



Reproductive trait shift in *Pinus contorta* helps explain invasion success in Aotearoa New Zealand

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Abstract: *Pinus contorta* is one of Aotearoa's worst weeds. Evidence suggests that its spread and growth rates in Aotearoa are greater than in its native range in North America, yet the underlying drivers remain poorly understood. In this study, we examine cone and seed traits of *P. contorta* across several major invasion sites in Aotearoa and compare their traits with values from the native range. Across six sites, the number of filled seeds per cone ranged from 1–146, with an average 74 seeds per cone, three times the number recorded in the native range and approximately 50% more than previous estimates for Aotearoa. Notably, one site (Craigieburn, Canterbury) averaged only 26 filled seeds per cone with a larger proportion of unfilled seeds. Cone length and seed holding capacity varied greatly within individuals with an average cone length of 43.6 mm, ranging from 15.9–62.0 mm. We predict that this increase in seed holding capacity has likely enhanced the invasion success of *P. contorta* by increasing propagule pressure in the environment. We found that the average number of seed scales per cone is similar between Aotearoa and the native range, and therefore we suggest that this trait shift towards a greater seed holding capacity may be due to an increase in the proportion of fertile scales.

Keywords: exotic species; forest; introduced; non-native; pine; *Pinaceae*; rapid adaptation; samara; seed potential, wilding conifer

Introduction

Plant invasions pose a significant threat to ecosystems worldwide, leading to substantial ecological and economic impacts (Dogra et al. 2010; Pyšek et al. 2020; Gioria et al. 2023). The success of invasions can be facilitated by shifts in traits between the native and invaded range that increase a plant's invasiveness (Hodgins et al. 2018). Shifts in traits related to invasiveness have been observed through numerous mechanisms including the reallocation of resources into growth after escaping enemies or competitors (Leishman et al. 2014), preadaptation (Elst et al. 2016; Mathakutha et al. 2019) or rapid adaptation to novel environments (Heberling et al. 2016; van Boheemen et al. 2019), and inter- or intra-specific hybridisation (Rius & Darling 2014; Hodgins et al. 2018).

Some of the most successful plant invaders in the Southern Hemisphere are non-native conifers, known as 'wilding conifers' in Aotearoa (Richardson et al. 2014). Wilding conifers are estimated to affect over 1.7 million hectares of Aotearoa, spanning both productive and conservation lands (Ministry for Primary Industries 2015) and threaten a further 7.5 million hectares (Wyatt 2018). Their rapid growth and spread has led to a number of ecological and economic impacts including outcompeting native species (Peltzer 2018), increasing fire risk (Simberloff et al. 2010), reducing land yield (Edwards et al. 2020), and supporting invasive mammal populations

(Carlin et al. 2024b). Prior work has shown that *Pinus contorta* Douglas ex Loudon, one of the most successful wilding conifers (Ledgard 2001), has higher cone production, growth, and spread rates in Aotearoa than compared with its native or other invaded ranges (Taylor et al. 2016).

The demonstrated trait shift exhibited by *P. contorta* in Aotearoa is unsurprising given the potential influences of hybridisation, enemy release, and environmental differences compared to its native range (Miller 1969; Cooper 1982; Miller & Ecroyd 1987). *Pinus contorta* is native to North America, with a range stretching from Baja, California, to Yukon, Canada (Bisbing et al. 2021). The four subspecies (*P. contorta* subsp. *bolanderi*, subsp. *contorta*, subsp. *latifolia*, subsp. *murrayana*), which vary in their form, growth rates, and cone traits (Table 1), were all introduced into Aotearoa and frequently planted together (Ledgard 1981 unpubl. data) allowing for potential intra-specific hybridisation. Field identification of subspecies in Aotearoa is difficult due to changes to phenotypes since their introduction, and that identification in the native range is largely informed by geographic location. *Pinus contorta* in Aotearoa has escaped interactions with specialist seed predators such as squirrels and crossbills which would normally impose selection pressures for increased cone defences in the native range including thicker scales, and a reduced frequency of serotinous cones (Critchfield 1957; Smith 1970; Koch 1996; Benkman et al. 2001; Edelaar & Benkman 2006; Parchman

Table 1. Summary statistics of cones and seeds from *Pinus contorta* subspecies in their native range (North America). Figures are presented for adult trees. MISM = mean individual filled seed mass.

Subspecies	Cone length (mm)	Cone circumference (mm)	Filled seed \bar{x}	MISM (mg)	Serotinous cone frequency	References
<i>bolanderi</i>	37.5	-	Unknown	2.0–2.9	Very Common	(Critchfield 1957; Koch 1996)
<i>contorta</i>	37.5–42.9	-	10–25 (Total seed* 10–46)	2.0–5.6	Uncommon	(Critchfield 1957; Jeffers & Black 1963; Koch 1996; Owens 2006)
<i>latifolia</i>	21.0–55.0	67.4–96.1	16–23 (Total seed* 16–46)	2.3–5.5	Very Common	(Clements 1910; Critchfield 1957; Ying et al. 1985; McGinley et al. 1990; Koch 1996; Owens 2006; Teste et al. 2011)
<i>murrayana</i>	44.6–45.7	-	16	3.8–8.2	None	(Critchfield 1957; Jeffers & Black 1963; Critchfield & Service 1980; Koch 1996)

*Estimates of total seed include unfilled seed.

et al. 2016). Serotinous cones can remain sealed on a tree for decades until an environmental trigger (high temperatures from wildfires) causes them to open, but in years without wildfires this makes them a reliable year-round food source to seed predators (Lotan 1976). Escaping these selection pressures could have allowed *P. contorta* to reallocate resources into growth or reproduction in Aotearoa. Additionally, all subspecies of *P. contorta* grow well in many parts of Aotearoa allowing usually stunted subspecies (e.g. subsp. *contorta*) to grow taller and faster than in the native range (Miller 1968, 1971; Shelbourne 1978; Miller 1986), suggesting that *P. contorta* is preadapted to the abiotic conditions of Aotearoa. Despite these observations, we currently have a poor understanding of how they may have influenced the invasiveness of *P. contorta* in Aotearoa.

Here we investigate cone and seed traits that could impact the reproductive potential of *P. contorta* in Aotearoa. We consider how cone length, seed holding capacity, seed mass, and number of cone scales compare between Aotearoa and its native range, and also consider whether these traits vary across populations nationally. As determinants of propagule pressure, cone and seed traits are crucial for understanding the spread rates of wilding conifers nationally and globally (Simberloff 2009; Simberloff et al. 2010; Taylor et al. 2016; Wyse & Hulme 2020a; Rajaonarivelo et al. 2022; Carlin et al. 2024a). Furthermore, if cone or seed traits vary between populations, this may aid in the identification of subspecies outside of their native range.

Methods

Site Selection

We selected six sites with major *P. contorta* invasions across Aotearoa (Ledgard 2001) that encompass variation in elevation, climate, latitude, soil, and land-use history (Table 2), which are known to affect *P. contorta* trait expression (Tinker et al. 1994). These sites represent similar introduction histories, and each possess a variety of stand densities, tree heights, and tree

ages. All six sites have a complex history of wilding conifer management including mechanical and chemical control efforts (National Wilding Conifer Control Programme 2019). Climate, soil, and elevation data were extracted for each site from WorldClim 2 (Fick & Hijmans 2017), ISRIC SoilGrids (Batjes NH et al. 2017; Batjes NH et al. 2020), and the *elevatr* R package (Hollister 2023).

Cone collection and processing

We identified untreated, self-established populations of coning *P. contorta* at each site and conducted cone collections from February to March of 2022–2024, except in the Waihōpai Valley where a single population was sampled in September 2022. At all other sites, at least two populations were sampled that were a minimum of 5 km apart from each other. Sampled trees within a population were greater than 50 m apart to reduce the chances of sampling direct siblings, and a minimum of 100 m from evidence of chemical control. Trees were only sampled if showing no signs of chemical control or disease which could impede cone development. Sampled trees represented a range of stand densities (lone trees–high density), ages (5–30), and heights (c. 1.5–25 m). Mature, closed cones were collected from the sampled trees across a range of crown heights (Carlin et al. 2024a). At least five cones were collected from each tree, except when a tree produced fewer than five cones, in which case all available sealed cones were collected. In areas with few large coning trees, such as the Craigieburn site, more than five cones were taken from some trees, with a maximum of 23 cones collected from a single tree. Cone length was measured before heating them in a drying oven at first at 30°C (non-serotinous cones) for 12 hours and then at 60°C (serotinous cones) if needed for an additional 12 hours to stimulate opening. Cones were dismantled by systematically removing scales from base to tip to ensure all seeds could be extracted before counting seed as either filled or unfilled (Appendix S1 in Supplementary Materials). The mean individual filled seed mass (MISM) was calculated for each cone to the nearest 0.1 mg. Seeds were removed from the samara prior to weighing.

A subset of 250 cones was selected to have their orthogonal widths measured, from which an approximate circumference

Table 2. Site characteristics of *Pinus contorta* populations in Aotearoa where samples were collected. For each site the approximate coordinates, sampled elevation range, and climatic summaries are provided. Minimum and maximum temperature are based on monthly climate averages.

Site	Longitude (DD)	Latitude (DD)	Populations sampled	Elevation range (m)	Soil group	Minimum temperature (C°)	Maximum temperature (C°)	Annual precipitation (mm)
Kaweka Range (Hawke's Bay)	176.2887	-39.4699	2	600–1050	Andosols	0.1	20.2	1732
Waihōpai Valley (Marlborough)	173.3993	-41.7250	1	1150	Cambisols	-0.5	18.4	1089
Clarence Valley (Canterbury)	172.8945	-42.4669	4	800–900	Cambisols	-0.7	18.1	1194
Craigieburn (Canterbury)	171.7290	-43.1780	3	800–900	Andosols	-1.2	18.6	1874
Lake Pukaki (Canterbury)	170.1381	-44.1943	3	600–650	Andosols	-1.3	21.7	704
Mid Dome (Southland)	168.5147	-45.6430	4	600–1050	Andosols	-2.2	19.4	995

Table 3. The total number of cones collected from each site and population, and the total number of trees from which cones were collected. Numbers in brackets signify the number of cones or trees that were included in a 250-cone subset that had their orthogonal measurements taken. Numbers in the site total column represent the number of trees and cones respectively, in the format “Trees | Cones”.

Site	Population	Trees	Cones	Site Total
Kaweka Range	A	7	28	16 70
	B	9	42	
Waihōpai Valley	A	5 (5)	29 (29)	5 29 (5 29)
Clarence Valley	A	10	50	39 187 (9 15)
	B	19 (9)	60 (15)	
	C	8	40	
	D	2	37	
Craigieburn	A	13 (2)	63 (11)	36 220 (18 128)
	B	8	40	
	C	15 (15)	117 (117)	
Lake Pukaki	A	19	70	29 120 (9 49)
	B	2 (1)	2 (1)	
	C	8 (8)	48 (48)	
Mid Dome	A	18	81	38 134 (11 29)
	B	10 (10)	10 (10)	
	C	3 (1)	27 (19)	
	D	7	16	
Total	17	163 (51)	760 (250)	-

was calculated using the Ramanujan formulae (Villarino 2005). A further subset of 43 cones from Waihōpai Valley and Mid Dome was selected to have their seed viability assessed, as well as counting and weighing their scales once dismantled. In addition to the total mass of seeds per cone and total mass of scales per cone, 10 randomly selected filled seeds and scales were weighed for each of the subset of 43 cones. Basal cone scales were not included in the scale count or total mass of scales as these do not produce filled seeds (Koch 1996). Two samaras (winged achenes, each including a seed) are typically produced per cone scale from the cone apical and middle scales, although the middle scales typically produce samaras of higher fecundity (Koch 1996). Seed viability testing followed standard protocol using a 1% tetrazolium chloride solution (Patil & Dadlani 2014).

The total number of filled seeds per cone was modelled as a function of cone length, serotiny, site, and their interactions using a generalised linear model (GLM) with a Poisson distribution. We initially specified a more complex model including collection year and serotiny as fixed effects and tree identification nested within population as a random effect, but the model was simplified to avoid convergence issues. Cone length and MISM per cone were each modelled with linear mixed effects models (LMMs) including tree identification nested within population as a random effect. The LMM to predict cone length included site and serotiny as fixed effects, whereas the LMM to predict MISM included cone length, site, their interaction, and serotiny as fixed effects. Collection year was excluded from all models due to having no apparent influence on the data. Where interaction terms were found to be

non-significant, they were removed, and the model was rerun.

To determine whether cone morphology (cone length:circumference ratio) is related to the number of filled seeds, we conducted a generalised linear mixed model with a Poisson distribution. We included cone morphology, site, and their interaction as fixed effects, and population as a random effect. To determine whether the number of cone scales was directly related to the number of filled seed within cones, we conducted a GLM with a Poisson distribution using the subset of 43 cones. Number of filled seeds was modelled by the number of scales, cone length, their interaction, and site. Pairwise post-hoc tests with the Tukey-method identified significant differences between comparisons. Effect sizes were considered significant if the 95% confidence interval did not overlap zero. All analyses were conducted using R version 4.3.1 (R Core Team 2023) using the *lme4* (Bates et al. 2015), *emmeans* (Lenth 2023), and *multcomp* (Hothorn et al. 2008) packages.

Results

We collected a total of 760 closed cones from 163 trees, including 126 serotinous cones (Table 3). The number of developed seeds found within a cone was considerably lower at the Craigieburn site than at all other sites (Table 4). The number of filled seeds found in cones ranged from 1–146 and, excluding Craigieburn, was an average of 74 seeds per cone. Cones from Craigieburn had an average of 26 filled seeds per cone, ranging from 1–92. Seed viability ranged from 50–100% of filled seed, with an average of 83.7% (± 0.9 SE) and was consistent across populations and sites. Filled seed mass for *P. contorta* in Aotearoa was within the known boundaries for all subspecies except subsp. *bolanderi* in their native range (Table 1), with a MISM in Aotearoa of 4.65 mg and an interquartile range of 3.96–5.62 mg (Table 4; Appendix S2).

Cones containing filled seed varied considerably in length (15.9–62 mm; Appendix S3) and circumference (49.7–110.0 mm; Appendix S4) between individuals and sites (Table 4). In Aotearoa, the average values for cone length were within the limits from the native range (Table 1). However, cones from all sites except the Clarence Valley were recorded exceeding the upper limit of cone length from the native range (Table 4). Cone circumference in Aotearoa was similar to that recorded in the native range (McGinley et al. 1990).

The number of filled seeds per cone increased with cone length for all sites ($\beta = 0.08$, 95% CI [0.07, 0.08], $p < 0.001$; Fig. 1a). Serotinous cones contained fewer seeds than non-serotinous cones at Mid Dome and the Clarence Valley (Fig. 1b), but we could not accurately determine this for other sites due to a lack of serotinous cones collected at other sites. The impact that increasing cone length had on increasing the number of filled seeds was highest in Craigieburn, and lowest at Mid Dome. Apart from serotinous cones from the Clarence Valley and Mid Dome, the remaining sites did not differ from one another in the amount that cone length influenced filled seed numbers (Fig. 1b). For serotinous cones from the Clarence Valley and Mid Dome, increasing cone length was associated with fewer filled seeds (Fig. 1).

The LMM to predict cone length had substantial explanatory power but most variation occurred among trees or populations, rather than by site ($R^2_{\text{conditional}} = 0.73$; $R^2_{\text{marginal}} = 0.27$). The main effects of site and serotiny were non-significant. However, there was a significant interaction

effect (site \times serotiny), with serotinous cones from Mid Dome being significantly larger than non-serotinous cones from the Clarence Valley (Appendix S3). The LMM to predict MISM had reasonable explanatory power, primarily driven by variation between trees or populations, rather than by site ($R^2_{\text{conditional}} = 0.56$; $R^2_{\text{marginal}} = 0.18$). Increasing cone length had a significantly positive effect on MISM, however neither site, serotiny nor their interactions had a significant effect.

The effect of cone morphology (length:circumference ratio) on the number of filled seed was significant and varied between sites (Fig. 2; Appendix S5). Longer, thinner, cones (positive values; Fig. 2) contained more filled seed at Craigieburn, Mid Dome, and Lake Pukaki. Conversely, shorter, fatter cones (negative values; Fig. 2) contained more filled seed in the Clarence Valley. Cones containing the highest number of filled seeds from the Waihōpai Valley did not tend towards either of the morphotype extremes.

Both the number of cone scales and the length of the cone significantly contribute to increasing the number of filled seed within cones (Appendix S6) However, there was a significant negative interaction between the number of scales and cone length ($\beta = -0.0003$, 95% CI [-0.00053, -0.00002], $p < 0.034$) suggesting that as cone length increases the number of scales becomes a worse predictor of the number of filled seeds. Only two sites were included in the 43-cone subset that had their scales counted (Waihōpai Valley and Mid Dome), with cones from Mid Dome containing more filled seeds than cones from the Waihōpai Valley (Appendix S7).

Discussion

Our results suggest a shift in the reproductive traits of *Pinus contorta* has occurred in Aotearoa compared to its native range, resulting in traits that have increased its invasiveness (Table 4; Fig. 1). Specifically, cones in Aotearoa hold three times more seed compared to any of the subspecies in the native range despite cones being a similar size (Table 4). These findings, in conjunction with prior work showing *P. contorta* produces more cones in Aotearoa than in its other ranges (Taylor et al. 2016), indicate that propagule pressure in Aotearoa will be significantly higher than estimates for the native range. Given that *P. contorta* is described as an “aggressive pioneer species” in its native range (Owens 2006), these trait shifts towards higher growth rates and fecundity experienced since arrival in Aotearoa help explain its invasion success. Cone traits including the seed holding capacity, cone length, and MISM were broadly consistent between populations in Aotearoa, except in the Craigieburn site where cones held significantly fewer filled seeds. The impact of cone morphology on number of seeds did however vary between sites, with both “short & fat” and “long & thin” morphotypes observed increasing the seed potential at different sites (Fig. 2).

In North America, large *P. contorta* cones typically contain 10–25 seeds up to a maximum of c. 50 seeds per cone (Critchfield 1980; Lotan & Perry 1983; Lotan & Critchfield 1990; Koch 1996; Owens 2006) or fewer for some subspecies (Table 1). The number of filled seeds is restricted by the number of fertile scales per cone, with each scale typically producing two ovules (Owens et al. 2005; Owens 2006). In the native range, *P. contorta* cones commonly have up to 100 scales but most scales (75–80) are sterile, meaning at most a cone can produce 40–50 seeds with its 20–25 fertile scales (Koch 1996; Owens 2006). In reality, the number of filled seeds is

Table 4. Summary statistics of *Pinus contorta* cones across the invaded range in Aotearoa. Average values and standard errors are shown. Approximate values from the native range, summarized across subspecies, are provided from Table 1 for ease of comparing between ranges. Mean individual filled seed mass (MISM) was calculated by dividing total seed mass by the number of filled seeds. Note that missing values (-) for cone circumference and the number of scales indicate insufficient cones from these sites were selected as part of the subset.

Site	Number of cones	Cone length (mm) \bar{x} (\pm SE)	Cone circumference (mm) \bar{x} (\pm SE)	Number of scales \bar{x} (\pm SE)	Filled seed \bar{x} (\pm SE)	MISM (mg) \bar{x} (\pm SE)	Serotinous cones present [†]
Kaweka Range (Hawke's Bay)	70	44.3 (\pm 0.7)	-	-	75.9 (\pm 3.8)	4.185 (\pm 0.120)	Unknown
Waihōpai Valley (Marlborough)	29	50.3 (\pm 0.9)	84.4 (\pm 2.7)	74.7 (\pm 5.3)	79.2 (\pm 3.5)	4.237 (\pm 0.180)	Yes
Clarence Valley (Canterbury)	187	38.5 (\pm 0.4)	76.0 (\pm 2.3)	-	68.4 (\pm 1.6)	4.047 (\pm 0.150)	Yes
Craigieburn (Canterbury)	220	39.4 (\pm 0.4)	79.6 (\pm 0.9)	-	26.3 (\pm 2.1)	4.863 (\pm 0.127)	Yes
Lake Pukaki (Canterbury)	120	44.4 (\pm 0.6)	61.4 (\pm 1.1)	-	83.0 (\pm 3.2)	4.886 (\pm 0.106)	Yes
Mid Dome (Southland)	134	47.4 (\pm 0.6)	72.0 (\pm 1.1)	48.0 (\pm 5.0)	74.0 (\pm 2.6)	4.574 (\pm 0.114)	Yes
New Zealand Average	760 (Total)	42.3 (\pm 0.3)	75.5 (\pm 0.8)	62.9 (\pm 4.2)	74.2* (\pm 1.2)*	4.503 (\pm 0.057)	Yes
Approximate Native Range Values	-	21–55	60–110	\leq 100	10–25	2.0–8.2	Subspecies Dependent

*Excluding Craigieburn where cones had significantly fewer filled seeds. [†]Estimating the frequency of serotinous cones was not accounted for in our sampling design.

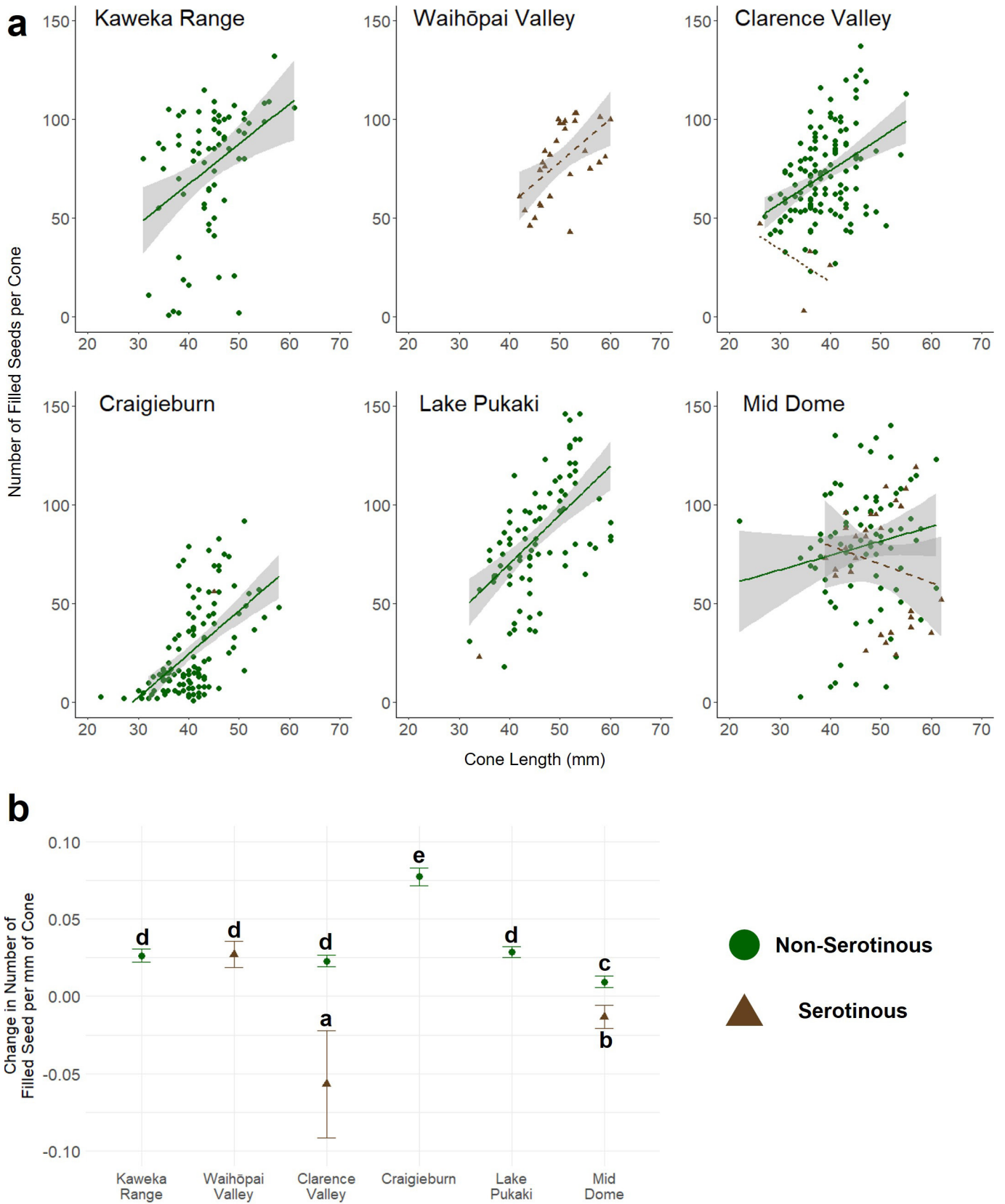


Figure 1. (a) Increasing *Pinus contorta* cone length is associated with an increased number of filled seeds per cone at each of the six assessed sites. Serotinous cones (brown) contained significantly fewer filled seeds than non-serotinous cones (green). (b) Values indicate the predicted change in number of seeds per cone for a 1 mm increase to the average cone length for each site. The estimated change in number of filled seeds per millimetre of cone was greatest for cones from Craigieburn and lowest for serotinous cones from the Clarence Valley. Larger serotinous cones from the Clarence Valley and Mid Dome contained fewer filled seeds than smaller serotinous cones. Error bars show a 95% confidence interval. Note, only serotinous cones were collected from the Waihōpai Valley.

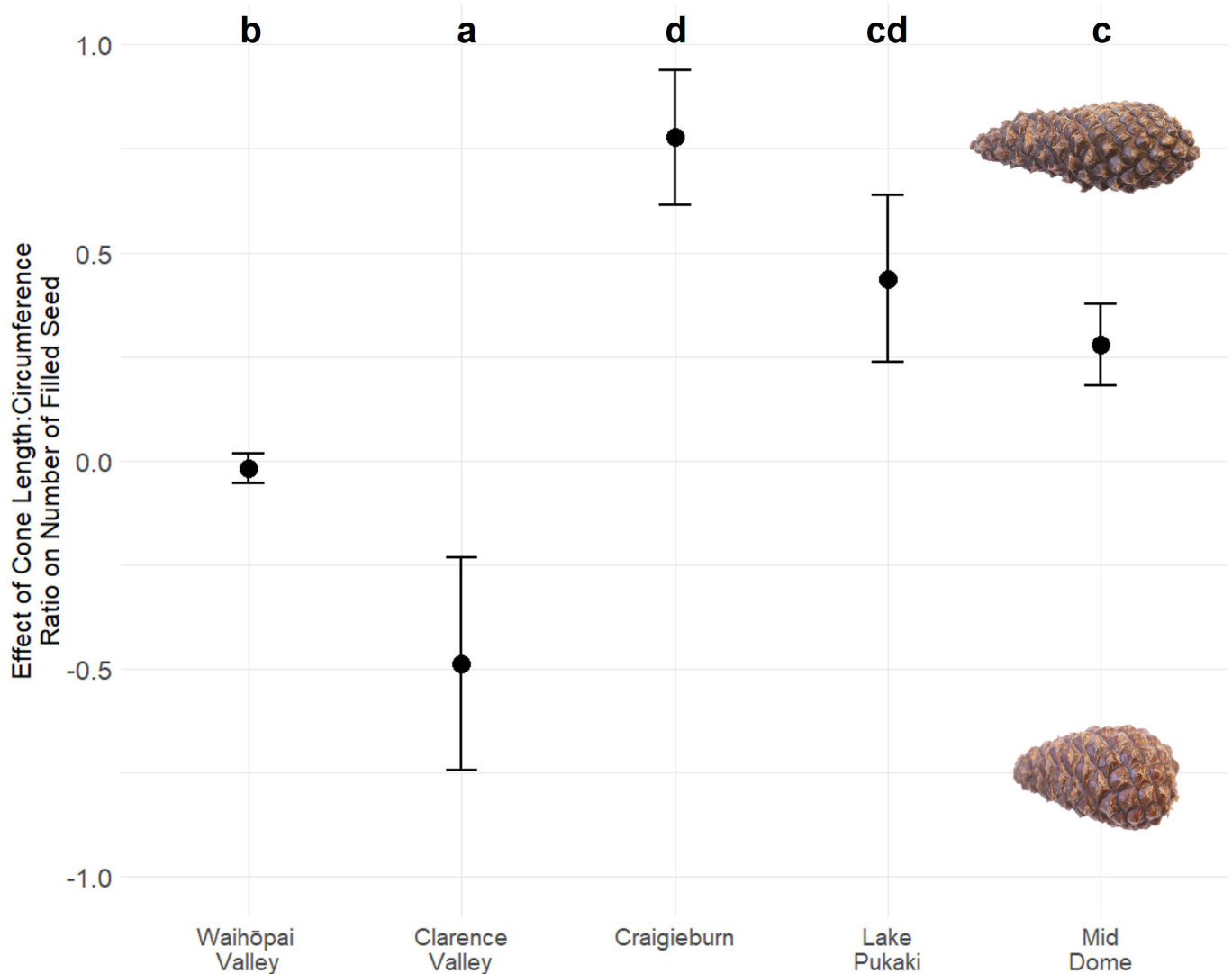


Figure 2. The effect that the cone length:circumference ratio (cone morphotype) has on the number of filled seeds per cone, at each of the six assessed sites. Higher ratio values indicate more filled seeds are found in long, thin cones (inset top right), and conversely, lower ratio values indicate more filled seeds are found in short, fat cones (inset, bottom right). Matching letters above groupings indicate that groups are not significantly different. Error bars show a 95% confidence interval.

further reduced by seed abortion after self-pollination, lack of pollination, seed insects, or other developmental interruptions (Owens 2006). In Aotearoa, we recorded an average of 74 filled seeds per cone, up to a maximum of 146 which is approximately three times that recorded in the native range. This result is also 48% greater than the estimate for Aotearoa provided by Miller (1973), and our estimate of filled seed numbers for the Clarence Valley are 40% greater than data provided by Wyse and Hulme (2020b) from Hamner Springs. We found cones averaged 63 seed scales (excluding sterile basal scales), ranging from 18 to 110. This suggests that the increase in cone seed potential in Aotearoa is due to a greater proportion of fertile seed scales, rather than more seed scales overall. Although we did not explicitly investigate the frequency of fertile vs sterile cone scales, we may estimate that approximately 50–60 scales are fertile per cone in Aotearoa, assuming that some seeds are still lost to mechanisms such as lack of fertilization, abortion after self-fertilisation, and other developmental delays.

If the observed trait shift is driven by an increase in the

proportion of fertile scales, this would help explain why cones from Craigieburn produced a similar number of filled seeds as those from the native range (Table 4). Craigieburn has a long *P. contorta* invasion history (Ledgard & Paul 2008) and has been one of the main focuses of the National Wilding Conifer Control Programme, leading to the removal of almost all adult coning trees from the wider area (National Wilding Conifer Control Programme 2019). As a result, few pollen-producing adults remain, so we would expect cross-pollination at Craigieburn—and consequently viable seed development—to be lower than at other sites. However, it is also possible that the lower number of filled seeds observed at Craigieburn may relate to site-specific conditions or a less successful lineage of hybrids resulting in less fertile offspring.

It is currently unclear whether these trait shifts were driven primarily by one or a combination of factors. Undoubtedly, release from seed predating invertebrates such as *Leptoglossus* spp. will reduce instances of post-fertilization seed abortion (Owens et al. 2005), however this does not account for

potential differences in the proportion of fertile scales. Given that seed predators in the native range impose intense selection pressure to develop cone defences such as thicker scales (Smith 1970; Siepielski & Benkman 2005; Edelaar & Benkman 2006; Parchman et al. 2016), it is reasonable to think that escaping these predators could allow resources to be reallocated into scale fertility. While we did measure the mass of a subset of cone scales (Appendix S7), we could not find comparable information from the native range. Cone circumference, which is similar between the native range and Aotearoa, is a poor proxy for changes in scale thickness due to the divergence of cone morphotypes across Aotearoa (Fig. 2). Hybridisation between sub-species remains a viable hypothesis for the increase in fertility however, is difficult to verify without genetic testing (Hovick & Whitney 2014). On top of this, the favourable growing conditions of Aotearoa (Miller 1971; Shelbourne 1978; Taylor et al. 2016) may be compounding any or all of these potential drivers (Abhilasha & Joshi 2009; Traveset & Richardson 2020).

Unfortunately, it is unclear from these results whether populations across Aotearoa represent distinct subspecies of *P. contorta* or are intraspecific hybrid mixes. Given that subspecies of *P. contorta* will readily hybridise (Critchfield 1957; Koch 1996; Owens 2006), and that introductions of *P. contorta* frequently resulted in the planting of subspecies together at the same sites (Ledgard 1981 unpubl. data; Cooper 1982), it is reasonable to think that self-established wilding conifers could have lost their primary subspecies distinctions through intraspecific hybridisation. Any loss of subspecies distinctions could be exemplified considering that subspecies (e.g. *P. contorta contorta*) express different growth forms in Aotearoa than they do in their native range (Miller & Ecroyd 1987). However, the significant difference in observed fertile cone morphotypes between the Clarence Valley and other sites (Fig. 2) may indicate that a different subspecies (or hybrid mix) is prevalent there compared to the other sites.

Here we have demonstrated that a trait shift in the seed potential of *Pinus contorta* cones has occurred in Aotearoa, increasing the species invasive potential. Although, exact calculations of propagule pressure still require detailed datasets of cone numbers across Aotearoa and must consider the density of the surrounding infestation, Taylor et al. (2016) have already shown that cone numbers are also higher than in the native range. These data provide crucial insights into the potential propagule pressure of *P. contorta* across much of Aotearoa.

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Additional information and declarations

Author contributions: TC, MS, and TP conceived the project. TP obtained the funding. TC, MS, and TP conducted all

fieldwork. TC processed the samples. TC conducted the data analysis and wrote the first draft. All authors contributed to manuscript revisions.

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Data and code availability statement: Upon acceptance, all data presented in this work will be made available at <https://github.com/TomC-93/VLR>

Ethics: All fieldwork and specimen handling was conducted with permissions from the Ministry of Primary Industries under sections 52 and 53 of the Biosecurity Act 1993.

Conflicts of interest: The authors have no conflicts of interest to declare.

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Supplementary Materials

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Differentiating between seeds

Appendix S2. Mean individual seed mass across sites

Appendix S3. Cone length across sites

Appendix S4. Cone circumference across sites

Appendix S5. Cone morphology across sites

Appendix S6. Model output from 43 cone subset

Appendix S7. Seed scale metrics across sites

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