Pollen thieves: Reproductive interference in Australian alpine angiosperm communities by invasive *Taraxacum officinale*

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Abstract

Flowering plants must compete with their peers to attract and reward animal pollinators in order to maximise the amount of conspecific pollen transferred to their ovules, and thus the number of their future offspring. When a flowering plant is introduced into a stable community, it can cause reproductive interference by limiting the amount of conspecific pollen received by native plants, leading to potential shifts in native plant abundance and diversity. We conducted a flowering plant transect and pollen analysis on pollinators sampled from flowers in the Australian Snowy Mountains, and found that invasive *Taraxacum officinale* (L.) Weber ex F.H. Wigg may potentially be limiting pollen transferred to native species by competing for pollinators and creating a pollen cross-contamination risk. *T. officinale* pollen was found on 31% of pollinators carrying native pollen, and on a further 12% of pollinators exclusively. It was particularly attractive to the Coleoptera sampled, 75% of which were found to be carrying *T. officinale* pollen, putting native plants that rely on the order's services at risk of pollen limitation. Furthermore, *T. officinale* produced proportionally more florets than any other native or invasive plant species across four transects. With climate change likely to boost abundance of the already ubiquitous weed, more research into the scale of its impact on the vulnerable Australian alpine flora communities is needed.

Key Words: pollen limitation, reproductive interference, competitive exclusion

Introduction

Flowering plants that rely on animal pollinators must attract and reward their visitors to ensure that visits are frequent, and long enough for pollination to occur at rates required to sustain successful reproduction (Fishman and Hadany 2015). When the plant–pollinator relationship is nonspecific, plants face great pressure to compete for pollinators, who typically visit more than one species of flower to meet their energy and nutritional needs (Fishman and Hadany 2015).

Competition for pollinators can result in the reproductive interference of a flowering plant species by one or more competing plant species (Nishida *et al.* 2014). When reproductive interference reduces a species' abundance by reducing its number of offspring, a positive feedback of competitive exclusion is created (Nishida *et al.* 2014): fewer offspring means the species' pollen comprises less of the pollinators' pollen load, leading to even fewer offspring in the following generation. Dwindling population sizes may lead to reduced fitness via inbreeding depression (Reed 2005; Phillips *et al.* 2014), although the association between inbreeding depression and extinction risk in plants is not well understood (Reed 2005).

In flowering plants, competition for pollinators can result in reproductive interference through pollen limitation (Miller *et al.* 2018), which can occur in two ways: via reduced pollinator visits/length of visits to the flowers of a particular species, or via pollen cross-contamination, whereby foreign pollen blocks the stigma of a flower from conspecific pollen by growing a pollen tube into its pistil (Miller *et al.* 2018; Nishida *et al.* 2014). Pollen cross-contamination can have a significant impact on seed set (the percentage of seeds in a flower that eventually germinate) (Matsumoto *et al.* 2010), and thus future species abundance. It should be noted that the latter experiment involved pollen cross-contamination between species of the same genus; it is possible that pollen cross-contamination between more distantly related species could be hindered by larger anatomical differences between the pollen tubes of one species and the carpels of another. This is supported by the work of Arceo-Gómez and Ashman (2016), who found that pollen cross-contamination between closely related species had a larger effect than that between less closely related species. In the Australian Alps, this would suggest that *T. officinale* potentially poses a larger pollen cross-contamination risk to other members of the Asteraceae family. Nishida *et al.* (2014) suggested that some flowering plant species may be capable of recognising and rejecting foreign pollen, but this is not yet supported by the literature. Arceo-Gómez *et al.* (2016) found that tolerance to heterospecific pollen cross-contamination came about due to changes to the pollen, rather than carpel, of the receiving flower.

When an introduced species causes reproductive interference, it has the potential to competitively exclude existing species in a plant community, potentially reducing the community's diversity. If the invader is more attractive or can offer a higher energetic or nutritional reward to pollinators, it has the potential to 'change the allegiance' of pollinators (Fishman and Hadany 2015), which could lead to decreased visitation rates and durations as well as an increased incidence of pollen cross-contamination for native plants. Although pollen cross-contamination is a common feature of life in flowering plant communities, detrimental effects on reproductive fitness are higher when the heterospecific pollen comes from an invasive plant than a fellow native plant (Arceo-Gómez and Ashman 2016).

The ubiquitous weed *Taraxacum officinale* (dandelion) has been introduced to the sensitive plant communities of the Australian alpine region, perhaps via seeds carried on vehicles and shoes (McDougall *et al.* 2005). Normally found in the vicinity of human habitation and activity, *T. officinale* is not listed among the weeds that pose a major or moderate threat to the national park areas (Johnston and Pickering 2015). However, an analysis of 1,400 quadrats from studies conducted between 1980 and 2005 suggests that *T. officinale* is one of only six invasive plants that were found in over 5% of the quadrats (being found in 9% of the quadrats) (McDougall *et al.* 2005). It is important to know whether *T. officinale* negatively impacts native flowering plant abundance and diversity via reproductive interference (specifically pollen limitation) as these possible impacts will be compounded by climate change, which is expected to increase the abundance and expand the distribution of invasive plants in the Australian Alps (McDougall *et al.* 2005; Scherrer and Pickering 2001) and the low level of specific plant-pollinator relationships at higher altitudes (Arroyo *et al.* 1982; Inouye and Pyke 1988). This lack of specialisation may heighten native alpine plants' vulnerability to competitive exclusion by generalist invasive plants. Increased abundance of *T. officinale* has already been correlated with an increase in pollen cross-contamination on native dandelions (*Taraxacum japonicum*) in Japan, resulting in competitive exclusion (Matsumoto *et al.* 2010). If *T. officinale* is found to pose a threat of similar magnitude to the native flowering plant communities of the Australian Alps, weed control measures could be introduced to mitigate the risk to native plant abundance.

We hypothesised that *T. officinale* is reducing pollinator visits to native Australian alpine flowering plants and increasing the risk of native flower pollen cross-contamination. We recorded the abundance of individual *T. officinale* plants and estimated the number of *T. officinale* florets in our transects, and then recorded the presence or absence of *T. officinale* pollen on the bodies of pollinators sampled from the flowers of Australian native alpine plants in a nearby area. The abundance, flower count and presence/absence of pollen on pollinators of the other major weed found in the area, *Trifolium* spp. (clover) was also recorded, and its potential role in pollen limitation compared to that of *T. officinale*.

Methods

Overview

We used data obtained from transects and a pollinator-pollen analysis to compare native flowering plant and invasive *T. officinale* and *Trifolium* spp. individual abundance, flower/floret abundance, and the proportion of pollinators carrying the pollen of a particular species. This enabled us to make inferences about the 'attractiveness' of *T. officinale* to pollinators relative to native flowering plants and the other major invasive species.

Location

Experiments were conducted in Perisher Valley, Australia, in an area of open heath adjacent to ski lodges and roads (-36.411°S, 148.406°E; elevation: 1,780 m a.s.l.). The native vegetation mostly comprised shrubs (*Grevillea australis, Hovea montana, Nematolepis ovatifolia, Olearia phlogopappa, Pimelea alpina*), with a smaller incidence of herbaceous flowering species (*Cardamine* spp. and *Ranunculus* spp.).

Date and weather conditions

We collected flower and pollinator samples between 9:09 am and 12:17 pm on 10–12 December 2018, and marked out transects between approximately 9 am and 11 am on 12 December 2018. Observationally speaking, weather was consistent over the three days, with light cloud cover. Using Kestrel weather meters, we recorded temperatures of approximately 18–21°C and wind speeds of approximately 0.3–2 km/h on the morning of 12 December.

Pollinator and flower collection

Pollinators were collected freely (without transects) and opportunistically (without a preference for a particular flower species or pollinator order) on site. We spaced ourselves randomly throughout the target area in an effort to minimise collection overlap. We caught pollinators in nets when they landed on a flower, swiftly transferring them into sterile, lidded plastic vials, and labelling the vials with identification codes. We recorded the flower species each pollinator was caught on.

We collected multiple cut flower heads representative of all the flower species observed in the area and swiftly placed them in separate plastic 'zip-lock' bags to prevent pollen cross-contamination in transit. Unknown species were identified, at least to genus level, using 'Kosciusko Alpine Flora' (Costin *et al.* 1979).

Pollen identification and count

We placed pollinators into a commercial freezer at -9°C for approximately one hour to euthanise them.

To make reference specimens for pollen identification, we observed the cut flower heads under a Kyowa Optical SD-2PL dissecting microscope to determine if pollen was present on their anthers.

Using a razor, we cut an approximately 2 mm^2 cube out of glycerine jelly imbued with pink dye (Wooller *et al.* 1983), picked up the cube with ethanol-rinsed, paper towel-dried tweezers, and dabbed it over the anthers of the flower. We then placed the cube of gel on a clean microscope slide, placed a cover slip over it, and melted it by holding a lit cigarette lighter beneath the slide for several seconds. The slide was labelled with the species of the flower the cube had been used to dab. We repeated the process for every flower species we collected, rinsing and drying the tweezers between samples.

We viewed the prepared slides under an Olympus Industrial and Scientific compound microscope at 400x total magnification and used our observations to create a pollen-species identification chart.

We repeated the pollen swabbing treatment on our pollinators, dabbing their entire bodies thoroughly with cubes of pink glycerine, and labelled the resulting slides with the pollinators' ID codes. We observed the pollinator slides as above, and recorded all pollen species on the slides with the aid of the identification chart. We did not directly count or estimate the quantity of the pollen grains found on each pollinator.

Finally, we recorded pollinators' scientific orders and attempted to identify them more narrowly using 'Field Guide to Wildlife of the Australian Snow-Country' (Green and Osborne 1994).

Transects

We marked out four 2 m wide, 50 m long transects, approximately 50 metres apart, with a measuring tape. Transect sites and angles were selected to encompass the range of vegetation in the area.

The flowering plant species name, number of plants currently or recently flowering (i.e. those with flowerheads that lacked petals and/or appeared desiccated), and number of flowers or, in composite flower species, florets, which are flowers in their own right (Elomaa *et al.* 2018), were recorded along each transect. For *T. officinale*, we used an estimate of 250 florets per head (Ianovici 2016), and for *Trifolium* spp. (clover) 150 florets per head (Lane *et al.* 2000). Native composite flower florets were large enough to be counted individually in three flower heads and then averaged for each particular species.

Data analysis

Plant incidence, flower/floret count, pollen load on pollinators in total and by taxonomic order, and the percentage of pollinators found to be carrying *T. officinale* for each native flower that they were collected from (visiting) were calculated and graphed in Microsoft Excel.

Results

Transects

Seventy-six individual plants in flower or recently in flower, comprising 12 different species, were found across the four transects. Of the 12 species, 10 were native to the region, and two were introduced: *T. officinale* and *Trifolium* spp. (clover). Twenty-two *T. officinale* plants (29% of the total number of plants), five *Trifolium* spp. (7%), and 49 native flowering plants (64%) were recorded (Figure 1). Of the native plants, *Pimelea alpina* had the highest incidence count (14 plants, 18%).

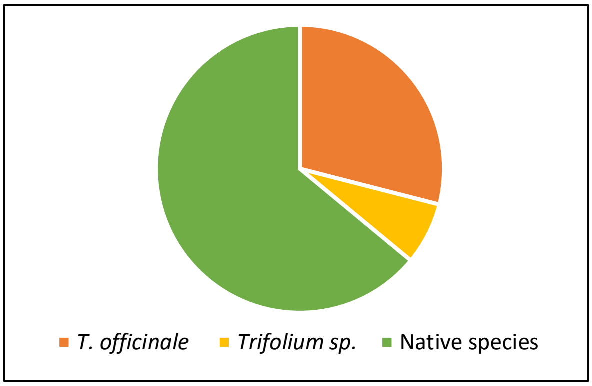

Figure 1: Total plant incidence count (no. of individual plants per species across all four transects).

A total of 79,590 estimated flowers or florets were recorded across the four transects. Of these florets, 23,750 were from *T. officinale* blooms that had finished flowering. A total floret count of 41,250 was recorded for *T. officinale* (52% of total flowers or florets in the transects), 2,100 for *Trifolium* spp. (3%) and 36,240 for native species (46%) (Figure 2). Of native species, *Nematolepis ovatifolia* had the most florets (17,711 florets, 22% of total flowers or florets).

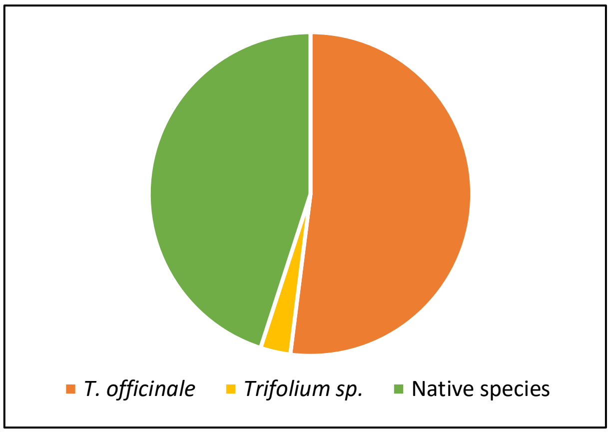

Figure 2: Total flower/floret (for composite flowers) count across four transects.

Pollen analysis

123 pollinators were examined, of which one was removed from the dataset because it lacked pollinator and flower species identification data. 77% of pollinators' carried the pollen of native species, 32% exclusively. The native Australian butterfly *Graphium macleayanus* was the only non-*T.officinales* carrier we were able to identify to species level. *Taraxacum officinale* pollen was found on 43% of pollinators, 12% exclusively (comprising 3% from pollinators caught on *T. officinale* and 9% from those caught on native species). *Trifolium* spp. pollen was found on 17% of pollinators, with zero pollinators carrying it exclusively. Eleven pollinators carried no observable traces of pollen (Figure 3). Only 3% of pollinators carried both *T. officinale* and *Trifolium* spp. pollen.

The pollen of only one native species was recorded on pollinators more often than *T. officinale* pollen: *Nematolepis ovatifolia*, at 49%.

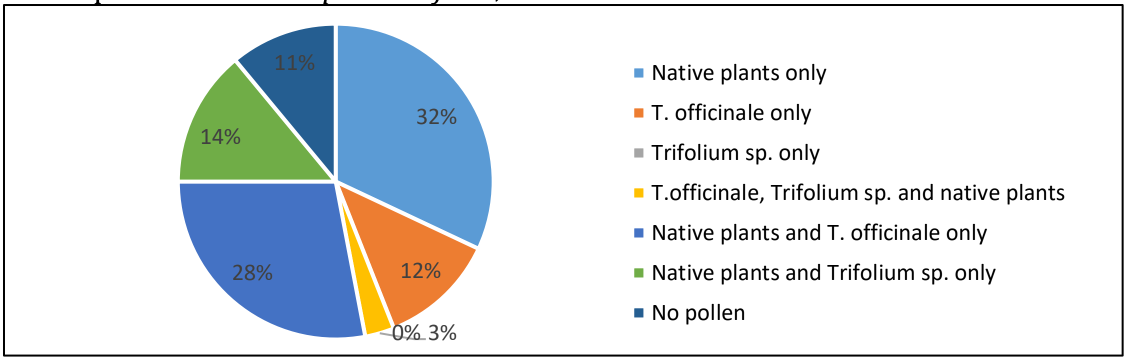

Figure 3: Pollen load on pollinators: Incidence of introduced (*T. officinale* and *Trifolium* spp.) and native pollen found on the bodies of pollinators as a percentage of total pollen incidence.

Most pollinators carrying mixed native and *T. officinale* pollen were Diptera (14 pollinators), followed by Hymenoptera (10 pollinators) and Coleoptera (7 pollinators). Lepidoptera and Hemiptera both had three mixed-pollen pollinators (Figure 4). Coleoptera carried the highest percentage, by insect order, of *T. officinale* pollen (75%, and 31% exclusively) although it accounted for only 13% of pollinators sampled. Hymenoptera (38%; 9% exclusively) and Diptera (45%, 10% exclusively) carried the least (Figure 5).

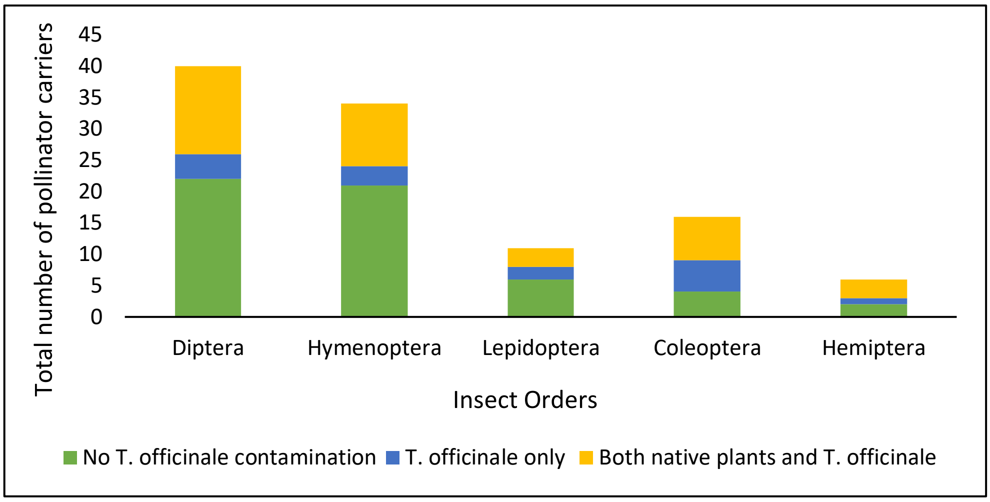

Figure 4: Pollen type found on pollinators by total number of pollinators sampled in each taxonomic order.

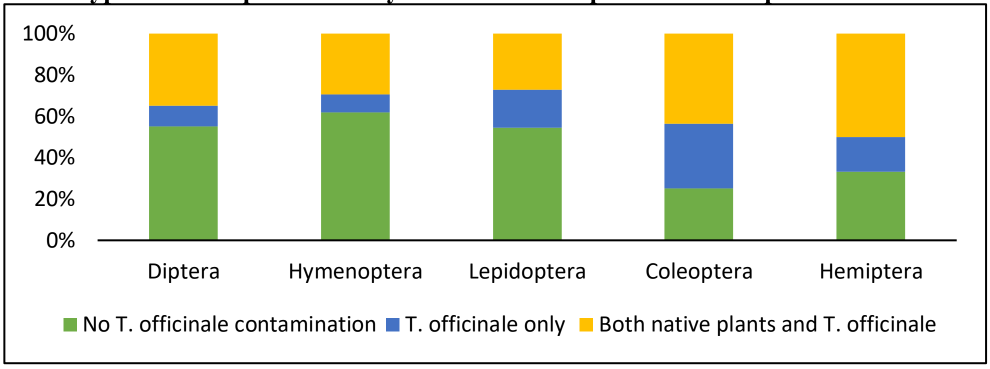

Figure 5: Pollen found on pollinators by pollen type and percentage of taxonomic orders.

Pollinators carrying *T. officinale* pollen were found to comprise from 8% (*Olearia phlogopappa var.*) to 75% (*Grevillea australis*) of total pollinators collected from a particular native flower species (Figure 6).

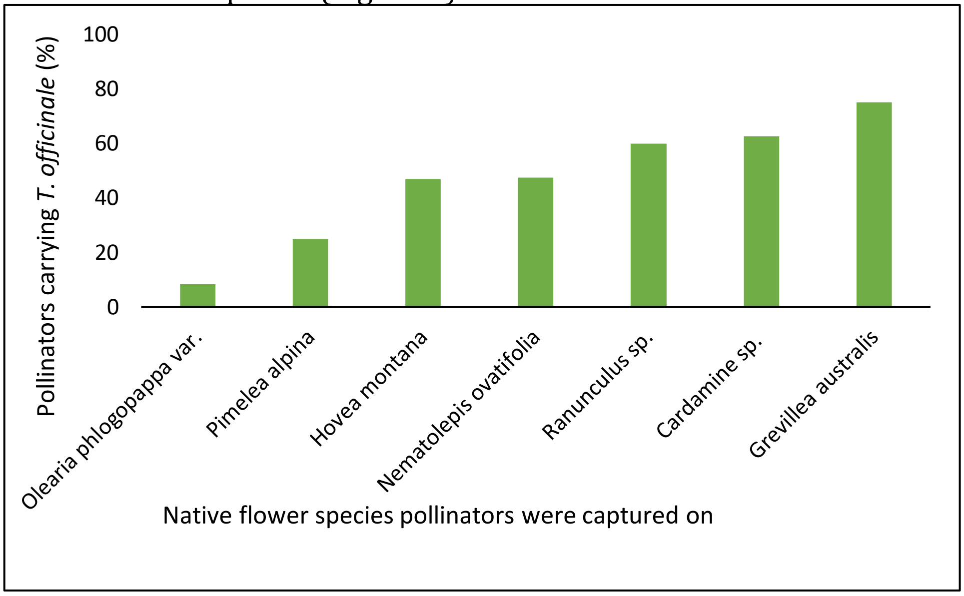

Figure 6: The percentage of pollinators found to be carrying *T. officinale* pollen by native flower species from which they were collected.

Discussion

Taraxacum officinale pollen was carried by a broad range of pollinators that also visited native alpine flowers, thus creating a potential pollen cross-contamination risk. Every order of insect collected had some specimens that carried *T. officinale* pollen to the exclusion of other species' pollen. For example, of 11 members of a Cantharidae species sampled, four carried only *T. officinale* pollen while pollen of seven native flowers was found spread among the remaining seven individuals. This tentatively suggests that, although the beetle species was capable of visiting a large range of native flowers in the area, some preferentially visited *T. officinale*, possibly reducing their pollination services to native flowers.

In a study on invasive plants at high elevations in New Zealand, Miller *et al.* (2018) observed that the abundance of introduced flowers did not affect visitation rates to native species. The fact that we observed 12% of pollinators carrying only *T. officinale* pollen suggests that it is affecting visitation rates to native species in the Australian Alps; that is, 12% of pollinators that may previously have been servicing native flowers instead foraged on *T. officinale*. A reduced pollinator visitation rate may have implications for the abundance of the native species that have to cope with a reduced pollen load resulting from fewer pollinator visits. The risk of pollen limitation via reduced pollinator visitation could potentially be mitigated if *T. officinale* and other introduced flowering plants are found to support a higher abundance of pollinators in a community due to the increased supply of nectar (Miller *et al.* 2018); a longitudinal study would be required to determine if this is the case in the Australian Alps. However, altered preferences of pollinators for the flowers of the new invaders may offset any possible benefit to native flowering plant communities from the higher pollinator loads.

With 31% of pollinators found to be carrying *T. officinale* and native pollen at the same time, a potential pollen cross-contamination risk exists for native species via stigma clogging. The cross-contamination risk was twice greater than that posed by *Trifolium* spp. (14% of pollinators). Greenhouse experiments assessing the ability of *T. officinale* pollen to obstruct the stigmas of native alpine flowers would help us to understand the potential risk this process could pose to native flowering plant abundance. But even if stigma clogging were not an issue (perhaps due to anatomical mismatches between *T. officinale* pollen and native alpine carpels), the mixed-carrying of invasive and native pollen could still lead to pollen limitation via fewer conspecific pollen grains carried per pollinator than in a community without *T. officinale,* leading to fewer ovules fertilised and thus fewer offspring. To better quantify the risk of cross-contamination, the study should be repeated with a pollen grain count (rather than only pollen species incidence) per pollinator recorded, and a heterospecific pollen grain count as a proportion of all pollen grains found on the stigmas and styles of native alpine flowers. This information could be combined with a longitudinal study of the abundance of native flowering plants and *T. officinale* in the Australian Alps to see if a causal relationship between pollen cross-contamination and reduced native plant abundance can be inferred. These studies should encompass both the heath (where our sampling took place) and herbfield communities of the Australian Alps, as the latter contain more members of the Asteraceae family and may thus be more vulnerable to *T. officinale* cross-contamination due to their closer phylogenetic relatedness to the weed (Arceo-Gómez and Ashman 2016)

Most pollinators were Diptera, which is consistent with earlier data on flowering plants of the region (Inouye and Pyke 1988); fortunately, they are at least risk (after Hymenoptera, the second most abundant pollinator) of 'changing allegiance' (Fishman and Hadany 2015), or spurning native pollen altogether in preference for *T. officinale*. Coleoptera's apparent attraction to *T. officinale* may put native species that rely heavily upon the order for pollination services (in our study, Coleoptera were largely found on *Grevillea australis* and *Cardamine* sp., species that also saw the highest number of *T. officinale*-carrying visitors) at risk of competitive exclusion via pollen limitation. Conversely, the *Graphium macleayanus* butterfly is one pollinator species upon which no *T. officinale* pollen was found, which may protect native flowers it services from pollen limitation. As the numbers of native flowers on which a 'pollination visit' from a *T. officinale*-carrying pollinator was observed differed widely by plant species (Figure 6), a better understanding of native plant and pollinator interactions on a species level would help to identify native plant species most at risk of having their pollen load reduced by the more attractive or rewarding *T. officinale*; more taxonomically precise studies are recommended in the region. Currently, *T. officinale* is a larger introduced threat than *Trifolium* spp., in terms of both its abundance and its apparent attractiveness to pollinators (being found on 12% of pollinators exclusively, even on those caught on a different species of flower, versus no pollinators exclusively carrying *Trifolium* spp.), suggesting that *Trifolium* spp. may be less attractive or nutritionally/energetically rewarding than *T. officinale*, although the lower abundance of *Trifolium* spp. may be reflected in these results. The low incidence of pollinators carrying the pollen of both invasives at the same time may suggest that they have different pollinator-attracting strategies. *T. officinale*'s investment in florets (in our transects, it had a 1.7× higher proportion of florets of the transect area than proportion of plants within it) and fast flower development (Ianovici 2016) may be additional strengths over *Trifolium* spp.

The processes and dynamics of a plant community's pollination strategies are complex and time- and weather-dependent; our study involved only one site at one elevation over a short period of time. To increase our confidence in the reproducibility of the results, the experiment should be repeated over the course of at least two growing seasons and at various sites of varied elevation across Kosciuszko National Park. It would be useful to contrast pollen species incidence counts at a site with *T. officinale* and other invasives, with a more pristine site relatively free of introduced flowering plants. Because the probability of ovule fertilisation cannot be directly estimated from pollination rates (Arroyo *et al.* 1985), and because we have not investigated whether the native species we recorded have tactics for preventing cross-contamination via stigma clogging (Miller *et al.* 2018; Nishida *et al.* 2014), it is important to record plant abundance in the communities over time to see whether *T. officinale* is actually growing in dominance (and potentially competitively excluding native species). Crucially, measures of abundance over time should be recorded within the same site the pollinator collection takes place on (a major limitation of our study; our transects and pollinator collection site were separated by a dirt road).

The risk of reproductive interference by *T. officinale* in native Australian alpine plant communities is likely to be amplified by climate change, as warmer conditions enable invasive plants to survive at higher elevations (McDougall *et al.* 2005; Scherrer and

Pickering 2001), and may keep *T. officinale* flower heads open for longer periods (Ianovici 2016), increasing chances of successful pollination. Conducting experiments at a range of elevations may help us to make predictions about the future risk of native flowering plant competitive exclusion and extinction.

Although more robust and longer-term studies are needed, our data suggest that *T. officinale* may be exerting a strong influence on pollinator visitation in a relatively small area of the Australian Alps, and deserves closer attention and possibly subsequent intervention to prevent a worst-case scenario of vulnerable native flowering species being competitively excluded to the point of extinction.

Conclusions

Our investigation into the potential competitive exclusion of native Australian alpine flowering plants by invasive *T. officinale* suggested the potential for pollen limitation via both reduced pollinator visits to native plants, and pollen cross-contamination and stigma-clogging risk. *Taraxacum officinale* attracted more pollinators than the second major invasive weed in the area, *Trifolium* spp., and all but one native plant species, *Nematolepis ovatifolia*. Twelve per cent of pollinators were found to be carrying only *T. officinale* pollen, representing a potential preference for the invasive over native flowering species. *Taraxacum officinale* seemed to be particularly attractive to the insect order Coleoptera (75% of sampled beetles carried its pollen), which may adversely impact native plant species that rely heavily upon the order for pollination services. Thirty-one per cent of pollinators were found to be carrying both *T. officinale* and native pollen, suggesting that a pollen cross-contamination risk could exist if pollinators transmitted *T. officinale* pollen to anatomically receptive native flower stigmas; this risk was halved in *Trifolium* spp.

Although not a weed of significance to the national park authorities in the Australian Alps (Johnston and Pickering 2015), our study suggests that *T. officinale* may be interfering in the reproduction of native flowering plant species. Further research into the scale of the impact of *T. officinale* on native plant abundance and diversity, and possible amplification of its impact by anthropogenic climate change, is needed if these unique, vulnerable plant communities are to be conserved.

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