

## Plant-pollinator interactions in sympatric exotic and native *Senecio* species: is facilitation or competition for pollinators occurring?

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### Abstract

The role of indirect interactions in invasion biology has rarely been addressed. Indirect interactions between two plant species may be mediated by shared pollinators: the presence of one plant species can have either a negative impact on pollination (and seed set) in another by competing for pollinators, or a positive effect by facilitating pollinator visitation. We investigated whether facilitation or competition for pollination was occurring between the closely related native *Senecio pinnatifolius* (A.Rich) and exotic *S. madagascariensis* (Poiret) in south-east Queensland. Visitation rates by honeybees and syrphid species, as well as seed set in each *Senecio* species, were assessed in naturally occurring mixed and pure stands. The exotic *S. madagascariensis* did not affect visitation rates to the native, but seed set of the native species was higher in mixed populations. The presence of native *S. pinnatifolius* caused a reduction in honeybee visits and an increase in syrphid visits to the exotic plant, but altered visitation patterns were not reflected in a change in seed set in the exotic.

**Keywords:** fireweed, indirect effects, invasive species, plant-pollinator interactions, visitation rates.

### Introduction

The colonization of new areas by invasive species is a major conservation issue, as in many cases it results in alterations to biodiversity and ecosystem function (Maron and Vila 2001, Agrawal and Kotanen 2003, Scherber *et al.* 2003). Various studies have investigated the impacts of invasive species on a system, generally focusing on direct mechanisms such as predation (Dickman 1996, Wilson *et al.* 1998, Kinnear *et al.* 2002) and competition (Cadi and Joly 2003, Kolb and Alpert 2003, Corbin and D'Antonio 2004, Miller and Gorcho 2004), or system-level impacts, which alter abiotic processes (Crooks 2002, Chornesky and Randall 2003). However, exotic and native species can also affect one another via indirect interactions, i.e. when changes

to interactions between two species occur as a result of the presence of a third (in this case invasive) species (Strauss 1991, Wootton 1994, Traveset and Richardson 2006, White *et al.* 2006). The impacts of such interactions might be positive, negative or neutral, for either or both of the species involved.

Mutualistic interactions, including plant-pollinator relationships, can be important in shaping natural systems and influencing the outcome of introductions (Richardson *et al.* 2000, Bruno *et al.* 2003). In self-incompatible, animal-pollinated plant species, plant-pollinator interactions can potentially be altered via indirect effects caused by the addition to the system of a new, simultaneously flowering plant species. Such indirect effects might occur via (i) competition – which includes both (a) competition for pollinators (exploitation competition), and (b) improper pollen transfer (interference competition) resulting in pollen interference or loss of conspecific pollen; or (ii) facilitation of pollination (Rathke 1983).

Plant species competing for the services of shared pollinators (exploitation competition) may or may not be closely related and may have similar or very different floral structures (Levin 1970, Rathke 1983). Several studies have shown decreased pollinator visitation rates to natives in the presence of more attractive exotic species (Chittka and Schurkens 2001, Ghazoul 2004, Moragues and Traveset 2005) (note though, that reduced visitation rates do not necessarily translate into reduced seed set, Ghazoul 2004). Alternatively, flowers of an invasive species may be *less* attractive to insect pollinators than flowers of native species, potentially limiting the establishment or spread of the invader. To our knowledge, no study has directly investigated the impact of the presence of a native species on pollinator visitation rates or seed set in a sympatric invasive species, although, in an analogous system, studies have shown that native species can compete with crop species for pollinators (Free 1963, Holm 1966).

Richardson *et al.* (2000) suggest that pollen limitation is rarely a constraint on the success of an invader because of the widespread distribution of generalist pollinators, which visit exotic as well as native plant species. Even in the absence of pollinator limitation however, the presence of one species can have a negative impact on another through improper pollen transfer (interference competition). This can result in reduced seed set either through pollen interference (when heterospecific pollen on a stigma interferes with fertilization of the ovules by conspecific pollen) (Galen and Gregory 1989, Brown and Mitchell 2001), or conspecific pollen loss (Campbell and Motten 1985, Bell *et al.* 2005).

Whilst negative impacts are the focus of the majority of studies, the presence of one plant species may instead have a positive facilitative effect on another by attracting greater numbers of pollinators to the area (Feldman *et al.* 2004, Moeller 2004). Facilitation is more likely to occur in plant populations of low density or of a small size (Rathke 1983) and has been recorded between sympatric native species (Campbell and Motten 1985, Moeller 2004, 2005). However, facilitation has rarely been shown to occur between exotic and native species. One exception is a study which demonstrated that the presence of an invader, *Carpobrotus* spp., had a facilitative effect on pollination in two co-occurring native species, *Cistus salvifolius* and *Anthyllis cytisoides* (Moragues and Traveset 2005).

The aim of this study is to determine whether facilitation of, or competition for, visits by shared pollinators is occurring between two species of *Senecio*, the native *S. pinnatifolius* and the invasive *S. madagascariensis*, in south-eastern Australia. Previous studies indicate that both species are self-incompatible, rely on insects for pollination, and share the same common floral visitors (Ali 1966, Radford 1997, authors' unpublished data). This creates the possibility for pollinator-mediated indirect interactions which, if present, may have the potential to affect both the invasion process and the impacts of the invader on the native species. This study took place in the middle of the flowering season of the native *S. pinnatifolius*, which coincides with the early stages of the *S. madagascariensis* flowering season. At this time of year, *S. pinnatifolius* plants and flowers are likely to occur at a greater density than *S. madagascariensis* plants and flowers, so we predict that the presence of the dominant native *S. pinnatifolius* is more likely to impact the invasive *S. madagascariensis*, than vice versa.

### Materials and methods

#### Study species

*Senecio madagascariensis*, fireweed, is an annual weed from South Africa that was first

recorded in Australia in 1918: it has since invaded large areas of farmland and grassland in south-eastern Australia (Radford *et al.* 1995, Radford 1997). In south-eastern Australia, *S. madagascariensis* flowers between the months of March and December (Radford 1997).

Closely related to *S. madagascariensis* is a group of sub-species belonging to the Australian native *S. pinnatifolius* complex. *Senecio pinnatifolius* is a herbaceous perennial (Ali 1966) whose geographic range overlaps with that of *S. madagascariensis* in Australia, but generally occurs in smaller, more scattered populations than the exotic (Radford 1997, Radford and Cousens 2000). *Senecio pinnatifolius* ssp. *lanceolatus*, the focus of this study, inhabits disturbed areas and pasture usually close to the edge of rainforest or moist eucalypt forest and flowers between January and June in south-eastern Australia (Radford 1997). There is a four month period of overlap between the flowering periods of the exotic and native *Senecio*. Previous studies have indicated that both species are self-incompatible and are likely to rely on insects as pollinators (Ali 1966, Radford 1997). The two species are morphologically similar; both produce similar-sized yellow capitula which occur in clusters on the plant, and floral visitors move freely between the two species when they grow together in the field (E. White, personal observation).

#### Study sites

This study was conducted using four 'population types', each represented by three replicate populations in south-east Queensland:

1. Three 'pure *S. pinnatifolius* stands': These were *S. pinnatifolius* populations which were at least five km from the nearest known *S. madagascariensis* populations. Two sites existed near Swanfels, (located at 28°07'S, 152°23'E and 28°08'S, 152°23'E respectively) and one was east of Hampton (27°22'S, 152°10'E);
2. Three 'pure *S. madagascariensis* stands': These comprised three populations of *S. madagascariensis* which were at least five km from the nearest known *S. pinnatifolius* populations. One was near Springbrook National Park (28°11'S, 153°16'E), a second at Mt. Tamborine (27°58'S, 153°12'E) and a third, just south of Beechmont (28°07'S, 153°10'E);
3. 'Mixed *S. pinnatifolius* stands': Three populations of *S. pinnatifolius* existing in close proximity (within 50 m) to *S. madagascariensis* populations. These included one just west of Queen Mary Falls (28°20'S, 152°21'E), one near Killarney (28°18'S, 152°21'E) and one on private land neighbouring the O'Reilly's section of Lamington National Park (28°13'S, 153°07'E).
4. 'Mixed *S. madagascariensis* stands': Three populations of *S. madagascariensis*

existing in close proximity (within less than 50 m) to *S. pinnatifolius* populations. These were in the same locations as those described for the mixed *S. pinnatifolius* stands.

All sites occur within an approximately 120 km length of the 'Border Ranges', a group of linked mountain ranges running along the eastern portion of the Queensland/New South Wales state border. All sites, regardless of location, occurred within a similar altitudinal range (between 550 m and 700 m ASL), had similar types of neighbouring vegetation (pasture and moist eucalypt forest or rainforest), and were surveyed between March and May when both species were flowering.

#### Quantity of pollen on insects

Honey bees (*Apis mellifera*) and hoverflies (syrphid species) are the two most common floral visitors to both *S. pinnatifolius* and *S. madagascariensis* at study sites in south-east Queensland (authors' unpublished data) and so it seemed likely that these species play an important role as pollinators. To confirm that these species were not only visiting flowers, but also carrying pollen, the following procedures were carried out.

Pollen grains of both *S. pinnatifolius* and *S. madagascariensis* were collected from flowers growing in the field, mounted on stubs, gold coated, examined and photographed under a scanning electron microscope at 800× magnification. Twelve specimens of *A. mellifera* and 13 specimens of syrphid flies found visiting *Senecio* flowers were collected from pure and mixed *S. pinnatifolius* and *S. madagascariensis* populations in south-east Queensland. Specimens were mounted individually on stubs (ventral side facing up), gold-coated, and examined under a scanning electron microscope at 400× magnification. Since it was difficult to determine exact number of pollen grains on an insect (particularly when pollen grains were extremely abundant and lying one on top of another) we recorded simply whether an insect was carrying <10, 10–50, 50–100 or >100 *Senecio* pollen grains. Body parts on which the pollen grains were found were also noted. Pollen contained in pollen sacs was visible on bees but was not included in the count because it was considered unlikely that the majority of these pollen grains would be transferred between plants.

#### Pollinator visits

Thirty random plants per population were used for floral visitor observations and observations were made on sunny days during which the temperature in the shade ranged between 17 and 23°C and wind gusts did not exceed 15 km h<sup>-1</sup>. Two observers monitored individual plants, recording the number of bees and hoverflies visiting flowers on a plant during a five

minute observation period, before moving to another plant. Since there were often several insects at a plant at any one time it was not possible to record how many flowers were visited by each insect.

Each observer conducted six, five-minute observations (as described above) per hour, between the hours of 10 am and 3 pm (it is during this time period that hoverflies and honeybees are most active on *Senecio* at this time of year, E. White, unpublished data). This procedure was performed by the two observers for one day per site for each of the six pure stands and two days per site for each of the mixed populations, in which one observer worked on one plant species and the second observer worked on neighbouring species simultaneously. Thus for each of the four population-types (i.e. for each treatment), a total of 13–15 hours of observations were conducted over a three-day period.

For each plant the following data were also recorded: height, number of open capitula, distance to nearest neighbour of same species, and whether or not the plant was in sun or shade during the time of observation. Plant density data were also obtained for each population-type using the PCQ method (Krebs 1989), using each of the 30 random plants per population-type as centre-points. Number of open capitula per plant for the four nearest neighbours to each of the 30 random plants was also recorded.

#### Seed-set

From each site, six or seven mature capitula (i.e. with shrivelled ray florets, containing mature seeds which were just about to be released) were collected from seven random plants, a total of 42–48 capitula per site. This was repeated for both species in mixed populations. Collections were made approximately two weeks after the pollinator observations were carried out. Seed set was determined by counting number of developed seeds per capitula.

#### Statistical analyses

All analyses were performed in SPSS v. 12.0.1. When variances were unequal, data were transformed by log<sub>10</sub>. Because data from individual sites were treated as a replicate of population-type, the factor 'site' was not included in any analysis.

**Quantity of pollen on insects** Using categorical data (categories were <10, 10–50, 50–100 and >100 pollen grains) a chi-squared test for association was performed to determine whether bees and hoverflies carried different amounts of pollen on their bodies.

**Effect of plant characteristics on visitation rate and time spent at plant** A range of variables can influence the attractiveness

of a plant to floral visitors. One-way ANOVAs were used to determine whether population-types differed in regard to density of plants, number of open capitula and plant height. In order to determine whether it was necessary to standardize the data to take into account any of these factors, multiple linear regression analyses (using the stepwise method) were performed for each of the four population-types separately, and for each of the two pollinator taxa within each population type. Dependent variables used were (i) number of visits per plant per five minute observation period (henceforth referred to as 'visitation rate') and (ii) time spent per insect per plant, and independent variables were: number of open capitula per plant, plant height and distance to nearest neighbour as independent variables.

Insect activity can also be influenced by micro-environmental variables, including level of sun or shade (Verma and Rana 1994, Kirchner *et al.* 2005). In order to test whether sun/shade was a factor that might explain differences in floral visitor activity between population-types, Pearson chi-squared tests were used to determine whether the number of observation periods conducted in a sunny position differed between population types. Independent-samples t-tests were performed for each population-type separately to establish whether bee/syrphid visits were more likely to occur in the sun or shade.

**Pollinator visits** One-way ANOVAs, followed by post-hoc Tukey tests, were used to determine whether (i) bee and (ii)

syrphid visits per plant per five minute observation period varied between population types.

**Seed set** A one-way ANOVA was used to determine whether differences existed in number of seeds set per capitulum between population types.

**Results**

*Quantity of pollen on insects*

Pollen grains of the two *Senecio* species were extremely similar morphologically, making it difficult to distinguish with any degree of certainty between the two species. However, both hoverflies and honeybees collected from mixed stands, as well as pure stands of each *Senecio* species, carried *Senecio* pollen on all body parts including legs, abdomen, thorax, head and mouthparts. Both of these insect taxa are therefore likely to act as pollinators for both *Senecio* species. Bees carried greater quantities of pollen than did hoverflies (df = 2;  $\chi^2 = 18.32$ ; P < 0.01).

*Vegetation structure*

Plant density was slightly lower in mixed *S. madagascariensis* stands than in other population-types (Table 1), but this difference was not significant (df = 3; f = 3.98; P = 0.05). Number of open capitula per plant and plant height did vary, however, between population types (df = 3; f = 205.76; P < 0.01 and df = 3; f = 398.54; P < 0.01 respectively), with plants in the *S. madagascariensis* population-types being smaller and having fewer open capitula than did *S. pinnatifolius* plants (Table 1).

*Visitation rates and plant characteristics*

Significant linear relationships existed between visitation rate and capitula number and/or plant height for both bees and syrphids. These relationships were weak and highly variable among population-types, however: overall R<sup>2</sup> values were low, ranging from 0.03 to 0.22, indicating that these variables accounted for only a small amount of the observed variation (Table 2). No significant relationship was

**Table 1. Vegetation structure of native *S. pinnatifolius* and exotic *S. madagascariensis* populations in pure and mixed stands (mean ±SE (n)). Letters in superscript denote groups (within columns) that are not significantly different from one another (P < 0.05).**

		Stem density m <sup>-2</sup>	Open capitula per plant	Height (cm)
Mixed stands	<i>S. pinnatifolius</i>	0.20 ± 0.05 (80) <sup>a</sup>	19.31 ± 1.69 (317) <sup>a</sup>	72.28 ± 2.27 (107) <sup>b</sup>
	<i>S. madagascariensis</i>	0.03 ± 0.01 (80) <sup>a</sup>	3.77 ± 0.26 (307) <sup>b</sup>	33.53 ± 0.93 (118) <sup>c</sup>
Pure stands	<i>S. pinnatifolius</i>	0.53 ± 0.13 (90) <sup>a</sup>	25.65 ± 3.11 (360) <sup>a</sup>	107.54 ± 2.01 (120) <sup>a</sup>
	<i>S. madagascariensis</i>	0.39 ± 0.10 (90) <sup>a</sup>	7.57 ± 0.44 (360) <sup>b</sup>	42.65 ± 1.18 (75) <sup>c</sup>

**Table 2. Summary of results of stepwise regression analyses for (i) amount of time spent per plant and (ii) visitation rate, by bees and syrphids to *Senecio pinnatifolius* and *S. madagascariensis* plants in mixed and pure stands. Independent variables include capitula number, plant height and distance to nearest neighbour (N.N. dist.). Values for non-significant variables, which were excluded from the stepwise analyses are not presented. \* = non-significant at the 0.05 level; Coef = coefficient; R<sup>2</sup> = overall R<sup>2</sup>.**

		Mixed stands						Pure stands						
		<i>S. pinnatifolius</i>			<i>S. madagascariensis</i>			<i>S. pinnatifolius</i>			<i>S. madagascariensis</i>			
		Capitula no.	N.N. dist.	height	Capitula no.	N.N. dist.	height	Capitula no.	N.N. dist.	height	Capitula no.	N.N. dist.	height	
Time spent per plant	Bees	Coef	0.09	0.07	0.31								0.23	
		t	3.60	3.54	2.56								2.46	
	P	<0.01	<0.01	<0.05									<0.05	
	R <sup>2</sup>		0.11		0.08			0.01*				0.04		
Syrphids	Coef											0.34		
	t											2.07		
	P											<0.05		
	R <sup>2</sup>		-0.05*		-0.02*			0.02*				0.09		
Visitation rate	Bees	Coef		0.46	0.35	-0.21	0.18			0.24			0.20	
		t			6.27	3.83	-2.29	2.40			2.48			2.04
		P			<0.01	<0.01	<0.05	<0.05			<0.05			<0.05
		R <sup>2</sup>		0.21		0.05		0.03			0.12			
	Syrphids	Coef	0.23	0.20		0.39	0.27			0.29				
		t	2.96	2.49		5.51	3.76			3.55				
		P	<0.01	<0.05		<0.01	<0.01			<0.01				
		R <sup>2</sup>		0.10		0.22		0.04*			0.08			



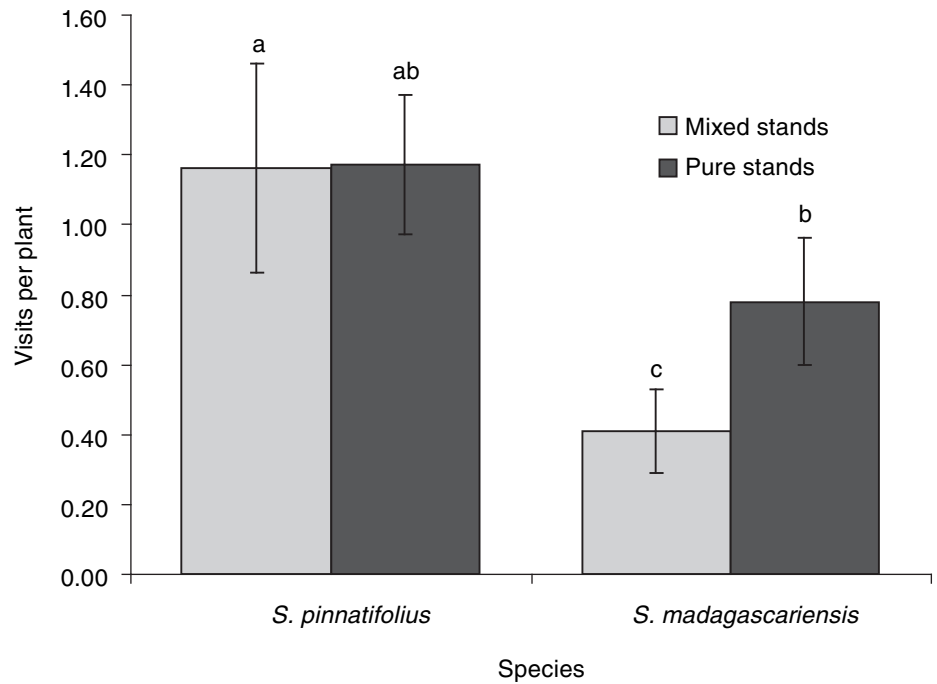
detected between visitation rate and distance to nearest neighbour (for bees) or visitation rate and plant height (for syrphids) in any population-type. Relationships between time spent at a plant by bee and syrphid visitors and number of open capitula, plant height and distance to nearest neighbour were also extremely weak or non-existent and highly variable among population-types (Table 2). Since we detected only weak and highly variable relationships between the measured individual plant characteristics and pollinator visitation rate and time spent at plant, per-plant visitation-rates data were not standardized to take into account any of these variables in subsequent analyses of results.

#### Pollinator visits

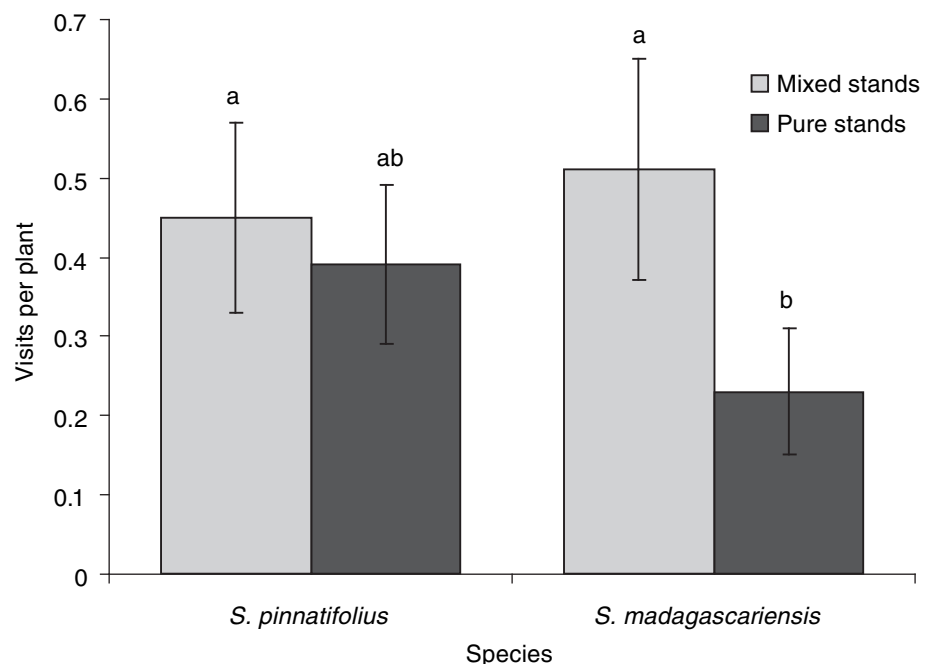
Bee visitation rate varied between population-types ( $df = 3$ ;  $f = 14.43$ ;  $P < 0.01$ ) (Figure 1). A post hoc Tukey test identified that *S. pinnatifolius* plants experienced a similar visitation rate regardless of whether or not *S. madagascariensis* grew nearby. Therefore, there is no evidence for either a facilitative or competitive effect of the exotic species on pollinator visits to the native in mixed populations. The visitation rate to pure *S. madagascariensis* stands did not differ significantly from the visitation rate to *S. pinnatifolius* in mixed stands. However, mixed *S. madagascariensis* stands recorded a significantly lower bee visitation rate than did pure *S. madagascariensis* stands and recorded a lower visitation rate than that recorded for *S. pinnatifolius* plants in either mixed or pure stands. This indicates a preference for the native *S. pinnatifolius* and possible competition for bee pollinators by the native *Senecio*.

Syrphid visits per plant also varied between population types ( $df = 3$ ;  $f = 4.05$ ;  $P < 0.01$ ) (Figure 2). Like bees, syrphids visited *S. pinnatifolius* plants at a similar rate regardless of whether or not the exotic species was present, indicating that the exotic species was having neither a facilitative, nor a competitive effect on visitation rates to the native in mixed stands. Visitation rates to *S. madagascariensis* plants in mixed stands were similar to those to the neighbouring *S. pinnatifolius* plants. However, in contrast to patterns of bee visitation, *S. madagascariensis* received lower visitation rates by syrphids in pure stands than when growing with the native *S. pinnatifolius*, indicating a potential facilitative effect of the native on visitation to the exotic.

Some evidence was obtained that pollinator visitation rates were higher in the sun than the shade for *S. pinnatifolius*, but not for *S. madagascariensis*, population-types (for bees in mixed *S. pinnatifolius* stands:  $df = 139$ ;  $t = 5.25$ ;  $P < 0.01$ ; and pure *S. pinnatifolius* stands:  $df = 170$ ;  $t = 3.45$ ;  $P < 0.01$ ; and syrphids in pure *S. pinnatifolius* stands:  $df = 129$ ;  $t = -3.57$ ;  $P < 0.01$ ). In



**Figure 1.** Bee visits per plant per five minute observation period for native *Senecio pinnatifolius* and exotic *S. madagascariensis* in pure and mixed stands. Bars represent mean  $\pm 2SE$ . Columns surmounted by the same letter are not significantly different ( $P < 0.05$ ) from each other.



**Figure 2.** Syrphid visits per plant per five minute observation period for native *Senecio pinnatifolius* and exotic *S. madagascariensis* in pure and mixed stands. Bars represent mean  $\pm 2SE$ . Columns surmounted by the same letter are not significantly different ( $P < 0.05$ ) from each other.

addition, different numbers of observation periods occurred in the sun between population-types ( $df = 3$ ;  $\chi^2 = 94.40$ ;  $P < 0.01$ ), with a greater number of observations periods being conducted on plants in the sun in *S. madagascariensis* population-types than in *S. pinnatifolius* population-types.

However, between-population-types variation in number of observation periods conducted in the sun does not adequately explain differences in floral visitor activity since the sunniest population-types (pure and mixed *S. madagascariensis* stands) recorded visitation rates similar to or

lower than the less sunny population-types (pure and mixed *S. pinnatifolius* stands (see Figure 1 and 2)).

#### Seed set

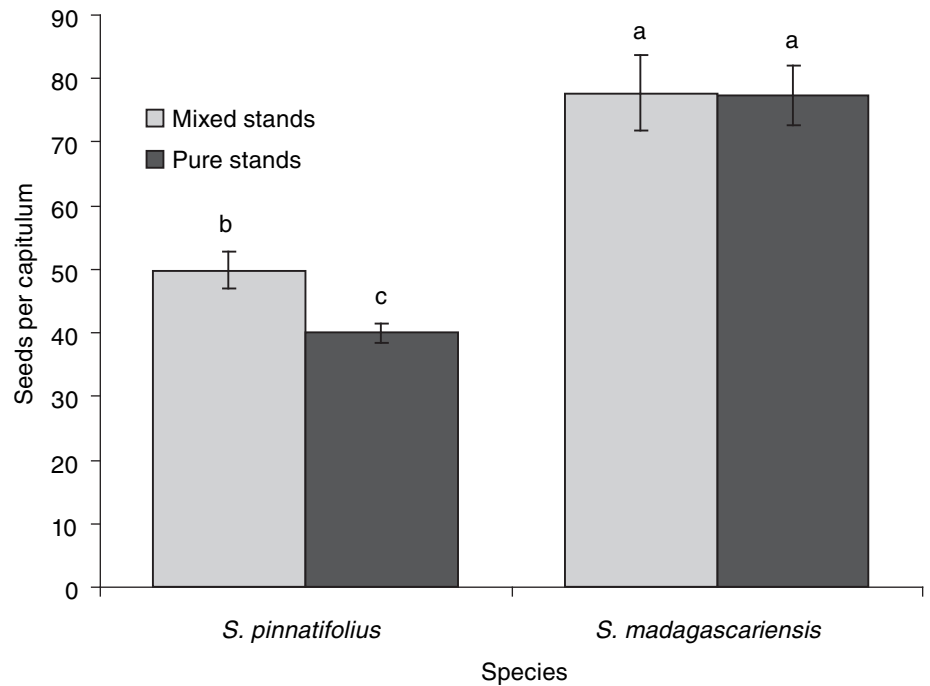
Seed set per capitulum varied between population-types (df = 3; f = 75.24; P < 0.01). A post-hoc Tukey test identified no difference in seed set between the two *S. madagascariensis* populations, and these set significantly more seeds per capitulum than did either *S. pinnatifolius* population type. *Senecio pinnatifolius* seed set was lower in pure stands than in mixed stands (Figure 3).

#### Discussion

We found no evidence therefore, that exotic *S. madagascariensis* was either competing for, or facilitating, pollinator visits to the native *S. pinnatifolius* at this stage in the flowering season. Native plants received similar numbers of bee and hoverfly visits regardless of whether or not the exotic species was present in the area. This most probably is due to the relatively low densities of *S. madagascariensis* flowers (compared with *S. pinnatifolius* flower density) during the study period.

Surprisingly, seed set in *S. pinnatifolius* was higher in mixed populations than when growing in isolation from the alien species. This is clearly not due to facilitation of pollinator visits by the presence of the alien species, but there are a number of possible explanations: (1) This may be due to abiotic factors not measured in this study, (2) Higher levels of herbivory have been recorded in pure populations of *S. pinnatifolius* (White *et al.* in press), which could have consequences for reproductive success in these plants, (3) seed set may be enhanced indirectly in mixed populations via hybridization. *Senecio pinnatifolius* and *S. madagascariensis* are known to hybridize (Radford 1997, Prentis *et al.* in press). If one species has greater male fitness (i.e. higher pollen germination rates) than another with which it is capable of hybridizing, seed set can be increased in the latter species when it receives pollen from the former (Anttila *et al.* 1998). If *S. madagascariensis* has higher male fitness than the native *Senecio*, seed set could be increased in mixed populations via this mechanism. Molecular studies show that *S. madagascariensis* does in fact, have a hybridization advantage, siring significantly more progeny to *S. pinnatifolius* maternal parents than expected based on proportional representation of the two species in sympatric populations (P. Prentis *et al.* in press). Further genetic work is currently underway to investigate this in greater detail.

Bees are likely to play a more important role than syrphids in pollination of *Senecio* species, since they carry significantly greater quantities of pollen and visited



**Figure 3.** Seeds set per capitulum for native *Senecio pinnatifolius* and exotic *S. madagascariensis* in pure and mixed stands. Bars represent mean seeds set per capitulum  $\pm 2SE$ . Columns surmounted by the same letter are not significantly different (P < 0.05) from each other.

capitula more frequently than did syrphids. The presence of the native *S. pinnatifolius* affected pollinator visitation rates to the alien *Senecio*, having opposite effects for bees and syrphids: bee visits to *S. madagascariensis* were significantly reduced by the presence of *S. pinnatifolius*, whilst syrphid visits increased. This may be due simply to differential responses of these two insect taxa to the presence of the native *Senecio*, with syrphid visits to *S. madagascariensis* being facilitated, whilst competition is occurring for bee visits. It is not uncommon for response to ecological variables to vary between pollinator species (Mitchell *et al.* 2004). However, interference competition between syrphids and honeybees might also be partially responsible for differences in visitation rates. Gross (2001) noted that Australian native bees were less likely to land on flowers of the shrub *Dillwynia juniperina* when honeybees were present. If, like native bees, syrphid activity is reduced by the presence of honeybees, syrphid visits to *S. madagascariensis* may increase in response to lower bee numbers when bees are attracted away from the alien to the more abundant flowers of the native species. If this were occurring, one would expect that syrphid visits to *S. pinnatifolius* plants would be reduced, relative to those to neighbouring *S. madagascariensis* plants. This was not the case here however, so this interaction probably does not fully explain differential syrphid visitation rates between mixed and pure *S. madagascariensis* stands.

Changes in pollinator behaviour, such as we have recorded, can have important consequences for plant reproduction and flowering patterns (Rathke 1983). In this case, however, altered visitation rates did not affect seed set in the exotic *Senecio*, indicating that either the facilitative and competitive effects cancelled each other out, or simply that *S. madagascariensis* is not pollen limited at these sites or at this point in its flowering period. Ghazoul (2004) also reported that although butterfly pollinator activity on the canopy tree species *Dipterocarpus obtusifolius* was significantly reduced in disturbed areas, this did not translate into a seed-set effect. He suggested that visits by other pollinator species probably compensated for reduced butterfly pollination. Given the generalist nature of plant-pollinator interactions and the widespread integration of exotic plants into the native plant-pollinator visitation web (Memmott and Waser 2002), it may be commonplace for reduced activity by one or two major pollinator taxa to be compensated for by visits from other generalist pollinators.

Depending on the point in the flowering season for the two *Senecio* species (e.g. at the end of the *S. pinnatifolius* flowering season, when exotic *S. madagascariensis* flowers are dominant), different scenarios might be observed than those which we report. Species such as the exotic and native *Senecio*, which have staggered flowering times, may indirectly act as mutualists by jointly maintaining pollinator populations at high levels over a longer time span

than would otherwise be the case (Waser and Real 1979). Alternatively, competitive interactions may be altered or reversed at different points in the flowering season, as pollinator preferences change in response to altered relative abundance of two or more plant species (Kephart 1983).

### Conclusions

The presence of the exotic *S. madagascariensis* had no effect on pollinator activity in the native *S. pinnatifolius* at the stage in the flowering season during which this study was conducted. This is not surprising considering the relatively low density of exotic flowers at this time. However, seed set in the native species was higher in mixed populations. Hybridization, if it is occurring, might have an impact on seed set and this issue warrants further investigation. In contrast, the presence of the native *S. pinnatifolius* did affect pollinator visitation rates to the exotic species, with bee visits being less frequent, and syrphid visits being more frequent (perhaps as a result of reduced interference competition with bees), though this did not result in alterations to seed set. In addition to commonly studied interactions such as competition, potential indirect interactions between invasive and native plant species should be taken into account when considering both management approaches for invasive plants and conservation strategies for native plant species.

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