



Research article

Influence of climate and regeneration microsites on *Pinus contorta* invasion into an alpine ecosystem in New Zealand

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Abstract: In many regions, alien conifers have spread widely at lower elevations and are increasingly found colonizing alpine areas. Although studies have addressed conifer invasions at low elevations, little is known about the rates and constraints on spread into higher elevations. Here, we assess the relative importance of climate and the availability of regeneration microsites on the establishment of the alien species *Pinus contorta* into a high elevation site in New Zealand. Spread has occurred from two stands planted at the elevation of the native treeline (1347–1388 masl) in the 1960s. Most stems established between 1350 and 1450 masl and *P. contorta* individuals were found up to 270 m above the original plantings. Although the population has increased by 180% in the last 20 years, population growth rate has been declining. Furthermore, comparisons with studies from other mountain ranges around the world and at low elevations in New Zealand suggest this is a relatively limited spread. Our results suggest that climate variation did not have a significant effect on establishment patterns, as opposed to availability of regeneration microsites. Soil and alpine mat microsites favoured establishment of *P. contorta* and, although these microsites did not appear to be saturated, microsite availability may be an important limiting factor for the spread of *P. contorta*. Thus management strategies should focus on preventing spread in addition to removing already established stems.

Keywords: biological invasions; climate change; dendrochronology; dispersal; forestry; microhabitat; *Pinus contorta*; recruitment; tree line; weed

1. Introduction

Compared to lower elevations, high elevation environments (i.e., alpine zones above the natural treeline) have been considered to be at low risk of plant invasion because of the harsh climatic conditions and lower human population density [1-4]. However, in the last decade, the presence of alien species in alpine zones has been increasingly documented around the world [4-8], and this trend is postulated to reflect greater human impacts at high elevations [4,9]. Together with increasing anthropogenic influence, propagule pressure and disturbance, climate change may further facilitate establishment of alien species in previously unsuitable environments [10-12] by mitigating unfavourable conditions associated with high elevation habitats.

Recent studies suggest that the suite of factors likely to promote range expansion of alien species into high elevation are precisely those that may lead to a steady decline in native species [12,13]. Thus, larger efforts are needed to estimate the risk of invasions into native communities. However, other factors potentially hampering the spread of alien species into alpine zones, such as biotic interactions [14], soil conditions [15] and microsite availability [16,17] may have been overlooked [18]. Therefore, a primary focus of current ecological research is to gain a better understanding of the drivers of invasion in order to develop more targeted management strategies.

As yet, current understanding of the consequences of plant invasion remains limited [19] and this is especially true in alpine zones. In contrast to the many alien herbaceous species that have colonized alpine zones, it might be expected that the establishment of alien trees above the native treeline would result in much more marked changes to ecosystem processes. Examples of alien tree invasions above native treelines are rare, but this phenomenon is increasingly being observed for alien conifer species [20-23]. This situation is relatively common in some regions of the Southern Hemisphere such as New Zealand, where treelines are composed of slow growing tree species such as *Nothofagus* sp. that show little or no upward expansion in response to climate change [24]. Such unresponsiveness to climate warming appears due to the many requirements this species has for successful establishment such as shelter, shade, mycorrhiza and nutrients [25]. The low tolerance of native tree species to the harsher climate found at high elevations results in a low competitive ability against invasive conifers [4,26]. Therefore, introduced conifers, such as pines, that are often pioneers and tolerant to temperature and drought stress as well as disturbance, can colonize high elevation habitats with limited interference from native tree species. This invasion has the potential to alter the structure of local treelines and impact subalpine vegetation.

Of particular concern is lodgepole pine, *Pinus contorta*, which has been widely introduced in several regions of the Southern Hemisphere for wood production, erosion control and forestry purposes [22,23,27,28]. *Pinus contorta* has been shown to have substantial and long lasting impacts in its invaded ranges, as besides reducing the diversity and abundance of native and endangered species [26], it negatively affects soil carbon and water balance, ultimately facilitating the establishment of other alien species at the expense of the local flora [29].

In New Zealand, *P. contorta* was introduced at the beginning of the 1900s and “wilding pines” have since spread across the lowlands covering approximately 150,000 ha by 2001 [30,31]. Multiple introductions exacerbated the invasion process, but provided evidence of the effect of propagule pressure on its spread [32]. Although numerous studies have addressed the invasion of *P. contorta* at low elevation, similar studies in alpine areas are limited. Thus, recent reports have raised concerns about the risks of spread into alpine areas [33], where *P. contorta* can recruit above the treeline,

located at 1350 masl, in the absence of competition from other trees [23,34]. Although it has been reported that the species can grow well at elevations up to 1600 masl [23], to our knowledge no study has quantified the rate of spread of *P. contorta* into high elevations. In the present study, we examined the spread of *P. contorta* from planted stands at one of the few alpine sites in the South Island of New Zealand where planting history and propagule pressure are known. We asked the following questions:

1. How rapid is the spread of *P. contorta* into alpine areas and is it comparable to rates observed in the lowlands?
2. Does climate variation influence recruitment and, if so, which variables are most important?
3. Is the availability of suitable regeneration microsites an important factor limiting the establishment of *P. contorta* in alpine areas?

Using the answers to these questions we explore the potential for further *P. contorta* invasion and discuss possible management options.

2. Materials and Method

2.1. Study site

The study site was located on a steep, highly eroded east-facing slope in the Craigieburn Range, South Island, New Zealand (43°10' S; 172°45' E). The native treeline-forming species (*Nothofagus solandri* var. *cliffortiodes* (Hook. f) Poole) gives way quickly to rocky scree fields, shrub and tussock grasslands above 1370 m [24,25]. As part of a series of forestry trials, two stands of *P. contorta* spp. *contorta* were planted above the *Nothofagus* treeline to examine the elevation limits of commercial forestry. The two stands, approximately 300 m apart, were planted for research purposes in 1962 (24 individuals; 1347 masl) and 1964 (multispecies trial planting including *Pinus contorta*, *Pinus ponderosa* and *Pinus mugo*, with a total of 40 individuals; 1388 masl) [25]. These two stands unintentionally provided an opportunity to assess the degree to which *P. contorta* could establish above the native treeline under conditions of relatively high propagule pressure.

2.2. Study species

Pinus contorta Dougl. ex. Loud., is native to the northwestern region of North America and Canada [35,36], and was initially planted in New Zealand for forestry purposes [8] and erosion control in mountain lands [23]. The species can begin reproducing after as little as five years [37]. Most cones mature within 12 months [38] and, in New Zealand, are non-serotinous [30]. Seeds are released shortly after maturation [39] in early autumn (March in New Zealand) or before the following growing season, generally beginning in October or November [40] when wind speed tends to be greatest [41]. Seeds of *P. contorta* are smaller than those of most pines [32], weighing approximately 4 mg [42], they are winged [43,44] and can be dispersed by wind up to 40 kilometers [30,37]. The species is shade intolerant [43,44] and previous studies showed that water holding capacity and soil moisture have a critical influence on the germination and early survival of *P. contorta* in its native range [45,46].

2.3. Field sampling

To assess establishment patterns of *P. contorta* into alpine zones, we established in February 2009 four sampling blocks running upslope starting at 1350 masl up to the maximum elevation reached by *P. contorta* (see Supporting Information for scheme of the sampling blocks—Figure S1). The maximum elevation was determined after a thorough search for individuals from the edge of the two planted stands to the ridgeline (1790 masl). Sampling blocks were situated between 10 and 150 m from the closest planted stand, and the maximum distance between sampling blocks was 120 m. Within each sampling block, we established at least five transect belts 50 m long and 2 m wide, with a total of 75 transect belts. Each transect belt ran parallel to the edge of the planted stands at intervals of 12.5 linear m, starting at 1350 m asl and ending at the maximum elevation reached by the species. Five transects were also laid within the planted stands to quantify these populations. The position of each transect belt was determined using a handheld eTrex GPS unit.

We identified and measured all *P. contorta* stems rooted within each transect. For each stem, we recorded the distance along the transect, stem height, basal diameter, presence of cones, tree class and age estimate. We categorized individuals in four tree classes according to their height and diameter: seedlings (basal diameter < 0.5 cm), saplings (0.5 < basal diameter < 4 cm), sub-adults (4 < basal diameter ≤ 10 cm) and adults (basal diameter > 10 cm). We used two methods to estimate stem age and year of recruitment, we counted internodes [47] for stems with diameters less than 3 cm, and counted the number of rings from increment cores or cross-sectional disks for stems with diameters greater than 3 cm. We cored stems or took disks by sawing stems at 20 cm above the ground because of the difficulty of coring stems at the root collar. We processed cores and disks according to the methods of Stokes and Smiley [48], and subsequently estimated the age by counting the rings with a binocular microscope, correcting for missing rings following Duncan [49]. It is well recognised that age estimates taken from above the root collar will underestimate age since establishment, because of the time taken for stems to grow to coring height [50,51]. To correct for this, we fitted a log-log regression between age and height for those individuals whose age was estimated by counting internodes. This allowed us to estimate the time taken to grow to coring height (on average, 4 years to reach 20 cm height) and so we added 4 years to the ages of the cored and sawed samples to estimate age since establishment (Figure 1).

Microsite occupancy and availability were also assessed along each transect. We determined the microsite into which each *P. contorta* stem had established by characterizing the area around each stem into six classes (Supporting information—Figure S2): rock outcrop, scree, bare soil, alpine mat (mainly composed of short-statured plants and bryophytes), tussock grassland, and shrubs (*Dracophyllum* sp., *Podocarpus nivalis* and *Aciphylla* sp.). Thus we used substrate characteristics as a proxy for the environmental conditions in which *P. contorta* individuals were growing. Microsite availability along each transect was estimated using a point intercept method, where the microsite was recorded at 1m intervals along the center of each transect (i.e., 50 samples per transect).

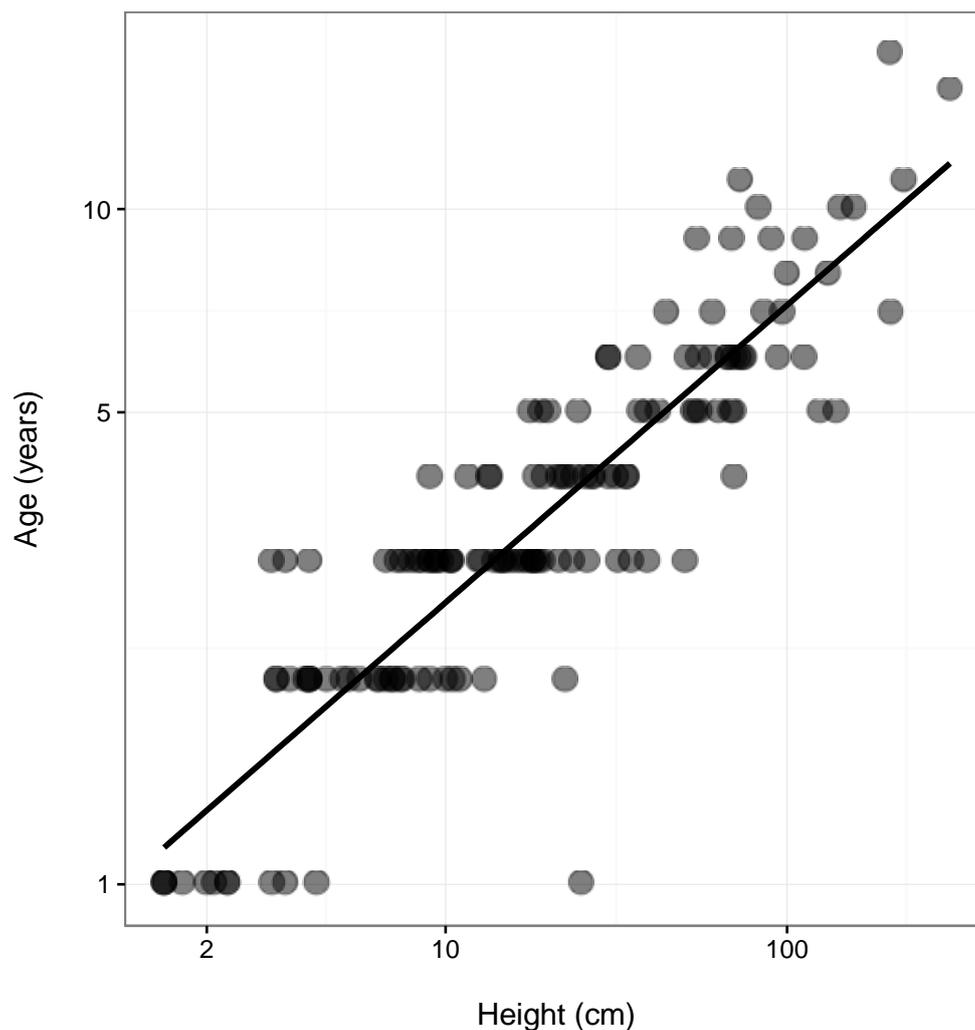


Figure 1. Regression between *P. contorta* height and age estimated by counting internodes. The regression line was used to estimate mean age at coring height (20 cm) to correct age estimates derived from cores and sections.

2.4. Climate data

Climate data were available from a meteorological station located at 914 masl, 4.2 km from the study area. Monthly temperatures (mean, minimum, maximum) and precipitation were downloaded for the period 1964–2008 (<http://cliflo.niwa.co.nz/>). We then calculated the annual average temperature and total precipitation for the austral growing (November through April) and dormant (May through October) seasons for each year.

2.5. Statistical analyses

Our data consist of the estimated age structure of *P. contorta* and the elevation and microsite in which trees were found. We used regression analyses to relate elevation (i.e., distance from the planted stands) to the number of recruits. To investigate population increase of *P. contorta* and

predict its invasion potential, we applied non-linear regressions to population size overtime by fitting two different models that assumed exponential or logistic growth, and compared the fit of these models to the data using AIC. The best model was then used to estimate the rate of population increase when rare (r) and the carrying capacity (K) of the sampled transects. These models assume a smooth rate of increase over time driven by constant values for r and K , but deviations from this average population growth curve will occur if the recruitment rate was lower (if below the curve) or higher (if above the curve) than expected in a given year. Such deviations could be driven by climate variation, with higher rates of recruitment in climatically favourable years and lower rates in less climatically favourable years. To test whether variation in climate could explain deviations in yearly recruitment away from the average population growth curve, we correlated the residuals around the growth curve with seasonal rainfall and temperature data. Furthermore, to allow for potential inaccuracies in our age estimates, we grouped individuals into age intervals of two and four years respectively, to allow for a dating imprecision of ± 1 or ± 2 years, and repeated the analysis.

To compare the microsites occupied by *P. contorta* stems with microsite availability, we first calculated availability as the percentage of all point intercepts classed as each microsite class. We then calculated occupancy as the percentage of microsites occupied by pines within each microsite class. Microsite preference was assessed as the ratio between occupancy and availability [52]. A ratio < 1 indicates that the microsite is occupied by *P. contorta* less than it would be expected given its availability, a ratio = 1 indicates that the microsite is occupied in proportion to its availability, and a ratio > 1 indicates a microsite occupied more often than would be expected given its availability. Significance was evaluated using chi-square tests. All statistical analyses were conducted using the statistical software R 3.1.2 [53].

3. Results

3.1. Demography

In total, 242 *P. contorta* individuals were sampled, with similar numbers of seedlings, (83) saplings (73), and subadults together with adults (86), with over half of the latter being reproductive (56). In total, we found 4 dead individuals, only one of which was found above the planted stands. Nearly one third of all stems (70) occurred within 10 m of the closest planted stand. The remaining individuals occurred up to 435 m linearly from these sources, across an altitudinal range of 272 m, and no stems were found above 1623 masl. Overall, we estimated a density of 290 trees/ha. Reproductive stems were observed up to 1601 masl and none of the individuals bearing cones were less than 12 years old. The majority of seedlings (93%) occurred within 10 m of a reproductive stem, but no seedlings were found above 1450 masl, indicating a lack of recent establishment, even though reproduction occurred above this elevation. We did not find evidence of establishment beyond the planted stands until 1987 (Figure 2, 3), over twenty years after the original planting date. Since the late 1980s, establishment has occurred annually up to 1450 masl, whereas above 1450 masl it has been episodic, primarily occurring since the 1990s (Figure 2).

Based on the spatial and temporal patterns of establishment, and the different distribution of tree classes across the elevation range, we divided our sample into two bands: a mid-elevation band (1349–1450 masl) composed of 219 individuals and a high-elevation band (1451–1623 masl) composed of 23 individuals, none of which were seedlings. For the 5 transects measured along the

edge of the planted stands, we recorded 156 individuals, with the oldest individual having established by at least 1960. Our age estimates suggest that approximately 25% of these individuals established between 1960 and 1987. Of these stems 18 individuals (12%) established between 1965 and 1987. Seedlings (55/156) and saplings (55/156) both accounted for 35% of stems, and adults and subadults together accounted for 30% of stems.

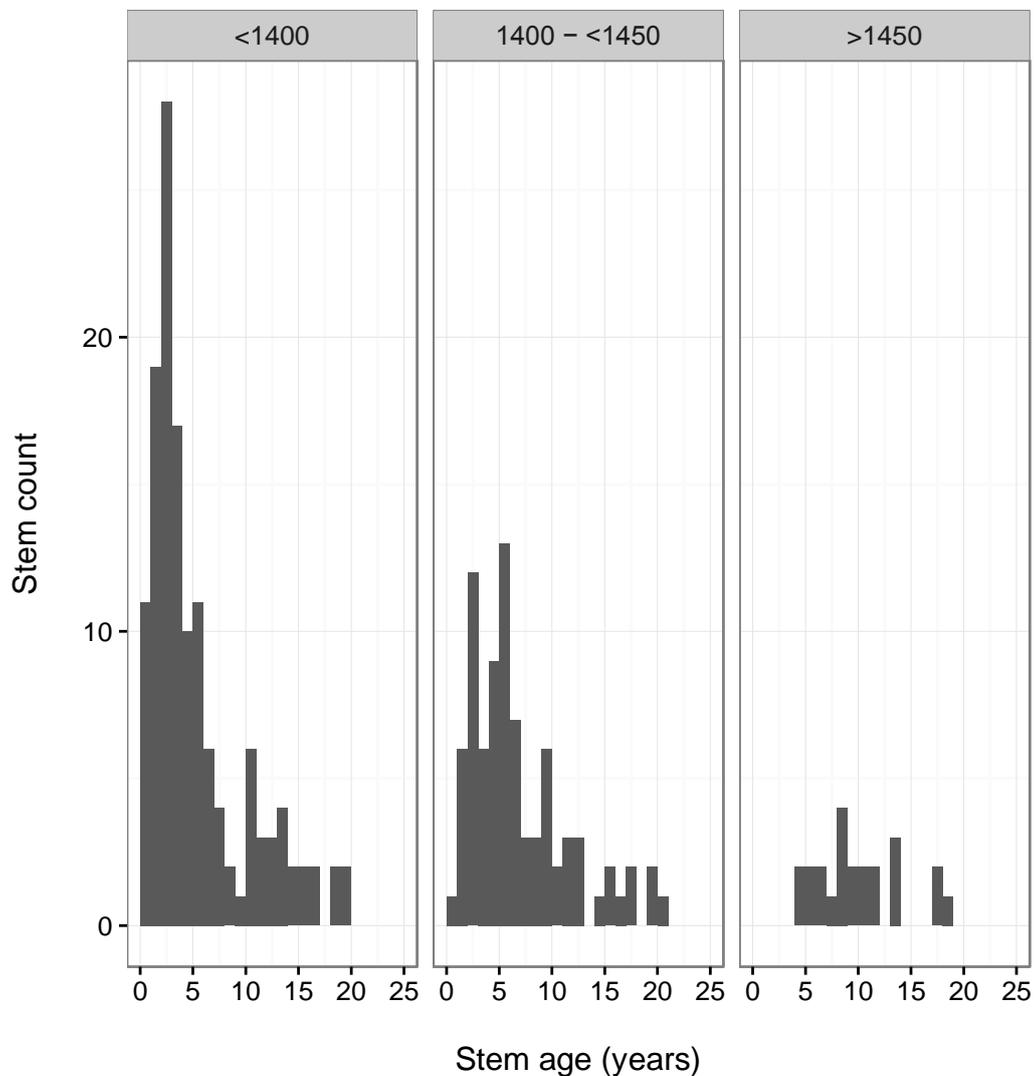


Figure 2. Number of stems by age class in three elevation bands (<1400 masl, 1400–1450 masl, >1450 masl). Since the late 1980s establishment has occurred in each year at elevations up to 1450 masl, whereas above 1450 masl establishment has been episodic and occurred mainly since 1990.

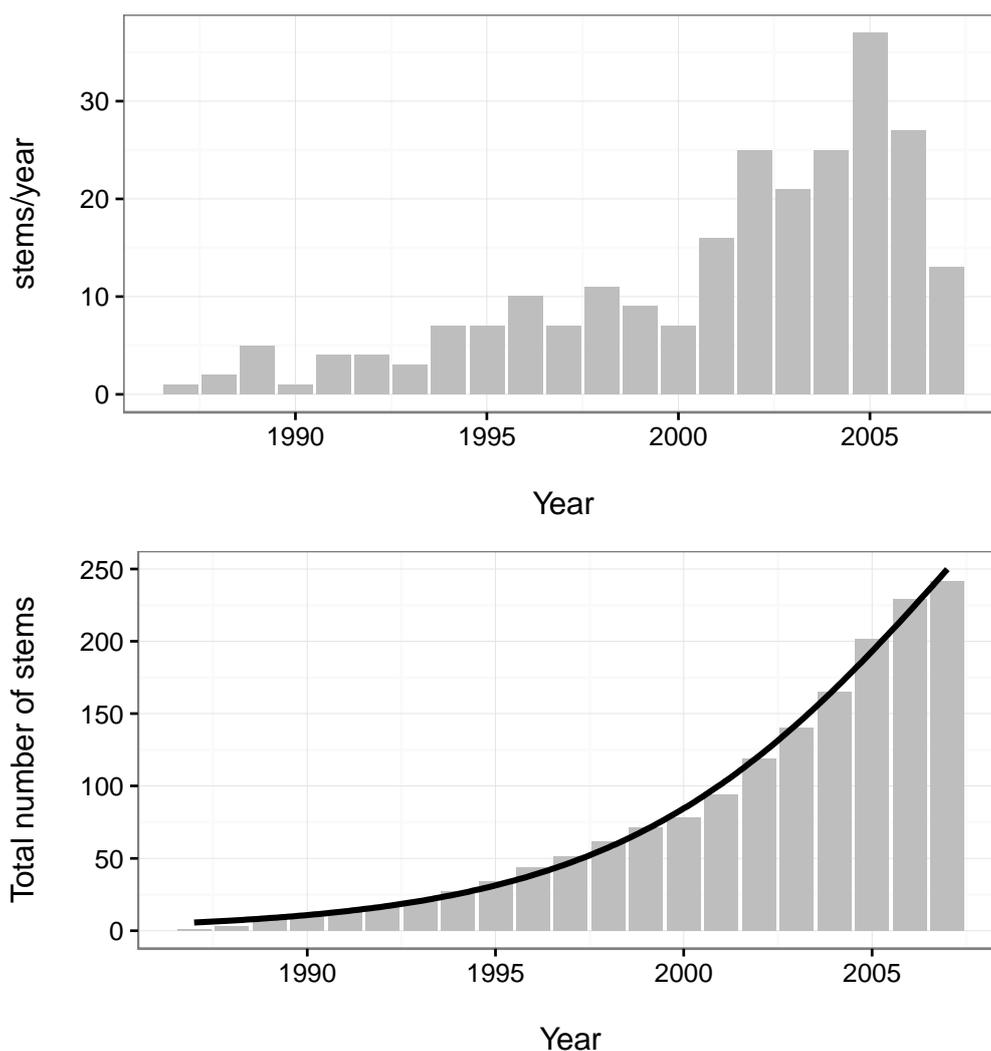


Figure 3. Upper figure: number of stems established beyond the planted stands in each year; lower figure: cumulative number of stems established beyond the planted stands with a fitted logistic growth curve.

3.2. Establishment patterns, climate and microhabitat

The number of *P. contorta* stems recorded on each transect declined with elevation ($R^2 = -0.0247$, $F = 18.84$, $df = 239$, p -value < 0.05). The logistic model (AIC = 131.2) was chosen over the exponential (AIC = 148.2) as the best descriptor of population growth (Figure 3), showing that the cumulative number of individuals increased through time, but that the rate of population growth was slowing. The rate of population growth when rare (r) was estimated as 0.22, and the population carrying capacity on the sampled transects (K) as 529. We did not find any significant correlations between climate variables and deviation in recruitment from the average growth curve (Supporting Information—Table S1, Figure S3). These results were unchanged when individuals were grouped into age-classes of two- and four-year intervals (Supporting Information—Table S1, Figure S4, S5). The prevailing wind direction during the period of seed release since the plantations were established was SE to SW, which was downhill.

The most common available microsites below 1450 masl were scree (51.2%), rock (17.3%), and shrub (11.9%), while above this elevation scree was dominant (78%). However, occupancy by *P. contorta* was highest in bare soil (76.6%) and alpine mat (48.4%) (Table 1, see Supporting Information—Table S2), which were the preferred habitats for establishment (Figure 4), and in which individuals occurred more than expected based on availability (chi-square: 1116.293, df = 5, p -value < 0.05). This preference was consistent across life stages (Table 1).

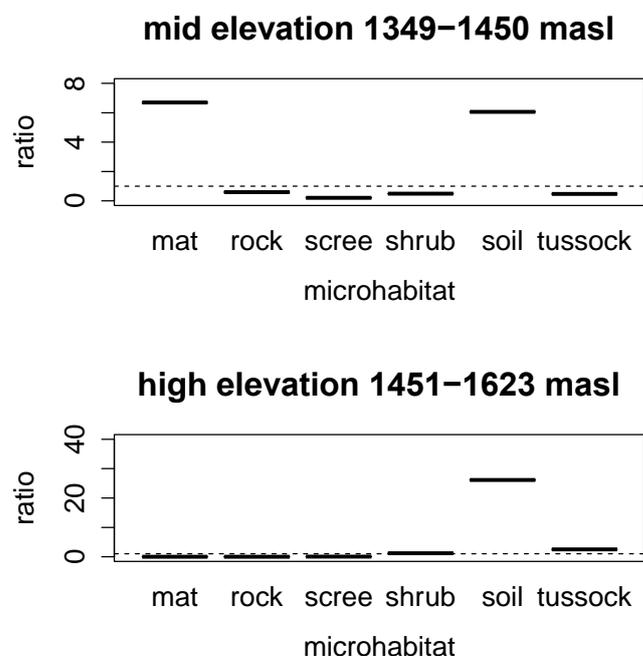


Figure 4. Microsite preference calculated as ratio of microsite occupancy to availability within each microsite class at mid- (1349–1451 masl) and high- (1451–1623 masl) elevation bands (thick lines). Dashed lines show the threshold value of ratio = 1. Values of the ratio above 1 indicate preference for a certain microsite class, in that occupancy is higher than would be expected according to availability.

Table 1. Number of individuals observed within each microsite class according to tree class (adults, subadults, saplings, seedlings) and results of Chi-square tests showing significant differences in occupancy across microsite classes.

Microsite	Adults	Subadults	Saplings	Seedlings
Mat	6	10	27	19
Rock	3	4	6	5
Scree	1	3	3	3
Shrub	2	4	7	2
Soil	25	27	25	54
Tussock	1	0	5	0
Chi-square	$\chi^2 = 68.73$ df = 5 $p < 0.001$	$\chi^2 = 60.75$ df = 5 $p < 0.001$	$\chi^2 = 48.06$ df = 5 $p < 0.001$	$\chi^2 = 156.63$ df = 5 $p < 0.001$

4. Discussion

Pinus contorta has invaded alpine areas in the Craigieburn Range in New Zealand, but at a slower rate compared to lowland invasions. Variation in climate did not account for annual fluctuations in recruitment around the overall population growth curve, whereas the availability of favourable regeneration microsites greatly affected species establishment. The limited availability of favourable regeneration microsites, together with the decline in population growth rate over time, suggest that the population of *P. contorta* at the Craigieburn range may be approaching saturation. However, given the high colonizing ability of the species, constant monitoring and implementation of management strategies are highly desirable.

4.1. Demography of invasion

The naturally regenerating *P. contorta* population above the planted stands has reached a density of approximately 300 trees/ha; a value at the lower limits of observations of *P. contorta* density in the Andes at 1420 masl [8,26]. Similarly, the population density and rate of population increase at low elevation sites in New Zealand is substantially higher than above the treeline. Ledgard and Paul [47] estimated that *P. contorta* density at 850 masl increased by almost 70 times (i.e., from 500 trees/ha to 34,550 trees/ha) in 10 years, whereas during the same period, the population at Craigieburn increased by approximately 25 times. Furthermore, a recent study estimated the density of a *P. contorta* population in New Zealand located between 785 and 1040 masl [54] to be 24,700 trees/ha, which is 85 times higher than the density estimated from our survey.

The increase in population size over time at Craigieburn is consistent with the high invasive potential of *P. contorta* [55] which is mirrored in the native range where the species is encroaching into meadows with negative effects on plant diversity [56]. In both the native and introduced range the species exhibits a wide tolerance for climate extremes [30,57]. However population growth at the Craigieburn Range may be inflated if it is primarily driven by recruitment of a large number of young stems, which then suffer high mortality. Although we did not monitor mortality, we recorded the presence of dead stems, finding only four dead individuals, three of which were within the planted stands, suggesting relatively low mortality rates of established stems. Our model suggests that *P. contorta* invasion into high elevations is unlikely to reach densities observed at lower elevations in New Zealand or in the Andes [8,26]. The current population appears to have reached more than half of the maximum number of individuals that can be supported at the study site, as evidenced by the estimated carrying capacity ($K = 529$). Such a trend is not entirely novel as decreasing density due to competition for limited microsites have been observed previously in New Zealand [47].

At the Craigieburn Range, a temporal lag in establishment is evident. Establishment above the planted stands only commenced in approximately 1987, almost 20 years after planting. Temporal lags in the spread of alien species after their introduction have been observed for pine species [4,58] and may reflect specific life history traits or changes over time in climatic and habitat conditions that assist spread [59]. A similarly low rate of establishment between 1975 and 1987 was observed at the edge of the planted stands, suggesting that the reason for this temporal lag may be at least in part due to unfavourable environmental conditions. In New Zealand, seeds of *P. contorta* are known to be dispersed over distances up to 40 km [27,30], however in our survey we found that the first

individuals to establish were located within about 0.1 km beyond the planted stands in bare soil. Remarkably, this is in contrast with a recent study showing that dispersal ability is a dominant factor at the early stages of a *P. contorta* invasion [60]. Furthermore, previous studies indicated that *P. contorta* produce cones as early as at 5 years [37], whereas we found no coning individuals younger than at least 12 years old. Thus both reproduction and establishment appear strongly constrained at these elevations.

Climate, although a critical factor affecting spread of numerous treeline species [61], was not a significant factor accounting for variation in the rate of population increase of *P. contorta* at our site (Supporting Information—Figure S3). The population has increased relatively steadily over time, suggesting relatively constant conditions for establishment (Figure 3). This suggests *P. contorta* recruitment is not tightly linked to climatic variation, which is consistent with the wide environmental tolerance of the species [62].

When looking at microsites, *P. contorta* stems were found mostly in bare soil and alpine mats, despite the relatively low availability of these two microsites classes (Table 1, Figure 4). Bare soil and alpine mats retain humidity that is beneficial for seedling survival [27], whereas tussock and shrubs may result in stronger competition for water and light especially during the early life stages [26,39,43]. Conversely, on rocky outcrops and scree, seedlings are exposed to harsh conditions and water run-off rapidly causes drought stress. *Pinus contorta* seedlings and saplings have shallow roots that penetrate soil only up to a depth of 10–15 cm, thus the species is highly susceptible to drought [35,36,45]. This effect may be especially relevant in high elevation habitats where steep slopes and shallow soil do not provide high water retention.

At our study site, the spread of *P. contorta* appears to be limited by source effects (i.e. higher establishment occurring close to the planted stands), longer time to reproduction and availability of microsites with higher potential water availability. Limited availability of favourable microsites may likely hinder successful establishment of seedlings, causing death during early life stages and curbing population growth rates.

4.2. Management implications

There is growing consensus among management and conservation experts that preventing recruitment of *P. contorta* (and in general alien conifers) should be emphasized over removing existing stands [33]. The focus on prevention is not only motivated by the elevated cost of removal of wilding conifers, but also by the fact that alien conifers, *P. contorta* among them, permanently offset soil abiotic and biotic properties preventing the recolonization of native species. Studies have shown that alien pines lead to soil acidification and to a reduction of exchangeable nutrients [63,64]. Furthermore, alien pines have been associated with a reduction of mycorrhizal species diversity compared to that found in *Nothofagus* forests [29,65]. Research by Paul & Ledgard [66] also showed that dead pine stands can have deleterious effects on the local vegetation as they favour the invasion of exotic grasses over native species [21,29].

In such a framework, our results fill a knowledge gap, as most of the data used by conservation strategists come from studies conducted at low elevation. Consistent with other studies [4,26], we show that the establishment of *P. contorta* into high elevation, although less dramatic than at lower elevations, remains a potentially large problem, as at high elevation there are no native species that can effectively outcompete and replace it.

Although considerable effort has been invested in eradicating *P. contorta* the species is still widespread in New Zealand. As highlighted by our results and by previous findings [67], not all microsites are favourable to the establishment of *P. contorta*. Thus, one step would be to increase the cover of native species such as tussock and shrubs where the survival of seedlings is hindered by shading and competition. This could be implemented by ameliorating grasslands through addition of fertilizer [31], which would increase their competitive ability against seedlings in the early life stages [68]. In addition, consistent with previous research [2], we recommend special attention should be paid to the removal of juvenile *P. contorta* in alpine areas, before individuals start coning, a practice that will prevent further spread at a lower economic and ecological cost compared to the removal of reproductive individuals. The unique setting of our study site, namely known initial propagule pressure and date of planting, was also its main limitation, as we could not extend our survey to other sites. Therefore, we have to be cautious in generalizing our results, and further studies should be carried out to validate the feasibility of our recommendations. Finally, our results suggest a physiological limit to expansion that will likely transfer to other sites; principally the availability of suitable microsites that limit population growth and spread. Regardless, colonization above the treeline should not be underestimated as, due to the lack of competitors, *P. contorta* cannot be replaced by native species at later successional stages [33,69] and should be closely monitored.

5. Conclusion

Our study found that *Pinus contorta* has been spreading into high elevation subsequent to plantings established in the 1960s at the Craigieburn Range. The establishment pattern is mainly constrained by limited availability of favourable microsites, whereas climate variation had surprisingly little effect on the rate of population growth. Our findings suggest that *P. contorta* may be approaching saturation of favourable microsites and thus it may not represent an immediate threat to high elevation native species. However, considering the potential for long distance dispersal and pioneer ability of this species, we recommend that studies examine in more detail the patterns of establishment in different mountain areas of New Zealand. Furthermore, constant monitoring of such populations is desirable to allow for early detection and removal of seedlings.

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Conflict of interest

We declare that we do not have any conflicts of interest.

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