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ORIGINAL ARTICLE

Complex planting histories of *Pinus contorta* subspecies and hybrids may help explain invasion success

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Abstract

Key message **Success of invasive non-native conifers in New Zealand may be in part due to introduced hybrids or unintentional hybridisation post-introduction, resulting in unexpected traits that impact control success.**

Abstract Exotic conifers are amongst the most successful weeds in the Southern Hemisphere, in part due to their frequent introductions for commercial forestry and sustainable land use. Multiple introductions of many species, subspecies, and races can help overcome genetic bottlenecks and shape unique invasive populations. Populations of *Pinus contorta*, the most vigorously spreading conifer in New Zealand, were believed to be dominated by a single non-serotinous subspecies, largely due to its perceived faster spread rate. However, recent work has identified serotinous cones in *P. contorta* stands leading to confusion around the identity of populations. Here, we investigated the historical planting literature to determine which *P. contorta* subspecies were introduced across New Zealand to better understand which traits may be expected in invasive populations. We also consider the effect that cone serotiny, expressed by two of four subspecies, may have on control operations by comparing the viability of serotinous seed banks in treated and untreated areas. We find that all four subspecies of *P. contorta* were established almost ubiquitously across New Zealand. Therefore, we postulate that invasive populations are unlikely to represent any one subspecies and observed trait shifts could be due to intentionally introduced hybrids or unintentional intermixing between subspecies. Additionally, we note that serotinous cone banks persist within herbicide-treated populations with no effect on seed viability. Despite lessening initial spread rates, cone serotiny may become more common across New Zealand by allowing populations to reinvade after herbicide treatments and confer fitness benefits as wildfires become more common under climate change.

Keywords *Pinaceae* · Subsp. *latifolia* · Subsp. *murrayana* · Subsp. *bolanderi* · Phylogeography · Invasion genomics

Introduction

Plant invasions are a widespread and recurring phenomenon that cause significant economic and environmental damage (Pyšek et al. 2020). When species are introduced into a new area, they typically undergo a lag-phase before becoming invasive (Gioria et al. 2023; Kowarik 1995), particularly if hampered by low genetic variation (Osunkoya et al. 2021). However, intentional introductions for productive agricultural, horticultural, ornamental, or forestry purposes can potentially reduce lag-phases for invasive species by rapidly establishing populations (Pyšek et al. 2011). Where species spread from provenance trials deliberately designed to include high genetic diversity (Alizoti et al. 2022; Park and Rodgers 2023), populations are less likely to suffer from genetic bottlenecks and are more likely to experience hybridisation between species or subspecies (Buhk and Thielsch

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2015; Hovick and Whitney 2014). Multiple introductions from diverse seed sources, as is often the case for intentionally introduced species, enhance genetic diversity and the potential for hybridisation, assisting potentially invasive populations to adapt and persist in the new environment (Gioria et al. 2023; Mounger et al. 2021).

Invasive conifer species are globally widespread tree weeds that cause significant environmental and economic damage (Nuñez et al. 2017; Sapere Research Group 2022). In Aotearoa New Zealand, invasive conifers, otherwise known as wilding conifers, are particularly pervasive in intermontane areas due to historic plantings for erosion control, forestry trials, and planting as amenity trees (Dickie et al. 2022; Peltzer 2018; Sapere Research Group 2022). Multiple species of invasive conifers have undergone trait shifts since their introduction to Aotearoa, New Zealand, that have increased their fitness both intentionally for commercial species, such as *Pinus radiata* D. Don (Burdon et al. 2008; Shelbourne et al. 2007), and unintentionally for non-commercial species such as *Pinus contorta* Loudon (Carlin 2025; Carlin et al. 2025b; Taylor et al. 2016). These trait shifts may be partially facilitated by hybridisation both within and between conifer species, as both inter- and intraspecific hybridisation in conifers are well-documented (Bisbing et al. 2021; Critchfield 1967; Cullingham et al. 2013; Dungey et al. 2013; Wachowiak & Prus-Głowacki 2008). The resulting hybrid offspring can present traits that may either positively or negatively affect their invasiveness.

Traits linked to invasiveness, such as growth rate and reproduction strategy (e.g. dispersal mechanisms, seed number, and seed longevity), vary among and within the 19 recognised invasive conifer species in New Zealand (NWCCP 2023b). One such trait is cone serotiny, which is an evolutionary adaptation where a proportion of cones remain closed and only open to release seeds in response to specific environmental triggers such as high temperatures from a fire (Connell and Slatyer 1977; Lamont et al. 1991; Lotan 1975, 1976; Muir and Lotan 1985; Vacek et al. 2022). Serotiny allows species to take advantage of the conditions of the seed-receiving environment after a fire when competition is reduced and the soil is rich in nutrients (Lamont et al. 2020; Lotan 1975, 1976). Some conifers produce no serotinous cones (e.g. *Pseudotsuga menziesii*; Miller and Knowles 1994) while others produce almost exclusively serotinous cones (e.g. *Pinus radiata*; Shelbourne 1978). Cone serotiny can also vary drastically within a species. For example, only two out of four *Pinus contorta* subspecies (i.e., subsp. *bolanderi*, subsp. *latifolia*) typically produce serotinous cones, with *P. contorta* subsp. *latifolia* having a highly variable occurrence of serotinous cone-bearing individuals (5–75%; Critchfield 1957; Parker and Benkman 2020). While serotiny is known to be a heritable trait (Hernandez-Serrano et al. 2014; Parchman et al. 2016; Talluto and Benkman 2014), serotinous cones produce fewer seeds than non-serotinous cones (Muir and Lotan 1985) and represent a trade-off between rapid reproduction and long-term fecundity assurance in fire-prone landscapes (Lamont et al. 2020). As such, it is reasonable to assume cone serotiny would be maladaptive for plant invasions in regions where the risk or occurrence of fire is low due to the retention of seed and subsequently slower spread rates (Ledgard 2001).

Pinus contorta is the most widespread invasive conifer species in Aotearoa, New Zealand (Ledgard 2001). Of the four subspecies of *P. contorta*, it is commonly believed that *P. contorta* subsp. contorta is the primary invader across much of Aotearoa, New Zealand (Ledgard 2001; Miller and Ecroyd 1987). This is due to the high frequency of its plantings and that subsp. *contorta* produces few (if any) serotinous cones, a trait considered to negatively correlate with population spread rates. However, recent work has identified serotinous cones in *P. contorta* populations across much of Aotearoa New Zealand, suggesting that other subspecies may be present in the invading populations (Carlin et al. 2025b). Unfortunately, visually distinguishing *P. contorta* subspecies in Aotearoa, New Zealand, is difficult as the species has undergone trait shifts since its introduction (Carlin 2025; Carlin et al. 2025b; Taylor et al. 2016).

Here, we investigated the planting history of *Pinus contorta*, to determine the original provenances of *P. contorta* invasions across Aotearoa New Zealand, and better understand which traits may be expressed in different populations. Additionally, as *P. contorta* is one of the main species managed by the National Wilding Conifer Control Programme (NWCCP), we sought to understand whether certain traits could allow some populations to persist through control treatments better than others. Specifically, we compared seed viability between serotinous cone banks from herbicide-treated and untreated areas.

Materials and methods

Study species

Pinus contorta is native to western North America, extending from Yukon Territory (Canada) to Baja California (Mexico) and from the Pacific coast as far east as South Dakota (USA), with four geographically distinct subspecies (Critchfield 1957; OECD 2010; Roche 1961): *P. contorta* subsp. *bolanderi*, subsp. *contorta*, subsp. *latifolia*, and subsp. *murrayana* (Fig. 1). In the native range, subspecies can be visually distinguished, and vary in traits that could affect invasiveness, such as the number of seeds produced per cone, growth rates, and maximum tree height (Fig. S1; Table S1; Critchfield 1957; Miller and Ecroyd 1987; Benkman et al. 2001). *Pinus contorta* subsp. *murrayana* is

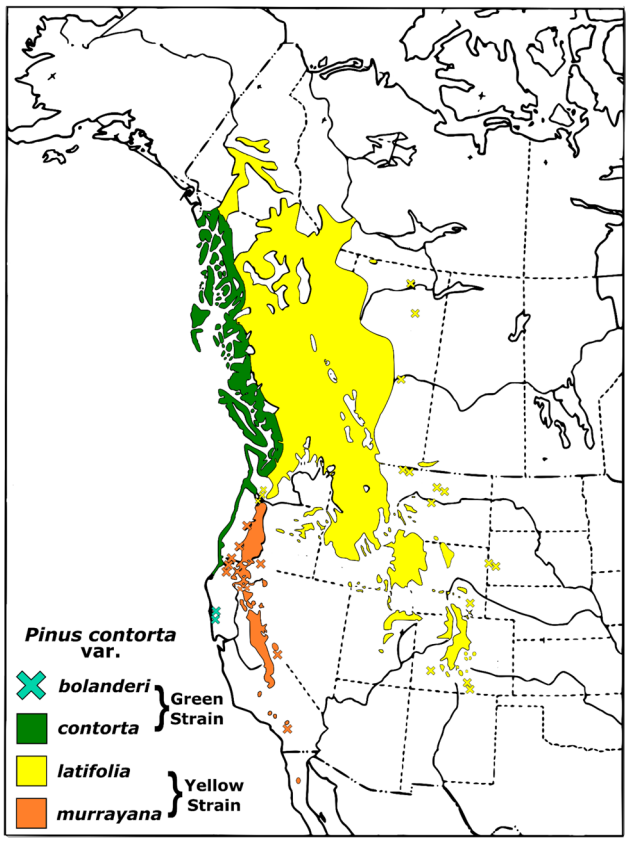


Fig. 1 Natural distribution of *Pinus contorta* subspecies in North America. Adapted from (Miller and Ecroyd 1987), based on data from Critchfield and Little (1966) and Critchfield (1957). Subspecies were frequently grouped into the green and yellow strains when introduced into New Zealand. State, territory, and province borders and major rivers are displayed

the only subspecies to shed its cones, typically every 1 to 5 years, rather than retain them indefinitely (Miller and Ecroyd 1987). *Pinus contorta* subsp. *latifolia* and subsp. *bolanderi* typically produce serotinous cones which open under higher temperatures as an adaptation to rapidly re-establish in fire-cleared landscapes (Lotan 1975, 1976; Muir and Lotan 1985; Vacek et al. 2022).

Subspecies of *P. contorta* can readily hybridise (Critchfield and Service 1980), such as in the northern margins where *P. contorta* subsp. *contorta* and subsp. *latifolia* border one another (Cope 1993). However, in the native range, geographic isolation and local adaptations largely maintain phenotypic differences between the four subspecies (Aitken and Libby 1994; Bisbing et al. 2021; Critchfield 1957). While some degree of gene flow does occur even across distant populations in the native range, this was shown to be insufficient to erode subspecies differences (Bisbing et al. 2021). Phenotypic differences between subspecies are also maintained via diverging selection pressures from cone predators (Benkman 1999; Benkman et al. 2001; Edelaar and Benkman 2006; Elliott 1988; Parchman et al. 2016; Siepielski and Benkman 2005; Smith 1970; Talluto and Benkman 2014, 2013). Where red squirrels (*Tamiasciurus hudsonicus*; Erxleben, 1777) co-occur with *P. contorta* they exert strong selection pressure on cone morphology towards smaller cones with fewer seeds (Benkman et al. 2001). In the absence of red squirrels, *P. contorta* and red crossbills (*Loxia curvirostra* Linn. [Pl. 200]) have coevolved, with *P. contorta* cones developing larger, thicker, overlapping scales, and crossbills developing shorter, deeper bills (Benkman et al. 2001; Parchman et al. 2016). Cone predation exerts selection pressure against serotinous cones, as these provide a year-round reliable food source, however, serotiny is retained by selection pressures from semi-frequent wildfires (Lamont et al. 2020).

Pinus contorta was introduced to Aotearoa, New Zealand, in the 1880s (Adams and Kensington 1909; Francis and Walzl 2009; Weston 1957) before establishment in state forests in 1902 and extensive seeding and planting in the 1920s and early 1930s (Benecke 1967) as part of government-initiated provenance trials for forestry and erosion control until the late 1960s (Cunningham and Roberts 1970). Planting of *P. contorta* in alpine areas and in pastoral shelterbelts waned after observations of rapid spread beyond established boundaries with guidelines restricting its planting in 1970 (Miller and Ecroyd 1987) until the eventual declaration of the species as an unwanted organism in the Biosecurity Act 1993 (Ministry of Agriculture and Forestry 1993). When introduced to New Zealand, samples of *Pinus contorta* subspecies were broadly categorised into the "green strain" (Coastal subspecies; *Pinus contorta* subsp. *contorta* and subsp. *bolanderi*) and the "yellow strain" (Inland subspecies; *Pinus contorta* subsp. *latifolia* and subsp. *murrayana*), meaning that some information relating to provenance was lost (Miller and Ecroyd 1987; Weston 1957; Zoete 1989). This provenance information was then further complicated by the initial plantings at Waiotapu and Kaingaroa (Central North Island, New Zealand) in 1941/42, appropriately named the Waiotapu and Kaingaroa strains, respectively, which became common seed sources for national plantings (Miller and Ecroyd 1987).

Literature review

We completed an extensive literature search of Google Scholar using combinations of the search terms in Table 1, followed by a search of Google Play Books (https://play.google.com/store/books/) for "*Pinus contorta*". As most planting history records were originally published as confidential reports, we repeated this search in the National Forestry Library database (hosted by the New Zealand Forest Research Institute) and ordered physical copies of any relevant non-digitised matches. In addition, we searched

Table 1 Terms used in literature searches of the National Forestry Library, National Library, Google Scholar, and Google Play Books

General terms	Subspecies-specific terms			
Provenance	*Bolanderi*	*Contorta*	*Latifolia*	*Murrayana*
Erosion planting	Bolander pine	Shore pine	Lodgepole pine	Sierra pine
Green strain		Coast pine	Rocky mountain pine	Tamarack pine
Yellow strain		Beach pine	Black pine	Murray pine
			Yellow pine	

the national library (https://natlib.govt.nz/) separately for "lodgepole", "contorta", and "murrayana" and examined digitised documents, including newspaper articles. "Murrayana" was included as a search term as *P. contorta* subsp. *murrayana* was previously labelled as "*Pinus murrayana*". All relevant search results were checked for mentions of individual subspecies or strains, alongside location information (Table S2). Where no provenance information was found for an area where *Pinus contorta* was known to be planted, in particular for major invasions, we submitted information requests to the relevant district councils and Department of Conservation Offices to gain access to non-digitised records. For records that did not contain coordinates, records were georeferenced by site location information to the best possible resolution. Records indicating planting of *P. contorta* without any indication of subspecies, strain, provenance, or seed source were not included.

Columns relate to pseudonyms for the subspecies variation at the column head (OECD 2010).

Sample collection and processing

Sealed, mature, serotinous cones were collected from October 2022–December 2023 across five sites across New Zealand representing major invasions of *P. contorta* that encompass variation in climate, elevation, latitude, soil, and land use history. These sites included Mid Dome (Southland), Craigieburn (Canterbury), Lake Pukaki (Canterbury), the Clarence Valley (Canterbury), and the Waihōpai Valley (Marlborough). Cones were collected both from healthy, living trees and from dead, standing trees treated with aerially applied herbicides (NWCCP 2023a). Cones were collected from a range of crown heights to account for within-tree variation in cone traits (Carlin et al. 2024a, b). Cones were presumed to be serotinous in the field if they were part of a previous years' cohort, yet remained sealed, and were confirmed to be serotinous by failing to open in a drying oven set at 30 °C for 24 h.

Cone age was defined as years since maturity, beginning at 1, with years since treatment recorded separately. The age of treatment varied from 1 to 8 years, with the earliest treatment occurring in the 2015/2016 season. Finding untreated cones older than 2 years old was uncommon at these sites, as the NWCCP prioritises control of coning populations, and as such, untreated cones were skewed to being younger than treated cones. Cone cohorts can be easily identified by their node position, with each full branch node or tree whorl representing a year. Cones that appear on sub-nodes mature in the same year as the more recently developed full node.

Viability and germination testing

After opening, cones had their seeds counted before viability testing using a standard protocol with a tetrazolium chloride (TTC) 0.1% solution (Patil and Dadlani 2014). Differences in the number of filled seeds and number of viable seeds between herbicide-treated and untreated cones were assessed using generalised linear mixed models (GLMMs) with a Poisson distribution. Both GLMMs included treatment and cone age as fixed effects and tree identity as a random effect. Differences in the proportion of viable seeds extracted from herbicide-treated and untreated cones were assessed using a generalised linear model (GLM) with a Binomial distribution. The GLM included treatment and cone age as fixed effects. We initially specified more complex models including site and the interaction between cone age and treatment, however, models were simplified to avoid convergence issues. Effect sizes were considered significant if the 95% confidence interval did not overlap zero. All models were conducted in R version 4.3.1 (R Core Team 2023) using the *lme4* package (Bates et al. 2015). Figures were generated using the *ggplot2* (Wickham 2016), *ggstatsplot* (Patil 2021), and *gghalves* (Tiedemann 2022) packages.

Results

Literature review

A total of 71 different articles were found that contained confirmed plantings of *P. contorta* subspecies, excluding repetitions of similar newspaper adverts from the National Library. Of these, 76 general locations were identified as having one or more subspecies of *Pinus contorta* planted (Fig. 2; Fig. S2, Table S2).

All four subspecies, and occasionally intraspecific hybrids, were widely planted across New Zealand (Fig. 2; Fig. S2). Records of *P. contorta* from opposing green and

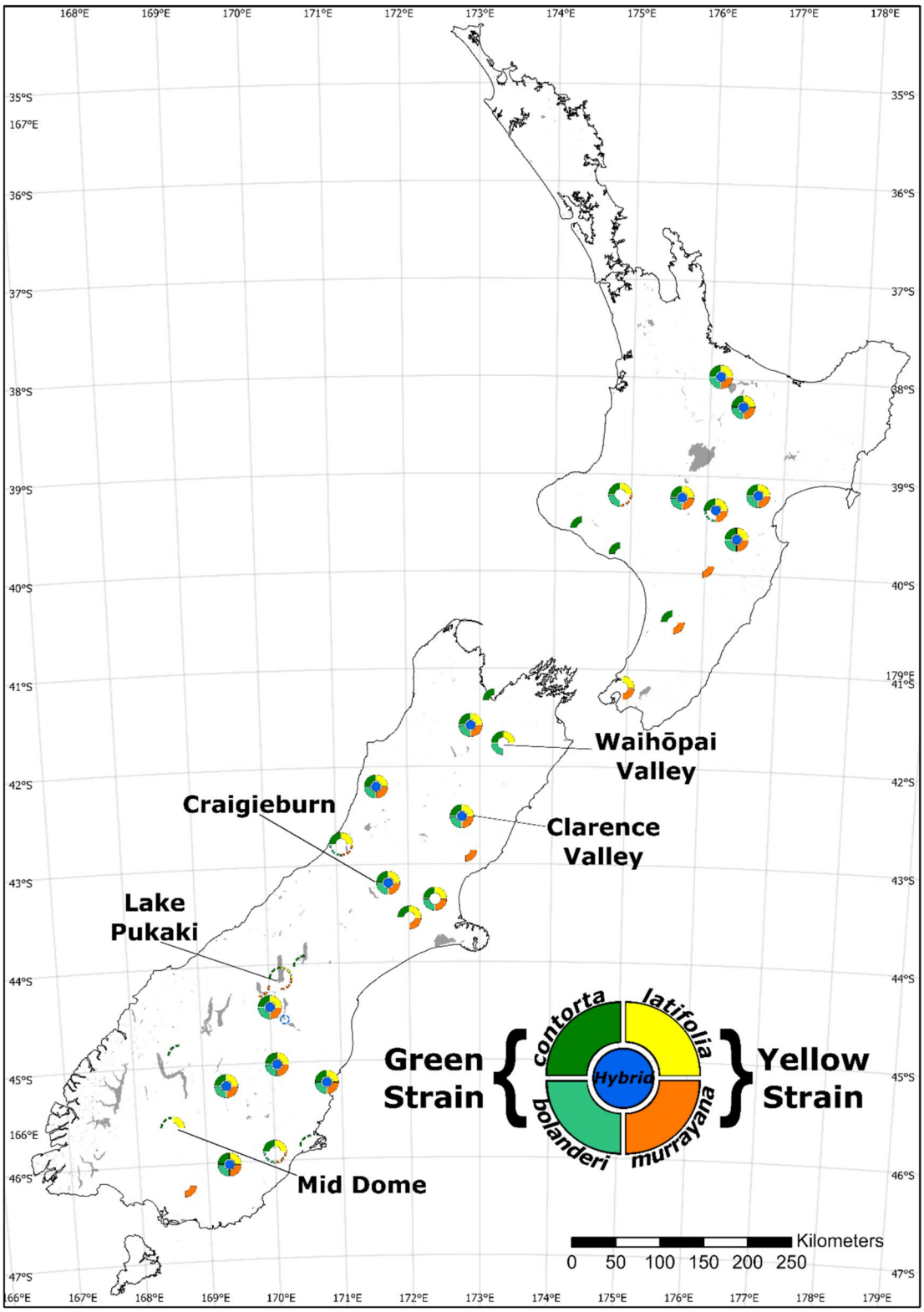


Fig. 2 A simplified map showing major locations of *P. contorta* plantings with known subspecies or provenance. Coloured quadrants indicate records of direct planting of that subspecies, with a blue inner circle indicating direct planting of intraspecific hybrids. Dashed coloured sections indicate no direct statements of subspecies planting but other identifying or suggestive information was present to imply the planting of a given subspecies. For display purposes, plantings within ~ 20 km of one another were grouped into a single symbol. Sites where serotinous cone collections occurred are labelled. Fig. S2 presents a higher resolution version of this map with all locations displayed separately

yellow strains were found planted directly next to one another or close by in most regions of New Zealand. Gisborne, Auckland, Northland and Waikato are exceptions where no planting records were located. Although two subspecies were known to be planted in Wellington, they were both part of the yellow strain. The planted subspecies resulting in major invasions of *P. contorta*, as identified in Ledgard (2001) and Paul (2013), are described in Table 2.

Viability of treated and untreated serotinous cones

A total of 135 serotinous cones were collected from October 2022 to December 2023 (Table 3). The average age of collected untreated and treated serotinous cones was 1.86 and 5.74 years, respectively. The average number of filled seeds found in untreated serotinous cones was 68.9 (± 3.4 SE) and 60.4 (± 3.2 SE) in treated cones. The average viability of developed seeds found in untreated cones was 85.7% (± 1.2% SE) and 83.8% (± 1.2% SE) in treated cones. The average number of viable seeds found in untreated cones was 59.1 (± 3.1 SE) and 51.0 (± 1.8 SE) in treated cones (Fig. 3). The oldest cones ($n = 18$) assessed were 10 years old from trees that had been treated 8 years prior; they held an average of 50.83 (± 2.7 SE) viable seeds.

The number of filled seeds was slightly greater in treated cones ($\beta_2 = 0.26$, 95% CI [0.10, 0.41], $z = 3.20$, $p = 0.001$), although this is likely not biologically significant given that most of the variance explained in the model was associated with tree identity ($R^2_{marginal} = 0.04$; $R^2_{conditional} = 0.92$). The number of viable seeds was likewise slightly greater in treated cones ($\beta_2 = 0.34$, 95% CI [0.16, 0.51], $z = 3.68$, $p = < 0.001$), although most of the variance was similarly explained by tree identity ($R^2_{marginal} = 0.01$; $R^2_{conditional} = 0.96$). The proportion of viable seeds per cone was unaffected by either cone age ($\beta_2 = -0.07$, 95% CI [− 0.82, 0.43], $z = -0.65$, $p = 0.52$) or treatment ($\beta_2 = 0.14$, 95% CI [− 1.13, 1.52], $z = 0.22$, $p = 0.83$). All model outputs are available in Table S3.

Cone age is defined as the number of years since development began, with age 1 representing a cone that matured in the previous season. Numbers within cells represent the number of untreated and treated cones, respectively

Discussion

Our findings indicate that all four subspecies of *P. contorta*, as well as intraspecific hybrids, were broadly planted across Aotearoa New Zealand (Fig. 2). Direct planting of hybrids may have helped shape invasive populations, and further intermixing between species may have occurred as subspecies were frequently planted together to compare performance. Although we did not directly assess the traits expressed at each site, we provide further evidence that cone serotiny is present across much of Aotearoa New Zealand, indicating that *P. contorta* subsp. *contorta* is unlikely to be the only subspecies responsible for invasive spread in Aotearoa New Zealand. As well as being an easily identifiable trait of some *P. contorta* subspecies, we show that cone serotiny may facilitate persistence of populations and possible re-invasion after control treatments with current best practises. Seeds from serotinous cones from dead, treated areas showed similar viability to cones from untreated areas, despite treated cones being older on average (Fig. 3).

Multiple subspecies were recorded as being planted in all regions across New Zealand with major *P. contorta* invasions (Fig. 2; Table 2), except for Mid Dome where only subsp. *latifolia* was planted, Hakataramea, where only subsp. *contorta* was planted, and Mt. Tarawera, for which no direct planting records were found. Despite finding no records for Mt. Tarawera, it is widely believed that the current invasion spread from plantings from both the south and west (Griffin 1989) and therefore likely originated from similar seed sources used at Waiotapu and Kaingaroa forests. As all subspecies were planted in these forests, and likely in shelterbelts of nearby properties, the invasion at Mt. Tarawera is likely similarly comprised.

By directly planting different *P. contorta* subspecies together, the geographic gene-flow barrier present in the native range was removed and, given *P. contorta* is wind-pollinated, likely resulted in rapid hybridisation between subspecies (Bisbing et al. 2021; Critchfield and Service 1980). This, as well as the potential for spreading directly planted hybrids, suggests that major invasions of *P. contorta* are unlikely to represent any single subspecies and likely represent populations of intraspecific hybrids. However, the degree of hybridisation will be based upon spatiotemporal variation in the proportion of each subspecies planted in any given area, and natural stochasticity in population genetics. If true, the resulting intraspecific hybrids may possess different traits than those reported for individual subspecies both in Aotearoa New Zealand, and in the native range, which could exacerbate their invasive potential. Whether hybridisation has contributed to the reported trait shifts *P. contorta* has undergone since arriving in Aotearoa New Zealand, is currently unclear (Carlin 2025; Carlin et al. 2025b; Taylor et al. 2016). Confounding effects, such as the release from cone- and seed-predators present in the native range (Benkman and Siepielski 2004; Carlin et al. 2024a, b; Parker and Benkman 2020; Talluto and Benkman 2014) or more favourable abiotic conditions in New Zealand, could also contribute to these trait shifts. Given the similarly complex introduction histories of other exotic conifers in New Zealand during the nineteenth and twentieth centuries, intraspecific hybridisation may also lead to unexpected trait expression

Table 2 Subspecies of *Pinus contorta* planted within or close to each of the major *P. contorta* invasions across Aotearoa New Zealand

Invasion location	Possible source plantings	Subspecies planted	References
Central Plateau	Karioi State Forest; Erua State Forest; Mount Ruapehu; National Park Township; Erua; Raurimu; Taurewa; Waikune Prison	*bolanderi*; *contorta*; *latifolia*; *murrayana*; *contorta* x *latifolia*; *contorta* x *murrayana*; *contorta* x *contorta**	(Cooper 1982; Cutler 1943; Francis and Walzl 2009; Hocking et al. 1944; Kenderdine 1945; Maddern Harris 1971; Miller 1968, 1971a, 1971b, 1986; Mohrdiek and Miller 1980; Shelbourne 1978; Shelbourne and Miller 1976; Shelbourne and Carson 2019; State Forest Service 1947; Thulin and Miller 1966; Wendelken 1956)
Kaweka range	Kaweka forest park	*contorta*; *latifolia*; *murrayana*; (maybe *bolanderi*)	(Cunningham and Roberts 1970; Miller and Ecroyd 1987; Shelbourne 1978)
Red Hills	Golden downs	*bolanderi*; *contorta*; *latifolia*; *murrayana*; *contorta* x *latifolia*; *contorta* x *murrayana*; *latifolia* x *murrayana*	(Maddern Harris 1971; Miller 1968, 1969, 1971b, 1976; Mohrdiek and Miller 1980; Shelbourne 1978; Shelbourne and Carson 2019; Thulin and Miller 1966)
Hakataramea	Benmore; Otemara; Aviemore; Kirkliston range	*contorta*; (maybe *murrayana*); (maybe intraspecific hybrids)	(Baker 1992; Department of Conservation 1992, 1993; Department of Lands and Survey 1985b)
Mid Dome	Mid dome (directly)	*latifolia*; (maybe *contorta*)	(Wendelken 1956)
Leatham State Forest	Leatham State Forest (directly); Garden Flat; Tommy's bluff; Fork Spur; Cow stream; Breezers Creek; Enchanted stream; Turkeys Nest Basin	*bolanderi*; *contorta*; *latifolia*	(Haywood 1974; Ledgard 2001; Ledgard 2002; Miller and Ecroyd 1987; Wildland Consultants 2011; Wishart 1984)
Clarence valley	Hanmer forest	*bolanderi*; *contorta*; *latifolia*; *murrayana*; *contorta* x *latifolia*; *contorta* x *murrayana*; *contorta* x *contorta**	(Miller 1971a, 1971b, 1973; Shelbourne 1978; Shelbourne and Carson 2019; Thulin and Miller 1966)
Craigieburn range	Hut Creek; Mount Cockayne; Cass; Helicopter Hill; Broken River; Craigieburn Valley; Craigieburn Arboretum; Grasmere Lodge; Mt Wall Creek	*contorta*; *latifolia*; *murrayana*; *contorta* x *latifolia*; *contorta* x *murrayana*; *latifolia* x *murrayana*; *contorta* x *P. banksiana***; *latifolia* x *P. banksiana*	(Baker 1974a, 1974b; Benecke and Baker 1968; Benecke and Morris 1975; Ledgard and Paul 2008; Ledgard 1981; Ledgard and Baker 1988; Wardle 1971, 1985)
Mackenzie Basin	Tara Hills Research Station (Omarama); Benmore; Otemara; Aviemore; Kirkliston Range; Coronet Peak; Tekapo; Bendhu Scientific Reserve; Lake Middleton; Mount Cook Station***	*bolanderi*; *contorta*; *latifolia*; *murrayana*; *contorta* x *latifolia*; *contorta* x *murrayana*; *latifolia* x *murrayana*	(Allan et al. 2018; Allen and Lee 1989; Baker 1992; Department of Conservation 1993; Department of Conservation 1992; Department of Lands and Survey 1985a, 1985b; Johnson 1990; Miller 1971a, 1971b, 1976; Miller and Ecroyd 1987; Molloy et al. 1976; Shelbourne and Carson 2019; Thulin and Miller 1966; Young 2016)
Blue mountains	Beaumont; Rankleburn; Crookston	*bolanderi*; *contorta*; *murrayana*	(Gimblett 1944; Maddern Harris 1971; Miller 1971b, 1973; Nelson 1942; Shelbourne and Carson 2019; Thulin and Miller 1966)
Mount Tarawera	None Found (Closest Records: Kaingaroa and Waiotapu Forests)	Undetermined (Closest Records would indicate: *bolanderi*; *contorta*; *latifolia*; *murrayana*; *contorta* x *latifolia*; *contorta* x *murrayana*; *contorta* x *contorta**)	See Table S2 for Closest Records

Table S2 provides a full list of subspecies planted locations

*Crossing of the same subspecies, from opposite ends of the subspecies range, ***Pinus banksiana* produces serotinous cones and readily hybridises with *P. contorta* (Cameron 1953; Little 1979; Lotan 1967; Moss 1949), ***No subspecies or seed source records found; however, records indicate substantial plantings occurred

Table 3 Number of serotinous cones collected across five sites of New Zealand

Site	Cone age (years)										
	1	2	3	4	5	6	7	8	9	10	Total
Clarence valley	–	4 | 1	0 | 3	0 | 27	0 | 2	0 | 1	0 | 2	0 | 1	–	–	4 | 37
Craigieburn	–	–	–	–	–	–	0 | 1	–	–	–	0 | 1
Mid Dome	–	31 | 7	1 | 0	2 | 2	–	–	–	0 | 3	–	0 | 18	34 | 30
Lake Pukaki	–	3 | 0	–	–	–	0 | 2	–	–	–	–	3 | 2
Waihōpai valley	19 | 0	–	5 | 0	–	–	–	–	–	–	–	24 | 0
Total	19 | 0	38 | 8	6 | 3	2 | 29	0 | 2	0 | 3	0 | 3	0 | 4	0 | 0	0 | 18	65 | 70

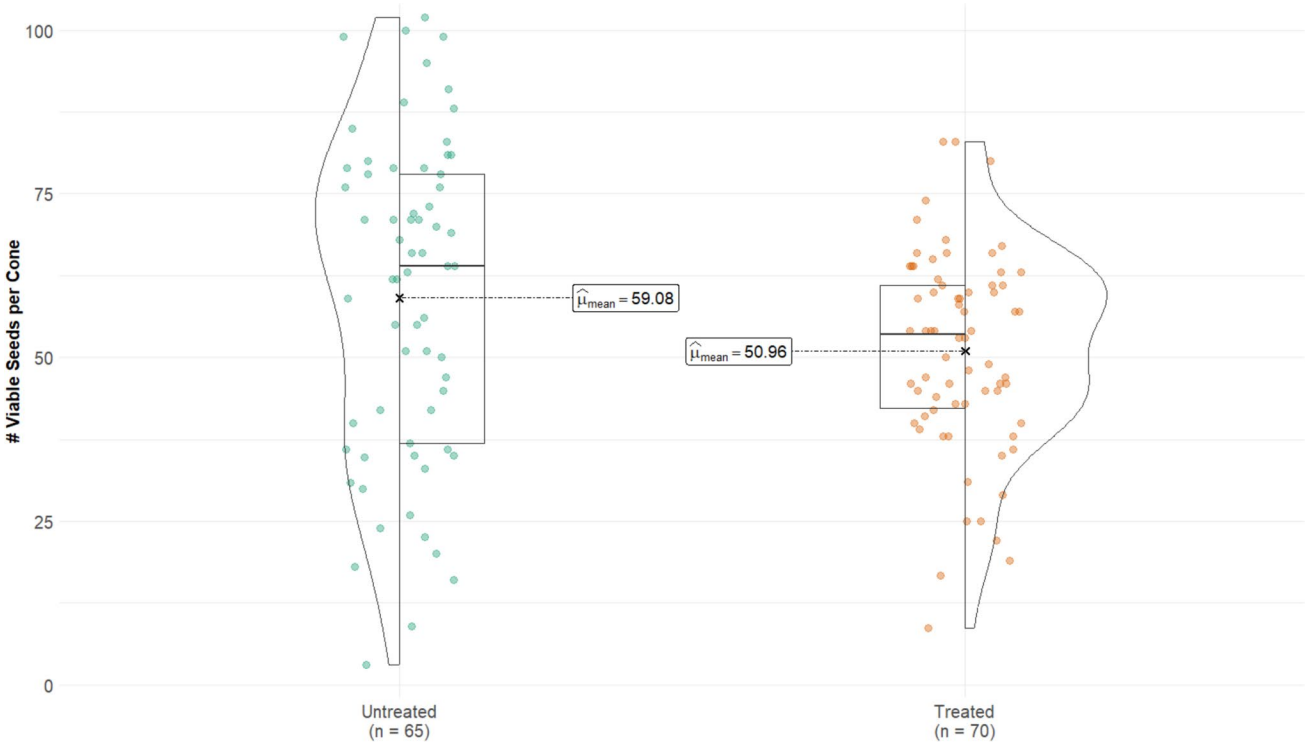


Fig. 3 Half-violin boxplots demonstrating that there are no significant differences in the number of viable seeds extracted from both untreated serotinous *Pinus contorta* cones and serotinous cones from herbicide-treated trees. Viability was assessed using 0.1% TTC solution. Half-Boxplots are displaying the median, interquartile range, and full range of data. Half-Violin plots display the distribution of viable seeds observed among cones. Black crosses represent the sample means

in those species (Table S4). Genomic analyses are required to investigate this further.

Where populations develop serotinous cones, which appear to be relatively common across New Zealand (Carlin et al. 2025b), our results indicate that these populations may be better adapted to persist through herbicide control treatments. Our experimental findings indicate that mature serotinous cones are unaffected by current aerial-foliar herbicide application (https://www.wildingpines.nz/good-practice-guides), with viability rates of extracted seed within the expected 70–90% range exhibited in the native range (Miller and Ecroyd 1987). This outcome indicates that reinvading populations may trend towards expressing greater proportions of serotiny. Aerial foliar spray application (AFSA) is a common wilding control method for dense infestations of *P. contorta* in the NWCCP and partially mimics the ecological effects of wildfire by killing most reproductively active individuals (NWCCP 2019). In contrast to fire, AFSA does not facilitate serotinous cone opening, but neither does the herbicide affect seeds within cones (Fig. 3; Carlin et al. 2025a). As such, AFSA-treated dead *P. contorta* forests may hold a substantial aerial bank of viable seeds in serotinous cones. In the native range, serotinous cones can persist on trees for decades without significant loss of viability, with the number of seeds stored in the subsp. *latifolia* cone bank stated to be in the millions per acre and 10 times

greater than the number of seeds produced annually (Lotan 1975; Lotan et al. 1985; Perry and Lotan 1979; Rhoades et al. 2022). While this would likely represent an overestimation of the aerial seed bank for many invasions across New Zealand that are comprised of younger trees, it indicates a substantial proportion of viable seed could remain in areas we assume to be fully treated.

While it is unclear whether conditions in Aotearoa, New Zealand, could regularly cause serotinous cones to open and disperse seed, requiring high temperatures or wildfire, these conditions are expected to become more common under climate change. Work on similar species has suggested that cones can get significantly hotter than the surrounding air temperature when exposed to the sun (Wyse et al. 2019), such as when pine needles are lost after AFSA operations. Additionally, controlled burns are considered as a wilding conifer control method (Ledgard 2009; Wilding Pine Network 2022), which could further select for serotiny in a population, reducing the efficiency of this method in the long term. While it is true that a severe canopy fire can kill seeds, *P. contorta* seedlings are extremely common after moderate fires in the native range (Anderson and Romme 1991). All of this combined suggests that some of our methods for controlling *P. contorta* could be selecting for serotinous trees, which may be more successful invaders under climate change (Lamont et al. 2020).

We can expect that certain traits, such as serotiny, will have different selection pressures in New Zealand than those imposed in the native range. In the native range, serotinous cones are selected for by fire (Lamont et al. 2020) but represent a reliable year-round food source and therefore also receive negative selection pressure from specialist cone predators (Talluto and Benkman 2014, 2013). With the absence of specialised cone predators in New Zealand, any existing positive selection pressures on serotiny could allow the proportion of serotinous trees to rapidly increase (Benkman and Siepielski 2004). We found the number of seeds counted within serotinous cones to be lower than average for *P. contorta* cones in New Zealand, which contain ~ 74 filled seeds per cone on average (Carlin et al. 2025b), which is consistent with data from the native range suggesting serotinous cones possess fewer seeds than non-serotinous cones (Muir and Lotan 1985; Parker and Benkman 2020).

Whether these findings indicate a need to consider meaningful changes to best long-term management practises is currently unclear and likely requires a more in-depth analysis both to quantify the proportion of the aerial cone bank that is serotinous and also better understand conditions that facilitate serotinous cone opening. However, when fires occur, land managers can and should expect *P. contorta* to readily regenerate and therefore may wish to consider treating the area again within 5 years post-fire, before the majority of the population have produced viable cones (Ledgard 2001). Cautious land managers may also wish to consider mulching areas, where possible, to remove the aerial cone bank (Paul and Ledgard 2009; Carlin et al. 2025a), although this can still result in regeneration (Cirelli et al. 2016). It is currently unclear whether other mechanisms can facilitate seed dispersal and reinvasion from serotinous cones, such as cone damage during canopy collapse or natural decay over time.

While this work likely represents the most comprehensive publicly available synthesised account of *P. contorta* plantings in Aotearoa New Zealand, it still likely underestimates the true extent due to the many individuals planted in private shelterbelts or elsewhere without record. Moreover, we focussed on records with confirmed subspecies identification, or with strong indications, and therefore the vast number of general plantings at the species level were not collated in this work.

Future work

Genetic analyses of significant invasive species in New Zealand have already provided valuable insight into invasion histories and genetic-based control techniques (Bond et al. 2023; Pattabiraman et al. 2022). Similar analyses on *P. contorta* would help elucidate the role of intraspecific hybridisation in wilding invasions and infer whether certain hybrid mixes lead to more successful invasions overall. Analyses of genetic variation among *Pinus contorta* subspecies have already been completed in the native range, providing a valuable comparison of the genetic makeup of each subspecies (Bisbing et al. 2021). Further work is required to determine how traits differ between New Zealand and native range populations, including those that may increase their invasiveness in the southern hemisphere.

Conclusion

All four subspecies of *Pinus contorta* were widely planted across Aotearoa New Zealand. Given the wind-pollinated nature of *P. contorta*, rapid hybridisation between subspecies is likely. The resulting traits expressed by populations across Aotearoa New Zealand, are unlikely to directly relate to any particular subspecies, and, therefore, trait data from the native range will likely differ from observations in Aotearoa New Zealand. Cone serotiny appears to be present across multiple populations, and aids in the retention of propagules after control efforts as they are unaffected by aerial herbicide regimes. Management efforts may result in populations trending towards greater serotiny expression, which may better adapt wilding populations to the effects of climate change. Genomic analyses to identify the genetic

variation amongst *P. contorta* in Aotearoa New Zealand may elucidate spatial variation in invasiveness correlated to their original planted populations.

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Data and code availability All data presented in this work is available at: https://github.com/TomC-93/VLR.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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