

Current rates of fruit removal and seed dispersal in New Zealand fleshy-fruited mountain plants

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Abstract: The New Zealand mountain flora is rich in fleshy-fruited species but many terrestrial frugivorous birds are extinct or declining, potentially putting seed dispersal mutualisms at risk. To determine whether fruits are currently being removed by animals, we measured removal rates of eight fleshy-fruited mountain plant species from five families over two fruiting seasons, at two sites in inland Canterbury. We compared fruit removal rates within cages (no animal access to fruits), on unmanipulated plants (open-access to fruits by all animals), and within lizard-only cages (large mesh). For the eight species, unmanipulated fruit removal rates were generally high, with overall percent fruit removal by the end of autumn ranging from 67% to 99% (mean 81%) in open-access treatments. Effects of cage treatments were significant for seven of the eight species, with 58–75% removal (mean 62%) in lizard-only treatments and 23–79% (mean 40%) in animal-exclusion cages. The largest difference in fruit removal between open-access and cage treatments was for the montane shrub *Aristotelia fruticosa* (98% vs 5% respectively) and the smallest was for *Coprosma petriei* (81% vs 65%, cage treatment effect non-significant). On average, fruit removal inside lizard-access cages was just over half of that on open-access plants, suggesting that lizards can move many fruits. Delays in fruit removal are unimportant provided that most fruits are removed before they rot, and levels of final fruit removal seen in this study provide no evidence for large-scale dispersal failure despite changes to the disperser fauna.

Keywords: Arthur's Pass; bird dispersal; Cass; *Coprosma*; exclusion cages; frugivory; *Gaultheria depressa*; lizard dispersal; mammal dispersal; subalpine–montane flora

Introduction

Fleshy-fruited plants generally rely on animals to eat their fruits and disperse their seeds. Frugivorous animals affect seed dispersal through the number of fruits they remove, and through where and in what condition seeds are deposited (Loiselle & Blake 1999; Jordano & Schupp 2000; Wenny 2000). Without fruit consumption by animals, dispersal and recruitment would be greatly reduced. Although consumption by animals may not always result in effective seed dispersal (Chapman & Chapman 2002; Cordeiro & Howe 2003), and undispersed fruits can still result in local regeneration (Robertson et al. 2006), consumption by animals greatly increases mean and maximum seed dispersal distances (Godoy & Jordano 2001; Wenny 2003; Shea 2007). Fruit removal rate is thus one important practical indicator of how well seed dispersal is currently working from the plant perspective (Kelly et al. 2004).

In New Zealand many terrestrial frugivorous bird species are extinct (Holdaway 1989; Tennyson 2010) or declining (Miskelly et al. 2008), possibly putting mutualisms such as seed dispersal at risk (Clout & Hay 1989; Kelly et al. 2010). The montane, subalpine and alpine (hereafter mountain) flora of New Zealand is relatively rich (12%) in fleshy-fruited plant species from many different families (Lord 1999). Despite the prevalence of fleshy fruits in the mountain flora, there are few obvious extant native frugivorous animals to disperse their seeds. In the Southern Alps of New Zealand, dispersal by native birds is probably restricted to only a few species, including kea (*Nestor notabilis*) and occasionally pipit (*Anthus novaeseelandiae*) (Clarke 1970; Young et al. 2012), falcon (*Falco novaeseelandiae*) (Young & Bell 2010), rock wren

(*Xenicus gilviventris*), and infrequent forest birds. Native lizards (Whitaker 1987; Lawrence 1997) and introduced birds (Clarke 1970) and mammals (Young 2012) may also act as dispersal agents for seeds of mountain fruits. Little is known about the effectiveness (quantity and quality) of lizards in seed dispersal of most New Zealand flora. Several lizard taxa are known to ingest some fruit and excrete viable seed of several montane grassland species (Whitaker 1987; Lawrence 1997). On predator-free Mana Island where lizards are abundant, Wotton (2002) showed lizards were dispersing large numbers of *Coprosma propinqua* fruits. There has been considerable speculation about some fleshy-fruited taxa being lizard-adapted, e.g. *Meliccytus alpinus* (Whitaker 1987; Lawrence 1997), although there is currently little empirical evidence supporting this.

In many areas of the Southern Alps, the original vegetation patterns have been substantially modified by nearly 1000 years of human-mediated impacts (especially burning and grazing) (Wardle 1991). While the natural upper limit of forest ranged from c. 1500 m above sea level (a.s.l.) in the northern South Island, down to 800 m a.s.l. in the south, subalpine grasslands and shrublands have replaced many of these forests, particularly east of the Main Divide of the Southern Alps. It is thus useful to look at fruit removal rates at both their natural (high elevation) sites and lower elevation sites as potential disperser fauna may change along an elevational gradient.

Within many of New Zealand's mountainous areas, the apparent lack of current native dispersers is concerning. This raises the question of whether seed dispersal mutualisms are functioning effectively. The main objective of this study was therefore to determine the effectiveness of current seed dispersal

by investigating fruit removal by animals (irrespective of the native versus exotic status of frugivores) for eight species of fleshy-fruited mountain plant species. If frugivore numbers are low, we hypothesise that high numbers of fruits will become overripe and remain on the plant later in the fruiting season, eventually falling off directly beneath the parent plant. Alternatively if frugivore numbers are adequate, we should expect high fruit-removal rates with low numbers of ripe and overripe fruits. Both removal rates and the proportion of ripe plus overripe compared with unripe (green) fruits are useful indices of dispersal service (Roberston et al. 2008). Cages of varying mesh size can be used to determine the contributions of different dispersal agents by allowing only species with body size smaller than the mesh size to enter. We aimed to determine the overall fate of fruits over time (i.e. the relative proportions of fruits that are removed versus becoming overripe and subsequently undispersed) so that we can begin to assess the current effectiveness of fruit removal by animals. This will enable us to assess how well dispersal mutualisms are functioning in New Zealand mountain ecosystems with the current depauperate native-frugivore fauna.

Little is known about the ecological and evolutionary significance of fruit colour polymorphisms and their maintenance, both in the New Zealand mountain flora and in general (Lee et al. 1998; Bach & Kelly 2007), but it is often assumed that fruit colour will affect removal rates by frugivores (Lee et al. 1988). Hence we also measured whether fruit removal differed between red- and white-coloured fruits in the polymorphic species *Leucopogon colensoi*.

Specifically we aimed to: (1) determine whether fruits from a range of mountain-plant species are being removed by animals; (2) determine the relative fruit removal rates by frugivore assemblage (i.e. all frugivores and only lizards); and (3) measure how fruit removal varies across a range of species, sites, elevations, and (in one species) fruit colours.

Methods

Study sites, vegetation and potential dispersers

Fieldwork was conducted at two sites – the Cass Mountain Research Area (43°02' S, 171°47' E), 5 km east of the eastern boundary of Arthur's Pass National Park, and Temple Basin (42°54' S, 171°34' E), within Arthur's Pass National Park, both in the Canterbury Region, South Island, New Zealand.

Both sites are characterised by areas of open high-country grassland, mixed shrubland, herbaceous and mat plants interspersed with scree, rock and small remnant forest patches. Cass is considerably drier than Temple Basin (1300 mm cf. 5000 mm mean annual rainfall), due to its location further east of the Main Divide (Burrows 1977). The vegetation at Cass is characterised by open grassland dominated by native fescue tussock and exotic grasses interspersed with mixed low-growing, dry-fruited shrubs and fleshy-fruited shrubs. Other low-growing, prostrate or sprawling mat plants are also present, many with fleshy fruits. At Temple Basin, vegetation at lower elevations is dominated by diverse tall shrubs among low-growing fleshy-fruited conifers (Podocarpaceae) and various shrubby and herbaceous angiosperms.

Very little is known about which lizard species are present in Arthur's Pass National Park (M. Lettink, Fauna Finders, Christchurch, pers. comm.; Department of Conservation Herpetofauna Database). Two lizard species are known in the Cass area: the Southern Alps gecko (*Woodworthia* "Southern Alps"); previously included in *Hoplodactylus maculatus* and the common skink (*Oligosoma polychroma*). Frugivorous birds present at both sites include native kea, pipit, and falcon plus several small exotic birds such as finches and skylarks (see Young et al. (2012) for a full list of birds present). Potential mammal dispersers at both sites include the Australian brushtail possum (*Trichosurus vulpecula*), European hare (*Lepus europaeus*), rabbit (*Oryctolagus cuniculus*), rats (*Rattus* spp.), hedgehog (*Erinaceus europaeus*), chamois (*Rupicapra rupicapra*), and red deer (*Cervus elaphus*) (see Young (2012) for details on mammalian dispersers at the sites). Cass is owned and managed by the University of Canterbury and therefore has different land management practices from Temple Basin (within a national park), principally through low-intensity sheep grazing (0.2 stock units ha⁻¹ year⁻¹) over parts of the 1775-ha Cass Mountain Research Area.

Study plants

At least 50 native fleshy-fruited plant species within 24 genera and 14 families occurred at the study sites. All fruits contained small seeds 0.4 to 6.0 mm length, within small fruits up to 12 mm (see appendix table A1 in Young et al. (2012) for species and details). Eight species were selected for this study, representing a range of plant families and fruit colours (Table 1). The selected species were those that were practical to use, depending on plant abundance, fruit availability,

Table 1. Species, fruit colour, sites and treatments used in fruit removal experiments over two fruiting seasons in the Canterbury Region, New Zealand. Note: many species are fruit-colour polymorphic, as listed; we used only the fruit colour outside brackets in case colour affected removal. For *Leucopogon colensoi* both red and white fruits were tested.

Species ¹	Family	Fruit colour used (not used)	2008 ²	2009 ²
<i>Corokia cotoneaster</i>	Argophyllaceae	Red (orange, yellow)	Cass L,H	
<i>Aristolelia fruticosa</i>	Elaeocarpaceae	Pink (red, white, black)	Cass L	
<i>Pentachondra pumila</i>	Ericaceae	Red	Cass H†	Cass H; Temple L,H‡
<i>Gaultheria depressa</i>	Ericaceae	White (pink)	Cass L,H	Cass L,H; Temple L,H
<i>Leucopogon colensoi</i>	Ericaceae	Red, white (pink)	Cass L,H	Cass L,H
<i>Muehlenbeckia axillaris</i>	Polygonaceae	White	Cass L	
<i>Coprosma propinqua</i>	Rubiaceae	Blue (white, yellow)	Cass L,H	Cass L,H
<i>Coprosma petriei</i>	Rubiaceae	Pale blue	Cass L	Cass L

¹Plant names follow the New Zealand Plant Names Database <http://nzflora.landcareresearch.co.nz/>.

²Treatments in 2008 = animal-exclusion cage and open; in 2009 = animal-exclusion cage, lizard-only cage, and open. Replicates = 5 per species/season/elevation/colour (except † = 4 and ‡ = 6). Cass and Temple (Basin) refer to the two study sites. L = low-, H = high-elevation sites. A blank means not studied in that season.

phenology, fruit longevity, sensitivity to fruit dislodgement during handling, and accessibility.

Fruit removal rates and treatments

For species with a wide elevational range, replicates were set up at both high- and low-elevation (m a.s.l.) sites (Cass low elevation = 650–800 m, Cass high elevation = 1000–1360 m; Temple Basin low elevation = 900–1100 m, Temple Basin high elevation = 1300–1700 m). During the start of the fruit ripening season (usually December to January), branches or parts of plants with at least 50 unripe fruits present were tagged (although most had more than 200 fruits to ensure large enough numbers to account for any losses occurring during counting when fruits were sometimes accidentally knocked off). Fruit fates were followed throughout the fruiting season (between 4 and 6 months) to determine the fate of fruits under situations of zero frugivore activity (animal-exclusion cage treatments) versus normal frugivore activity (open-access, non-cage treatments). The numbers of unripe, ripe, overripe, dead or aborted and fallen fruits were counted approximately every 4 weeks in both treatments. Numbers of dead, aborted and fallen fruits were summed and classified as ‘unavailable’ for primary seed dispersal. All fruits (other than those deemed ‘unavailable’) that were unaccounted for at each count were considered ‘removed’ from the plant, i.e. eaten and dispersed by an animal, and overall fruit removal was calculated based on this.

We defined unripe fruits for all species as being green, hard and smaller than mature fruits. We defined fruits as being ripe (available to be eaten) when the colour had largely changed from green to its mature colour (see Table 1), and the fruit pulp had softened and become sweeter (to the human taste). Overripe fruits became wrinkled, and were generally considered to be less attractive for frugivore selection. The percentage of fruits going from unripe to overripe during the 4–6 months in the absence of dispersal or predation could be determined from the monthly counts. Fruits in the ‘removed’ category were considered separately to fruits that had fallen off either into mesh bags (on bagged treatment branches) or loose on the ground under the plant (or on top of the foliage for mat-forming species such as *Coprosma petriei*). Because fruits in the ‘fallen’ category were problematic to account for, mostly due to the difficulties in accurately counting fallen fruits beneath or within foliage, results in this category are likely to be substantially underestimated. Consequently, the calculations for ‘total percent of fruits removed’ are likely to be overestimated in the cage treatments (which should be zero, or close to). If frugivore visitation was adequate, we would expect lower numbers of ripe and overripe fruits in open-access treatments compared with high numbers of ripe, overripe and accumulated fallen fruits for plants in cage treatments.

Two of the fruiting species used in this study posed complications for fruit counts and thus accurately measuring levels of fruit removal. *Pentachondra pumila* and *Muehlenbeckia axillaris* flowered continuously until late summer, suggesting that unripe fruits would continue to appear throughout summer and autumn if pollination and fruit set were successful. This made fruit ripening and fruit removal measurements difficult, particularly for *M. axillaris*, which produced new flowers at a very rapid rate; hence this species was only used in the 2008 season and dropped in 2009. For *P. pumila*, flower numbers were easier to count and monitor. Therefore, we counted flowers and fruits over time for *P. pumila* and used this species in 2008 and 2009. We also had to

drop a ninth species (*Podocarpus nivalis*, Podocarpaceae) that we had been keen to include as its fruits are preferred by kea (Young et al. 2012). However, *Podocarpus nivalis* produces new green fruits throughout the entire year and it ultimately proved impossible with our methods to reliably determine fruit removal rates for this species.

2008 fruiting season

In 2008 fruit removal experiments were performed only at Cass. Branches were assigned to one of two treatments – caged to exclude all frugivores (cage) and open-access to any frugivore (control). For shrubby species, tagged branches for the two treatments were usually located within an individual plant, but for prostrate plants, treatments were placed on different plants within 5 m of each other. Cages for prostrate plants (mesh size 4 mm) or muslin bags for shrubs (mesh size 1 mm) were applied to branches after flowering, or at the ‘green fruit’ stage (between December and February depending on species and elevation). For some species, there were already low levels of ripening fruits by the time the experimental set-up was complete.

2009 fruiting season

In 2009 the number of study species we used decreased from eight to five, and a second site (Temple Basin, Arthur’s Pass National Park) was introduced for comparison. The same experiments were performed but an extra treatment was added (at both sites) to test whether lizards were removing fruits and how this compared with fruit removal rates in cage and open-access treatments. Cages with 2.5-cm mesh size, large enough to allow lizard access while excluding larger animals, were added to branches or sections of mat plants in the same fashion as previously described. This mesh size could allow access by mice (*Mus musculus*) and large invertebrates such as grasshoppers (Orthoptera; see Young 2012) and weta (Anostomatidae; Larsen & Burns 2012), but we believe those groups probably removed few fruits. At Cass mice are only regularly seen around buildings. Weta densities are limited by rodent predation, and for some weta species (*Hemideina* spp.) preference for fruits is low (Wyman et al. 2011). These impressions were reinforced by 425 hours of infrared video surveillance of fruiting plants at Cass, spanning day and night. The video captured seven vertebrates eating fruits, including one ship rat (*Rattus rattus*), but no mice. Several weta were seen in the videos but none ate any fruits. We have no information about mice and weta densities at Temple Basin but the site is higher elevation and wetter than Cass, both of which might reduce the density of those animals.

Statistical analysis

Generalised linear models (GLMs) were used to test for differences in fruit removal rates between levels of animal exclusion treatments, sites, years and elevations across the fruiting period, using plants as replicates. Tests were performed separately for each species. The response variable used in analyses for each species was the final proportion of fruits removed at the last count in the fruiting season (usually May or June, but for high-elevation treatments at Temple Basin, the last count was in April just before heavy snowfalls). The response variable was binomial (final proportion of fruits removed out of the maximum number of fruits present at the start of the study). A priori tests showed data were overdispersed; therefore, a quasibinomial error term was specified.

To estimate the proportion of all dispersed fruits that lizards were capable of removing, we compared the additional removal rate with lizard-only access (i.e. 'lizard-only' minus 'caged' final percent gone) to the additional removal with open access (i.e. 'open' minus 'caged' final percent gone). This does not necessarily indicate that lizards actually removed that same percentage of fruits from the open-treatment plants, only that they would be capable of doing so if other animals did not remove them first.

Results

Through each season, fruits ripened gradually and were removed or fell off, as illustrated by one example, *Gaultheria depressa*, which showed a significant effect of site, but no effect of elevation or year, on the end-of-season percent of fruits gone (Table 2). The open-access treatments for *G. depressa* show the highest levels of percent of fruits gone through time (Fig. 1). Although in this example there were no significant differences in final percent fruit removal between low- and high-elevation

plants (Table 2, Fig. 1), there was a noticeable delay in fruit ripening for *G. depressa* at higher elevations, particularly at Temple Basin. For analysis, we used the outcome (fruits gone versus still present) at the final count, which was usually in May or June (see Methods). In some cases, especially at higher elevations and the Temple Basin site, the fruits were buried under snow after that time. It is possible that remaining fruits would be dispersed in spring after snowmelt, but here we only analyse removal in autumn.

The animal-exclusion cage treatments reduced autumn fruit removal for all species (Fig. 2). For open (uncaged) plants, mean fruit removal by season's end averaged 81% across the eight species (range 67–99%). Those means are generally high, and suggest that most species of plant are getting most fruits dispersed by the end of autumn, although that is least certain for *Muehlenbeckia axillaris* where fruit disappearance was 79% even inside cages. The reductions of fruit removal by caging treatments were significant for seven of the eight species (Table 2, Fig. 2), and on average reduced fruit removal by half (from a mean of 80.5% in open treatments to a mean of 40.3% in caged treatments). The largest reduction was in *Aristotelia fruticosa*

Table 2. Significance tests of predictors for overall percent fruit removal at end of the fruiting season, based on separate quasibinomial generalised linear models for each species. Significant effects are in bold.

Species ¹	Predictors	d.f.	Deviance	Residual d.f.	Residual deviance	F	P-value
<i>Gaultheria depressa</i>	NULL			76	3532.1		
	Elevation	1	1.54	75	3530.6	0.06	0.801
	Year	1	22.17	74	3508.4	0.92	0.341
	Site	1	514.62	73	2993.8	21.34	<0.001
	Treatment	2	1371.25	71	1622.5	28.44	<0.001
	Site × Treatment	2	169.45	69	1453.1	3.51	0.035
<i>Pentachondra pumila</i>	NULL			46	1557.31		
	Year	1	197.53	45	1359.78	12.46	0.001
	Elevation	1	7.73	44	1352.05	0.49	0.49
	Site	1	0.75	43	1351.30	0.05	0.83
	Treatment	2	635.10	41	716.20	20.03	<0.001
	Site × Treatment	2	77.78		638.43	2.45	0.10
<i>Coprosma propinqua</i>	NULL			49	2212.8		
	Year	1	0.00	48	2212.7	0.00	0.99
	Elevation	1	123.69	47	2089.1	4.17	0.047
	Treatment	2	459.97	45	1629.1	7.76	0.001
<i>Coprosma petriei</i>	NULL			24	300.29		
	Year	1	0.149	23	300.14	0.01	0.91
	Treatment	2	53.514	21	246.63	2.28	0.13
<i>Leucopogon colensoi</i>	NULL			91	5452.9		
	Year	1	24.56	90	5428.4	0.752	0.39
	Elevation	1	12.88	89	5415.5	0.395	0.53
	Colour	1	1.47	88	5414.0	0.045	0.83
	Treatment	2	2635.62	86	2778.4	40.386	<0.001
	Colour × Treatment	2	79.83	84	2698.6	1.221	0.30
<i>Corokia cotoneaster</i>	NULL			19	968.71		
	Elevation	1	0.40	18	968.31	0.01	0.91
	Treatment	1	445.36	17	522.94	15.31	0.001
<i>Aristotelia fruticosa</i>	NULL			9	992.80		
	Treatment	1	969.83	8	22.98	352.25	<0.001
<i>Muehlenbeckia axillaris</i>	NULL			9	234.153		
	Treatment	1	177.79	8	56.368	31.49	<0.001

¹Plant names follow the New Zealand Plant Names Database <http://nzflora.landcareresearch.co.nz/>.

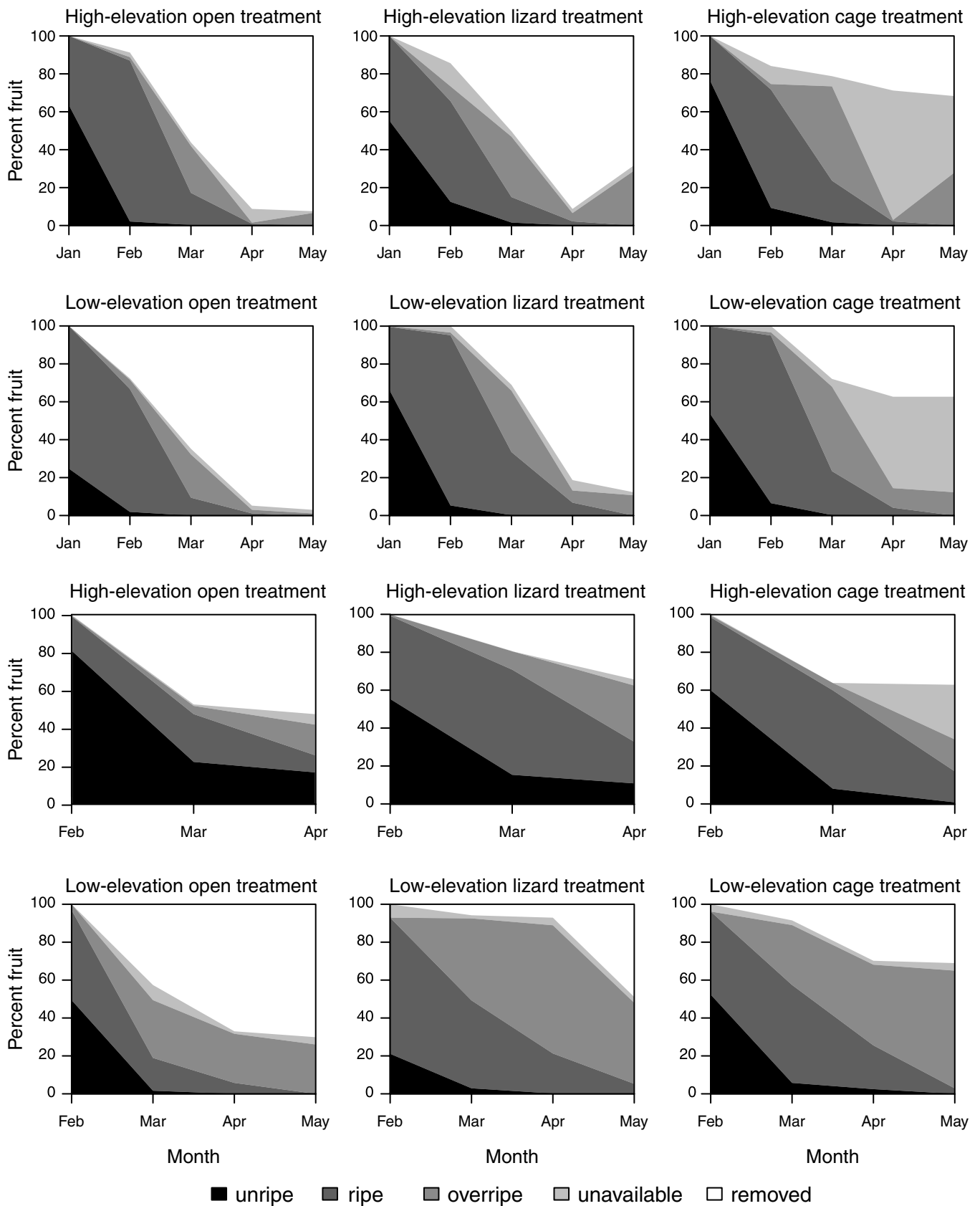


Figure 1. Fruit ripening and removal rates over time for *Gaultheria depressa* during the 2009 fruiting season at Cass (top two rows) and Temple Basin (bottom two rows), at low- and high-elevation sites, under open-access, lizard-access, and caged treatments. The percent fruit ‘unavailable’ category accounts for all dead or fallen fruits that are unavailable for primary seed dispersal by animals.

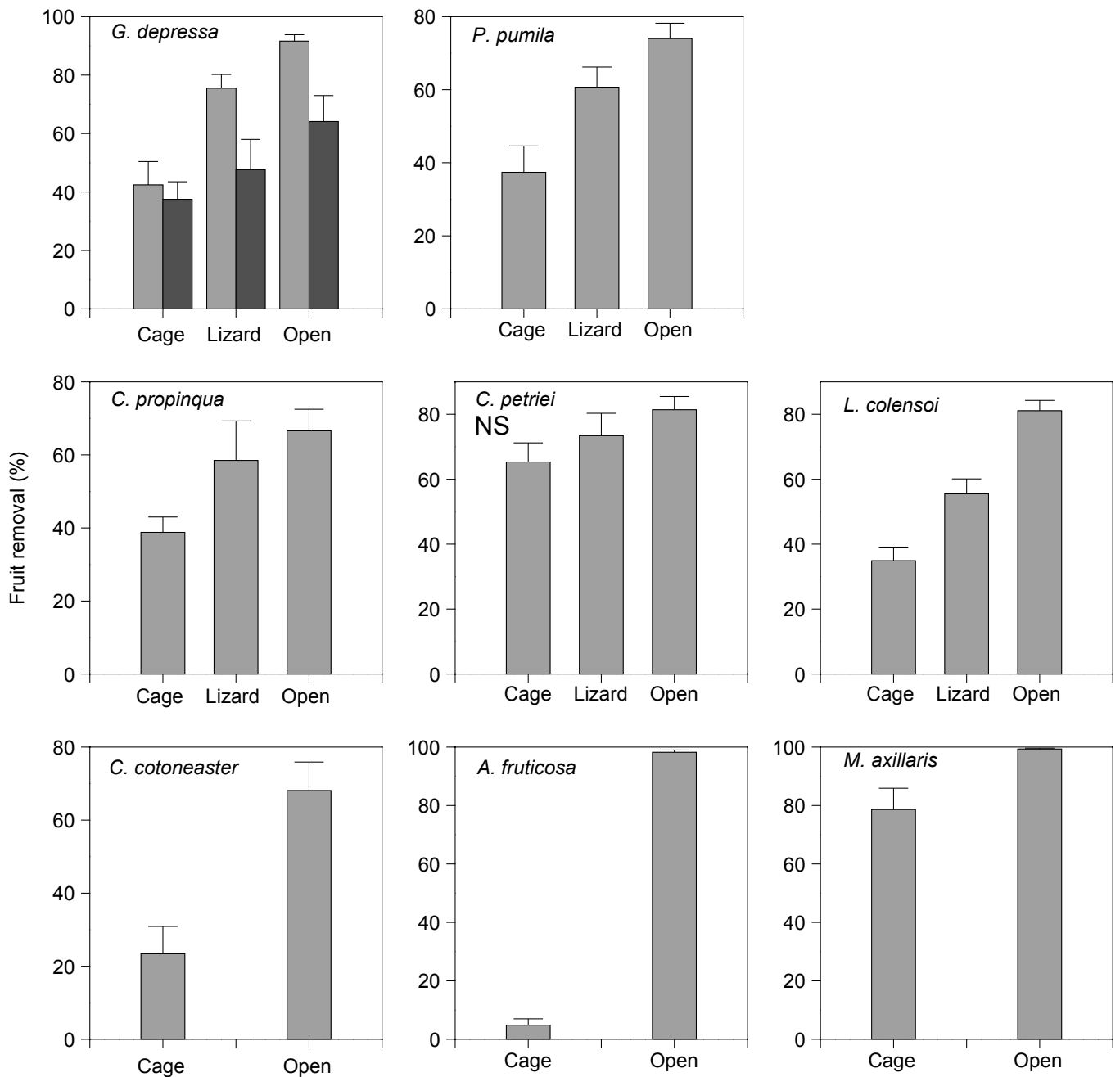


Figure 2. Mean final fruit removal rates (with SEMs) over autumn for eight fleshy-fruited mountain species (see Table 1 for full species names). Treatment was significant for all species except *Coprosma petriei* (Table 2). Where the site × treatment interaction was significant (*Gaultheria depressa*), treatment means are shown separately for Cass (light grey) and Temple Basin (dark grey); otherwise treatment means are for both sites combined (*Pentachondra pumila*) or for the sole site at Cass (all other species). NS = treatment effects not significant in *Coprosma petriei*.

(98% removal in open, 4% in cage) and the smallest was in the non-significant *Coprosma petriei* (81% open, 65% cage).

Where lizard-only cages were used, removal rates were intermediate between open and fully caged for all five species (Fig. 2). Across the six cases spanning five plant species, lizard removal (mean 61.9%) was just over halfway from caged removal (mean 42.7%) to all-animal (open-access) fruit removal (mean 76.5%). That suggests lizards would be capable of taking about half of all fruits that were observed to be removed (to be exact, $(61.9 - 42.7) / (76.5 - 42.7) = 0.56$ times as many fruits). This ratio was highest in *Coprosma*

propinqua (lizards alone removed 0.71 times as many fruits as removed by all animals) and lowest in *Gaultheria depressa* at Temple Basin (0.38).

There was a significant interaction between site and treatment for *Gaultheria depressa*, which was because removal rates were similar between the two sites inside cages, but were lower for lizard-access and open-access plants at Temple Basin. This suggests there were fewer visits to *G. depressa* plants at Temple Basin. However, for the only other species tested at both sites, *Pentachondra pumila*, there was no significant site effect (Table 2).

In the one species where we tested two different colour forms (*Leucopogon colensoi*, with red and white fruits), there was no significant effect of colour overall and no significant interaction (Table 2). Therefore, in this species, removal rates were not affected by fruit colour.

Discussion

Is fruit removal failing?

Fruit removal rates for these eight montane, subalpine, and alpine fleshy-fruited plants were generally high (81% averaged across all open-access treatments) under the current suite of available native and exotic frugivores. The removal rates in this study were comparable with studies overseas. Herrera (1984) found total removal rates of 89–100% for seven shrub species in Spain, while in Australia the shrub *Coprosma quadrifida* had 84% of fruits removed by 14 bird dispersers (French et al. 1992). In South Carolina, USA, removal rates averaged 72% across 22 species (McCarty et al. 2002). Hence these New Zealand mountain flora results are similar to those reported overseas, where fewer faunal losses have occurred.

Only a few New Zealand studies have monitored fruit fate over time to determine levels of dispersal service. At low elevation on Mana Island, which at the time had no mammalian predators present and large numbers of lizards, Wotton (2002) reported removal of *Coprosma propinqua* inside cages at levels not much higher than our study (47% vs 39% respectively), but much higher removal rates for open-access fruits (96% on Mana vs 67% in our study) and for lizard-only treatments (93% vs 59%). How much the higher removal rates by animals are attributable to the lower elevation versus the predator-free habitat is unknown. Kelly et al. (2004) monitored fruit ripening and removal over 4 years for two Loranthaceous mistletoes growing on host mountain beech (*Fuscospora cliffortioides*, previously *Nothofagus solandri* var. *cliffortioides*) at Craigieburn Forest Park (20 km from Cass). For both *Alepis flavida* and *Peraxilla tetrapetala*, there was no evidence of dispersal limitation, with very few (<5%) ripe fruits present on plants at any one time and >90% of the total fruit crop removed. These were higher fruit removal rates than for many species in our study. For some species (e.g. *Gaultheria depressa*) large numbers of ripe fruits (20–70%) were often present at any given time in open-access treatments, suggesting slower fruit removal than for the mistletoes at Craigieburn. At Craigieburn, mistletoes are one of only a few fleshy-fruited species available in these low-diversity mountain beech forests that occur widely east of the Main Divide (Wardle 1991; Murphy & Kelly 2001). This lack of alternative foods may encourage higher removal rates for mistletoe fruits. Conversely, at Cass, there are many fruiting species present. Consequently, fruit removal of individual species could be lower, particularly if frugivores display preferences for certain species and if fewer frugivores are present.

Does this suggest dispersal limitation for some alpine fleshy-fruited species? Robertson et al. (2008) compared fruit removal rates on the New Zealand mainland with those on offshore Kapiti Island (a bird sanctuary with high bird densities) and found lower proportions of ripe and overripe fruits (0.9%) on uncaged branches at Kapiti than the mainland (up to 40%), suggesting rapid removal by birds. Both Kelly et al. (2004) and Robertson et al. (2008) suggest that as long as fruits are being removed at some point before they rot and

fall below the parent plant, delays in fruit removal may have negligible fitness consequences. In this respect, our findings of mean percent fruit removal by June (before winter snow cover settles) of 67–99% by the current suite of available seed dispersers argues against any widespread dispersal failure in these eight plants, despite changes to the disperser fauna.

Robertson et al. (2008) assumed that fruit removal in *Fuchsia excorticata* measured the level of mutualism service provided by native birds. However, because introduced mammals can also consume large numbers of fruits, it can be difficult to determine whether birds or mammals are removing these fruits. Alternative methods such as faecal analysis, direct observation and video recording should therefore be considered in order to evaluate the role of birds relative to other dispersers (Young et al. 2012). Final percentage of the fruit crop removed and fruit removal rates depend on a variety of factors such as attractiveness (Willson & Whelan 1990), conspicuousness (Lee et al. 1988), fruit crop size, and neighbouring fruit crop availability (Blendinger & Villegas 2011). Investigations into fruit removal should therefore consider these other factors when monitoring fruit fates to determine quantitative measures of seed dispersal effectiveness.

Fruit removal by lizards

Fruit removal in lizard-access (2.5-cm mesh) cages was usually less than for open-access plants. This was not surprising as the cages were designed to exclude all the large frugivores (birds and large mammals), and lizard densities are now generally much lower on mainland New Zealand than in predator-free habitats. In contrast, on predator-free Mana Island, Wotton (2002) found removal in lizard-access cages was very similar to open-access removal. More surprising was that in our study, despite their apparent low densities, lizards managed to remove about half as many fruits from the lizard-access treatments as the entire suite of frugivores removed from open-access treatments, suggesting an unexpectedly large potential contribution by lizards. Literally speaking, the lizard-access cages also allowed entry by other small animals such as mice and invertebrates, although, as discussed in Methods, lizards were probably the main animal responsible for fruit removal. In a separate study at the same sites (Young 2012), artificial lizard retreats were used to monitor which lizard species were present, their spatial distribution, and their effectiveness as seed dispersers. Preliminary results suggest that the common skink and Southern Alps gecko were widespread at Cass but not particularly abundant, but not recorded at Temple Basin. This could explain why there was little difference in final fruit removal between lizard-only cages and animal-exclusion cages for *Gaultheria depressa* at Temple Basin.

Overwintering fruit

Final fruit counts ceased for this study each year between April and June because of snowfall, which covers plants. The highest plants monitored at Temple Basin were at nearly 1700 m elevation. Many plant species with animal-dispersed fruits grow at similar elevations to this across much of the South Island. However, because of snow cover that can persist until late spring and settle again from late summer (Shanks et al. 1990), they have a relatively short season available to ripen and disseminate their fruits (Kudo 1992). In this study we found that undispersed ripe fruits can remain on the plant over the winter months for some species (particularly *Corokia cotoneaster*, and less commonly in *Coprosma propinqua*) and

may be dispersed after winter snow melts in the following spring. This can happen while the next season's green fruit crop is developing and ripening. This is also the case for *Peraxilla tetrapetala* at Cragieburn (~ 950 m elevation), where some fruits ripen as late as January the next year (Kelly et al. 2004).

Extinct frugivores

Of all the study species, *Corokia cotoneaster* fruits were usually the slowest to be removed, with many individual plants bearing large quantities of ripe fruit late in autumn. This would suggest *C. cotoneaster* has one of the least-preferred fruits. Its fruits have a seed enclosed inside a large and hard endocarp (Webb & Simpson 2001) covered by a very thin fruit pulp, which offers relatively little reward to frugivores. However, fruits (particularly *C. cotoneaster* in mid-Canterbury) were abundant in the diets of many extinct herbivorous moa species (Dinornithiformes) (Burrows et al. 1981; Burrows 1989; Horrocks et al. 2004; Wood et al. 2008). Seeds with hard endocarps are common in species that moa are known to have eaten (e.g. *Cyathodes*, *Leucopogon*, *Myrsine*, and *Corokia* species), so it is possible (albeit untestable) that the slow removal of *C. cotoneaster* is a result of the extinction of moa.

Fruit colour polymorphisms and frugivore guilds

We investigated whether fruit colour polymorphism was an important factor in determining levels of fruit removal in *Leucopogon colensoi* and found no difference in final percent fruit removal between red- and white-fruited plants. There is little known about the ecological and evolutionary significance of fruit colour polymorphisms and their maintenance, both in the New Zealand mountain flora and in general (Lee et al. 1988; Bach & Kelly 2007), but it is often assumed that fruit colour will affect removal rates by frugivores (Lee et al. 1988). Birds are reportedly more attracted to red fruits over light-coloured fruits (Willson & Whelan 1990). The similar removal rates we found for red and white fruits in *L. colensoi* could suggest that New Zealand birds are more flexible; after all, bellbirds are known to forage on *Peraxilla tetrapetala* fruit (Kelly et al. 2004), which are green when ripe, and *Fuchsia excorticata* flowers (Robertson et al. 2008), which are green when producing nectar. Alternatively, the lack of preference for red could result from an important dispersal contribution from introduced mammals (Young 2012). Day and night video evidence collected during a separate related study showed that most mammals (hedgehog, possum and rat) and lizards (skinks) filmed eating fruits did so at night, while most bird frugivory occurred by day (apart from kea, which fed on fruit day and night) (Young 2012). Therefore, it is possible that nocturnally foraging mammals, which are relatively novel frugivores of New Zealand fleshy-fruited plants, have no preference for certain fruit colours and remove red and white fruits at roughly the same rate.

In conclusion, overall unmanipulated fruit removal rates were generally high while rates of fruit removal by lizards were also moderately high for all eight species studied. Fruit removal in some species was slow; however, most fruits were removed by the end of autumn in most of the study species. Delays in fruit removal are probably of little importance provided that most fruits are removed before they rot. Final fruit removal levels seen in this study provide no evidence for large-scale dispersal failure despite changes to the disperser fauna. The next step is to determine which animals are acting as seed dispersers (both native and exotic), and their post-dispersal

effects on seeds, such as deposition into appropriate microsites and effects of gut passage on germination, growth and survival.

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