is the first comprehensive trait evaluation of New Zealand's naturalised flora and comparison to the native flora. This information is needed as a basis for risk assessment given the large number of introduced plant species in New Zealand that continues to naturalise at a steady rate (Gatehouse 2008; Howell 2019). Of the 1798 naturalised plant species included in our dataset as of 2020, 1689 were previously classed as naturalised and 70 as casual (Howell and Sawyer 2006), and 39 species were not previously listed. Currently, an additional 1043 casual non-native plant species are known to occur in New Zealand (Brandt et al. 2020a; Schönberger et al. 2020a, b), many of which are managed locally to prevent subsequent naturalisation and spread. Time (i.e. overcoming lag phases, Kowarik 1995), global change (Bradley et al. 2010; Sheppard et al. 2016) and increasing transport networks and infrastructure (Hulme et al. 2008) are

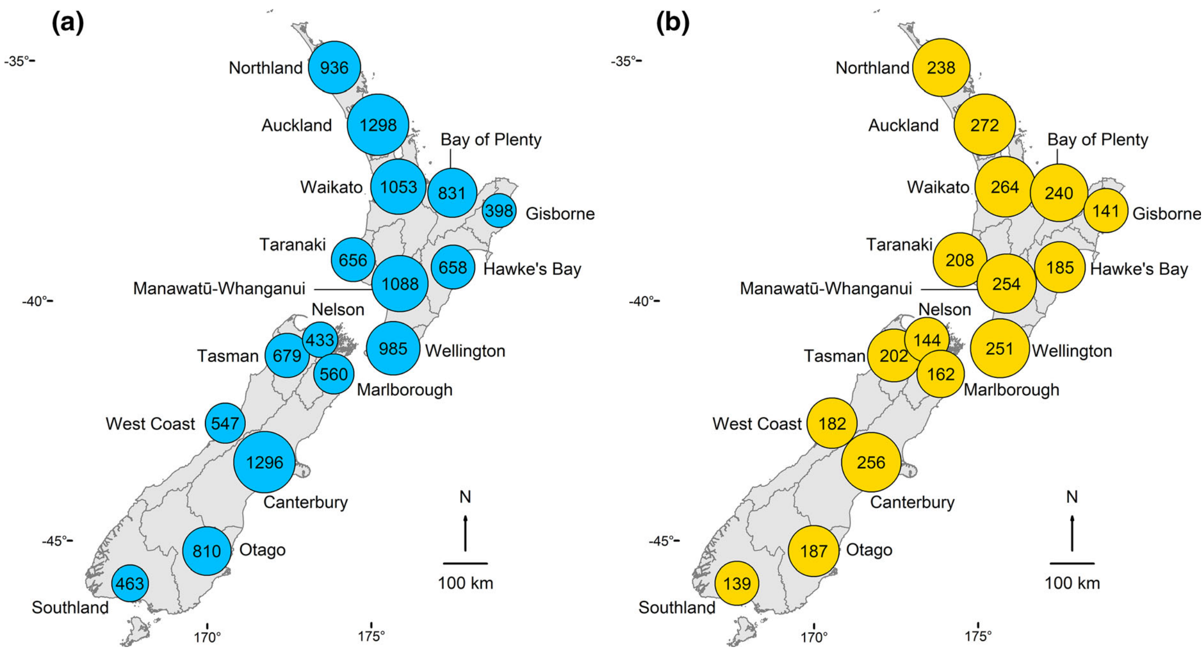

Fig. 4 The distribution of (**a**) all naturalised plant species and (**b**) environmental weeds within the 16 political regions of New Zealand

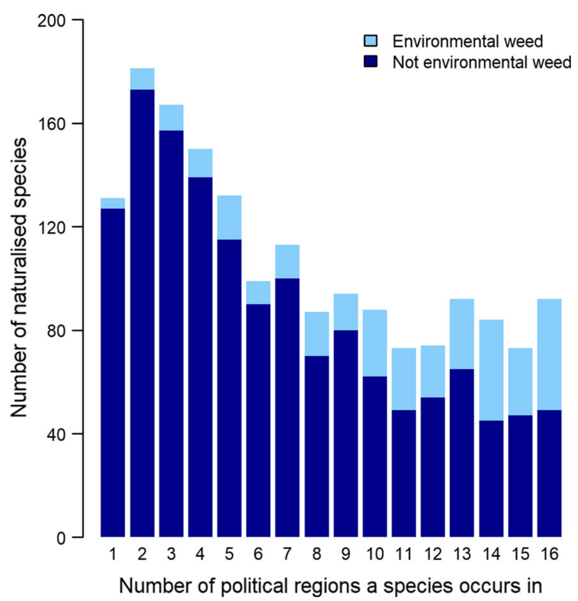

Fig. 5 The frequency at which naturalised plant species occur in the 16 political regions of New Zealand

likely to drive both further naturalisation from the non-native pool and increased abundance and distribution of currently naturalised species.

Taxonomic comparisons

The ratio of naturalised-to-native plant species in New Zealand (78.2 naturalised per 100 native species) well exceeds the current global median for both islands (48.1 naturalised per 100 native species) and mainland regions (7.8 naturalised per 100 native species; Essl et al. 2019). Introduction effort and climate matching to species' native ranges both appear to contribute to this high rate of plant naturalisation, as a similar proportion of temperate species introduced to Australia and New Zealand have naturalised, whereas a greater proportion of introduced tropical species have naturalised in Australia (Diez et al. 2009). Plant families overrepresented in naturalised floras worldwide are also overrepresented in New Zealand's naturalised flora. Poaceae has the greatest number of naturalised species in New Zealand (250 species), as in Australia (Dodd et al. 2015) and 26 other regions around the world (Pyšek 1998). The next two largest plant families in New Zealand, Asteraceae (178 species) and Fabaceae (114 species), are also the next families with the most non-native species worldwide (Pyšek 1998) and in Australia (Dodd et al. 2015). Other well-represented families in New Zealand (Brassicaceae and Solanaceae) are also prominent worldwide and in Australia. In an assessment of 187 species considered weeds in pastures in New Zealand, Poaceae and Asteraceae were by far the most species-rich families (24% and 23% respectively of the total number of species; Bourdôt et al. 2007). The most species-rich families of environmental weeds in New Zealand are the same as those that are naturalised, although Rosaceae form a greater proportion.

Despite the native and naturalised floras sharing the most species-rich dicot and monocot families, the naturalised flora is taxonomically distinct overall. This is most apparent in the gymnosperms with the introduction of Pinaceae, a family originally almost absent from the Southern Hemisphere (Richardson 1998) that naturalises vigorously in temperate regions worldwide (Essl et al. 2011; Pyšek 1998). In contrast to Australia, Pinaceae is among the 20 most successful families to naturalise in New Zealand per introduction effort (Diez et al. 2009) and naturalisation of introduced conifer taxa is ongoing (Howell 2019). Pinaceae are by far the most species-rich gymnosperm family among New Zealand's environmental weeds (Howell 2008; Howell 2019). Additionally, certain large families in the native flora are nearly or completely absent from the naturalised flora, including Hymenophyllaceae in the ferns and Orchidaceae in the monocots. Orchidaceae is a family from which very few species naturalise globally (Daehler 1998; Pyšek 1998).

Plant growth forms and life histories

The naturalised flora of New Zealand is more herbaceous and less woody than the native flora and has a greater proportion of obligate annual species. The subset of the naturalised flora that are considered environmental weeds contains a higher proportion of woody species, most likely because tall woody plants are thought to have much greater effects on communities and ecosystems than lower-statured species (Grime 1998). However, low biomass species can also have strong deleterious effects on native biodiversity (Bernard-Verdier and Hulme 2019; Peltzer et al. 2009; Standish et al. 2001), and this should be taken into account in future assessments. In contrast to the environmental weeds controlled on conservation lands in New Zealand, pastoral weeds are predominantly herbaceous species (Bourdôt et al. 2007).

This coarse comparison does not reflect variation in plant growth or strategies that are known to be important within different taxonomic groupings. For example, although the number of naturalised tree species in New Zealand is similar to the number of native tree species (195 vs. 229 respectively), many of the naturalised species are shade-intolerant colonisers of disturbed habitats (e.g. within Pinaceae and Salicaceae; Dansereau 1964; Richardson 1998) or deciduous species, whereas these growth strategies are uncommon in the native tree flora (Lusk et al. 2015; McGlone et al. 2004; Wardle 1991). The number of naturalised grasses is also similar to the native grasses (250 vs. 193 Poaceae respectively), but often naturalised species are shorter-lived, faster-growing, and turf-forming compared to the long-lived, slow-growing bunchgrasses common in the native flora (Craine and Lee 2003), and this distinction holds within major genera (e.g., *Poa, Festuca*). Information about plant functional traits that are linked to growth rates, capacity to invade disturbed habitats, and high fecundity are needed to determine differences within growth forms between native and naturalised species (e.g., Levine et al. 2003).

Native species, naturalised species, and environmental weeds are overwhelmingly perennial, but the number of annual plants among the naturalised flora is an order of magnitude greater than the native flora. The relatively small number of native annual plants is remarkable in a temperate flora (Wardle 1991), but is driven by past conditions in New Zealand of almost complete forest dominance prior to human settlement. Human settlement has created a new niche in the form of nutrient-rich disturbed sites that some annual plant species favour (Cowie and Werner 1993; Fernández Ales et al. 1993; Pouteau et al. 2015). Although annual plants scarcely feature among the environmental weeds that are subject to control in New Zealand, they can exert a disproportionate influence on ecosystem properties. For example, non-native annuals colonising a New Zealand floodplain altered the soil microbial community structure and increased soil carbon, microbial biomass, and abundance of microbial-feeding and predatory nematodes relative to plant communities dominated by native perennials, perhaps because high SLA and foliar N, as well as short lifespan, resulted in their rapid decomposition and inclusion in soils (Peltzer et al. 2009). Non-native annuals are also likely to exert competitive effects, making native plant dominance in some ecosystems less likely (Fukami et al. 2013). While perennial species predominate among both the native and naturalised floras, many naturalised perennials preferentially colonise deforested habitats, and are often dominant over native perennial "ruderal" species (sensu Grime 2001) during the early stages of both primary (e.g., Bellingham et al. 2005; Brummer et al. 2016; Drake 2011) and secondary successions (e.g., Bellingham and Coomes 2003; Dickie et al. 2014; Sullivan et al. 2007). Some genera of "ruderal" perennials are represented by both native and naturalised species, e.g., many *Senecio* (22 of 24 native and 4 of 7 naturalised species that can grow as perennials) and all *Rytidosperma* species (21 and 9 species respectively; Brandt et al. 2020a).

Functional differences: case study of tree leaf N

Naturalised trees had higher leaf N_{area} than native trees on average, which might suggest a greater productivity of naturalised species than natives given the tight association between leaf N_{area} and photosynthetic capacity (Hikosaka and Hirose 2000). Moreover, the difference in leaf N_{area} remained significant regardless of leaf habit (i.e. deciduous, evergreen), in contrast to leaf trait comparisons made between co-occurring native and non-native woody species within a single New Zealand forest (Heberling and Mason 2018). Relatively high nutrient fluxes associated with disturbance and climate change, and positive plant-soil feedbacks by productive non-native species having greater litter decomposition rate and nutrient uptake, may further promote invasions of these productive naturalised tree species (Jo et al. 2017; Lake and Leishman 2004).

Our findings for native vs. naturalised tree leaf N concur with previous studies suggesting that functional differences between native and naturalised plant species in New Zealand could drive changes in multiple ecological processes and ecosystem functions. For example, resistance to mammalian grazing is thought to be low in the native flora compared to the naturalised flora (Craine et al. 2006; Lee 1998), and presence of bird rather than mammalian browsers may have given rise to distinct growth forms such as divarication in native woody plants (McGlone et al. 2010). Moreover, mesocosm experiments with co-occurring native and naturalised woody species demonstrated that native plants had lower N-based defences against herbivory than naturalised species (Kurokawa et al. 2010). Similarly, many naturalised species have leaf or structural characteristics making them more flammable than native species, and this can in turn create vegetation types that are more pyrogenic compared to native-dominated vegetation (Wyse et al. 2018). However, the consequences of such functional differences for ecological processes can depend on the spatial scale at which they arise and the community's environmental context (Gross et al. 2013; Heberling and Mason 2018; Henn et al. 2019). Collecting additional data on plant functional traits to fill gaps in existing databases would enable comparisons across the full plant community at local scales, which may provide greater insight into the potential impacts of functional distinctions between native and naturalised species (Hulme and Bernard-Verdier 2018).

Distribution of naturalised plant species

The distributional analyses must be interpreted with some caution as the underlying GBIF dataset has taxonomic and spatial biases (Meyer et al. 2016). For example, herbarium records in New Zealand suffer from significant spatial biases associated with proximity to population centres (Aikio et al. 2011). However, we feel confident that the trend for greater numbers of naturalised species and environmental weeds in the larger, more populated, and more northerly political regions provides an accurate representation of differences in distribution, and agrees with previous summaries of naturalised species distributions at the regional scale within New Zealand (Gatehouse 2008; Williams and Cameron 2006). Regional differences in naturalised species numbers likely reflect past invasion pathways (e.g., imported commodities and stowaways), but also suggest future invasion pathways through vectored or unaided natural spread from occupied to unoccupied regions should be evaluated (Hulme et al. 2008). Thus, our observation that many naturalised species appear to remain localised, compared to distributions of species already considered environmental weeds, may highlight a current opportunity for eradication or control of some naturalised species having high invasive potential.

Implications

Information on species' characteristics, function, and distribution are needed to refine risk assessment for current and future naturalised species. Our inventory of the naturalised flora of New Zealand highlights certain taxonomic and functional aspects which distinguish it from the native flora, which could translate into greater ecosystem impacts than would naturalisation of species with similar traits (Wardle et al. 2011). In contrast, naturalisation risk can be higher if newly-arriving species are close relatives of the native flora, at least at larger spatial scales, such as regions (Diez et al. 2008). However, functional distinctiveness may be more valuable than relatedness in predicting naturalisation risk because different traits are important throughout different stages of invasion (Bennett 2019; Nunez-Mir et al. 2019). We show that the naturalised flora of New Zealand contains a higher proportion of herbaceous and annual species than the native flora, and that a subset of the naturalised flora (i.e. trees) tends to differ in certain leaf traits from its native counterpart, which could influence both further spread and ecosystem impacts. Filling gaps in functional trait information of both the native and naturalised plant species of New Zealand (e.g. for herbaceous species) would allow additional comparisons that could improve predictions of further invasion and measurable impact (e.g., by identifying traits driving invasiveness; Nunez-Mir et al. 2019). Improving predictions of naturalisation probability and impact based on trait information as well as introduction effort could subsequently inform prioritisation of weed management (Blackburn et al. 2014; McGregor et al. 2012; Nunez-Mir et al. 2019), with the goal of reducing expected rather than perceived impacts.

Our whole-flora comparisons were not structured to account for species co-occurrence or shared environmental conditions. Previous work has shown that distinctive growth form, life history, and resource allocation patterns between native and naturalised plant species within a New Zealand community can alter community and ecosystem properties (Peltzer et al. 2009). Thus, more comprehensive comparisons between native and naturalised species at multiple spatial scales and taxonomic resolutions is required to better describe and understand the consequences of their functional distinctions.

Conclusions

Here, we present the whole native and naturalised vascular floras of New Zealand, including environmental weeds, and explore their differences in three key areas: taxonomic composition, growth strategies, and functional differences in tree leaf N. We also show that all regions of New Zealand are highly invaded in terms of the number of naturalised species, and that naturalised species considered environmental weeds are widely distributed throughout New Zealand. These distinctions of the naturalised from the native flora are especially important to consider when predicting potential impacts of naturalised species, both individually and as a whole. The potential for invasion by non-native species to fill functional gaps in the native flora, leading to subsequent impacts, is not unique to New Zealand or other islands (Lewerentz et al. 2019).

This inventory of the naturalised flora of New Zealand and accompanying information on plant attributes also contributes to the global need for accessible data on species naturalisation to better understand the current and future causes and consequences of invasion (e.g., van Kleunen et al. 2019). A focus on documenting ongoing naturalisation and spread within introduced regions in an easily-accessible format (e.g. online lists) is also essential as comprehensive updates to naturalisation status in the literature become less frequent (e.g., 15 non-native conifer taxa in New Zealand with newly-documented wild populations since 2008; Howell 2019) and barriers to naturalisation might be rapidly overcome, such as a female plant being introduced where only male plants previously occurred (Dawson 2016) or colonisation by specialist pollinators (Gardner, Early 1996). Our whole-flora treatment helps identify gaps in available information on plant species traits and distribution of naturalised plant species within New Zealand, as well as suggesting the need for in-depth exploration at finer resolution, both taxonomically and spatially, in future work.

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Authors' contributions AJB, PJB, RPD, JJS, and DAP conceived the ideas for the paper. AJB, TRE, JDF, CJH, MSM, and SJR assembled the data and AJB, TRE, and IJ analysed the data. All authors contributed significantly to the writing of the manuscript.

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Data availability The datasets used to compare taxonomic composition, growth forms and life histories (Brandt et al. 2020a, https://doi.org/10.7931/cfvb-z286; Brandt et al. 2020b, https://doi.org/10.7931/ky4e-7h98), and tree leaf traits (Brandt, Richardson 2020, https://doi.org/10.7931/wjf8-2234) between the native and naturalised floras, and to estimate the distribution of naturalised plant species in New Zealand (Etherington and Brandt 2020, https://doi.org/10.7931/nt3a-b734) are archived in DataStore: The Manaaki Whenua – Landcare Research Data Repository (https://datastore.landcareresearch.co.nz/).

Code availability R scripts used in the workflow to estimate distribution of naturalised plant species in New Zealand are available on the Manaaki Whenua – Landcare Research Data Repository (Etherington and Brandt 2020, https://doi.org/10.7931/nt3a-b734).

Compliance with ethical standards

Conflict of interest None.

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