



Future climates are predicted to alter the potential distributions of non-native conifer species in New Zealand

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Abstract: Non-native conifers constitute a significant threat to the ecology and biodiversity of many of New Zealand's native ecosystems and species. From the top down, the potential distributions of non-native conifer species are governed by climate suitability, which alongside variables such as the availability of suitable habitats and a source of propagules determines whether an area of land will be susceptible to invasion by a given species. Here, we undertook a novel study to quantify potential distributions as defined by climate suitability for all 55 non-native conifer species in New Zealand using ecological niche modelling. Using current and future climate data, we then predicted how climate change may affect the potential distributions of these species. For most conifer species currently of concern from a management perspective, the total potential distribution is predicted to decline in future climates, with the largest reductions occurring for *Pinus contorta*. However, the climatically suitable land area for species such as *Pinus pinaster* and *Pinus patula* is predicted to increase in the future, while for species such as *Pinus radiata* future losses of suitable climate space in the North Island are approximately balanced by gains in the South Island. Although there is a great deal of variation at the individual species level, the vast majority of New Zealand will have climate suitable for a non-native conifer species both now and in the future. While data and methodological limitations associated with ecological niche modelling means we are more confident about increases than decreases in potential distributions, our results can be used to guide the management of non-native conifers in New Zealand and contribute to invasion risk assessments for these species. Our data and methodology can also be used to contribute to invasion risk modelling in other areas of these conifer species' introduced ranges throughout the Southern Hemisphere.

Keywords: alien plant, climate change, convex hull, ecological niche modelling, fundamental niche, invasive species, Mahalanobis distance, species distribution modelling, weed, wilding conifers

Introduction

Worldwide, conifer species have been planted extensively outside their native ranges for purposes such as forestry, erosion control, shelter, and amenity plantings, particularly in the Southern Hemisphere (Richardson & Rejmánek 2011; Castro-Díez et al. 2019). Consequent naturalisation and invasive spread of these species within their introduced ranges has had substantial ecological and economic impacts in many regions (Nuñez et al. 2017), including negative effects on biodiversity values, modification of soil processes and fire regimes, and reductions to the productivity of agricultural land (Franzese et al. 2017; Nuñez et al. 2017; Taylor et al. 2017; Peltzer 2018). Consequently, considerable resources are invested in the control of non-native conifer invasions globally, with Aotearoa New Zealand at the forefront of management of these species (Richardson & Higgins 1998; Nuñez et al. 2017).

Within New Zealand, introduced non-native conifers underpin commercial forestry, worth around NZ\$5 billion a year, yet invasion by wilding conifers is arguably one of

New Zealand's most serious and intractable weed problems (Hulme 2020). Naturalisation and increasing distribution of wilding conifers is ongoing, such that wildings have been estimated to occupy around 1.8 million ha and could cover 28% of New Zealand's land area by 2050 (MPI 2014; Howell 2016; Wyatt 2018). The cost of wildings through impacts on ecological communities, ecosystem processes, economy, and cultural values is conservatively estimated at NZ\$4.6 billion over the next 30 years (Wyatt 2018), while land managers, government agencies, and communities collectively spending NZ\$10s of millions each year managing this problem with these costs increasing by around 30% per year (MPI 2014). Despite current management efforts, the total area invaded has increased by approximately 6% per year since management has commenced (Howell 2016). As a consequence, a goal for wilding conifer invasion to be stopped or contained nationally by 2030 was stipulated in the 2015 National Strategy for Wilding Conifer Management (MPI 2014). However, the information or data needed to understand the potential distribution of wildings currently and in the future remains unresolved.

Less than half of the 28 naturalised conifer species in New Zealand (Howell 2019) are thought to be responsible for most wilding conifer spread, with *Pinus contorta* (lodgepole pine), *Pinus nigra* (Corsican pine), *Pseudotsuga menziesii* (Douglas fir), and *Larix decidua* (European larch) among the most commonly managed wilding conifer species (Froude 2011). However, future threats are likely from additional naturalised or casual conifer species present in New Zealand (Howell 2019), which should therefore undergo invasive species risk assessments. A key component of such risk assessments (Andersen et al. 2004) is an estimate of the potential distribution of a species (Venette et al. 2010). Although there are many abiotic, biotic, and dispersal factors that interact to ultimately dictate a species distribution (Soberón & Peterson 2005), climatic variables represent a top-down limiting factor that can predict where conifers could invade (Essl et al. 2011; Nuñez & Medley 2011).

Climatic risk assessments can greatly improve our understanding of future invasion risks. For example, ecological niche modelling (or species distribution modelling) that uses known occurrences of species in environmental space, can be used to identify the set of environmental conditions under which a species can exist currently or in the future (Peterson 2003). Because climate is an abiotic factor, ecological niche modelling is best approached using the fundamental niche (Soberón & Peterson 2005), which can be defined as an n -dimensional hypervolume that corresponds to the environmental conditions in which the species could persist indefinitely (Hutchinson 1957). Identifying geographic locations that have environmental conditions within the fundamental niche enables maps of potential distribution to be produced that can help inform invasion risk (Peterson 2003). While the fundamental niche of a species is relatively stable and will only change slowly through evolutionary processes, more rapid processes such as climate change could result in geographic locations shifting in or out of the fundamental niche (Jackson & Overpeck 2000). Therefore, climate change could result in increases or decreases in the potential distributions of non-native conifers across New Zealand, leading to changes to the risks of invasive spread posed by these species.

Given the relatively large number of non-native conifers found in New Zealand coupled with ongoing climate change, our objective was to assess invasion risk from the top-down perspective of current and future climates. This was done by first building ecological niche models for each non-native conifer species and then mapping the potential distribution of non-native conifers present in New Zealand under current and future climatic conditions. We further distinguished non-native conifer species as either naturalised species with self-maintaining wild populations or casual species with sporadic or non-persistent wild populations (Howell 2019) to reflect differences in progression towards invasiveness. Overall, this study provides new insights into the current and potential future potential distributions of a major group of biological invaders across New Zealand.

Methods

Climate data

We used the Climatologies at High resolution for the Earth's Land Surface Areas (CHELSA) bioclimatic BIOCLIM variables, as the original BIOCLIM variables have previously

been demonstrated to be useful for predicting climatically suitable areas for tree species (Booth 1985). The data were obtained for the 1979–2013 climatic period and have a global extent with 30 arc-second (c. 1 km²) resolution (Karger et al. 2017).

We sought a minimal set of ecologically relevant BIOCLIM variables that captured climatic variation in New Zealand, as it is critically important to choose explanatory variables that have direct ecological relevance (Fourcade et al. 2018) and that are uncorrelated (Dormann et al. 2013), especially as we are extrapolating our niche models across time and climatic space. Also, as we were modelling the fundamental niche which describes environmental limits for a species, we focussed on frost and drought tolerance as ecologically relevant climatic factors that have strong effects on conifer seedling mortality in New Zealand (primarily through frost heave and subsequent desiccation, and freezing and desiccation of sensitive seedling tissues), and hence limit the distributions of naturalised conifers in New Zealand (Benecke 1967; Ledgard 1979; Wardle 1985; Allen & Lee 1989; Burdon & Miller 1992). We used “BIOCLIM6 minimum temperature of the coldest month” to capture niche limitations around frost tolerance, and both “BIOCLIM9 mean temperature of the driest quarter” and “BIOCLIM17 precipitation of the driest quarter” in combination to capture niche limitations around drought tolerance. We limited our analyses to these three BIOCLIM variables as these variables are highly correlated with all other potentially ecologically relevant BIOCLIM variables within New Zealand (McCarthy et al. 2021), and as such are expected to capture most of the climatic variation.

When modelling a species' future response to climate change it is critical to recognise the inherent uncertainty of this task, and that careful consideration must be given to representing this uncertainty within the modelling (Beaumont et al. 2008). We chose to model future conditions for the 2061–2080 climatic period provided by CHELSA (Karger et al. 2017), for which a wide range of possible predictions exist based on various combinations of a relative concentration pathway (RCP) implemented by a global circulation model (GCM). We chose to consider the RCP 2.6, 4.5, 6.0, and 8.5 scenarios to be equally possible, and have followed the Intergovernmental Panel on Climate Change by assuming that each GCM is equally valid (Maslin 2014). However, as some GCMs use very similar approaches, it is important to recognise that by including all available GCMs the results will be biased towards approaches that are more commonly applied (Knutti et al. 2013). Therefore, of the CHELSA 2061–2080 GCMs that provided predictions for all four RCPs, we used a hierarchical similarity clustering of GCM outputs (Knutti et al. 2013) to select 10 GCMs (BCC-CSM1-1, MIROC5, GFDL-CM3, MRI-CGCM3, GISS-E2-R, HadGEM2-AO, CCSM4, IPSL-CM5A-LR, CSIRO-Mk3-6-0, MIROC-ESM), whose predictions were spread across the range of possible future conditions and as such should represent a fair reflection of future climate uncertainty.

For the purposes of mapping the potential distributions in New Zealand, the global climatologies were clipped and reprojected to a 1 km² grid of cells covering the three main islands of New Zealand plus nearshore islands. Those 1 km² grid cells that currently consist of $\geq 50\%$ inland water (LINZ 2021) were then reclassified as unavailable for conifer distribution. The current climate conditions of New Zealand demonstrate that there are strong climatic gradients in New Zealand meaning that there could be regional variation in the potential distributions

of different conifer species (Figs 1 a–c). The future climate conditions measured as the median across all four RCPS and 10 GCMs indicates that the minimum temperature of the coldest month will increase modestly across New Zealand (Fig. 1d), the mean temperature of the driest quarter will mostly increase across New Zealand including some very significant localised increases (Fig. 1e), and the precipitation of the driest quarter across New Zealand could increase as much as decrease but that these changes could be locally significant (Fig. 1f).

Species data

We focussed our study on 28 naturalised (Table 1) and 27 casual (Table 2) non-native conifer species in New Zealand (Howell 2019). For each species, we obtained global occurrence data from the Global Biodiversity Information Facility (GBIF) (Edwards et al. 2000), limiting the data obtained to occurrences recorded as having reliable geographic locations. The use of global occurrence data, as opposed to data solely from New Zealand, is critically important for a climate change study,

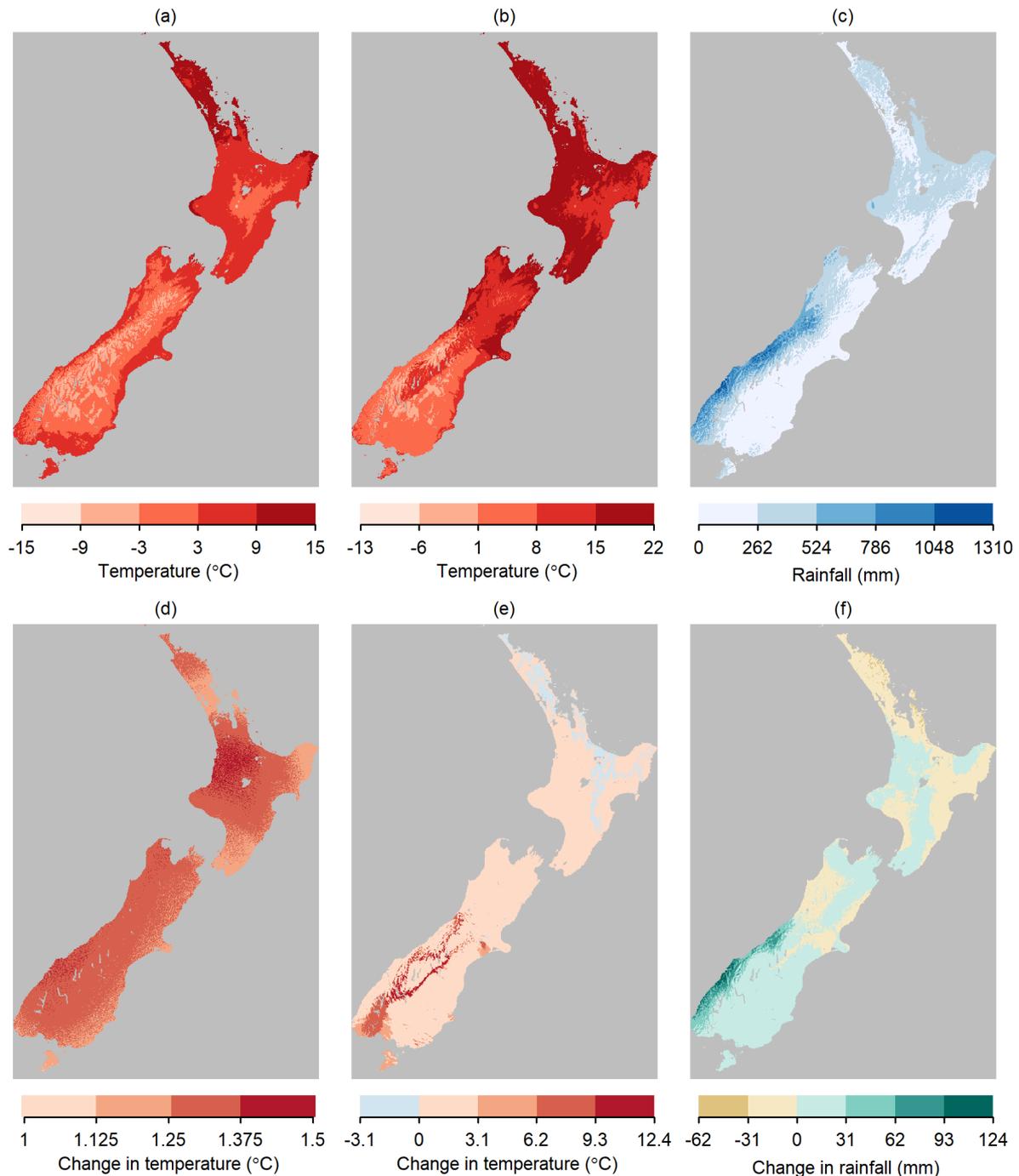


Figure 1. Current climate conditions and associated future climate change in New Zealand. Current conditions for the period 1979–2013 are shown for (a) BIOCLIM6, minimum temperature of the coldest month, (b) BIOCLIM9, mean temperature of the driest quarter, and (c) BIOCLIM17, precipitation of the driest quarter. Future climate change is for the period 2061–2080 and is shown as the median change across the four relative concentration pathways and 10 global circulation models used in the analysis for (d) BIOCLIM6, (e) BIOCLIM9, and (f) BIOCLIM17.

Table 1. Summary information for naturalised non-native conifer species analysed within this study. The 28 naturalised species are listed by their percentage point gain or loss of potential distribution areas for New Zealand. The potential distribution area as a percentage of New Zealand is given for the 1979–2013 and 2061–2080 the climatic periods, along with the number of clean GBIF global species occurrences used to build the ecological niche models, and the number of those global occurrences that were from New Zealand.

Species	Percentage point change	1979–2013 potential area (%)	2061–2080 potential area (%)	<i>n</i> (Global)	<i>n</i> (New Zealand)
<i>Araucaria heterophylla</i>	+7.8	36.7	44.5	160	18
<i>Cupressus lusitanica</i>	+7.4	40.1	47.5	130	3
<i>Pinus patula</i>	+5.4	9.0	14.4	116	4
<i>Callitris rhomboidea</i>	+5.2	17.7	22.9	258	2
<i>Pinus pinaster</i>	+3.1	51.6	54.7	488	11
<i>Cryptomeria japonica</i>	+2.9	79.2	82.1	323	23
<i>Cupressus macrocarpa</i>	+1.6	42.3	43.9	293	51
<i>Cupressus sempervirens</i>	+1.2	50.2	51.4	527	0
<i>Pinus halepensis</i>	+1.2	23.8	25.0	494	1
<i>Pinus radiata</i>	+1.2	67.1	68.3	754	141
<i>Pinus muricata</i>	-0.3	5.9	5.6	45	10
<i>Pinus taeda</i>	-0.6	38.8	38.2	288	1
<i>Pinus banksiana</i>	-1.6	4.1	2.5	329	0
<i>Pinus ponderosa</i>	-2.0	11.9	9.9	632	5
<i>Pinus monticola</i>	-2.3	12.3	10.0	271	0
<i>Abies nordmanniana</i>	-2.9	21.0	18.1	165	0
<i>Abies grandis</i>	-3.9	24.9	21.0	458	2
<i>Sequoia sempervirens</i>	-4.2	28.6	24.4	179	6
<i>Pinus mugo</i>	-4.7	18.1	13.4	505	6
<i>Pinus strobus</i>	-5.3	22.6	17.3	1242	1
<i>Picea sitchensis</i>	-6.9	48.9	42.0	848	0
<i>Pinus sylvestris</i>	-7.0	46.9	39.9	1886	3
<i>Larix decidua</i>	-7.1	33.5	26.4	1207	11
<i>Pinus nigra</i>	-7.1	59.2	52.1	652	16
<i>Pseudotsuga menziesii</i>	-7.2	67.8	60.6	1511	75
<i>Pinus contorta</i>	-7.9	45.0	37.1	1097	35
<i>Taxus baccata</i>	-8.0	56.6	48.6	1493	22
<i>Picea abies</i>	-8.1	56.9	48.8	1788	0

as it maximises the chance of including climatic conditions that do not currently exist in New Zealand but may in the future (Peterson et al. 2011; Atwater et al. 2018).

Because the natural history data that forms the backbone of GBIF will have errors and contain sampling bias (Graham et al. 2004), we followed existing advice (Zizka et al. 2020; Sillero & Barbosa 2021) and cleaned the GBIF occurrences in the following manner to minimise potential errors and to maximise suitability to our question. To be temporally consistent with the climatologies, while also trying to maximise sample size, we limited occurrences to those from 1970 onwards. To be spatially consistent with the climatologies, only occurrences with a known spatial uncertainty ≤ 1 km and with supporting coordinate precision were included. Occurrences were also removed if they were not located in the country in which they were recorded, or if they fell in a global climatology grid cell with no data. Having extracted the climatic data for each remaining occurrence, to minimise sampling bias in climatic space, an environmental filter was applied (Varela et al. 2014) to ensure that occurrences were at least 1°C apart on the minimum temperature of the coldest month and the mean temperature of the driest quarter axes, and 25 mm apart on the precipitation of the driest quarter axis.

Ecological niche modelling

Recognition of the inevitable uncertainties in both estimating the fundamental niche of a species, and with projecting the

niche into the future, is critically important for invasive species risk mapping (Venette et al. 2010). Blonder (2018) suggests bootstrapping (Efron 1979; Diaconis & Efron 1983) as a possible method to obtain a confidence, or conversely uncertainty, estimate for niche models, and we have adopted this approach as bootstrapping has been shown to work well in similar modelling contexts (Verbyla & Litvaitis 1989; Etherington & Lieske 2019). We therefore repeated the modelling process for each species for 500 bootstrapped samples, with the result being the mean of the 500 bootstrap models.

We chose a presence-only ecological niche modelling framework, as we had neither absence data nor the ability to reliably define a relevant background area, which ideally would require us to know the area surveyed and the area available to each species, both of which are unknown. We selected the convex hull approach (Walker & Cocks 1991) to model the fundamental niche for each non-native conifer species as it has several properties which lend itself to this application. Namely, convex hulls require only presence data, do not require the specification of any model fitting parameters, and only assume that a niche is convex in shape (Blonder 2018). This latter assumption is of particular importance as it aligns with the shape of the niche we are modelling at a conceptual level (Hutchinson 1957).

Convex hulls are sensitive to outliers and can produce misleadingly large niche estimates (Blonder 2018). Therefore,

Table 2. Summary information for casual non-native conifer species analysed within this study. The 27 casual species are listed by their percentage point gain or loss of potential distribution areas for New Zealand. The potential distribution area as a percentage of New Zealand is given for the 1979–2013 and 2061–2080 the climatic periods, along with the number of clean GBIF global species occurrences used to build the ecological niche models, and the number of those global occurrences that were from New Zealand.

Species	Percentage point change	1979–2013 potential area (%)	2061–2080 potential area (%)	<i>n</i> (Global)	<i>n</i> (New Zealand)
<i>Araucaria bidwillii</i>	+5.5	14.7	20.2	107	1
<i>Pinus elliotii</i>	+2.8	18.4	21.2	151	0
<i>Podocarpus elatus</i>	+1.8	3.1	4.9	138	0
<i>Afrocarpus falcatus</i>	+1.7	1.8	3.5	106	2
<i>Pinus pinea</i>	+1.1	21.8	22.9	333	1
<i>Callitris oblonga</i>	+0.7	2.4	3.1	45	0
<i>Cupressus arizonica</i>	+0.4	29.1	29.5	174	3
<i>Pinus canariensis</i>	+0.3	0.4	0.7	101	0
<i>Pinus coulteri</i>	0.0	0.0	0.0	97	0
<i>Abies pinsapo</i>	-0.1	1.8	1.7	45	1
<i>Cedrus atlantica</i>	-0.9	19.8	18.9	179	0
<i>Pinus wallichiana</i>	-1.5	11.1	9.6	58	0
<i>Chamaecyparis pisifera</i>	-1.7	8.7	7.0	56	1
<i>Cedrus deodara</i>	-1.8	37.2	35.4	203	0
<i>Juniperus virginiana</i>	-2.0	64.2	62.2	912	0
<i>Pinus uncinata</i>	-2.5	7.9	5.4	101	0
<i>Larix kaempferi</i>	-3.8	20.0	16.2	310	0
<i>Chamaecyparis lawsoniana</i>	-5.7	50.9	45.2	443	21
<i>Juniperus communis</i>	-6.2	58.0	51.8	3051	2
<i>Thuja occidentalis</i>	-6.2	28.3	22.1	780	0
<i>Tsuga heterophylla</i>	-6.7	38.5	31.8	777	1
<i>Thuja plicata</i>	-7.0	53.7	46.7	742	2
<i>Abies alba</i>	-7.8	39.6	31.8	820	0
<i>Cunninghamia lanceolata</i>	-	-	-	41	1
<i>Pinus thunbergii</i>	-	-	-	35	0
<i>Podocarpus elongatus</i>	-	-	-	19	0
<i>Podocarpus macrophyllus</i>	-	-	-	42	1

we used the Mahalanobis distance (Mahalanobis 1936) statistic to identify outliers. After each bootstrap sample was generated, we calculated the probability that each occurrence in the bootstrap sample was an outlier (Etherington 2019) using a minimum covariance determinant approach (with $k=0.95$); an approach that has been demonstrated to be robust to sample size, error, and bias (Etherington 2021). Precipitation values were log-transformed and all variables were converted to *z*-scores (Gregory 1978) for the Mahalanobis distance calculations to help ensure the assumption of multi-variate normality was appropriate, and to aid visualisation. Occurrences were then eliminated if their Mahalanobis distance probability was > 0.99 (Fig. 2).

The fundamental niche was then defined using a convex hull constructed around the remaining occurrences. Using the convex hull, the climatic suitability of any current or future location in New Zealand could be assessed by determining if the climate at that location and time fell within the convex hull (suitable), or outside the convex hull (not suitable). For each bootstrap sample, one of the 40 possible futures formed by the ten future climate GCMs under the four RCPs was chosen at random to explore possible futures.

Predictions were made for the New Zealand 1 km² resolution climate grids, and when the mean of all bootstrap samples was taken, this resulted in potential distribution maps on a scale from 0 (never climatically suitable) to 1 (always climatically suitable) with values in between representing

the degree of uncertainty, and 0.5 representing maximum uncertainty. As well as producing current and future potential distribution maps, the difference between these two maps was calculated to show the spatial pattern of any changes in potential distribution. To collectively examine the potential distribution of those conifers currently of regional concern, for both time periods we also calculated the maximum potential conifer distribution across all 13 conifer species listed on regional pest management plans: *Larix decidua*, *Pinus contorta*, *Pinus monticola*, *Pinus mugo*, *Pinus muricata*, *Pinus nigra*, *Pinus patula*, *Pinus pinaster*, *Pinus ponderosa*, *Pinus radiata*, *Pinus sylvestris*, *Pinus uncinata*, *Pseudotsuga menziesii*. The value of each grid cell in the maps resulting from this analysis was the maximum suitability score (from 0–1) of the corresponding grid cells from the individual species maps. The difference between these two maps was calculated to examine changes in potential distribution for any non-native conifer of regional concern.

For all 55 non-native conifer species, national scale summaries of the potential distribution area were calculated for the 1979–2013 and 2061–2080 time periods. To incorporate the modelling uncertainty, the potential distribution area was calculated as the sum of the area of each grid cell multiplied by the uncertainty of each grid cell. The potential distribution area was then expressed as a percentage of the total area of New Zealand, defined by the number of 1 km² grid cells of mainland New Zealand plus nearshore islands. Changes in

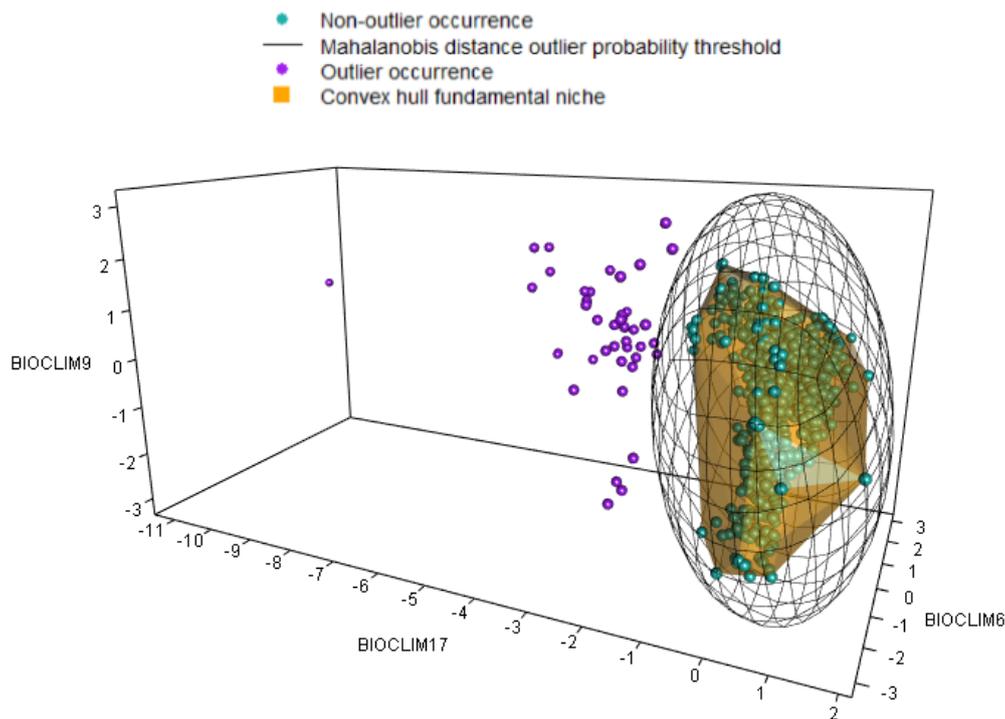


Figure 2. Example of convex hull fundamental niche modelling with Mahalanobis distance outlier detection. The points represent global occurrences of *Pinus radiata* in three-dimensional climate space formed by: minimum temperature of the coldest month (BIOCLIM6), mean temperature of the driest quarter (BIOCLIM9), and precipitation of the driest quarter (BIOCLIM17). Precipitation values were log-transformed and all variables were converted to z-scores. The elliptical shape shows the Mahalanobis distance threshold used to detect outliers, and the polyhedral shape is the convex hull around the remaining non-outlier points that defines the climatic fundamental niche of *Pinus radiata*.

potential distribution areas between time periods were then calculated as a percentage point change (for example, a change from 68% to 70% is a +2 percentage point change).

All analyses were undertaken using R version 3.5.3 (R Core Team 2019) using functionality from the MASS version 7.3-51.1 (Venables & Ripley 2002), rgbif version 1.3.0 (Chamberlain & Boettiger 2017), sf version 0.7-6 (Pebesma 2018), raster version 2.9-5 (Hijmans 2019), rgl version 0.100.30 (Adler & Murdoch 2019), rnaturland version 0.1.0 (South 2017), and compGeometeR version 1.0 (Barber et al. 1996; Etherington & Omondiagbe 2021) packages.

Results

All 55 non-native conifer species were identified within GBIF with a $\geq 97\%$ taxonomic confidence. After error cleaning and bias filtering the data from the resulting download (GBIF.org 2021), a median of 491 (range 45–1886) occurrences for each naturalised species (Table 1) and 138 (range 19–3051) occurrences for each casual species (Table 2) were used for the niche modelling. Models built with very small sample sizes are unlikely to be reliable, and thus we chose to limit our ecological niche modelling to those species with ≥ 45 occurrences, which enabled all 28 naturalised species and 23 of the 27 casual species to be analysed.

When aggregated at a national scale, the potential distribution areas were often very large. For naturalised species, the median potential distribution area was 37.8% (range 4.1–79.2%) for the period 1979–2013 and 37.7% (range 2.5–82.1%) for the period 2061–2080 (Table 1). In contrast,

the potential distribution areas for the casual species were smaller, with a median potential distribution area of 19.8% (range 0–64.2%) for the period 1979–2013 and 20.2% (range 0–62.2%) for the period 2061–2080 (Table 2).

When aggregated at a national scale the changes in potential distribution area for each species were generally quite small and were similar between naturalised (percentage points: median -2.2 , range -8.1 – $+7.8$) and casual (percentage points: median -1.5 , range -7.8 – $+5.5$) species (Tables 1 and 2). In contrast, the spatial patterns of changes in potential distribution within New Zealand varied markedly among species. For example, while *Pinus radiata* (radiata pine) was predicted to have a small increase in potential distribution at the national scale, this resulted from losses in northern New Zealand being balanced by gains in southern New Zealand (Fig. 3). This contrasts with other species such as *Araucaria heterophylla* (Norfolk Island pine) that had consistent gains across New Zealand (Fig. 4) or *Pinus mugo* (dwarf mountain pine) that had consistent losses across New Zealand (Fig. 5).

When considering the naturalised conifers most problematic from a management perspective in terms of their capacity to spread (*Larix decidua*, *Pinus contorta*, *Pinus mugo*, *Pinus muricata*, *Pinus nigra*, *Pinus pinaster*, *Pinus ponderosa*, *Pinus radiata*, *Pinus sylvestris*, and *Pseudotsuga menziesii*; Froude 2011), most species (8 of 10) showed an average reduction in the potential climatically suitable land area within New Zealand (Table 1). Of these species, the largest decrease in suitable area is predicted for *P. contorta* (-7.9 percentage points; Fig. 6), and the largest increase in suitable area is predicted for *P. pinaster* ($+3.1$ percentage points; Fig. 7). The species highlighted in these examples (Figs 3–8) represent

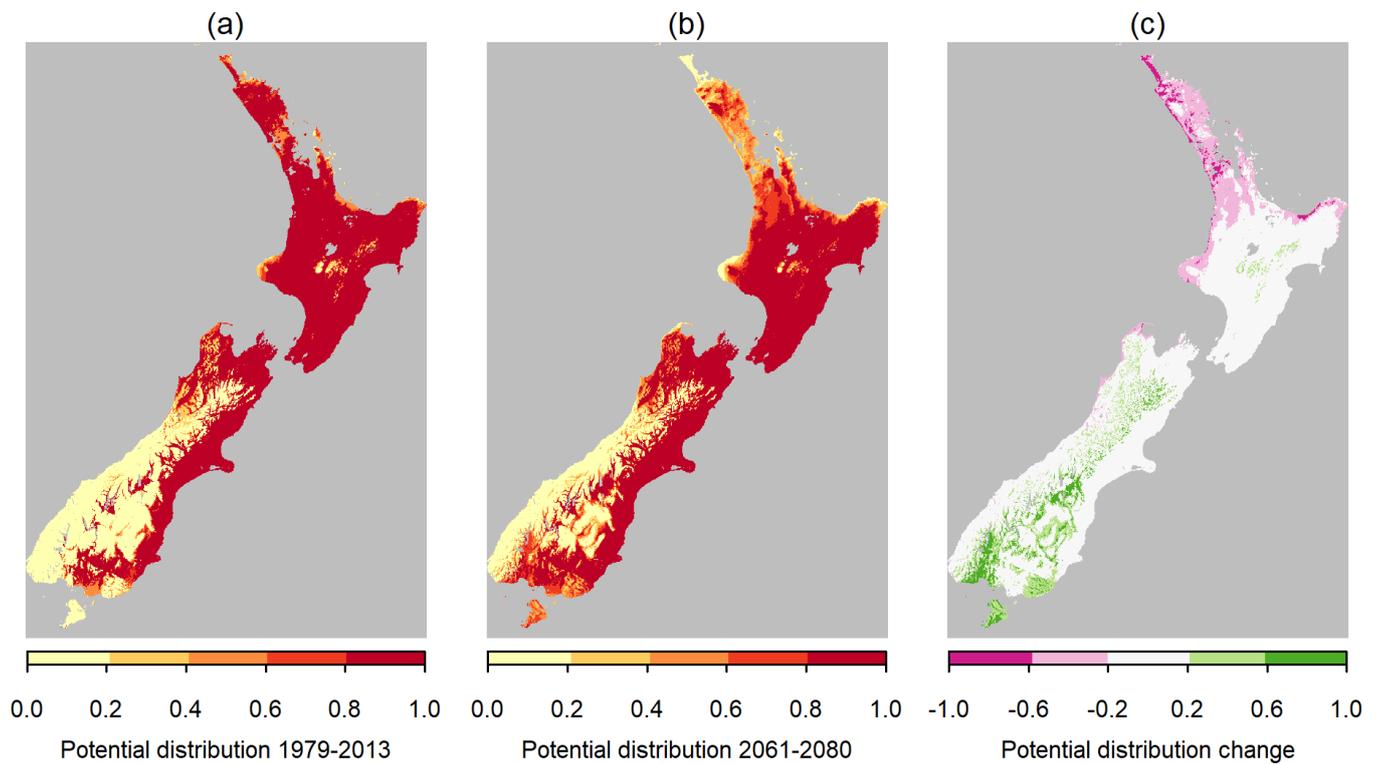


Figure 3. Potential distribution maps of *Pinus radiata* from a climate perspective. The potential distributions maps show climatic suitability on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

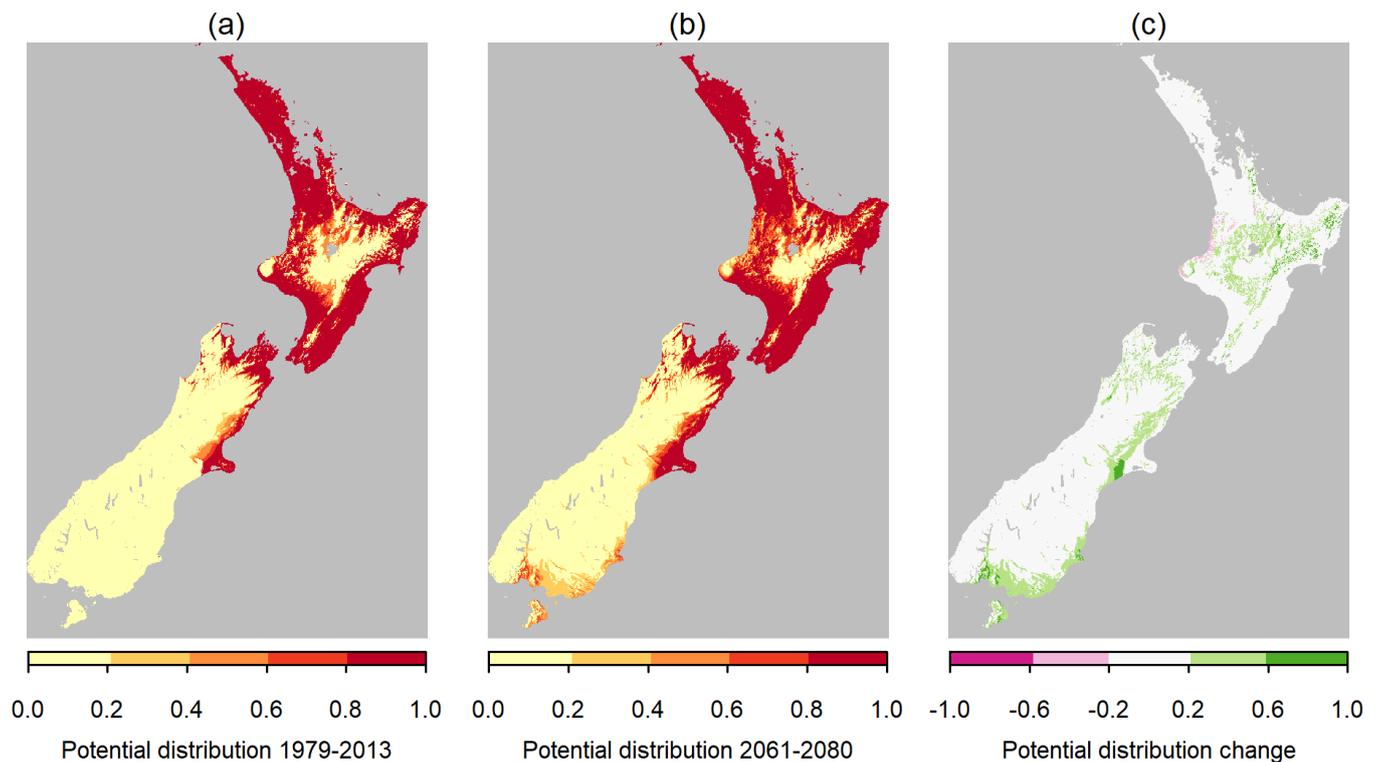


Figure 4. Potential distribution maps of *Araucaria heterophylla* from a climate perspective. The potential distributions maps show climatic suitability on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

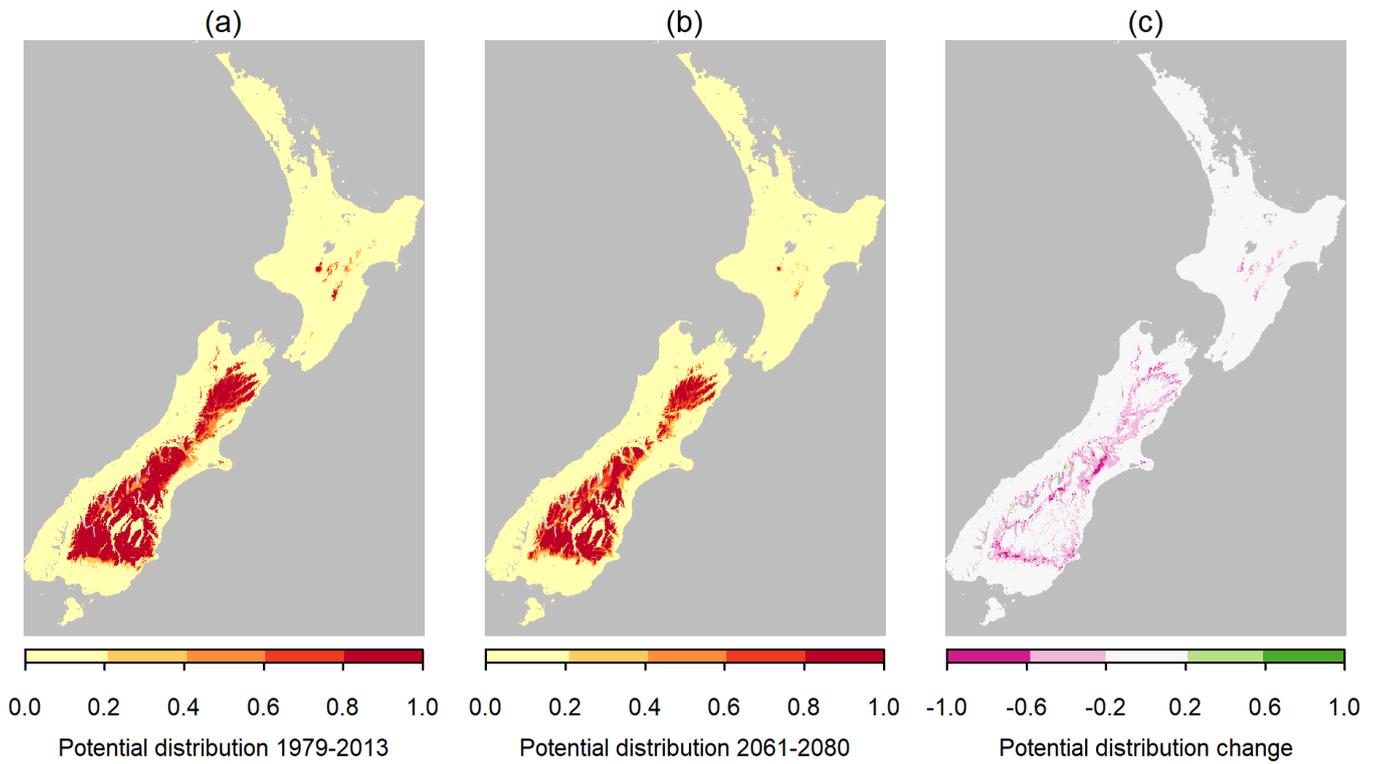


Figure 5. Potential distribution maps of *Pinus mugo* from a climate perspective. The potential distributions maps show climatic suitability on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

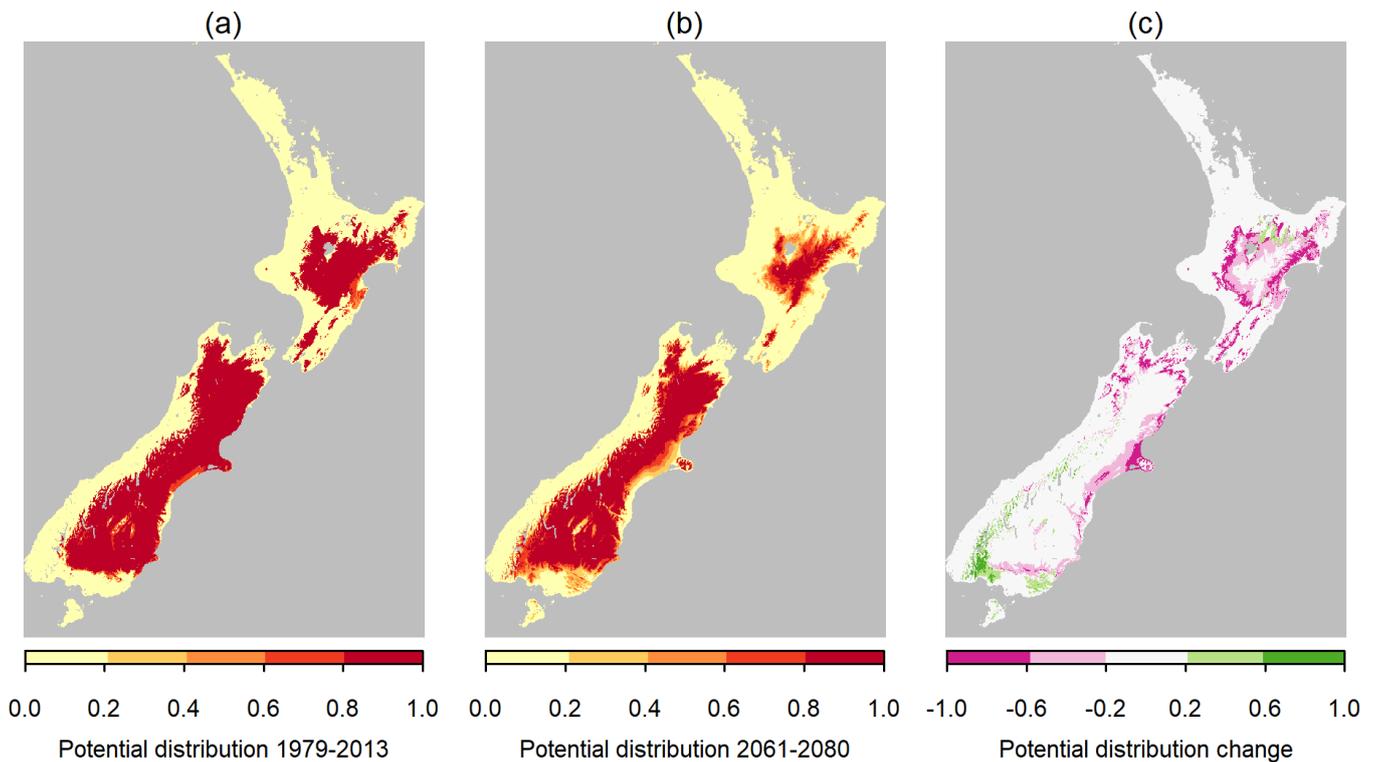


Figure 6. Potential distribution maps of *Pinus contorta* from a climate perspective. The potential distributions maps show climatic suitability on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

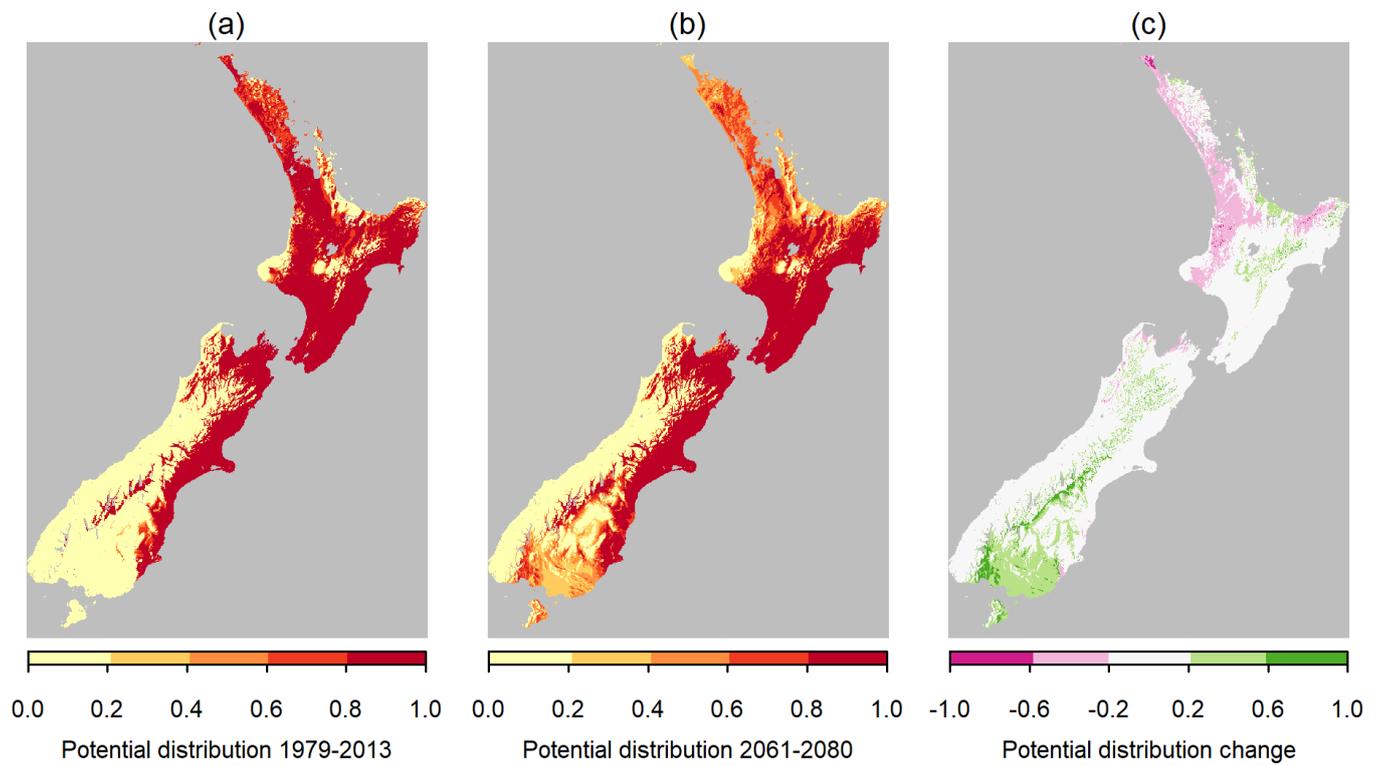


Figure 7. Potential distribution maps of *Pinus pinaster* from a climate perspective. The potential distributions maps show climatic suitability on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

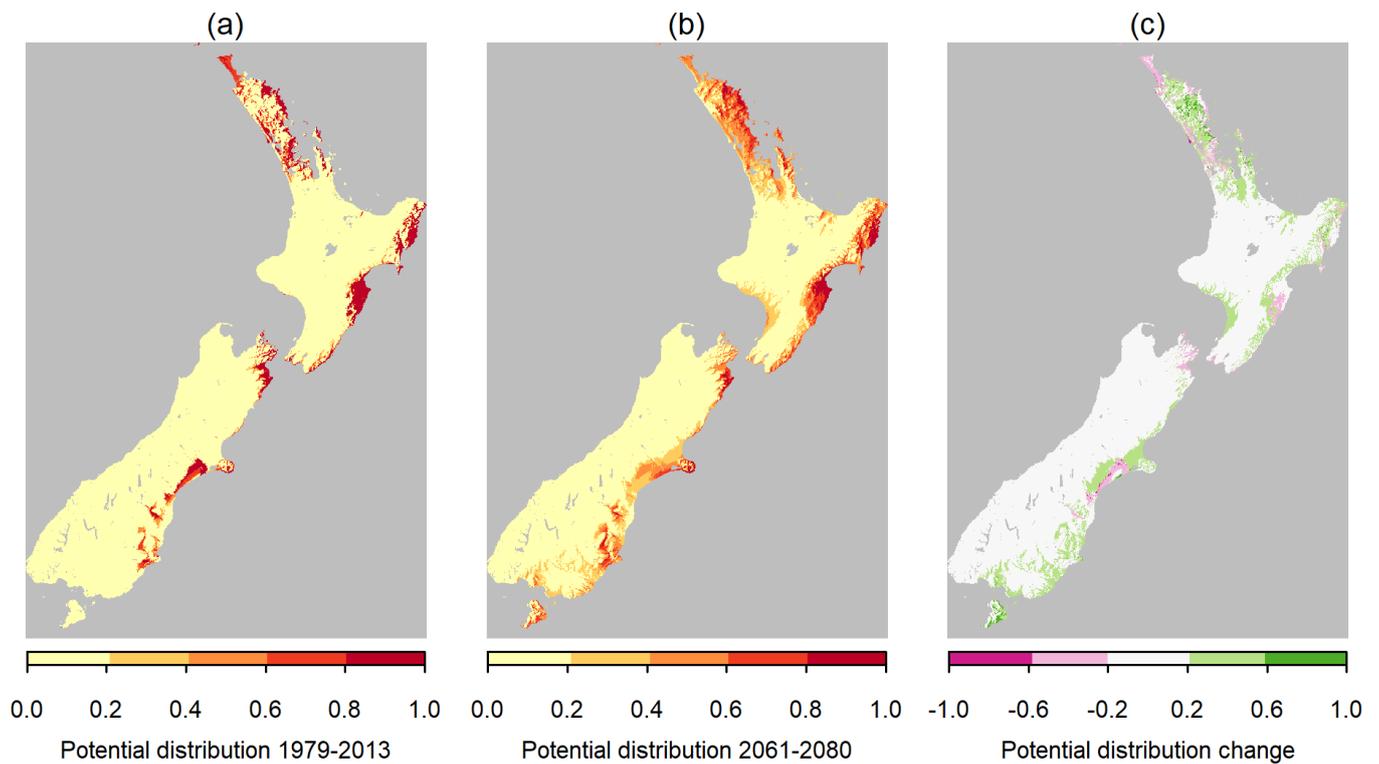


Figure 8. Potential distribution maps of *Pinus patula* from a climate perspective. The potential distributions maps show climatic suitability on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

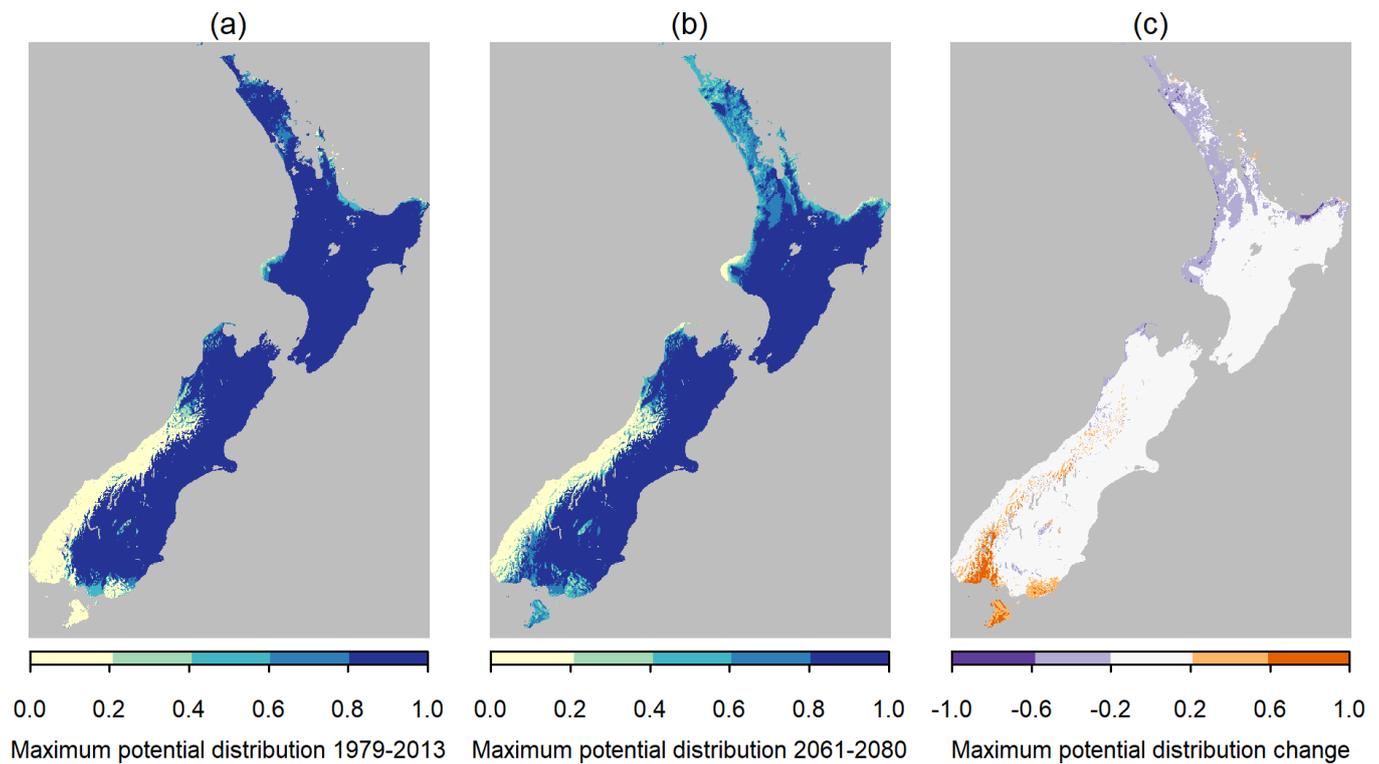


Figure 9. Maps of maximum potential distribution across all conifer species listed on New Zealand regional pest management plans (*Larix decidua*, *Pinus contorta*, *Pinus monticola*, *Pinus mugo*, *Pinus muricata*, *Pinus nigra*, *Pinus patula*, *Pinus pinaster*, *Pinus ponderosa*, *Pinus radiata*, *Pinus sylvestris*, *Pinus uncinata*, *Pseudotsuga menziesii*). The potential distribution maps show the maximum climatic suitability across all species on a scale from 0 to 1 for (a) the period 1979–2013 and (b) the period 2061–2080, with (c) showing the change in suitability between the two periods.

species that were exemplars of spatial patterns or extremes of overall change. For those interested in other species, maps for all species are provided openly in the supplementary materials alongside the associated data and code.

Regarding the combined risk from any of the non-native conifers of regional concern, the majority of New Zealand is climatically suitable for at least one species of conifer listed on the 16 regional pest management plans, both now (Fig. 9a) and in the future (Fig. 9b). There are some reasonably widespread slight decreases in climate suitability in the northern parts of the country, and some localised but more significant increases in climate suitability in the southern parts of the country (Fig. 9c).

Discussion

From a climate perspective the vast majority of New Zealand is currently suitable for at least one conifer species, including those of particular concern, demonstrating that the issue of wilding conifers is of national importance. The potential distribution of many non-native conifers is relatively large, meaning that climate is unlikely to be a limiting factor for the invasion of many species. Known wilding species such as *Pinus nigra* and *Pseudotsuga menziesii* (Howell 2008) have potential distributions that cover over half of New Zealand, which supports ongoing control efforts to prevent their even wider spread. There are also casual species such as *Juniperus* spp. that have similarly large potential distributions, indicating

that these species have the capacity to become very widely distributed. Species risk assessments for casual species should therefore recognise that while some non-native conifers may currently have comparatively localised distributions, those conifers with larger potential distributions could pose a significant future risk.

Looking to the future, it seems that the effects of climate change are more likely to shift the spatial arrangement of non-native conifer potential distributions, rather than eliminating any species. For example, climatic conditions for *Pinus radiata* are projected to become less suitable in northern regions and more suitable in southern and upland regions (Fig. 3), a pattern that likely a result of warming temperatures and is consistent with results from ecophysiological models (Watt et al. 2019). Even those species such as *Pinus contorta* that had more significant reductions in their potential distributions still retain large areas that are climatically suitable (Fig. 6). Therefore, the effects of climate change on non-native conifer distributions are most likely relevant at more regional scales where there is the possibility that some regions may become climatically suitable for some species, or unsuitable for others. This underlines the importance of regional decision making in the management of non-native conifers as priorities are likely to vary among regions. To support this regional decision making we are openly sharing maps and data to allow for regional assessments. We would also encourage regional authorities to share knowledge on their respective weeds and weed control efforts, as a current weed in one region may be a future weed for another. For example, *Pinus patula* is currently listed

on the regional pest management strategy for Marlborough only (Wyse & Hulme 2021b) but our models suggest that in the future the climatically suitable area for this species may expand into other regions such as Canterbury and Otago (Fig. 8). Because management is most effective at the earliest stages of invasion, knowledge of which weed species could occur in the future should be used to target species for early eradication or to prevent future invasion at the regional scale. We conclude that while the climatic suitability for individual conifer species may increase or decrease locally, the vast majority of New Zealand could be at risk from at least one wildling conifer species both now and in the future.

It is critical to reinforce that our analyses represent minimum estimates of the climatically suitable conditions. A fundamental limitation to ecological niche modelling of invasive species is data availability (Peterson 2003), and the predictions for those species with minimal data (Tables 1 and 2) should be treated with greater caution. A good example of this issue is *Pinus coulteri* that only had 97 occurrences after our data cleaning process, none of which were in New Zealand, and as such was predicted to have no suitable climates in New Zealand. But this prediction is clearly incorrect as *P. coulteri* is known to have naturalised in two ecological regions of New Zealand (Howell 2019). Much of the available species data was lost as it did not record location uncertainty, but to get reliable results from ecological niche modelling it is absolutely critical to use occurrence data that are known to match the resolution of the climatic variables (Sillero & Barbosa 2021). To improve these kinds of models we therefore need to increase the amount of occurrence data available for non-native conifers that are located with sufficient precision and have recorded the location uncertainty in their metadata. This could be done either by collecting new data, or by updating the metadata of existing data. Another major source of species data loss was from environmental filtering to remove bias from areas of climate space that were oversampled. Given there were often minimal occurrence data from New Zealand (Tables 1 and 2), it would be extremely beneficial for additional data to be collected. Additional occurrence data that is targeted towards any areas currently predicted as being outside a potential distribution would be particularly valuable as these data would occur in under-sampled parts of New Zealand's climatic space where additional data would better describe the full extent of a species' fundamental niche and potential distribution. The additional figures and potential distribution data for all species provided alongside this research could support such targeted data collection. Finally, despite some high-quality occurrences in certain New Zealand locations, the model may not classify the location as suitable as these rare occurrences in climatic space are classified as outliers in relation to more abundant data for other parts of climatic space. For example, an occurrence of *P. patula* has been reliably recorded from near Rotorua, but being rare and climatically distant from other occurrences it is classified as an outlier, so in our model this region is not currently considered climatically suitable (Fig. 8).

This issue of data availability for ecological niche modelling is exacerbated in the context of invasive species risk assessments. It is extremely common for invasive species to occupy climatic conditions in their introduced range that are not present in their native range, meaning that ecological niche modelling using data only from the native range is likely to underpredict the fundamental niche and potential distribution of an invasive species (Atwater et al. 2018; Perret et al. 2019). Not relying on occurrence data from the native range

reinforces the need to collect non-native conifer occurrence data in New Zealand and elsewhere in the introduced ranges, as we cannot depend on occurrences in a species' native range to provide a reliable prediction of the potential distribution in the introduced range. The data availability issue is further exacerbated in the context of climate change, as future climate conditions may be novel, with no present-day climate analogue. As a result, it is currently impossible to collect data that would confirm if novel future climates will be within a species' fundamental niche (Peterson et al. 2011).

The general issue of data availability for ecological niche modelling, combined with the invasive species and climate change contexts of this research, reinforces that our predictions are best interpreted as minimum estimates of the climatically suitable conditions. While we feel confident that those areas expected to be climatically suitable now and in the future are indeed likely to be suitable, it is quite possible that currently unsuitable climates or apparent losses of climate suitability are a result of data limitations rather than ecological processes. In addition, although we have considered climate as the only top-down limiting factor of invasion risk, we recognise that this risk will also be affected by other abiotic, biotic, and dispersal processes that will ultimately dictate the invasion risk of these conifer species (Allen & Lee 1989; Essl et al. 2011; Nuñez & Medley 2011; Wyse et al. 2019; Wyse & Hulme 2021b).

For instance, while our models are appropriate for national and regional scale assessment, at the finer scales at which individual trees operate abiotic factors such as microclimate (Lembrechts et al. 2019) would be expected to refine our models by representing highly localised effects of topography on temperature and moisture gradients (Bennie et al. 2008; Kopecký et al. 2021). Other abiotic factors relating to soil geochemistry and drainage have also been shown to be important for explaining plant distributions (Buri et al. 2020).

The addition of biotic interactions adds an additional layer of complexity, but will be necessary to improve ecological niche models (Anderson 2017). The suitability of the available habitat, in terms of the land use practices and plant community composition, are critical for determining the likelihood that a conifer seedling will be able to successfully establish at a site. Community composition and grazing pressure are both crucial for determining the establishment success of non-native conifers, as high grazing pressure reduces the likelihood of seedling establishment (Ledgard 1994), while conifer establishment success generally decreases with increasing vegetation cover (Ledgard 2001; Lloyd et al. 2016). However, of the dominant wildling conifers, *Pseudotsuga menziesii* is the most shade tolerant and can also invade native forest (Lloyd et al. 2016). Further, the successful establishment of these conifer species is dependent on the presence of suitable mycorrhizal fungi (Dickie et al. 2010), although such species are becoming reasonably ubiquitous in most areas, with their spread facilitated by non-native herbivore species such as the European red deer (*Cervus elaphus*) and the Australian brushtail possum (*Trichosurus vulpecula*) (Wood et al. 2015). It is also worth noting that where there is simultaneous invasion from multiple non-native conifers there will also be competitive and mutualistic biotic interactions between non-native conifers will add an additional layer of complexity to the invasion process.

As many of the naturalised and casual conifer species currently have quite limited distributions, each occurring in just a few of New Zealand's ecological regions (Howell 2019), a final intrinsic component of a species' invasion risk profile is its dispersal ability. The conifer species that represent the

greatest concern for management are all wind-dispersed, where the tallest species and those with the lowest seed terminal velocities (typically species with the smallest seeds) have the greatest dispersal potentials (Wyse & Hulme 2021a, 2021b). For such species, the species' dispersal abilities have been shown to strongly predict their historic spread rates within New Zealand (Wyse & Hulme 2021b). In addition, human-mediated processes may also act as important dispersal pathways for the species (Auffret et al. 2014), with forestry planting effort in particular likely to facilitate spread and the likelihood that a species will become naturalised (McGregor et al. 2012). The inclusion of conifer species in major afforestation efforts across New Zealand such as the Billion Trees Initiative, might inadvertently facilitate additional naturalisation or spread of these species by increasing future propagule pressure.

Finally, a full risk assessment must also consider aspects beyond potential distribution, such as the severity of the ecological impacts of the species (Andersen et al. 2004), but we hope that our minimum potential distribution maps can form part of a fuller risk assessment that contributes to our understanding and management of the issue of wilding conifers. For example, current management practice of removing wildings at scale is largely driven by the failure of past efforts to contain or slow their increased distribution and abundance (Froude 2011). But our estimates of current and future potential distributions could support a more proactive approach to landscape-scale management of invasive trees through regional predictions of changes in the climatic suitability for invaders. Our findings also support the general call for including detection and monitoring of invasive populations, and more specifically, how niche-based sampling frameworks could be deployed to detect predicted changes in future distributions, thus increasing management efficiency through early intervention (Panetta 2007; Wilson et al. 2014). More generally, improved understanding and management of landscape-scale invaders necessitates linking management to research (Funk et al. 2020), and the large-scale long-term control of wilding conifers is a globally important example of how such linkages can be made (Nuñez et al. 2017). To that end all the data and code underlying our analyses have been made openly available such that where useful they can form part of more complex localised risk assessments. For example, in the future any national strategy for the control of non-native conifers could include a more regional perspective on prioritising species control that better recognises regional differences in potential distributions, and a longer-term perspective that includes potential distributional shifts due to climate change.

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Author contributions

All authors conceived the study. TRE and SVW developed the methodology. TRE conducted all data analyses. All authors wrote the manuscript.

Data and code availability

All data and figures are released under a CC-BY 4.0 (Attribution) license, while all code is released under a MIT license, both of which are openly available at <https://doi.org/10.7931/654j-wh37>.

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