Biol Invasions (2023) 25:39–60
https://doi.org/10.1007/s10530-022-02892-6

ORIGINAL PAPER

The right tree in the right place? A major economic tree species poses major ecological threats

P. J. Bellingham · E. A. Arnst · B. D. Clarkson · T. R. Etherington · L. J. Forester · W. B. Shaw · R. Sprague · S. K. Wiser · D. A. Peltzer

Received: 3 February 2022 / Accepted: 28 July 2022 / Published online: 13 August 2022

Abstract Tree species in the Pinaceae are some of the most widely introduced non-native tree species globally, especially in the southern hemisphere. In New Zealand, plantations of radiata pine (*Pinus radiata* D. Don) occupy *c*. 1.6 million ha and form 90% of planted forests. Although radiata pine has naturalized since 1904, there is a general view in New Zealand that this species has not invaded widely. We comprehensively review where radiata pine has invaded throughout New Zealand. We used a combination of observational data and climate niche modelling to reveal that invasion has occurred nationally. Climate niche modelling demonstrates that while current occurrences are patchy, up to 76% of the land area (i.e. 211,388 km^2) is climatically capable of supporting populations. Radiata pine has mainly invaded grasslands and shrublands, but also some forests. Notably, it has invaded lower-statured vegetation, including three classes of naturally uncommon ecosystems, primary successions and secondary successions. Overall, our findings demonstrate pervasive and ongoing invasion of radiata pine outside plantations. The relatively high growth rates and per individual effects of radiata pine may result in strong effects on naturally uncommon ecosystems and may alter successional trajectories. Local and central government currently manage radiata pine invasions while propagule pressure from existing and new plantations grows, hence greater emphasis is warranted both on managing current invasions and proactively preventing future radiata pine invasions. We therefore recommend a levy on new non-native conifer plantations to offset costs of managing invasions, and stricter regulations to protect vulnerable ecosystems. A levy on economic uses of invasive species to offset costs of managing invasions alongside stricter regulations to protect vulnerable ecosystems could be a widely adopted measure to avert future negative impacts.

P. J. Bellingham (✉) · E. A. Arnst · T. R. Etherington ·
S. K. Wiser · D. A. Peltzer
Manaaki Whenua – Landcare Research, Lincoln 7640,
New Zealand
e-mail: bellinghamp@landcareresearch.co.nz

P. J. Bellingham
School of Biological Sciences, University of Auckland,
Auckland 1142, New Zealand

B. D. Clarkson
Environmental Research Institute, University of Waikato,
Hamilton 3240, New Zealand

L. J. Forester
Northland Regional Council, Private Bag 9021,
Whangārei 0148, New Zealand

W. B. Shaw
Wildlands Consultants, Te Ngae, PO Box 7137,
Rotorua 3042, New Zealand

R. Sprague
CarbonCrop NZ, Nelson 7010, New Zealand

Keywords Climate niche models · Forest ecosystem processes · Naturally uncommon ecosystems · Research–management interface · Species' distribution models · Succession

Introduction

Some of the most widely introduced tree species globally are Pinaceae, deliberately established for a range of services including timber, fibre, amenity value and soil conservation (Richardson et al. 1994; Essl et al. 2010; McGregor et al. 2012). Nearly 4% of the world's forests are plantations, established primarily to provide timber and wood products (Pawson et al. 2013). In the southern hemisphere, non-native *Pinus* species are the most widely grown in plantations (Richardson et al. 1994). Radiata pine (*Pinus radiata*, or Monterey pine) is native to North America, where it is narrowly distributed along the Californian coast, but is one of the most widely planted tree species worldwide (> 4 million ha), with the largest plantations in New Zealand and Chile (> 1.5 million ha each) and Australia (0.77 million ha; Mead 2013).

In New Zealand, radiata pine is by far the largest contributor to its forestry industry, comprising 90% of the total plantation area, supplies most domestic wood products, and is the third largest export earner, contributing c. 3% of GDP (Roche 1990, 2017; NZFOA 2020). The near-complete reliance of New Zealand's forest industry on radiata pine is remarkable internationally (Castro-Díez et al. 2019). Its economic benefits are well documented, but there is a view that this species is relatively unimportant as a biological invader despite its widespread introduction effort (Froude 2011; Wyse and Hulme 2021a, b; see also Williams and Wardle 2007).

The potential negative environmental and ecosystem impacts of invasive non-native pines are well documented, resulting from a combination of high introduction effort, subsequent widespread naturalization and invasion, and relatively high growth rates and early reproductive maturity (Richardson et al. 1994; Simberloff et al. 2010; McGregor et al. 2012; Rejmánek and Richardson 2013). However, invasive pines vary widely in both biomass and potential effects across different ecosystems and scales (Rouget et al. 2001; Williams and Wardle 2005; Curtis et al. 2019). This has prompted major efforts to better understand the causes and consequences of pine invasion, and how to integrate this knowledge into management (e.g., Nuñez et al. 2017; Sapsford et al. 2020). Because of widespread increases in the distribution, abundance and ecological impacts of non-native pines, there are increasing efforts to contain or remove these invaders at the landscape scale (Froude 2011; Rundel et al. 2014; Nuñez et al. 2017). What is unresolved is how landscapes are managed for species that can simultaneously have benefits and negative impacts depending on their location (Sapsford et al. 2020); radiata pine is an excellent species for evaluating these complexities.

Radiata pine has naturalized from commercial plantations and amenity plantings and invaded native ecosystems across the southern hemisphere including Chile (Bustamante and Simonetti 2005; Becerra and Montenegro 2013), Argentina (Franzese et al. 2020), Australia (Williams and Wardle 2005, 2007; Baker and Murray 2010; Calviño-Cancela and van Etten 2018), and South Africa (Richardson and Brown 1986; van Wilgen et al. 2016). In many of these systems, positive feedbacks between radiata pine invasion and fire are common because pines contribute more flammable litter than native species (Baker et al. 2007; Franzese et al. 2020) and can promote crown fires (Richardson and Brown 1986; Burrows et al. 1989). Many invasive non-native Pinaceae in New Zealand, notably *Pinus contorta*, *P. nigra*, and *Pseudotsuga menziesii*, are widely controlled to prevent or minimize their effects on ecosystems and biodiversity (e.g., Ledgard 2001; Dickie et al. 2014a; Hulme 2020). In contrast, radiata pine naturalized by at least 1904 but has been considered "only a minor escape" that is only "occasionally extensively naturalized in scrub and herbaceous vegetation downwind from plantations" (Webb et al. 1988), and this view of radiata pine as a minor invasive species has prevailed for over three decades. For example, its characterisation as an invasive weed (as it is in Australia; Baker and Murray 2010) does not feature in policy decisions in New Zealand. A major afforestation initiative in New Zealand ("One Billion Trees", https://www.teururakau.govt.nz/funding-and-programmes/forestry/one-billion-trees-programme/) will likely increase the area of radiata pine plantation and thus propagule pressure, yet its potential as an invasive species and its effects in natural ecosystems has not been considered. We are now at the stage of requiring evidence for invasion risk and potential impacts at the local to regional scales needed to guide policy and management of both plantation forestry and environmental weeds (Hulme 2020).

More generally, New Zealand has developed approaches to conservation and biosecurity management relatively rapidly at a national scale because it is a small island nation, some of which, such as eradication of invasive mammals from islands and species translocations, have been applied globally (Simberloff 2019). In the case of invasive plants in New Zealand, high numbers of species from across major biogeographic regions coupled with long naturalization histories have prompted concerted national management responses, providing general insights into the large-scale management of invasive species and prioritisation of plant biosecurity risks worldwide (Nuñez et al. 2017; Hulme 2020; Sapsford et al. 2020; Brandt et al. 2021).

In this paper, we reassess Webb et al.'s (1988) view of radiata pine as only a minor invasive species in New Zealand, more than 30 years later. We present the first comprehensive review of where invasive radiata pine occurs in New Zealand, and evaluate the potential climatic suitability for radiata pine to invade nationally. We assess radiata pine invasions in three classes of natural ecosystems that are naturally uncommon and geographically confined (Williams et al. 2007), many of which are threatened by increasing dominance by invasive, non-native plants (Holdaway et al. 2012). We also evaluate the extent to which radiata pine is a feature of successional ecosystems, including primary successions and secondary successions. An overarching goal of this work is to provide the evidence needed to improve management of non-native species at the landscape-scale that simultaneously provide benefits and negative impacts that are location- or context-dependent (Hulme 2020; Sapsford et al. 2020).

Methods

Current distribution of invasive radiata pine in New Zealand

To identify occurrences of invasive radiata pine in New Zealand, we used: (i) plot records from the National Vegetation Survey (NVS) databank (Wiser et al. 2001; https://nvs.landcareresearch.co.nz/ on 1 May 2020); (ii) herbarium records from the New Zealand Virtual Herbarium (https://www.nzherbaria.org.nz/ on 13 June 2019) and physical records in individual herbaria; (iii) records from the citizen science initiative i-Naturalist (https://inaturalist.nz/ on 17 July 2019) where locations and photographs were clearly marked as invasive, with additional observations from Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.lowakv on 9 November 2018). Our approach was conservative, scrutinising all potential records to ensure that we admitted only documented invasions. We determined invasions on offshore islands from floras of 264 northern New Zealand islands (spanning 34–38°S and 172–179°E; Mologni et al. 2021), and records from other islands (Atkinson 1997). To establish the current environmental range of invasive radiata pine occurrences, we extracted the 0.5% and 99.5% percentiles from 100 m resolution environmental layers of elevation, mean annual temperature, and annual precipitation for each of these records (McCarthy et al. 2021).

Potential distribution of radiata pine in New Zealand

A global set of reliably georeferenced radiata pine occurrences was obtained from GBIF (GBIF.org 2020). Global climatologies for the period 1979–2013 with a 30 arc second (ca. 1 km) grid resolution (Karger et al. 2017) were used to define climate space. We used mean annual temperature and annual precipitation because these variables are the strongest predictors of species distributions (Barbet-Massin and Jetz 2014) and easily interpreted. To maximize the suitability of the radiata pine occurrences for niche analysis, GBIF occurrences were retained if they were: (1) temporally consistent with climatologies (i.e., recorded during 1972–2020); (2) recorded with a known spatial uncertainty ≤ 1 km (i.e., to ensure spatial consistency with the climatologies); (3) located within 0.1 degrees of the country to which they were recorded, located inside the climatology data range, not located within a 1 km grid for another observed occurrence, and not recorded as managed or cultivated.

Because we were interested in where radiata pine could potentially occur, we modelled its fundamental niche as a multivariate ellipse (Soberón and Peterson 2020) derived using Mahalanobis distances

(Etherington 2019). To meet assumptions of multivariate normality annual precipitation values were log-transformed, and then both mean annual temperature and annual precipitation data were rescaled to z-scores such that the units of climatic space were the same in all dimensions. Because GBIF data are known to be highly biased (Meyer et al. 2016), a climatic space filter was applied to reduce the effects of sampling bias in climatic space by ensuring all occurrences were at least 0.1 z-scores away from any other occurrence (Varela et al. 2014).

After cleaning the data for errors and bias, 1281 observations were available for niche analysis. The fundamental niche was defined as the climatic space with a Mahalanobis distance chi-square probability ≤ 0.99, using a minimum covariance determinant approach (with $k = 0.95$), which is robust to any remaining occurrence errors or bias (Etherington 2021). Fundamental niche models were generated as the mean of results from 1000 bootstrap resamples (Efron 1979; Diaconis and Efron 1983; Verbyla and Litvaitis 1989; Etherington and Lieske 2019). The fundamental niche of radiata pine was then applied to New Zealand's current climate to map the potential distribution of radiata pine. The area of New Zealand that is climatically suitable to support a population of radiata pine was calculated as a weighted sum of the potential distribution values, but excluding those 1 km^2 grid cells that consisted of $\geq 50\%$ of inland water (LINZ 2021a, LINZ 2021b). All analyses were done using R software (R Core Team 2019) with the MASS (Venables and Ripley 2002), virtualNicheR (Etherington and Omondiagbe 2019), rnaturalearth (South 2017), raster (Hijmans 2020), sf (Pebesma 2018), and rgbif (Chamberlain and Boettiger 2017) packages.

Determining ecosystems invaded by radiata pine

We extracted data from vegetation plots archived in the NVS databank where radiata pine had been recorded and data were collected following consistent relevé-based methods (Hurst and Allen 2007). Many of these plots have been assigned to a national classification that quantitatively defined woody and non-woody vegetation types (Wiser and De Cáceres 2011, 2013; Wiser et al. 2016). Previously unclassified plots were assigned to a vegetation type following the procedures defined in these earlier publications, where possible. All plots were further categorized into a physiognomic class (e.g. grassland, fernland, herbfield) based on the summed cover of different species groups, following Atkinson (1985). We also reviewed published literature from across studies of New Zealand ecosystems invaded by radiata pine, and, for some of these ecosystems, we present new data.

Results

Current distribution of invasive radiata pine in New Zealand

Observations of invasive radiata pine extend nearly the full latitudinal range of New Zealand (Fig. 1a), and were present between 1 and 1060 m elevation, 6–16 °C mean annual temperature, and 548–2813 mm annual precipitation. Invasive radiata pine occurs on 34 (12.8%) of 266 northern New Zealand islands for which there are comprehensive floras (Atkinson 1997; Mologni et al. 2021). The 34 islands are, on average, nearly 7 times greater in area than the overall mean of 266 islands (1631 ± 854 [SEM] ha vs. 242 ha), nearly half as close, on average, to the mainland (5.4 ± 1.3 km vs. 9.6 km), and more often with permanent human settlement (62% of islands are inhabited vs. 15.4%). Radiata pine has also naturalized on another 8 islands off the northern South Island coast (40.5–41.5°S); an island (45.7°S) close to Dunedin, southern South Island (Atkinson 1997); and on Rekohu/Chatham Island, c. 800 km east of the South Island of New Zealand (Fig. 1b), which is permanently inhabited. The higher incidence of radiata pine invasion on islands with permanent human settlement is likely to coincide with planting radiata pine for shelter, fuelwood, or timber, so that invasive radiata pines on many islands are most likely derived from local seed sources (e.g. Cameron and Davies 2013) rather than long-distance dispersal from mainland populations (see also Wyse and Hulme 2021b).

Potential distribution of radiata pine in New Zealand

The climatically suitable areas for radiata pine were in the warmer and drier regions of New Zealand, which is consistent with radiata pine's native range in coastal southern California, with only the coldest and wettest climates of New Zealand predicted to be outside the

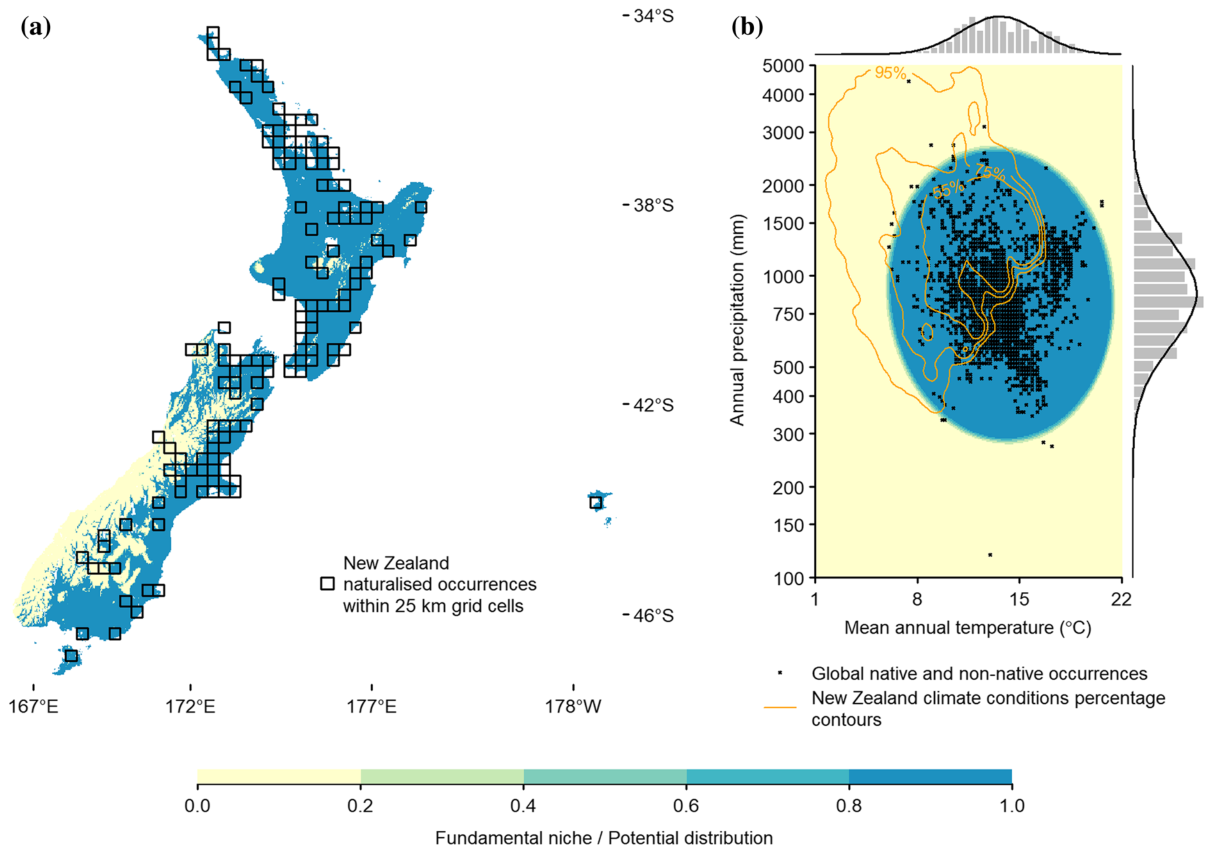

Fig. 1 Current invasive range and ecological niche modelling of the fundamental niche and potential distribution of non-native *Pinus radiata* in New Zealand. **a** The national 25 km grid squares containing confirmed occurrences of invasive *P. radiata;* potential distribution of *P. radiata* (blue shading) is predicted by the species' fundamental climatic niche. **b** The estimated fundamental niche (blue shading) of *P. radiata* calculated from global native and non-native occurrence data using Mahalanobis niche modelling. For context, contours show the climate space containing 55, 75, and 95% percentiles for the current climatic conditions of New Zealand, and the histograms show the distribution of occurrences for each climate variable

fundamental niche (Fig. 1b). The occurrence data conformed well to the Mahalanobis distance method's assumption of multi-variate normality, and the results from the bootstrap resampling were highly consistent, indicating the fundamental niche model is reliable (Fig. 1b). Therefore, the potential distribution of radiata pine is likely to include most of New Zealand aside from relatively high elevation (> 1000 m) and high rainfall (> 2000 mm year^{-1}) regions of the centre and west, especially southwest, of the South Island (Fig. 1a). While confirmed presences of radiata pine in New Zealand are currently patchy and localized, the total area that is climatically capable of supporting populations is estimated as 76% of New Zealand's land area (or 211,388 km^2; Fig. 1a).

Ecosystems invaded by radiata pine in New Zealand

Of 101 relevé plots nationally that we were confident contained invasive radiata pine, 56 had been collected in a manner consistent with those supporting previous quantitative vegetation classifications. Of the 56 plots with suitable data, 31 (55%) could be classified to a previously defined vegetation type, whereas the composition of the remainder was not consistent with previously defined vegetation types. Instead, these were assigned to physiognomic types (Table 1). There were an equal number of plots in grasslands, fernland and herbfields versus successional shrublands in which radiata pine had invaded (21 plots in each of the groups, both 38% of the

Table 1 Summary of different vegetation types in New Zealand in which invasive *P. radiata* has been recorded as present in relevé plots

Vegetation	Plots (n)
Grassland, herbfield, fernland	
Festuca novae-zelandiae–Poa colensoi–Anthoxanthum odoratum/Leucopogon fraseri tussockland	11
Indigenous grassland	6
Adventive grassland	1
Fernland	1
Herbfield	2
Shrubland	
Kunzea ericoides/(*Coprosma rhamnoides–Leptecophylla juniperina*) shrubland	5
(*K. ericoides*)/*C. rhamnoides*/*Dactylis glomerata–A. odoratum* successional shrubland	4
K. ericoides–Cyathea dealbata–(*Leptospermum scoparium*)/*Leucopogon fasciculatus* (*C. rhamnoides*) forest and tall shrubland	4
L. scoparium shrubland	1
Discaria toumatou–Coprosma propinqua/*A. odoratum–D. glomerata* shrubland	1
Ulex europaeus–Cordyline australis shrubland	1
Indigenous shrubland (including subshrubs)	4
Adventive shrubland	1
Forest	
Weinmannia racemosa–C. dealbata – Knightia excelsa (*Beilschmiedia tawa*)/*L. fasciculatus* forest	2
C. dealbata–Melicytus ramiflorus–Freycinetia baueriana–Ripogonum scandens forest	1
Nothofagus solandri–(*Nothofagus fusca*)/*Coprosma microcarpa – L. fasciculatus* forest	1
Indigenous Woodland	5
Indigenous Forest	1
Exotic Conifer Forest	2
Exotic Conifer Woodland	2

Plots invaded were either assigned to non-woody (Wiser et al. 2016) or woody (Wiser and De Cáceres 2011, 2013) vegetation types (number of plots per type) or, where this was not possible, categorized into physiognomic classes, following Atkinson (1985)

total) and fewer plots in forests were invaded (14 plots, 25% of the total).

Naturally uncommon ecosystems

Radiata pine has invaded at least three classes of naturally uncommon ecosystems (Table 2; Fig. 2): (1) geothermal, (2) gumlands, and (3) inland cliffs, scarps, and tors. Geothermal ecosystems include heated ground (dry), hydrothermally altered ground (now cool), acid rain systems, fumeroles and geothermal streamsides. Vegetation structure ranges from nearly bare ground to moss and herbfields to shrublands to forest. Radiata pine invades the woody vegetation (Burns 1997; Boothroyd 2009; Beadel et al. 2018), where it can become structurally dominant, occupying areas > 10 ha (Table 2). Increasing ground temperatures in these ecosystems can kill mature radiata pine trees; conversely, cooling substrate temperatures can allow more radiata pine to establish. Radiata pine and *Pinus pinaster* are the principal invaders in geothermal areas (Burns 1997; Beadel et al. 2018).

Gumlands are mosaics of dry and wet heathlands in warm temperate northern New Zealand on infertile, podzolized soils that formerly supported forests dominated by *Agathis australis* (Enright 1989), and are locally prone to waterlogging, often because of silica clay or ironstone pans (Clarkson et al. 2011). These ecosystems are fire-prone, with fire disturbance likely to have increased through human ignition (Clarkson et al. 2011). Radiata pine invades gumlands throughout their range (Table 2; also Wilcox 2014), along with other non-native pyrogenic species such as *Hakea sericea* and *Ulex europaeus*. Radiata pine grows relatively rapidly and taller than

Table 2 Naturally uncommon ecosystems in New Zealand in which radiata pine is invasive

Ecosystem	Location	Latitude/longitude	Elevation	Details of invasion	References
Geothermal	Waikato Region	38° 22′ S–38° 25′ S; 176° 7′ E–176° 17′ E	240–1760 m	Invasive in 34 of 49 geothermal ecosystems across 13 sites, from scattered trees to stands covering > 10 ha	Wildland Consultants (2014)
	Bay of Plenty Region	38° 2′ S–38° 48′ S; 176° 3′ E–176° 43′ E	40–500 m	Invasive in 20 of 46 geothermal ecosystems across 13 sites	Wildland Consultants, unpublished data (2020)
	Bay of Plenty Region	38° 2′ S–38° 48′ S; 176° 3′ E–176° 43′ E	40–500 m	Invasive in 3 of 166 plots (4–100 m^2) across 38 sites	Smale et al. (2018)
	Te Kopia Scenic Reserve (95 ha)	38° 24′ S; 176° 13′ E	410 m	Radiata pine or *Pinus pinaster* invaded 4 of 10 plots (25 m^2) in shrublands	Burns (1997)
Gumlands	Northland Region	34° 24′ S–36° 4′ S; 172° 43′ E–174° 35′ E	10–340 m	Invasive in 27 of 31 gumlands–abundant in one, sparse (< 1 ha^{-1}) in 19, and confined to the margins of 7	L.J. Forester, unpublished data (2017)
	Northland Region	34° 28′ S–36° 54′ S; 172° 47′ E –174° 38′ E	10–310 m	Invasive in 1 of 15 gumlands, assessed in 100 m^2 plots in each site	Clarkson et al. (2011)
	Northland Region	35° 13′ S–35° 51′ S; 173° 8′ E–173° 54′ E	20–310 m	Invasive in 2 of 4 gumlands, assessed in 400 m^2 plots in each site	E.A. Arnst, unpublished data (2016)
Inland cliffs, scarps, and tors	Banks Peninsula	43° 48′ S; 172° 51′ E	500–900 m	Invasive in 3 of 7 plant communities on basic cliffs, scarps, and tors	Wiser and Buxton (2009)
	Mount Ararat, Ōmihi (2 ha)	43° 3′ S; 172° 50′ E	250–310 m	Invasive in species-poor short-statured (ca. 3 m tall) woody communities and open sites on cliffs, scarps, and tors on quartz sandstone	Walls (2013)

the resident native woody gumland vegetation (c. 1 m tall or less; Esler and Rumball 1975; Clarkson et al. 2011), becoming locally structurally dominant, and potentially hastening succession from short heaths to forest that occurs on some gumlands (Enright 1989).

Inland cliffs, scarps, and tors formed from bedrock of varying chemistry occur throughout New Zealand (Williams et al. 2007). Radiata pine invades at least two of these kinds of ecosystems, on basalt and quartz sandstone (Table 2), usually as isolated individuals but, when established, attains far greater height and biomass than resident native plant species.

Primary successions

Radiata pine often invades with other Pinaceae species during primary succession (Table 3). On volcanic substrates, it is more common than *Pinus pinaster* as an invader of lava and scoria on Rangitoto (Brown and Wilcox 2007), and mainly

Fig. 2 *Pinus radiata* has invaded a wide range of ecosystems across New Zealand, including successional vegetation and naturally rare ecosystems such as: **a** geothermal ecosystems (Wairakei, Waikato, photo: Rowan Sprague); **b** inland basic cliff (Banks Peninsula, Canterbury, photo: Rowan Buxton); **c** abandoned marginal land undergoing secondary succession (Northland, photo: Peter Bellingham); **d** gumland heaths (Northland, photo: Ceres Sharp); **e** inland cliffs (Waikato river, photo: Rowan Sprague); **f** coastal dunes (Northland, photo: Ceres Sharp)

invades scoria at lower elevations on Mount Tarawera (Table 2). Much of New Zealand is mountainous and landslides are common because of unstable underlying bedrock, tectonism, and high rainfall events and storms including cyclones (e.g., Marden and Rowan 1993). Radiata pine is often planted to reduce the likelihood of landslides in erosion-prone terrain, yet it can invade landslides that form within extensive areas of natural forest (> 2000 km^2; Table 3). Radiata pine has been widely planted on mobile coastal sand dunes, initially to stabilize them to prevent sand movement into agriculture, and later, once pine growth rates were found to be rapid, as a timber crop (McKelvey 1999). Seedlings of radiata pine establish on stable sand, and this study supports Wardle's (1991) prediction that, wherever there is a seed source in areas with 500–6000 mm annual rainfall, radiata pine will increasingly dominate primary succession on coastal sand dunes (Table 3).

Secondary successions

Radiata pine invasions are also widespread in secondary successions (Table 4), with radiata pines rapidly growing in height and becoming emergent over the resident successional communities. Invaded ecosystems are mostly low elevation grasslands and shrublands (< 400 m a.s.l., Table 4) including those dominated by native as well as by non-native species (Table 1). Secondary successions invaded by radiata pine are often in areas previously used for agriculture and then either abandoned or farmed less intensively (Standish et al. 2008; Wilson 2008). Widespread successions through native Myrtaceae shrubs and trees (*Lepospermum scoparium* and *Kunzea* spp.; Wardle

Table 3 Primary successions in New Zealand in which radiata pine is invasive

Primary succession	Location	Latitude, Longitude	Geology, Elevation	Details of invasion	References
Volcanic	Rangitoto (2311 ha)	36° 47′ S; 174° 51′ E	Basalt shield and scoria cone, 0–260 m, erupted c. 1450 and 1510	Invasive on lava and scoria since 1900, with trees up to 36 cm diameter (40 years old) in 1954, and locally dominant by 1980s. Controlled since 1980, but still invading in 2021	Hannken (1954), Brown and Wilcox (2007)
	Mount Tarawera	38° 13′ S; 176° 30′ E	Rhyolitic domes, 650–1110 m, erupted 1886	Invasive on bare scoria since 1962–1964; scattered emergent trees by 1979, and locally dominant (with other pine species) by 1991. Controlled since 1991 but still invading lower elevations in 2021	Dickinson (1980), Clarkson and Clarkson (1991), P. Cashmore, (Department of Conservation, pers. comm.) (2020)
Landslides	Te Urewera (2127 km^2)	38° 9 S–38° 49′ S; 176° 40′ E–177° 26′ E	Greywacke overlain by rhyolitic pumice, 300–1250 m	Invasive on landslides mostly 8–11 km east of Kāingaroa radiata pine plantation (2900 km^2) but up to 20 km east. In 2020, tree diameters declined west to east, suggesting a colonization gradient. Also invasive on bare gravel floodplains	Shaw (1990), B. Lett (Department of Conservation, pers. comm., 2020)
Coastal dunes	Kokotā	34° 35′ S; 172° 59′ E	Sand, 2–20 m	Invasive on bare dunes in 2020 from nearly plantation	L.J. Forester, unpublished data 2020
	Ngunguru	35° 38′ S; 174° 30´ E	Sand, 2–10 m	Invasive on bare dunes in 2020	L.J. Forester, unpublished data 2020
	Dunes beside Lake Humuhumu (70 ha)	36° 20′ S; 174° 7′ E	Sand, 30–110 m	Dominant over previously bare dunes in 2020, colonized from an adjacent plantation	L.J. Forester, unpublished data 2020
	Waitarere	40° 32′ S; 175° 11′ E	Sand, 2–10 m	Invasive in sparse grass cover on seaward side of plantation	Campbell (1998)
	Waikouaiti Beach	45° 37′ S; 170° 40′ E	Sand, 2–10 m	Abundant on seaward side of plantations	Johnson (1992)
	Warrington Beach	45° 43′ S; 170° 36′ E	Sand, 2–10 m	Frequent on seaward side of plantations	Johnson (1992)

Table 4 Secondary successions in New Zealand in which radiata pine is invasive

Location	Latitude, Longitude	Geology, Elevation	Circumstances of succession	Co-occurring native woody species	Co-occurring non-native woody species	References
Aotea (Great Barrier Island)	36° 12′ S; 175° 27′ E	Greywacke and andesite, 2–360 m	Logging and burning	*Kunzea robusta*, *Leptospermum scoparium*	*Erica lusitanica, Hakea gibbosa*, *H. sericea*	Perry et al. 2010, Wyse et al. 2018
Kawau Island	36° 26′ S; 174° 29′ E	Basalts and sandstone, 2–60 m	Agricultural abandonment, 1940s		*Pinus pinaster*	Gardner 1993
Maunga Kākaramea (Rainbow Mountain)	38° 18′S; 176° 28′E	Dacitic dome adjoining geothermal ecosystems, 400–743 m	Recurrent fires	*L. scoparium*, *Pterophylla racemosa*	*Pinus contorta*, *P. nigra*, *P. strobus*	Watt 1986
Taita	41° 10′ S; 174° 58′ E	Greywacke, 40–224 m	Agricultural abandonment, 1930s, fires	*L. scoparium*	*E. lusitanica*, *Ulex europaeus*	Druce 1957, Wardle 1991
Abel Tasman National Park	40° 57′ S; 173° 3′ E	Granite, 2–310 m	Agricultural abandonment, 1930s	*Kunzea ericoides*, *L. scoparium*, *Leptecophylla juniperina*, *Leucopogon fasciculatus*	*E. lusitanica*, *Hakea salicifolia*, *H. sericea*, *P. pinaster*	Esler 1962, Wardle 1991
Marlborough Sounds	41° 9′ S; 174° 0′ E	Greywacke, 2–c. 400 m	Agricultural abandonment, 1920s–1930s, fires	*L. scoparium*	*Cytisus scoparius*, *E. lusitanica*, *U. europaeus*	Wassilieff 1982
Smothering Gully, Ōmihi	43° 3′ S; 172° 51′ E	Sandstone and mudstone, 150–280 m	Agricultural abandonment, 1980s	*K. robusta*	*P. nigra*	Giller 2013
Banks Peninsula	43° 46′ S; 172° 53′ E	Basalt overlain with loess, 2–900 m	Agricultural abandonment, 1920s–1990s, fire	*K. robusta*, *Melicytus ramiflorus*, *Podocarpus laetus*	*C. scoparius*, *Sambucus nigra*, *U. europaeus*	Wilson 1992, Wyse et al. 2022

1991) are also commonly invaded by shade-intolerant radiata pine (Tables 1, 4); the low leaf area of these Myrtaceae species (Whitehead et al. 2004) may permit its establishment. Recurrent fire is likely to have promoted radiata pine invasions in some secondary successions by retarding succession, reducing leaf area, and presenting open sites favourable for the establishment of radiata pine (Druce 1957; Wassilief 1982; Wardle 1991; Wyse et al. 2018). Enhanced propagule pressure after establishment of new radiata pine plantations near invaded successional vegetation, from the late 1970s onward, is a probable reason for ongoing invasion, e.g., in Abel Tasman National Park (https://www.janszoon.org/assets/documents/Wilding%20conifer%20control%20.pdf) and the Marlborough Sounds (Marlborough District Council 2015). When uncontrolled in secondary successions, radiata pine can dominate, forming tall, closed canopy forests, e.g., c. 40 years after agriculture was abandoned on Kawau Island (Gardner 1993).

Discussion

The evidence we present challenges previous (Webb et al. 1988) and current views that radiata pine is a minor invader in New Zealand (see also Wyse and Hulme 2021a, b). Rather, radiata pine is a nationally invasive tree (Fig. 1), which occurs across primary and secondary successions (Tables 3, 4) and naturally uncommon ecosystems dominated by low statured vegetation (Table 2). The discrepancy between Webb et al.'s (1988) view and our findings could, in part, be a function of residence time: a major expansion of radiata pine plantation area in the 1970s–1980s including into new regions (Roche 1990) would scarcely have reached reproductive maturity or dispersed seed until our analyses > 30 years after Webb et al's (1988) findings. Additionally, previous work on invasion of non-native conifers in New Zealand has focussed on montane grasslands invaded primarily by *Pinus contorta*, *P. nigra* and *Pseudotsuga menziesii* (e.g., Ledgard 1994; 2006) whereas radiata pine invasions are most prevalent in lowland regions.

Several attributes or traits of radiata pine explain both its invasiveness and absolute abundance in the ecosystems it invades (Rejmánek and Richardson 1996; McGregor et al. 2012; Wyse and Hulme 2021a, b). For example, rapid growth rates of radiata pine, in height and biomass, far outstrip any native woody species: plantations of radiata pine have annual dry-matter production approximately double most native Nothofagaceae forests, tree radial diameter increments an order of magnitude greater than most native trees, and within 22 years have biomass equivalent to most old-growth native podocarp-broadleaf and Nothofagaceae forests (Wardle 1991; McGlone et al. 2022). The effects of invasive radiata pine on ecosystem productivity and function, whether measured by biomass (Grime 1998), litterfall, or asymmetric competition resulting from its greater height and diameter growth, are likely to be large in the immediate neighbourhood of any individual that establishes (Sapsford et al. 2020; see also Franzese et al. 2017). Moreover, radiata pine is functionally distinct from native- and many non-native-dominated communities it invades because of its novel ecotomycorrhizal associations (Dickie et al. 2010) and relatively high flammability (Perry et al. 2014; Gómez-González et al. 2022).

Invasion current range and potential

Our ecological niche modelling demonstrates that most climatic conditions across New Zealand occur within radiata pine's estimated fundamental niche and are thus climatically suitable for its establishment (Fig. 1). Relatively few observations of invasive radiata pine were recorded for some colder or wetter regions, but absence of occurrence data is not strong evidence for climatic unsuitability because of observer biases (Atwater et al. 2018); therefore, our results should be interpreted as minimum estimates of the fundamental and potential niche. Wide national distribution was also described by Howell (2019) based on herbarium records within broad ecological regions (McEwen 1987), where radiata pine occurred in 56 regions—more than twice as many as other invasive Pinaceae species that currently attract greater concern and management (*Pinus contorta* and *P. nigra*, 23 regions each; *Pseudotsuga menziesii*, 26 regions; *Larix decidua*, 17 regions). In addition, our estimates are based on current climate conditions but if New Zealand's climate warms and dries, as future climate scenarios predict, then radiata pine's potential distribution is likely to increase (Etherington et al. 2022). This example adds to a growing recognition internationally that rates of naturalization and invasion are dynamic, either dampening or accelerating under future climates, thus requiring better understanding of how climate and invasions interact to predict future invasion risk (Caplat et al. 2013).

In addition to presence-only observational data used to estimate species distributions, we used both plot- and site-based data to better understand the scale and importance of radiata pine invasion. We observed relatively low incidence of radiata pine invasion from plot-based data at the 0.04 ha scale but much higher incidence for site-based data at the > 1 ha scale (Table 2). These differences between data sources reflect both different sampling objectives and ability to detect early invasions or any sparsely distributed population. For example, plot-based data typically quantify absences or the abundance of species in communities, but are thus sensitive to replication, stratification by vegetation or land use type, spatial bias and representativeness (e.g., Holdaway et al. 2014). In contrast, site-based surveys typically generate presence-only qualitative data about species but have larger spatial grain and higher detection probability for populations compared with plot-based data but are uninformative for some processes such as habitat suitability (Garrard et al. 2008). Both approaches can be combined to scale up low probability distributions or occurrence of plant populations (e.g., Peltzer et al 2008; see also Isaac et al. 2020), or alternatively, hierarchically nested plots can be used to evaluate the scale-dependence of observations (e.g., Stohlgren et al. 1995). Overall, a combination of plot- and site-based data can be used in combination to understand current and future distributions of biological invaders, and to better understand changes in invasion rates or ecological effects. This approach is generalisable across species and different regions (see also Wilson et al. 2018; Etherington et al. 2022).

There is little information on abundance of radiata pine in New Zealand, aside from plot-based assessments within a few sites. Such information is required to confidently estimate impacts at larger spatial scales using, for example, EICAT or SEICAT systems (Blackburn et al. 2014; Bacher et al 2018). Even without this information, studies on invasive pines in New Zealand and internationally show that high ecological impacts of radiata pine are likely, based on at least large range and high per-unit effects (Parker et al. 1999; Sapsford et al. 2020; Latombe et al. 2022). However, studies of the per-unit effects of radiata pine in New Zealand ecosystems are needed to inform programmes to manage its invasion.

Invasive radiata pine as a transformer of naturally uncommon ecosystems

Invasion by trees into largely treeless habitats is a global concern (Rundel et al. 2014), and the spread of non-native radiata pine into naturally rare ecosystems exemplifies this issue (Table 2). Radiata pine invasion in gumland heaths is analogous to its invasion of mesic fynbos in South Africa (Richardson and Brown 1986); in both systems, initial invasion by radiata pines was closest to plantations. As in invasions of fynbos, even young radiata pines grow rapidly in height to exceed the c. 1 m tall gumlands and achieve far greater biomass and height than the resident flora in < 10 years, and can positively feedback to increase fire frequency, thus maintaining low-statured and invasible vegetation (Clarkson et al. 2011; Tepley et al. 2018; Wyse et al. 2018). Invasion by radiata pine on inland cliffs, scarps, and tors, likely pre-empts native woody plants from re-establishing following deforestation of these systems through a combination of relatively high propagule pressure, growth and occupancy of restricted habitat or microsites for establishment (Wiser and Buxton 2009). We documented radiata pine invasion into three broad classes of naturally uncommon ecosystems but, since unpublished data shows it invades many other rare ecosystems (e.g., coastal cliffs, gravel beaches), data for the extent of radiata pine invasion and ecosystem effects throughout the invasive range of radiata pine worldwide is warranted to understand effects on rare ecosystems, and for prioritising management (e.g., by assessing its invasion against the IUCN Red List of rare ecosystems; Holdaway et al. 2012).

Invasive radiata pine in successions

Multiple lines of evidence point to increasing potential effects of radiata pine in successions. Its rapid accrual of biomass compared with co-occurring native and most other non-native species suggests that the per-individual effects of this species are high (Sapsford et al. 2020), but population-level impacts are currently low because many sites are in the early stages of the invasion process. This suggests that for many sites or successions, early detection and containment remain the most effective management strategies for radiata pine (Simberloff et al. 2013; Hulme 2020).

Radiata pine may also fill a ‘functional gap’ in the New Zealand flora (Dansereau 1964; Wilson and Lee 2012), exerting relatively large potential impacts through functional dissimilarity (Wardle et al. 2011). This supports a view that deflected trajectories in primary succession can be driven by “pre-emptive invasion of unusual species” that alter soil nutrient concentrations and microclimates (Walker and del Moral 2003). For example, *Pinus* species colonize recent surfaces generated by volcanic eruptions globally (e.g., Tagawa 1964; del Moral and Wood 1993; Ohtsuka et al. 2013) and, in New Zealand, radiata pine colonises lava flows (Brown and Wilcox 2007) and ejecta (Clarkson and Clarkson 1991) on which there is no functional analogue in the native flora. Potentially indicative of its ecosystem effects, *Pinus nigra* planted on lava flows in Sicily caused weathering of primary minerals throughout the soil profile, depletion of base cations, and release of aluminium in the topsoil (Certini et al. 2001). Radiata pine invasions can also alter secondary successions through co-invasions with mutualists; alteration of plant community composition; and feedbacks with fire regime (Tepley et al. 2018; Sapsford et al. 2020). For example, radiata pine can exacerbate fire intensity on islands thus shifting secondary successions toward a subset of more fire-tolerant species than would otherwise occupy these islands (e.g., Kawau and Great Barrier (Aotea) Islands; Gardner 1993; Wyse et al. 2018). Together, these observations suggest that invasive pines have strong potential to alter both primary and secondary successions, but empirical tests of these impacts both in New Zealand and more generally are scarce, suggesting that the mechanisms and magnitude of these effects warrant renewed investigation.

Both plot- and site-based data revealed that radiata pine rarely invades alone to generate monodominant vegetation, but often co-occurs with other non-native species. What is largely unknown is how novel combinations of non-native species interact to either amplify or dampen their effects in communities or ecosystem processes. For example, co-invasion by radiata pine and nitrogen-fixing, woody non-native species such as Scotch broom (*Cytisus scoparius*) and gorse (*Ulex europaeus*) might have larger biogeochemical impacts than either species alone because of complementary effects on P and N respectively. Similarly, many invasive plant species in New Zealand that co-occur with pines can alter fire behaviour or may exacerbate fire behaviour (Taylor et al. 2017). Moreover, these same species may benefit from increased fire intensity or frequency through increased post-fire establishment (e.g., *Hakea sericea* in gumlands) or reductions in abundance of less fire-resistant native species. How radiata pine alters successions either directly, or through indirect effects including with co-invading species, is largely unknown. However, given both the global occurrence of pine invasions into successional systems, a greater understanding of the role that invasive pines like radiata pine have in ecosystems is required for shaping ecosystem restoration and conservation efforts (e.g., Becerra & Montenegro 2013; Taylor et al. 2017; Nuñez et al. 2021). Greater emphases are needed on building the evidence base for impacts however, including primary data for invader distribution and abundance (Wilson et al. 2018) and their impacts on social and ecological systems (Blackburn et al. 2014; Bacher et al 2018). Such evidence is required both for multiple purposes including prioritisation of landscape-scale management and developing cost–benefit analyses for supporting investment in invader management (e.g., van Wilgen et al. 2014, 2016; Nuñez et al 2021).

Dispersal and invasions of radiata pine

Despite international evidence of high potential invasion risk by radiata pine (e.g., its z-score of Rejmánek & Richardson 1996; see also Grotkopp et al. 2002; McGregor et al. 2012), a commonly held view in New Zealand is that it mostly invades close to established populations because it has poorer dispersal ability and slower maturity than some other invasive pine species (Wyse and Hulme 2021a). Several lines of evidence suggest that radiata pine can invade further than previously expected. Observational data from known point sources to invasive populations suggest that long-distance dispersal is possible. For example, downwind colonisation of landslides throughout a large tract of native forest, Te Urewera, is most likely to originate from propagule sources at Kāingaroa > 20 km away (Shaw 1990); this may be due in part to sheer spatial mass effects, where the source plantation is ca. 190 000 ha. The role of birds or mammals in radiata pine seed dispersal in

New Zealand is unknown, but long-distance dispersal of radiata pine is mediated by parrots in Australia (Batianoff 2005) and pigs in Argentina (Nuñez et al. 2013). Recent work on seed traits of radiata pine validated against empirical observations of dispersal from known sources demonstrates that some propagules within individual trees have large wings that allow them to travel at least 1.5 km at wind speeds of only 2 m s^{-1} (Wyse and Hulme 2021b; Wyse et al. 2022), and higher windspeeds are common in New Zealand, and cause long distance dispersal of radiata pine from plantations in the South Island (Hunter & Douglas 1984). Long-distance dispersal of radiata pine over several km should thus be anticipated rather than dispersal over a few hundred metres as is currently assumed and used by managers (e.g., in the 'wildings spread risk calculator' to predict spread risk from plantations; see also Froude 2011; Strang et al. 2015; Wyse and Hulme 2021a,b).

Managing invasions of an economically important tree

A major consideration of managing some invasive plant species is that, depending on the site considered, the same species can be an environmental weed in one situation and economically beneficial in another (Dickie et al. 2014b; Nuñez et al. 2021). This is exemplified by goals within New Zealand's national strategies of "the right tree in the right place" (MPI 2014, national wilding conifer control strategy) and "right tree, right place, right purpose" (One Billion Trees afforestation initiative: https://www.mpi.govt.nz/forestry/funding-tree-planting-research/one-billion-trees-programme/about-the-one-billion-trees-programme/). More generally, because non-native species can be viewed as either beneficial or harmful depending on environmental and social context, this can generate conflicting views on their management (Dickie et al. 2014b; Edwards et al. 2020; Yletyinen et al. 2021). As such, the costs and benefits of invasive species' impacts or their management require information on both ecological effects alongside information on social and economic values.

Rigorous cost–benefit analyses demonstrate accelerating costs of managing species as invasion proceeds, and some benefits of species for economic activities or carbon sequestration that are readily quantified (e.g., Wise et al. 2012; Wyatt 2018; see also Castro-Díez et al. 2019). However, the value of some processes, services or impacts of invasive species cannot easily be quantified, or have complex responses to invader abundance (e.g., Mason et al. 2017; Panetta and Gooden 2017; Bartz and Kowarik 2019). For example, a cost–benefit analysis for non-native Pinaceae in New Zealand demonstrated a 38:1 benefit:cost (Wyatt 2018). However, this analysis was highly conservative because it only considered costs to primary industry through invasions, water availability, fire risk, and future savings to management costs over 50 years, and it did not include costs to biodiversity or carbon because of difficulties in valuing damage and uncertainties around markets respectively. Economic justifications for invader management have been well developed elsewhere, for example, for non-native tree invasions in South Africa (see de Wit et al 2001; Wise et al 2012). Cost–benefit analyses could be more widely applied both to understand the net ecological, social and economic effects of invasions and their management, but also aid to understand how short-term management or investments can have longer-term benefits (van Wilgen et al. 2014).

National cost–benefit analyses are likely to oversimplify the complex nature of effective management at regional or site scales. For example, many invasive plant management efforts either fail to meet their stated management goals or do not carry out rigorous evaluations of success (e.g., Wilson et al. 2014) including the wider values or benefits beyond invader removal that typically occur at the site scale (Reid et al. 2009). Implicit goals of invasive pine management can range from conservation of sites and native species to sustained water yield in catchments and maintenance of landscape values (MPI 2014; Gawith et al. 2020; Edwards et al. 2020). As a consequence, there are opportunities to more closely link ecological knowledge with management to avoid or mitigate the impacts of major biological invaders such as radiata pine include resolving: (1) when do low-density invasions matter? Eradication is rarely feasible and ongoing invasion requires knowledge of abundance–impact relationships to avoid negative effects or legacies of invasions (Sofaer et al. 2018; Sapsford et al. 2020). Similarly, evidence is essential to determine how much control is needed relative to the distribution and abundance of the invader, and how much it would cost to meet management goals (e.g., van Wilgen et al. 2016); (2) what evidence is required to evaluate management success? Internationally there is a move to collect a minimum set of core data to better understand and manage tree invasions (Wilson et al. 2014, 2018; Brundu et al. 2020). Because the outcomes of invasive species removal are variable (Kettenring and Adams 2011), it is also essential to evaluate the performance of different management strategies (Funk et al. 2020); and (3) understand the potential future risks of invasion. Given predicted changes to climate, land use, and disturbance regimes, we should anticipate that invasion risk is dynamic over decades and planning land use or management strategies should consider this dynamism (Caplat et al. 2013; Macinnis-Ng et al. 2021; Etherington et al. 2022). As an example, management of 'wilding conifers' in New Zealand has a clearly stated national goal of stopping or containing invasion by non-native conifers by 2030, estimated to cost > $110 million USD (Wyatt 2018) and, in some areas (e.g. Northland Region and coastal parts of Marlborough District), most of these costs focus on controlling invasive radiata pine. Actual costs of controlling radiata pine invasions are currently hard to determine because agencies often concentrate on multiple species of Pinaceae, amongst which radiata pine is sometimes the most abundant invader. More explicit costs of its management will be needed, including costs resulting from re-invasions, both from incomplete management, and ongoing propagule pressure from existing and new plantations. How long-term management of invasive pines in New Zealand is unresolved. Understanding the costs and benefits associated with invasions and their management over the longer-term is essential to developing approaches to both value and invest in such large-scale and long-term efforts (see also Graham et al. 2019; Peltzer et al. 2019).

In light of our findings, we recommend the following changes to afforestation and biosecurity policies and legislation in New Zealand: (1) a levy on new non-native conifer forests; and (2) stricter afforestation regulations, incorporating recommended changes and addressing gaps recently identified (Wyse et al. 2021a, 2021b). The levy could be used for surveillance and clearance of new invasions, and stricter afforestation regulations should mitigate the risk of future conifer spread including into areas that climate change renders more suitable for colonization (Etherington et al. 2022). Since radiata pine is the most likely species to be planted in new areas and has the largest propagule pressure, these changes to policies will be critical to curb ongoing invasion. A more detailed assessment of current investments in management, both direct and in-kind, is needed to determine whether such a levy alongside other investments, is sufficient to achieve the national goal of stopping or containing invasions. Similar approaches have also been proposed in South Africa to offset the impacts of plantations on water availability, but were unsuccessful because the levy was insufficient to compensate for the negative impact on water or ongoing invasion (Tewari 2005).

Recent syntheses demostrate the growing direct and indirect economic costs of invasive species globally (e.g., Diagne et al. 2021; Welsh et al. 2021; Zenni et al. 2021). However, the costs and benefits of non-native species vary among locations, and along the invasion pathway. For example, economic costs of invader management are often borne later, and in different locations, from original sources (Lovett et al. 2016). Here we provide an example to help overcome this issue for invasive conifers, which are economically valuable species but also major invaders globally (Richardson and Rejmánek 2004; Nuñez et al. 2017). In New Zealand, most costs of managing invasive conifers are currently met by by short-term central government funding and long-term stable mechanisms to fund management are lacking (Hulme 2020). Levies would address the large commercial plantations that provide propagule pressure but other measures will also be needed to fund long-term management. Propagule pressure from invasive trees, including radiata pine, derives from widespread non-commercial plantings for soil conservation, amenity and shelter, thus management requires multiple incentives, regulatory or economic tools for their management (e.g., Hulme 2020; Yletyinen et al. 2021). The findings and solutions presented here are globally relevant and provide critical information to improve management in other countries at earlier stages of managing these invaders (Nuñez et al. 2017; see also Brundu et al. 2020).

Conclusion

We used plot- and site-based data and ecological niche models to demonstrate that invasive radiata pine occurs far more widely across New Zealand than previously appreciated. Niche modelling based on climatic suitability suggests that its distribution could be much wider than current plot or observational data indicate. The wide distribution of invasive radiata pine is partly explained by its wide introduction as a plantation and amenity species, but also reflects far greater spread risk than previously assumed because of long-distance (at least 1.5 km) seed dispersal. Radiata pine has potentially large, but largely undocumented, effects in many primary and secondary successions and across multiple naturally uncommon ecosystems. Although management of invasive radiata pine is already widespread in New Zealand and other southern hemisphere countries, more proactive planning is needed given ongoing large-scale afforestation efforts and potential future increases in invasion. A levy on economic uses of invasive species to offset costs of managing invasions alongside stricter regulations to protect vulnerable ecosystems could thus be more widely adopted to prevent or avert future negative impacts.

Acknowledgements We acknowledge the use of data drawn from the National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz/), including the use of data drawn from the Natural Forest plot data collected between 2002 and 2014 by the LUCAS programme for the Ministry for the Environment. We thank knowledgeable practitioners for information about invasive conifer observations and management: Brad Lett (formerly Department of Conservation, Murupara) for western Te Urewera; Ceres Sharp and Don McKenzie (Northland Regional Council) for Northland; and Andrew Macalister for the Marlborough Sounds. Hamish Maule assisted with determining the invasion status of occurrence records. Fabio Mologni provided calculations of island invasions. We thank three anonymous reviewers for thoughtful and constructive comments on this manuscript.

Author contributions PJB and DAP developed initial ideas for this paper, all authors made conceptual and written contributions to the manuscript, and interpretation of results.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. We thank the New Zealand Ministry of Business, Innovation and Employment for financial support through the Endeavour research programme Winning Against Wildings (Grant Number C09X1611).

Availability of data and material Data will be made publicly available upon manuscript acceptance. (as a time-stamped collated dataset in DataStore: https://www.landcareresearch.co.nz/tools-and-resources/databases/datastore/).

Code availability Custom code for the niche models will be made publicly available upon manuscript acceptance.

Declarations

Conflicts of interest We declare no conflict of interest.

Consent for publication All authors consent for this manuscript to be published in Biological Invasions.

References

Atkinson IAE (1985) Derivation of vegetation mapping units for an ecological survey of Tongariro National Park, North Island, New Zealand. N Z J Bot 23:361–378. https://doi.org/10.1080/0028825X.1985.10425343

Atkinson IAE (1997) Problem weeds on New Zealand islands. Sci Conserv 42:1–58

Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. Nature Ecol Evol 2:34–43. https://doi.org/10.1038/s41559-017-0396-z

Bacher S, Blackburn TM, Essl F, Genovesi P, Heikkilä J, Jeschke JM, Jones G, Keller R, Kenis M, Kueffer C et al (2018) Socio–economic impact classification of alien taxa (SEICAT). Methods Ecol Evol 9:159–168. https://doi.org/10.1111/2041-210X.12844

Baker AC, Murray BR (2010) Relationships between leaf-litter traits and the emergence and early growth of invasive *Pinus radiata* seedlings. Weed Res 50:586–596. https://doi.org/10.1111/j.1365-3180.2010.00805.x

Baker AC, Murray BR, Hose GC (2007) Relating pine-litter intrusion to plant-community structure in native eucalypt woodland adjacent to *Pinus radiata* (Pinaceae) plantations. Aust J Bot 55:521–532. https://doi.org/10.1071/BT06135

Barbet-Massin M, Jetz W (2014) A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. Divers Distrib 20:1285–1295. https://doi.org/10.1111/ddi.12229

Bartz R, Kowarik I (2019) Assessing the environmental impacts of invasive alien plants: a review of assessment approaches. NeoBiota 43:69–99. https://doi.org/10.3897/neobiota.43.30122

Batianoff GN (2005) Notes on *Pinus radiata* D. Don (Pinaceae): an invasive woody weed in the Stanthorpe Shire, Queensland. Proc Royal Soc Qld 112:71–75

Beadel S, Shaw W, Bawden R, Bycroft C, Wilcox F, McQueen J, Lloyd K (2018) Sustainable management of geothermal vegetation in the Waikato Region, New Zealand, including application of ecological indicators and new monitoring technology trials. Geothermics 73:91–99. https://doi.org/10.1016/j.geothermics.2017.11.001

Becerra PI, Montenegro G (2013) The widely invasive tree *Pinus radiata* facilitates regeneration of native woody species in a semi-arid ecosystem. Appl Veg Sci 16:173–183. https://doi.org/10.1111/j.1654-109X.2012.01221.x

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W et al (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12:e1001850. https://doi.org/10.1371/journal.pbio.1001850

Boothroyd IK (2009) Ecological characteristics and management of geothermal systems of the Taupo Volcanic Zone, New Zealand. Geothermics 38:200–209. https://doi.org/10.1016/j.geothermics.2008.12.010

Brandt AJ, Bellingham PJ, Duncan RP, Etherington TR, Fridley JD, Howell CJ, Hulme PE, Jo I, McGlone MS, Richardson SJ, Sullivan JJ, Williams PA, Peltzer DA (2021) Naturalised plants transform the composition and function of the New Zealand flora. Biol Invasions 23:351–366. https://doi.org/10.1007/s10530-020-02393-4

Brown PM, Wilcox MD (2007) Exotic vascular flora. In: Wilcox MD (ed) Natural history of Rangitoto Island. Auckland Botanical Society, Auckland, pp 87–100

Brundu G, Pauchard A, Pyšek P, Pergl J, Bindewald A, Brunori A, Canavan S, Campagnaro T, Celesti-Grapow L, De M et al (2020) Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts. NeoBiota 61:65–116. https://doi.org/10.3897/neobiota.65.58380

Burns B (1997) Vegetation change along a geothermal stress gradient at the Te Kopia steamfield. J Royal Soc N Z 27:279–293. https://doi.org/10.1080/03014223.1997.9517539

Burrows ND, Woods YC, Ward BG, Robinson AD (1989) Prescribing low intensity fire to kill wildings in *Pinus radiata* plantations in Western Australia. Austral for 52:45–52. https://doi.org/10.1080/00049158.1989.10674535

Bustamante RO, Simonetti JA (2005) Is *Pinus radiata* invading the native vegetation in central Chile? Demographic responses in a fragmented forest. Biol Invasions 7:243–249. https://doi.org/10.1007/s10530-004-0740-5

Calviño-Cancela M, van Etten EJ (2018) Invasive potential of *Eucalyptus globulus* and *Pinus radiata* into native eucalypt forests in Western Australia. For Ecol Manag 424:246–258. https://doi.org/10.1016/j.foreco.2018.05.001

Cameron EK, Davies NC (2013) Changes in the wild vascular flora of Tiritiri Matangi Island, 1978–2010. N Z J Ecol 37:307–342

Campbell DJ (1998) Salt-wind induced wave regeneration in coastal pine forests in New Zealand. Can J for Res 28:953–960. https://doi.org/10.1139/x98-073

Caplat P, Cheptou PO, Diez J, Guisan A, Larson BM, MacDougall AS, Peltzer DA, Richardson DM, Shea K, van Kleunen M, Zhang R (2013) Movement, impacts and management of plant distributions in response to climate change: insights from invasions. Oikos 122:1265–1274. https://doi.org/10.1111/j.1600-0706.2013.00430.x

Castro-Díez P, Vaz AS, Silva JS, van Loo M, Alonso Á, Aponte C, Bayón Á, Bellingham PJ, Chiuffo MC, DiManno N et al (2019) Global effects of non-native tree species on multiple ecosystem services. Biol Rev 94:1477–1501. https://doi.org/10.1111/brv.12511

Certini G, Sanjurjo MJ, Corti G, Ugolini FC (2001) The contrasting effect of broom and pine on pedogenic processes in volcanic soils (Mt. Etna, Italy). Geoderma 102:239–254. https://doi.org/10.1016/S0016-7061(01)00017-9

Chamberlain SA, Boettiger C (2017) R Python, and Ruby clients for GBIF species occurrence data. PeerJ Prepr 5:e3304v1. https://doi.org/10.7287/peerj.preprints.3304v1

Clarkson BD, Clarkson BR (1991) A century of change on Mt Tarawera. In: Clarkson BD, Smale MC, Ecroyd CE (compilers), Botany of Rotorua. Forest Research Institute, Rotorua, pp 79–84

Clarkson BR, Smale MC, Williams PA, Wiser SK, Buxton RP (2011) Drainage, soil fertility and fire frequency determine composition and structure of gumland heaths in northern New Zealand. N Z J Ecol 35:96–113

Curtis CA, Pasquarella VJ, Bradley BA (2019) Landscape characteristics of non-native pine plantations and invasions in southern Chile. Austral Ecol 44:1213–1224. https://doi.org/10.1111/aec.12799

Dansereau P (1964) Six problems in New Zealand vegetation. Bull Torrey Bot Club 91:114–140. https://doi.org/10.2307/2483613

del Moral R, Wood DM (1993) Early primary succession on the volcano Mount St. Helens J Veg Sci 4:223–234. https://doi.org/10.2307/3236108

de Wit M, Crookes D, van Wilgen BW (2001) Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. Biol Invasions 3:167–178

Diaconis P, Efron B (1983) Computer-intensive methods in statistics. Sci Am 248:116–130

Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJ, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592:571–576. https://doi.org/10.1038/s41586-021-03405-6

Dickie IA, Bolstridge N, Cooper JA, Peltzer DA (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. New Phytol 187:475–484. https://doi.org/10.1111/j.1469-8137.2010.03277.x

Dickie IA, St John MG, Yeates GW, Morse CW, Bonner KI, Orwin K, Peltzer DA (2014a) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. AoB Plants 6:plu056. https://doi.org/10.1093/aobpla/plu056

Dickie IA, Bennett BM, Burrows LE, Nuñez MA, Peltzer DA, Porté A, Richardson DM, Rejmánek M, Rundel PW, Van Wilgen BW (2014b) Conflicting values: ecosystem services and invasive tree management. Biol Invasions 16:705–719. https://doi.org/10.1007/s10530-013-0609-6

Dickinson BR (1980) The flora and vegetation of the high domes of Mount Tarawera, Rotorua, New Zealand. PhD dissertation, University of Waikato, Hamilton, New Zealand

Druce AP (1957) Botanical survey of an Experimental Catchment, Taita, New Zealand. DSIR Bulletin 124, DSIR, Wellington

Edwards P, Stahlmann-Brown P, Thomas S (2020) Pernicious pests and public perceptions: Wilding conifers in Aotearoa New Zealand. Land Use Policy 97:104759. https://doi.org/10.1016/j.landusepol.2020.104759

Efron B (1979) Bootstrap methods: another look at the Jackknife. Ann Stat 7:1–26

Enright NJ (1989) Heathland vegetation of the Spirits Bay area, far northern New Zealand. N Z J Ecol 12:63–75

Esler AE (1962) Botanical features of Abel Tasman national park. Trans Royal Soc N Z (botany) 1:297–311

Esler AE, Rumball PJ (1975) Gumland vegetation at Kaikohe, Northland, New Zealand. N Z J Bot 13:425–436. https://doi.org/10.1080/0028825X.1975.10430335

Essl F, Moser D, Dullinger S, Mang T, Hulme PE (2010) Selection for commercial forestry determines global patterns of alien conifer invasions. Divers Distrib 16:911–921. https://doi.org/10.1111/j.1472-4642.2010.00705.x

Etherington TR (2019) Mahalanobis distances and ecological niche modelling: correcting a chi-squared probability error. PeerJ 7:e6678. https://doi.org/10.7717/peerj.6678

Etherington TR (2021) Mahalanobis distances for ecological niche modelling and outlier detection: implications of sample size, error, and bias for selecting and parameterising a multivariate location and scatter method. PeerJ 9:e11436. https://doi.org/10.7717/peerj.11436

Etherington TR, Lieske DJ (2019) [Re] Resampling methods for evaluating classification accuracy of wildlife habitat models. ReScience C 5:#4

Etherington TR, Omondiagbe OP (2019) virtualNicheR: generating virtual fundamental and realised niches for use in virtual ecology experiments. J Open Source Softw 4:1661. https://doi.org/10.21105/joss.01661

Etherington TR, Peltzer DA, Wyse SV (2022) Predicted climate-change impacts on the distributions of suitable climates for exotic conifers in New Zealand. N Z J Ecol 46:3473. https://doi.org/10.20417/nzjecol.46.14

Franzese J, Urrutia J, García RA, Taylor K, Pauchard A (2017) Pine invasion impacts on plant diversity in Patagonia: invader size and invaded habitat matter. Biol Invasions 19:1015–1027

Franzese J, Raffaele E, Blackhall M, Rodriguez J, Soto AY (2020) Changes in land cover resulting from the introduction of non-native pine modifies litter traits of temperate forests in Patagonia. J Veg Sci 31:223–233. https://doi.org/10.1111/jvs.12847

Froude VA (2011) Wilding conifers in New Zealand: status report. Prepared for the Ministry of Agriculture and Forestry. Bay of Islands, New Zealand, Pacific Eco-Logic Ltd

Funk JL, Parker IM, Matzek V, Flory SL, Aschehoug ET, D'Antonio CM, Dawson W, Thomson DM, Valliere J (2020) Keys to enhancing the value of invasion ecology research for management. Biol Invasions 22:2431–2445. https://doi.org/10.1007/s10530-020-02267-9

Gawith D, Greenaway A, Samarasinghe O, Bayne K, Velarde S, Kravchenko A (2020) Socio-ecological mapping generates public understanding of wilding conifer incursion. Biol Invasions 22:3031–3049. https://doi.org/10.1007/s10530-020-02309-2

GBIF.org (2020) GBIF Occurrence Download, https://doi.org/10.15468/dl.yvcf3c

Gardner RO (1993) Some plants of Kawau Island. Auckl Bot Soc Newsl 48(2):23–27

Garrard GE, Bekessy SA, McCarthy MA, Wintle BA (2008) When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. Austral Ecol 33:986–998. https://doi.org/10.1111/j.1442-9993.2008.01869.x

Giller M (2013) The vegetation of smothering Gully, Omihi Hills, North Canterbury. Canterb Bot Soc J 44:43–49

Gómez-González S, Paniw M, Blanco-Pastor JL, García-Cervigón AI, Godoy O, Herrera JM, Lara A, Miranda A, Ojeda F, Ochoa-Hueso R (2022) Moving towards the ecological intensification of tree plantations. Trends Plant Sci 27:637–645. https://doi.org/10.1016/j.tplants.2021.12.009

Graham S, Metcalf AL, Gill N, Niemiec R, Moreno C, Bach T, Ikutegbe V, Hallstrom L, Ma Z, Lubeck A (2019) Opportunities for better use of collective action theory in research and governance for invasive species management. Conserv Biol 33:275–287. https://doi.org/10.1111/cobi.13266

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. Am Nat 159:396–419. https://doi.org/10.1086/338995

Hannken PB (1954) Tree felling expedition. Auckland Bot Soc Newsletter 11(4):2–3

Hijmans RJ (2020) raster: Geographic data analysis and modeling. R package version 3.3–7, URL https://www.R-project.org/

Holdaway RJ, Wiser SK, Williams PA (2012) Status assessment of New Zealand's naturally uncommon ecosystems. Conserv Biol 26:619–629. https://doi.org/10.1111/j.1523-1739.2012.01868.x

Holdaway RJ, McNeill SJ, Mason NWH, Carswell FE (2014) Propagating uncertainty in plot-based estimates of forest carbon stock and carbon stock change. Ecosystems 17:627–640. https://doi.org/10.1007/s10021-014-9749-5

Howell CJ (2019) Naturalised status of exotic conifers in New Zealand. N Z J Bot 57:227–237. https://doi.org/10.1080/0028825X.2019.1626744

Hulme PE (2020) Plant invasions in New Zealand: global lessons in prevention, eradication and control. Biol

Invasions 22:1539–1562. https://doi.org/10.1007/s10530-020-02224-6

Hunter GG, Douglas MH (1984) Spread of exotic conifers on South Island rangelands. N Z J For 29:78–96

Hurst J, Allen R (2007) The Recce method for describing New Zealand vegetation: field protocols. Landcare Research New Zealand, Lincoln

Isaac NJ, Jarzyna MA, Keil P, Dambly LI, Boersch-Supan PH, Browning E, Freeman SN, Golding N, Guillera-Arroita G, Henrys PA, Jarvis S (2020) Data integration for large-scale models of species distributions. Trends Ecology Evol 35:56–67. https://doi.org/10.1016/j.tree.2019.08.006

Johnson PN (1992) The sand dune and beach vegetation inventory of New Zealand. II. South Island and Stewart Island. DSIR Land Resources Scientific Report Number 16, DSIR Land Resources, Christchurch. 278 p

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Sci Data 4:170122. https://doi.org/10.1038/sdata.2017.122

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. J Appl Ecol 48:970–979. https://doi.org/10.1111/j.1365-2664.2011.01979.x

Latombe G, Catford JA, Essl F, Lenzner B, Richardson DM, Wilson JR, McGeoch MA (2022) GIRAE: a generalised approach for linking the total impact of invasion to species' range, abundance and per-unit effects. Biol Invasions. https://doi.org/10.1007/s10530-022-02836-0 (**in Press**)

Ledgard NJ (1994) A form for assessing the risk of conifer spread in the South Island high country. NZ For 39:26–27

Ledgard N (2001) The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. For Ecol Manag 141:43–57. https://doi.org/10.1016/S0378-1127(00)00488-6

Ledgard N (2006) Mitigating worries with wildings. NZ J For 50:20–23

LINZ (Toitū Te Whenua Land Information New Zealand) (2021a) NZ Lake Polygons (Topo, 1:50k). https://data.linz.govt.nz/layer/50293-nz-lake-polygons-topo-150k/ (Accessed 27 Aug 2021)

LINZ (2021b) NZ Chatham Island Lake Polygons (Topo, 1:50k). https://data.linz.govt.nz/layer/50088-nz-chatham-island-lake-polygons-topo-150k/ (Accessed 27 Aug 2021)

Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert KF, Orwig DA, Campbell FT, Rosenthal J, McCullough DG et al (2016) Non-native forest insects and pathogens in the United States: Impacts and policy options. Ecol Appl 26:1437–1455. https://doi.org/10.1890/15-1176

MPI (Ministry for Primary Industries) (2014) The right tree in the right place: New Zealand wilding conifer management strategy 2015–2030. A non-regulatory strategy for the management of wilding conifers in New Zealand. Ministry for Primary Industries of New Zealand, 40 pp. ISBN: 978–0–477–10511–8

Macinnis-Ng C, Mcintosh AR, Monks JM, Waipara N, White RS, Boudjelas S, Clark CD, Clearwater MJ, Curran TJ, Dickinson KJM et al (2021) Climate-change impacts exacerbate conservation threats in island systems: New Zealand as a case study. Front Ecol Environ 19:216–224. https://doi.org/10.1002/fee.2285

Marden M, Rowan D (1993) Protective value of vegetation on tertiary terrain before and during Cyclone Bola, East Coast, North Island, New Zealand. N Z J For Sci 23:255–263

Mason NWH, Palmer DJ, Vetrova V, Brabyn L, Paul T, Willemse P, Peltzer DA (2017) Accentuating the positive while eliminating the negative of alien tree invasions: a multiple ecosystem services approach to prioritising control efforts. Biol Invasions 19:1181–1195. https://doi.org/10.1007/s10530-016-1307-y

McCarthy JK, Leathwick JR, Roudier P, Barringer JR, Etherington TR, Morgan FJ, Odgers NP, Price RH, Wiser SK, Richardson SJ (2021) New Zealand Environmental data stack (NZEnvDS): a standardised collection of spatial layers for environmental modelling and site characterisation. N Z J Ecol 45:3440. https://doi.org/10.20422/nzjecol.45.31

McEwen WM (1987) Ecological regions and districts of New Zealand. Department of Conservation, Wellington, p 125

McGlone MS, Bellingham PJ, Richardson SJ (2022) Science, policy and sustainable indigenous forestry in New Zealand. N Z J For Sci 52:8. https://doi.org/10.33494/nzjfs522022x182x

McGregor KF, Watt MS, Hulme PE, Duncan RP (2012) What determines pine naturalization: species traits, climate suitability or forestry use? Divers Distrib 18:1013–1023. https://doi.org/10.1111/j.1472-4642.2012.00942.x

McKelvey P (1999) Sand Forests: a historical perspective of the stabilisation and afforestation of coastal sands in New Zealand. Canterbury University Press, Christchurch

Mead DJ (2013) Sustainable management of *Pinus radiata* plantations. Food and Agriculture Organization of the United Nations (FAO) Forestry Paper No. 170

Meyer C, Weigelt P, Kreft H (2016) Multidimensional biases, gaps and uncertainties in global plant occurrence information. Ecol Lett 19:992–1006. https://doi.org/10.1111/ele.12624

Mologni F, Bellingham PJ, Tjørve E, Cameron EK, Wright AE, Burns KC (2021) Similar yet distinct distributional patterns characterize native and exotic plant species richness across northern New Zealand islands. J Biogeogr 48:1731–1748. https://doi.org/10.1111/jbi.14110

Nuñez MA, Hayward J, Horton TR, Amico GC, Dimarco RD, Barrios-Garcia MN, Simberloff D (2013) Exotic mammals disperse exotic fungi that promote invasion by exotic trees. PLoS ONE 8:66832. https://doi.org/10.1371/journal.pone.0066832

Nuñez MA, Chiuffo MC, Torres A, Paul T, Dimarco RD, Raal P, Policelli N, Moyano J, García RA, van Wilgen BW, Pauchard A, Richardson DM (2017) Ecology and management of invasive pinaceae around the world: progress and challenges. Biol Invasions 19:3099–3120. https://doi.org/10.1007/s10530-017-1483-4

Nuñez MA, Davis KT, Dimarco R, Peltzer DA, Paritsis J, Maxwell BD, Pauchard A (2021) Should tree invasions be used in treeless ecosystems to mitigate climate change? Front Ecol Environ 19:334–341. https://doi.org/10.1002/fee.2346

NZFOA (New Zealand Forest Owners' Association) (2020) https://www.nzfoa.org.nz/images/Facts_Figures_2019_20_Web_FA3-updated.pdf

Ohtsuka T, Negishi M, Sugita K, Iimura Y, Hirota M (2013) Carbon cycling and sequestration in a Japanese red pine (*Pinus densiflora*) forest on lava flow of Mt. Fuji Ecol Res 28:855–867. https://doi.org/10.1007/s11284-013-1067-4

Panetta FD, Gooden B (2017) Managing for biodiversity: impact and action thresholds for invasive plants in natural ecosystems. NeoBiota 34:53–66. https://doi.org/10.3897/neobiota.34.11821

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Pawson SM, Brin A, Brockerhoff EG, Lamb D, Payn TW, Paquette A, Parrotta JA (2013) Plantation forests, climate change and biodiversity. Biodivers Conserv 22:1203–1227. https://doi.org/10.1007/s10531-013-0458-8

Pebesma E (2018) Simple features for R: standardized support for spatial vector data. R J 10:439–446

Peltzer DA, Ferriss S, FitzJohn RG (2008) Predicting weed distribution at the landscape scale: using naturalized *Brassica* as a model system. J Appl Ecol 45:467–475. https://doi.org/10.1111/j.1365-2664.2007.01410.x

Peltzer DA, Bellingham PJ, Dickie IA, Houliston G, Hulme PE, Lyver PO'B, McGlone M, Richardson SJ, Wood J, (2019) Scale and complexity implications of making New Zealand predator-free by 2050. J Royal Soc N Z 49:412–439. https://doi.org/10.1080/03036758.2019.1653940

Perry GLW, Ogden J, Enright NJ, Davy LV (2010) Vegetation patterns and trajectories in disturbed landscapes, great barrier Island, northern New Zealand. N Z J Ecol 34:311–323

Perry GLW, Wilmshurst JM, McGlone MS (2014) Ecology and long-term history of fire in New Zealand. N Z J Ecol 38:157–176

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reid AM, Morin L, Downey PO, French K, Virtue JG (2009) Does invasive plant management aid the restoration of natural ecosystems? Biol Conserv 142:2342–2349. https://doi.org/10.1016/j.biocon.2009.05.011

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661. https://doi.org/10.2307/2265768

Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive alien species – 2013 update of the global database. Divers Distrib 19:1093–1094. https://doi.org/10.1111/ddi.12075

Richardson DM, Brown PJ (1986) Invasion of mesic mountain fynbos by *Pinus radiata*. S Afr J Bot 52:529–536. https://doi.org/10.1016/S0254-6299(16)31486-7

Richardson DM, Rejmánek M (2004) Conifers as invasive aliens: a global survey and predictive framework. Divers Distrib 10:321–331. https://doi.org/10.1111/j.1366-9516.2004.00096.x

Richardson DM, Williams PA, Hobbs RJ (1994) Pine invasions in the southern hemisphere: determinants of spread and invadability. J Biogeogr 21:511–527. https://doi.org/10.2307/2845655

Roche M (1990) History of New Zealand Forestry. New Zealand Forestry Corporation Ltd, Auckland

Roche M (2017) Forest governance and sustainability pathways in the absence of a comprehensive national forest policy — The case of New Zealand. For Policy Econ 77:33–43. https://doi.org/10.1016/j.forpol.2015.12.007

Rouget M, Richardson DM, Milton SJ, Polakow D (2001) Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecol 152:79–92. https://doi.org/10.1023/A:1011412427075

Rundel PW, Dickie IA, Richardson DM (2014) Tree invasions into treeless areas: mechanisms and ecosystem processes. Biol Invasions 16:663–675. https://doi.org/10.1007/s10530-013-0614-9

Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD II, Green JL, Hulme PE, Nuñez MA, Orwin KH et al (2020) Towards a framework for understanding the context-dependencies of the impacts of non-native tree species. Funct Ecol 34:944–955. https://doi.org/10.1111/1365-2435.13544

Shaw WB (1990) Update on wild pines in Te Urewera national park. Rotorua Bot Soc Newsl 19:11–12

Simberloff D (2019) New Zealand as a leader in conservation practice and invasion management. J Royal Soc N Z 49:259–280. https://doi.org/10.1080/03036758.2019.1652193

Simberloff D, Nuñez MA, Ledgard NJ, Pauchard A, Richardson DM, Sarasola M, Van Wilgen BW, Zalba SM, Zenni RD, Bustamante R, Peña E (2010) Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. Austral Ecol 35:489–504. https://doi.org/10.1111/j.1442-9993.2009.02058.x

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66. https://doi.org/10.1016/j.tree.2012.07.013

Smale MC, Wiser SK, Bergin MJ, Fitzgerald NB (2018) A classification of the geothermal vegetation of the Taupō Volcanic Zone, New Zealand. J Royal Soc N Z 48:21–38. https://doi.org/10.1080/03036758.2017.1322619

Soberón J, Peterson AT (2020) What is the shape of the fundamental Grinnellian niche? Theoretical Ecol 13:105–115. https://doi.org/10.1007/s12080-019-0432-5

Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader abundance and impact. Ecosphere 9:e02415. https://doi.org/10.1002/ecs2.2415

Standish RJ, Sparrow AD, Williams PA, Hobbs RJ (2008) A state-and-transition model for the recovery of abandoned farmland in New Zealand. In: Hobbs RJ, Suding KN (eds) New models for ecosystem dynamics and restoration. Island Press, Washington DC, pp 189–205

Stohlgren TJ, Falkner MB, Schell LD (1995) A modified-Whittaker nested vegetation sampling method. Vegetatio 117:113–121. https://doi.org/10.1007/BF00045503

Strang S, Richards K, Weir P (2015) National environmental standard for plantation forestry. N Z J For 60(3):20–25

South A (2017) rnaturalearth: world map data from Natural Earth. R package version 0.1.0 https://CRAN.R-project.org/package=rnaturalearth

Tagawa H (1964) A study of the volcanic vegetation in Sakurajima, south-west Japan I. Dynamics of vegetation pattern and succession. Jpn J Bot 19:127–148

Taylor KT, Maxwell BD, McWethy DB, Pauchard A, Nuñez MA, Whitlock C (2017) *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire. Ecology 98:678–687. https://doi.org/10.1002/ecy.1673

Tepley AJ, Thomann E, Veblen TT, Perry GLW, Holz A, Paritsis J, Kitzberger T, Anderson-Teixeira KJ (2018) Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. J Ecol 106:1925–1940. https://doi.org/10.1111/1365-2745.12950

Tewari DD (2005) Should commercial forestry in South Africa pay for water? Valuing water and its contribution to the industry. Water SA 31(3):319–326. https://doi.org/10.4314/wsa.v31i3.5221

van Wilgen BW, Richardson DM (2014) Challenges and trade-offs in the management of invasive alien trees. Biol Invasions 16:721–734. https://doi.org/10.1007/s10530-013-0615-8

van Wilgen BW, Fill JM, Baard J, Cheney C, Forsyth AT, Kraaij T (2016) Historical costs and projected future scenarios for the management of invasive alien plants in protected areas in the Cape Floristic Region. Biol Conserv 200:168–177. https://doi.org/10.1016/j.biocon.2016.06.008

Varela S, Anderson RP, García-Valdés R, Fernández-González F (2014) Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37:1084–1091. https://doi.org/10.1111/j.1600-0587.2013.00441.x

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York

Verbyla DL, Litvaitis JA (1989) Resampling methods for evaluating classification accuracy of wildlife habitat models. Environ Manage 13:783–787. https://doi.org/10.1007/BF01868317

Walker LR, del Moral R (2003) Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, Cambridge

Walls G (2013) Southern rata (*Metrosideros umbellata*) in the Omihi Hills, North Canterbury. Canterbury Bot Soc J 44:34–42

Wassilieff MC (1982) Secondary succession in the lowland forests of the Marlborough Sounds Maritime Park. PhD thesis, Victoria University of Wellington, New Zealand

Wardle P (1991) Vegetation of New Zealand. Cambridge University Press, Cambridge

Wardle DA, Bardgett RD, Callaway RM, van der Putten WH (2011) Terrestrial ecosystem responses to species gains and losses. Science 332:1273–1277. https://doi.org/10.1126/science.1197479

Watt V (1986) Pine invasion on Maungakakaramea (Rainbow Mountain). MSc thesis, University of Waikato, Hamilton, New Zealand

Webb CJ, Sykes WR, Garnock-Jones PJ (1988) Flora of New Zealand Volume IV. Botany Division, DSIR, Christchurch

Welsh MJ, Turner JA, Epanchin-Niell RS, Monge JJ, Soliman T, Robinson AP, Kean JM, Phillips C, Stringer LD, Vereijssen J et al (2021) Approaches for estimating benefits and costs of interventions in plant biosecurity across invasion phases. Ecol Appl 31:e02319. https://doi.org/10.1002/eap.2319

Whitehead D, Walcroft AS, Scott NA, Townsend JA, Trotter CM, Rogers GN (2004) Characteristics of photosynthesis and stomatal conductance in the shrubland species mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*) for the estimation of annual canopy carbon uptake. Tree Physiol 24:795–804. https://doi.org/10.1093/treephys/24.7.795

Wilcox MD (2014) Vascular plants of Ahipara, Kaitaia area and Karikari Peninsula, Northland. Auckland Bot Soc Bull 31:1–252

Wildland Consultants (2014) Geothermal vegetation of the Waikato Region, 2014. Waikato Regional Council Technical Report 2015/07. 539 pp

Williams MC, Wardle GM (2005) The invasion of two native eucalypt forests by *Pinus radiata* in the Blue Mountains, New South Wales, Australia. Biol Conserv 125:55–64. https://doi.org/10.1016/j.biocon.2005.03.011

Williams MC, Wardle GM (2007) *Pinus radiata* invasion in Australia: identifying key knowledge gaps and research directions. Austral Ecol 32:721–739. https://doi.org/10.1111/j.1442-9993.2007.01760.x

Williams PA, Wiser S, Clarkson B, Stanley MC (2007) New Zealand's historically rare terrestrial ecosystems set in a physical and physiognomic framework. N Z J Ecol 31:119–128

Wilson HD (1992) Banks ecological region. Protected natural areas programme survey report No. 21. Department of Conservation, Christchurch

Wilson HD (2008) Vegetation of Banks Peninsula. In: Winterbourn M, Knox G, Burrows C, Marsden I (eds) The Natural History of Canterbury. Canterbury University Press, Christchurch, pp 251–278

Wilson JB, Lee WG (2012) Is New Zealand vegetation really 'problematic'? Dansereau's puzzles revisited. Biol Rev 87:367–389. https://doi.org/10.1111/j.1469-185X.2011.00202.x

Wilson JRU, Caplat P, Dickie IA, Hui C, Maxwell BD, Nuñez MA, Pauchard A, Rejmánek M, Richardson DM, Robertson MP, Spear D (2014) A standardized set of metrics to assess and monitor tree invasions. Biol Invasions 16:535–551. https://doi.org/10.1007/s10530-013-0605-x

Wilson JRU, Faulkner KT, Rahlao SJ, Richardson DM, Zengeya TA, van Wilgen BW (2018) Indicators for monitoring biological invasions at a national level. J Appl Ecol 55:2612–2620. https://doi.org/10.1111/1365-2664.13251

Wise RM, van Wilgen BW, Le Maitre DC (2012) Costs, benefits and management options for an invasive alien tree species: the case of mesquite in the Northern cape. J Arid Environ 84:80–90. https://doi.org/10.1016/j.jaridenv.2012.03.001

Wiser SK, Bellingham PJ, Burrows LE (2001) Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. N Z J Ecol 25(2):1–17

Wiser SK, Buxton RP (2009) Montane outcrop vegetation of Banks Peninsula, South Island, New Zealand. N Z J Ecol 33:164–176

Wiser SK, De Cáceres M (2013) Updating vegetation classifications: an example with New Zealand's woody vegetation. J Veg Sci 24:80–93. https://doi.org/10.1111/j.1654-1103.2012.01450.x

Wiser SK, Hurst JM, Wright EF, Allen RB (2011) New Zealand's forest and shrubland communities: a quantitative classification based on a nationally representative plot network. Appl Veg Sci 14:506–523. https://doi.org/10.1111/j.1654-109X.2011.01146.x

Wiser SK, Thomson FJ, De Cáceres M (2016) Expanding an existing classification of New Zealand vegetation to include non-forested vegetation. N Z J Ecol 40:160–178. https://doi.org/10.20417/nzjecol.40.18

Wyatt S (2018) Benefits and costs of the wilding pine management programme, Phase 2. Report prepared for the New Zealand Ministry of Primary Industry, Wellington. https://www.wildingconifers.org.nz/assets/Uploads/Benefits-and-Costs-of-the-Wilding-Pine-Management-Programme-Phase-2.pdf

Wyse SV, Perry GLW, Curran TJ (2018) Shoot-level flammability of species mixtures is driven by the most flammable species: implications for vegetation-fire feedbacks favouring invasive species. Ecosystems 21:886–900. https://doi.org/10.1007/s10021-017-0195-z

Wyse SV, Hulme PE (2021a) Dispersal potential rather than risk assessment scores predict the spread rate of non-native pines across New Zealand. J Appl Ecol 58:1981–1992. https://doi.org/10.1111/1365-2664.13947

Wyse SV, Hulme PE (2021b) Limited evidence for a consistent seed mass–dispersal trade-off in wind-dispersed pines. J Ecol 109:284–293. https://doi.org/10.1111/1365-2745.13477

Wyse SV, Etherington TR, Hulme PE (2022) Quantifying the risk of non-native conifer establishment across heterogeneous landscapes. J Appl Ecol 59:1608–1618. https://doi.org/10.1111/1365-2664.14170

Yletyinen J, Perry GLW, Burge OR, Mason NWH, Stahlmann-Brown P (2021) Invasion landscapes as social–ecological systems: role of social factors in invasive plant species control. People Nat 3:795–810. https://doi.org/10.1002/pan3.10217

Zenni RD, Essl F, García-Berthou E, McDermott SM (2021) The economic costs of biological invasions around the world. NeoBiota 67:1–9. https://doi.org/10.3897/neobiota.67.69971