The impact of bridal creeper (*Asparagus asparagoides*) on native ground-cover plant diversity and habitat structure

Claire J. Stephens[A], **José M. Facelli**[B] and **Andrew D. Austin**[A,C]
[A] Australian Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Sciences, The University of Adelaide, South Australia 5005, Australia.
[B] School of Earth and Environmental Sciences, The University of Adelaide, South Australia 5005 and Cooperative Research Centre for Australian Weed Management, Australia.
[C] Corresponding author: School of Earth and Environmental Sciences, Darling Building, The University of Adelaide, South Australia 5005, Australia.
Email: andy.austin@adelaide.edu.au

Summary
This study investigated the impacts of one of Australia's most serious environmental weeds, bridal creeper (*Asparagus asparagoides*), on a diverse native ground-cover plant community in *Eucalyptus* woodland. Bridal creeper is a creeping geophyte with an extensive root system of tuber-bearing rhizomes that has the potential to cover large areas of ground with dense foliage. Despite being a well-recognized 'Weed of National Significance' and its obvious overall impact in invaded areas, there are very few quantitative studies of the effects of this weed on native plant diversity and the habitat it invades. In a comparison of adjacent invaded and non-invaded habitat the impact of bridal creeper was found to be detrimental. There was a significant decrease in total species richness and frequency of native ground-cover plants in invaded areas, however the total species-richness and frequency of exotic species were not significantly reduced. There was a significant negative correlation between weed intensity (per cent cover) and the number of native and exotic species. A reduction of open, mossy patches and an increase in the level of *Eucalyptus* leaf litter in invaded habitat also suggests that bridal creeper has the potential to modify habitat structure. The possible consequences of the replacement of a species-rich and open ground-cover habitat into a closed homogenous one with increased leaf litter are discussed.

Keywords: ***Asparagus asparagoides*, environmental weed, *Eucalyptus* woodland, leaf litter, species diversity.**

Introduction
Exotic plants that invade and naturalize in native habitats are one of the greatest threats to natural ecosystems worldwide (Vitousek *et al.* 1997, Groves and Willis 1999, Dukes and Mooney 2004). Through direct competition with native plant species or by changing ecological conditions to the detriment of natives, weeds can reduce the abundance of native species in communities resulting in the formation of monospecific stands, or depauperate assemblages of tolerant species (e.g. Braithwaite *et al.* 1989, Griffin *et al.* 1989, Clouse 1999, Blossey *et al.* 2001). Since little is known about the effects of many of the most serious environmental weeds in Australia, there is an urgent need for research into their impacts on biodiversity, community structure and ecosystem processes (Adair and Groves 1998). *Asparagus asparagoides* (L.) Druce (Asparagaceae), commonly known as bridal creeper, was introduced into Australia from South Africa in the late 19th Century as an ornamental garden plant. It is now categorized as a 'Weed of National Significance', and has naturalized in a range of soil and habitat types including wet and dry sclerophyll forests, mallee shrubland, creek and river banks and coastal vegetation across south-western Western Australia, South Australia, Victoria and coastal New South Wales (Groves and Willis 1999, Agriculture and Resource Management Council of Australia and New Zealand 2001, Morin *et al.* 2006). The species is a creeping geophyte with an extensive root system of tuber-bearing rhizomes that has the potential to cover large areas of ground, shrubs and tree trunks with dense foliage (Raymond 1999). Both native and exotic frugivorous birds consume the fleshy red berries and can disperse seeds over considerable distances. This leads to the invasion of undisturbed habitats where, unlike the majority of environmental weeds (Vitousek *et al.* 1997, Adair and Groves 1998), it will successfully germinate without any type of soil disturbance (Stansbury 1996, Raymond 1999). In most regions the above-ground biomass senesces in early summer leaving the root system which re-shoots again in autumn.

Raymond's (1999) comprehensive ecological study of bridal creeper concluded that eradicating the weed from Australia would be a difficult, if not an impossible task. As it can smother large areas, bridal creeper was predicted to be modifying the ground-cover habitat it invades, thus affecting associated native biota. Indeed, bridal creeper is considered a threat to a range of native herbs, lilies and orchids across southern Australia (Sorensen and Jusaitis 1995, Groves and Willis 1999, Agriculture and Resource Management Council of Australia and New Zealand 2001, Bickerton 2001) and has been experimentally shown to reduce the cover of a variety of regenerating native ground-cover and shrub species (Turner and Virtue 2006). Therefore, this study aimed to determine the impact of bridal creeper on the native plant community and associated habitat variables in *Eucalyptus* woodland typical of the type of native habitat invaded by the weed in southern Australia and provide baseline data for further investigations into its impacts on higher trophic levels such as terrestrial invertebrates.

Methods
Study site
This study was conducted in Mount Billy Conservation Park (CP) (35°25'72"S, 138°35'82"E) on the Fleurieu Peninsula, South Australia. The park is 208 ha, with an elevation ranging from 100–216 m a.s.l. and is surrounded by cleared grazing land, except for the southern end that adjoins an uncleared area surrounding the Hindmarsh Valley Reservoir. Mean maximum summer temperatures range from 24–27°C and mean maximum winter temperatures from 13–15°C. The area has a strong winter rainfall pattern with a mean annual rainfall of 766 mm (Bureau of Meteorology, Melbourne).

Mt Billy CP contains mallee, woodland and forest habitats and, due to its history as a fenced-off catchment for a drinking-water reservoir, has remained in a relatively natural state with minimum disturbance. Over 430 native plant species have been recorded in the park, with a particularly high diversity of ground-cover herbs, ferns, lilies and orchids (R. Taylor personal communication 2000). The habitat within Mt Billy CP used for this study was medium-height eucalypt woodland with a moderately open canopy of *Eucalyptus leucoxylon* F.Muell. (South Australian blue gum) and *E. fasciculosa* F.Muell. (pink gum), a sparse mid-story of *Acacia pycnantha* Benth. (golden wattle), *Dodonaea viscosa* Jacq. (sticky hop-bush), and *Xanthorrhoea semiplana* F.Muell. (flat-leafed grass-tree), and a diverse, low ground-cover of native herbs and grasses. Bridal creeper was by far the dominant exotic plant species in the park.

Vegetation and habitat survey
As bridal creeper invades and smothers the ground-cover habitat, the focus of this study was the native ground-cover plant community. Eight pairs of native (control) and bridal creeper-invaded transects (15 m × 1 m) were established in two locations (sites) approximately 100 m apart within the woodland. An underlying assumption when using such a multi-site comparison technique is that the species composition of invaded areas is the same or similar to control areas prior to invasion. Thus, as pre-invasion states cannot be determined, care needs to be taken to match control and weed-invaded habitats (Adair and Groves 1998). In contrast to many invasive plant species, bridal creeper can establish without prior habitat disturbance (Stansbury 1996, Raymond 1999). As such, areas could be chosen with the same history and no prior soil or fire disturbance in both invaded and native habitat. Transect locations in both native and invaded habitats were primarily selected based on the presence or absence of bridal creeper. However, effort was made to control for natural between-site microhabitat variability by locating transects in the same habitat (open spaces among eucalypt trees), and away from the edge of native and invaded patches to limit the effect of changes in microhabitat and community structure that can occur at the edge of a habitat (Schowalter 2000). In addition, transect pairs were placed parallel along the hill to account for the sloping habitat and were established similar distances away from the base of large eucalypt trees that seasonally shed large amounts of bark that covered the ground-cover vegetation. The area beneath these trees also would have been the invasion points of the weed and may have originally had different microhabitats prior to invasion (Stansbury 1996; Raymond 1999). Tree canopy cover was similar above each transect (around 70%) and each bridal creeper invaded transect was located within 10 m of a native transect. The rust fungus biological control *Puccinia myrsiphylli* (Thüm.) G.Winter was released outside the experimental transects at Mt Billy CP during the study and there was no evidence of its presence in these transects during this time (CJS personal observations).

Transects in native habitat were established in patches with little or no bridal creeper, while weed-invaded transects had considerable cover of bridal creeper. Within each transect, using 24 randomly placed 10 × 10 cm quadrats, the following measurements were recorded: the per cent cover in 5% increments of bridal creeper, leaf litter, moss (bryophytes), and bare ground (measured independently, thus did not total to 100%), and the identity of each plant species (recorded as presence/absence). As bridal creeper and native plants senesce over summer, the plant survey was undertaken in spring (September 2000). This was when bridal creeper was at its maximum growth and coincided with the maximum growth and presence of flowers and seed heads of native species that allowed for their identification. Many grasses could not easily be identified in the field during the survey due to lack of seed heads, thus were recorded as 'Poaceae sp.'. When separating plant species into native and exotic species for analysis, 'Poaceae sp.' were grouped with the native species, however it is likely that some were exotic. To account for the seasonal differences in habitat structure, the per cent cover of bridal creeper and leaf litter was also recorded once every four weeks from April 2001 to May 2002 in 24 random quadrats (10 × 10 cm) within each transect. An indication of vertical habitat structure was also recorded by measuring the maximum height of the vegetation, including bridal creeper (or litter or bare ground), at 60 random points within each transect.

Data analysis
The data were analysed using the number of species (counts) and species frequency. Bridal creeper was included in the analysis only as an explanatory (habitat) variable, not as a plant species. As native and bridal creeper transects were paired, the differences in plant species richness and frequency and the per cent cover of bridal creeper, litter, moss and bare ground between native and invaded transects were analysed using paired t-tests using GraphPad Prism (ver. 4.0 for Macintosh, GraphPad Software, San Diego California USA). The per cent cover of bridal creeper, vegetation height and litter cover in invaded and non-invaded transects over time were compared using repeat measures analysis of variance (ANOVA) using GraphPad Prism with Bonferroni post-tests to determine which sample dates differed for invaded and non-invaded transects. The relationship between the level of bridal creeper invasion (per cent cover) and plant species richness was examined using linear regression in GraphPad Prism. Non-metric multi-dimensional scaling (NMDS) using PC-ORD (ver. 4.25) was used to examine plant community composition and habitat variables. Non-metric multi-dimensional scaling is generally considered to be the most effective ordination method for community data (McCune and Grace 2002). The NMDS was run using the Sørensen distance measure and the 'Auto-pilot: slow and through' option in PC-ORD and significant habitat variables were overlaid as correlation vectors to further investigate the arrangement of transects in the ordination. Native and exotic species in invaded and non-invaded transects were also examined by comparison of their ranked mean frequencies.

Results

Plant species richness
A total of 74 ground-cover plant species were recorded. Of these, 47 species were native and 27 were exotic, mostly annual pasture grasses and weedy herbs, presumably from surrounding farmland. Areas invaded by bridal creeper had significantly lower plant species richness (t = 4.708, P = 0.0022) (Figure 1a) and species frequency (t = 5.618, P = 0.0008) (Figure 1b) than non-invaded habitat. When native and exotic species were examined separately, only the number (t = 5.267, P = 0.0012) (Figure 1a) and frequency (t = 7.664, P = 0.0001) (Figure 1b) of native species were significantly different. The number of exotic plant species recorded were not significantly different between invaded and non-invaded transects (t = 2.103, P = 0.0736) (Figure 1a), nor was species frequency (t = 0.7719, P = 0.4654) (Figure 1b).

A strong negative relationship was found between the per cent cover of bridal creeper and the total number of plant species (R^2 = 0.9037, P <0.0001), the number of native (R^2 = 0.8120, P <0.0001), and number of exotic species (R^2 = 0.9005, P <0.0001) (Figure 2).

Community composition
The ordination of transects showed that bridal creeper and native transects clearly separated based on plant frequency and species composition, particularly along Axis 1 where the bridal creeper transects cluster on the right with the native transects to the left (Figure 3). This separation can be related to an overlay of environmental variables showing that the per cent cover of moss, the total number of plant species and the number of native plant species correlated with the plant community recorded from transects in native habitat, whereas increasing litter cover and per cent cover of bridal creeper correlated with transects in invaded habitat (Figure 3).

The ranked frequency of native plant species (Figure 4a) revealed that most species found in invaded transects were also those more frequently recorded in native transects. Thus, the assemblage of native plants remaining in habitat invaded by bridal creeper is a subset of the ground-cover plant community. However, most exotic plant species (Figure 4b) are found in both native and invaded transects.

Bridal creeper and habitat variables
The per cent cover of bridal creeper recorded from native transects ranged from 0–10 (mean 0.86%) and from invaded transects 0–100 (mean 58.69%) (t = 18.41, P <0.0001). There was no significant difference in the small per cent of bare ground

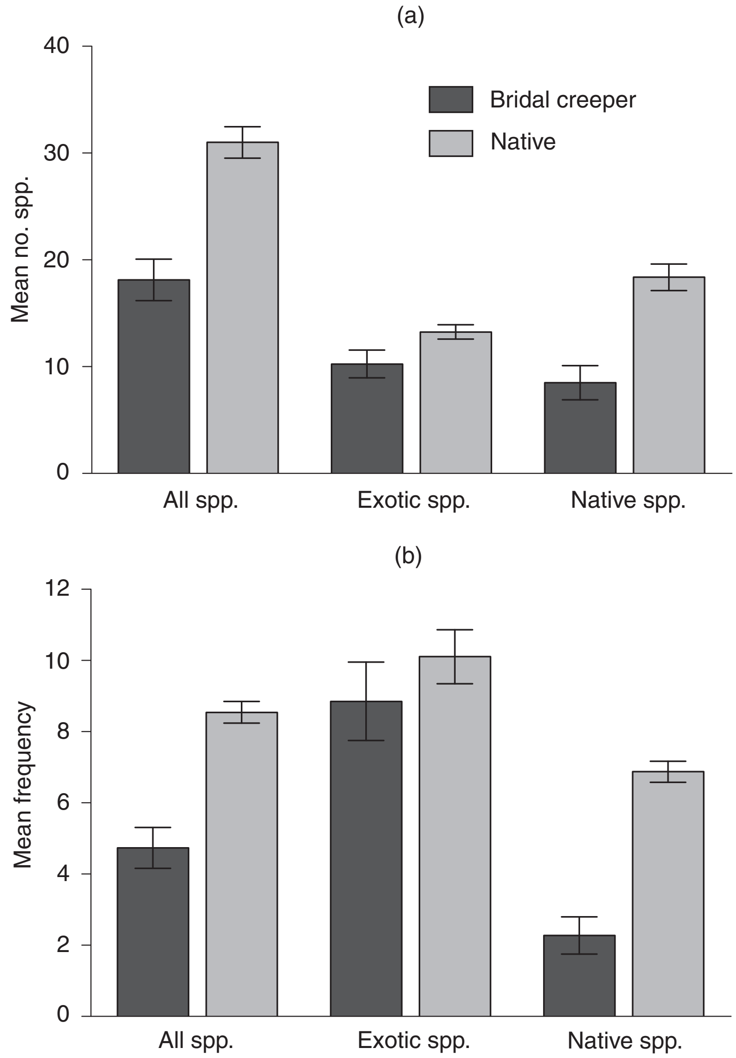

Figure 1. Mean (±SE) (a) number and (b) frequency of all, native, and exotic ground-cover plant species recorded from bridal creeper (n = 8) and native (n = 8) transects.

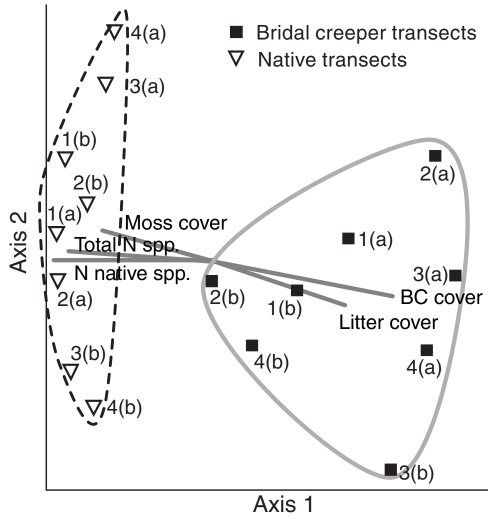

Figure 3. Two-dimensional ordination (NMDS) of plant frequency and species composition. The numbers next to each transect correspond to transect pairs and letters in brackets correspond to sites (a and b). The model explains 87.8% of the total variation (Axis 1 = 85.1%, Axis 2 = 2.7%) and the superimposed vectors (constrained to R^2 = 0.5) show the correlation between plant species and environmental variables. The length of each vector indicates the strength of the correlation and the orientation the direction of increase. Distance measure: Sørensen; final stress for the 2-dimensional solution = 6.82649; final instability = 0.00001; number of iterations = 56.

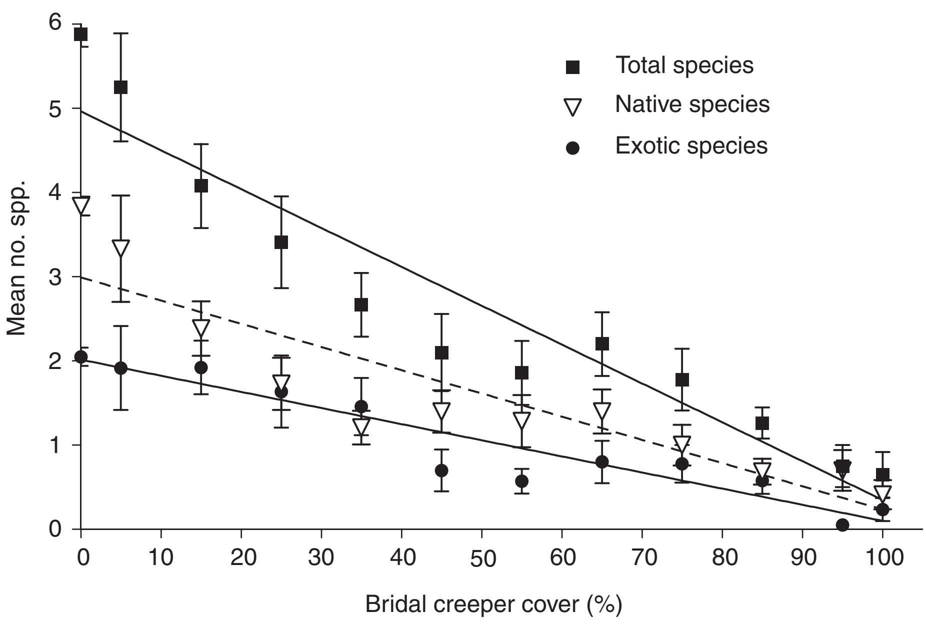

Figure 2. Relationship between the per cent cover of bridal creeper and mean (±SE) number of ■ total (R^2 = 0.9037, P <0.0001), ▽ native (R^2 = 0.8120, P <0.0001), and ● exotic (R^2 = 0.9005, P <0.0001) plant species (n = 384 quadrats).

(t = 1.122, P = 0.2987), however there was a higher per cent cover of leaf litter recorded from bridal creeper transects (t = 5.529, P = 0.0009) and a greater cover of moss in native transects (t = 4.825, P = 0.0019) (Figure 5).

As previously reported from other Mediterranean climates in Australia (Raymond 1999, Morin *et al*. 2006), the above-ground biomass of bridal creeper was strongly influenced by sample date ($F_{1,98}$ = 1524.61, P <0.0001). The per cent cover of bridal creeper peaks in the winter and spring months, decreases significantly over summer as the weed senesces, and rapidly increases again in autumn as it re-shoots (Figure 6a). There was a significant interaction effect between sample date and habitat ($F_{13,98}$ = 26.30, P <0.0001), indicating there were differences in the amount of bridal creeper between native and invaded transects over time. However, this was due to the large differences in the amount of bridal creeper cover in invaded transects

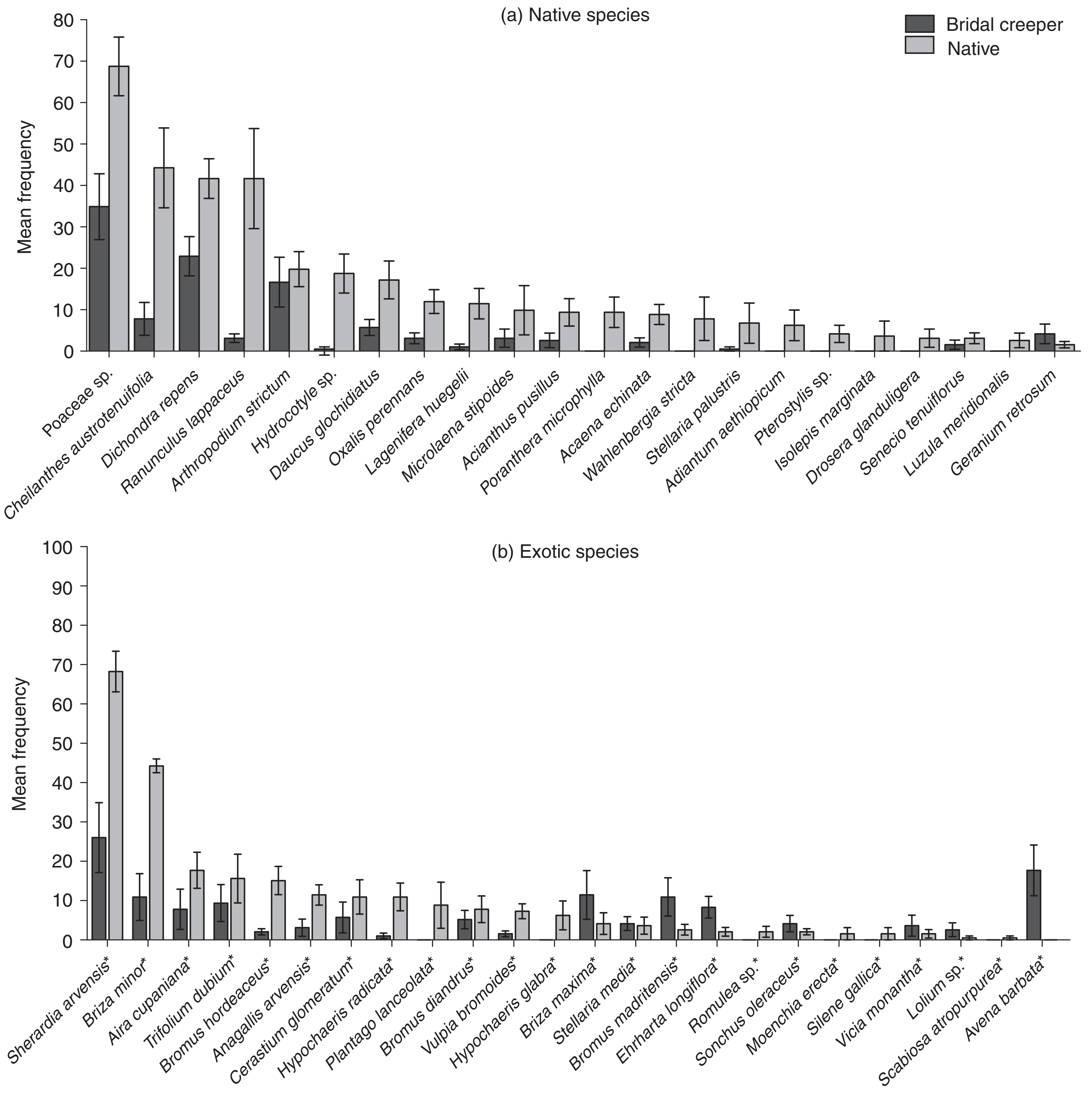

Figure 4. Mean (±SE) frequency of (a) native plant species and (b) exotic plant species (*) from bridal creeper and native transects. For comparison, plant species have been ranked by descending frequencies in native transects and species with a mean frequency of <2% were not included for ease of illustration.

between winter/spring and summer/autumn. Reflecting the choice of transect locations, bridal creeper cover was constantly greater in invaded transects ($F_{13,98}$ = 1.09, P = 0.3341) (Figure 6a).

Vegetation height was also significantly effected by sample date ($F_{1,98}$ = 692.30, P <0.0001) and habitat ($F_{13,98}$ = 8.75, P <0.0001), with taller vegetation (bridal creeper) in invaded transects. The maximum height of bridal creeper peaks over the same period as its per cent cover. The vegetation in non-invaded areas also follows a similar pattern, although the difference between seasons is not as great (Figure 6b). There were significant interaction effects between habitat and time for vegetation height ($F_{13,98}$ = 26.41, P <0.0001), and post-tests showed there were significant differences in mean height for all sample dates, except for the last sample in April 2002 (Figure 6b).

Both sample date ($F_{1,98}$ = 306.35, P <0.0001) and habitat ($F_{13,98}$ = 5.44, P <0.0001) significantly influenced the amount of leaf litter recorded. There was also a significant interaction between sample date and habitat ($F_{13,98}$=2.30, *P*=0.0104). Post-tests revealed that during autumn and early winter, when there is the greatest litter cover in both habitats, there was no difference in leaf litter between invaded and non-invaded habitat. As the season progressed however, there was a decline in litter cover in native transects while it remained fairly constant in invaded transects, resulting in significant differences in cover between bridal creeper and native habitats (Figure 6c).

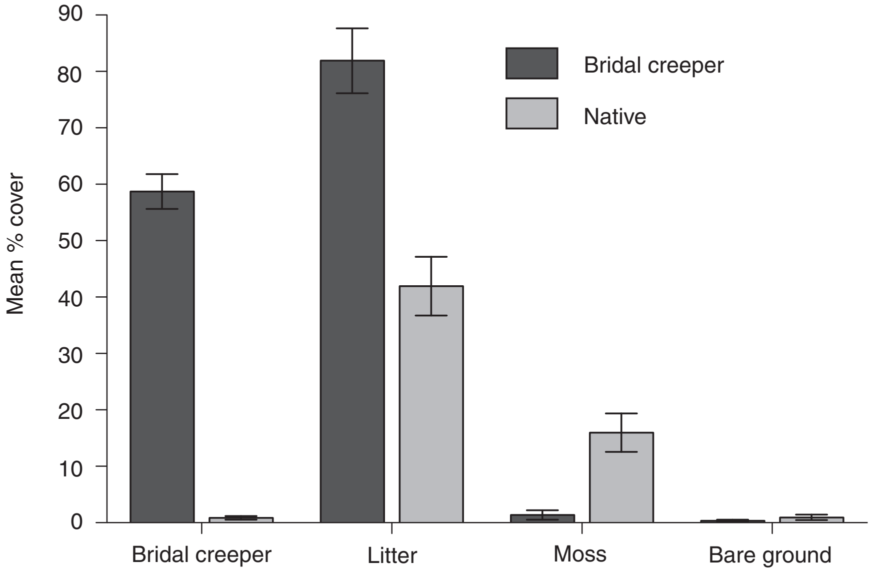

Figure 5. Mean (±SE) per cent cover of bridal creeper, litter, moss, and bare ground from bridal creeper (*n* = 8) and native (*n* = 8) transects.

Discussion

Bridal creeper and native plant species

The results of this study confirm that the invasion of bridal creeper has a negative effect on native plant biodiversity by reducing both species richness and abundance (frequency) (Figure 1). Those species remaining in invaded areas were the most abundant species from the control transects (Figure 4), suggesting that rare species, with naturally low frequencies, were the first to be displaced by bridal creeper. This may have an impact on future invasions, or has possibly even facilitated the spread of bridal creeper, as it has been shown that a reduction in plant species richness at a local scale via the loss of rare species can increase the invasibility of a system (Lyons and Schwarta 2001).

There was a negative relationship between increasing bridal creeper cover and decreasing number of native ground-cover species such that when bridal creeper cover was 90–100%, no other native ground-cover species were recorded (Figure 2). This response to weed invasion where some measure of weed infestation (e.g. per cent cover of bridal creeper) increases uniformly in relation to a decrease in some biodiversity value (e.g. native plant species richness) has been previously reported in Australia (e.g. Braithwaite *et al.* 1989) and described by Adair and Groves (1998) ('Type II model'). This model predicts that any level of weed reduction will result in an increase in biodiversity values. Thus, it may be predicted that a decrease in bridal creeper below 90–100% cover will lead to an increase in the number of native plant species present in the study area (Figure 2). Alternately, intervention such as herbicide use or biological control agents that prevent high levels of bridal creeper should maintain higher numbers of plant species.

Bridal creeper's stem density can reach >90 stems m^{-2} (around 80% cover), shading the soil and ground-cover habitat and reducing the amount of light reaching the soil by up to 94% (Raymond 1999), which in other systems has been shown to reduce under-story forb abundance and species richness (Carson and Root 2000). Although not directly measured in the current study, bridal creeper's above-ground biomass was likely to be greater than that of native species as vegetation height was constantly greater in bridal creeper transects (Figure 6b). Furthermore, the greater per cent cover of moss in native areas (Figure 5) also indicates a more open habitat with less vegetation cover. This suggests that bridal creeper probably has increased resource use (such as water, light and nutrients) in invaded areas.

The majority of bridal creeper's biomass (over 80%) is in the root tubers (Raymond 1999). Up to 6000 individual tubers per square metre with an above ground biomass averaging between 70–80% cover has been reported for this species in other south-eastern Australian habitats (Raymond 1999). Extrapolating to the current study, where the mean per cent cover of bridal creeper was around 60% (Figure 5) and often reached 100%, the below ground biomass is likely to be reaching similar levels at Mt Billy CP. It is possible that competition with bridal creeper's massive root system for nutrients, water and 'space' below ground has more of an impact on native plants than the more ephemeral shading effect of its aboveground foliage (Groves and Willis 1999). Phenological and morphological similarities between bridal creeper and the endangered greenhood orchid *Pterostylis arenicola* in South Australia are considered to be the likely cause for the negative relationship between bridal creeper cover and orchid numbers, as both the orchid and weed grow from underground tubers over autumn and winter, and both fruit and senesce during spring and summer (Sorensen and Jusaitis 1995, Groves and Willis 1999). This may be also an issue in the current study where there were many native geophytes and other annual and perennial species that senesce and shoot or re-shoot at the same time as bridal creeper. Invasive plant species have also been shown to reduce fungal diversity and abundance, including mycorrhizal species (Goodwin 1992, Allen *et al.* 1995). This has implications not only for decomposition processes, but also for the many orchid species with specific mycorrhizal symbionts (Jones 1988) growing in this and other woodland habitats. Thus, further investigation of the impacts of bridal creeper's underground root system is required to determine the impact on fungal communities.

The total species-richness and frequency of the other exotic plants in the habitat (mostly pasture species) were not significantly reduced in bridal creeper invaded areas (Figure 1). It is possible that many of these species are more tolerant of bridal creeper invasion than many native species because they are also 'weedy', possessing many characteristics such as the ability to capture resources earlier and faster than natives that have allowed them to be successful invaders. However, there was a negative relationship between bridal creeper cover and exotic plant species-richness (Figure 2) and many of the exotic species recorded also had reduced frequencies in invaded habitat (Figure 4b). Therefore, in this study system, bridal creeper has a detrimental effect on, and eventually displaces, both native and exotic species. Turner and Virtue (2006) also recorded reduced cover of exotic species in bridal creeper invaded areas. The displacement of exotic species suggests that invasion by bridal creeper does not trigger a complete invasion meltdown (Simberloff and von Holle 1999), i.e. bridal creeper does not seem to facilitate the invasion of other plant species. However, further studies that address other key components of the ecosystem, such as invertebrates, are required to confirm this.

Leaf litter

The invasion of bridal creeper also modifies some of the physical characteristics of the ground level habitat, such as moss and leaf litter cover (Figure 5). Increased litter may have also contributed to the lower plant species richness (and moss cover) in invaded areas as leaf litter often has a

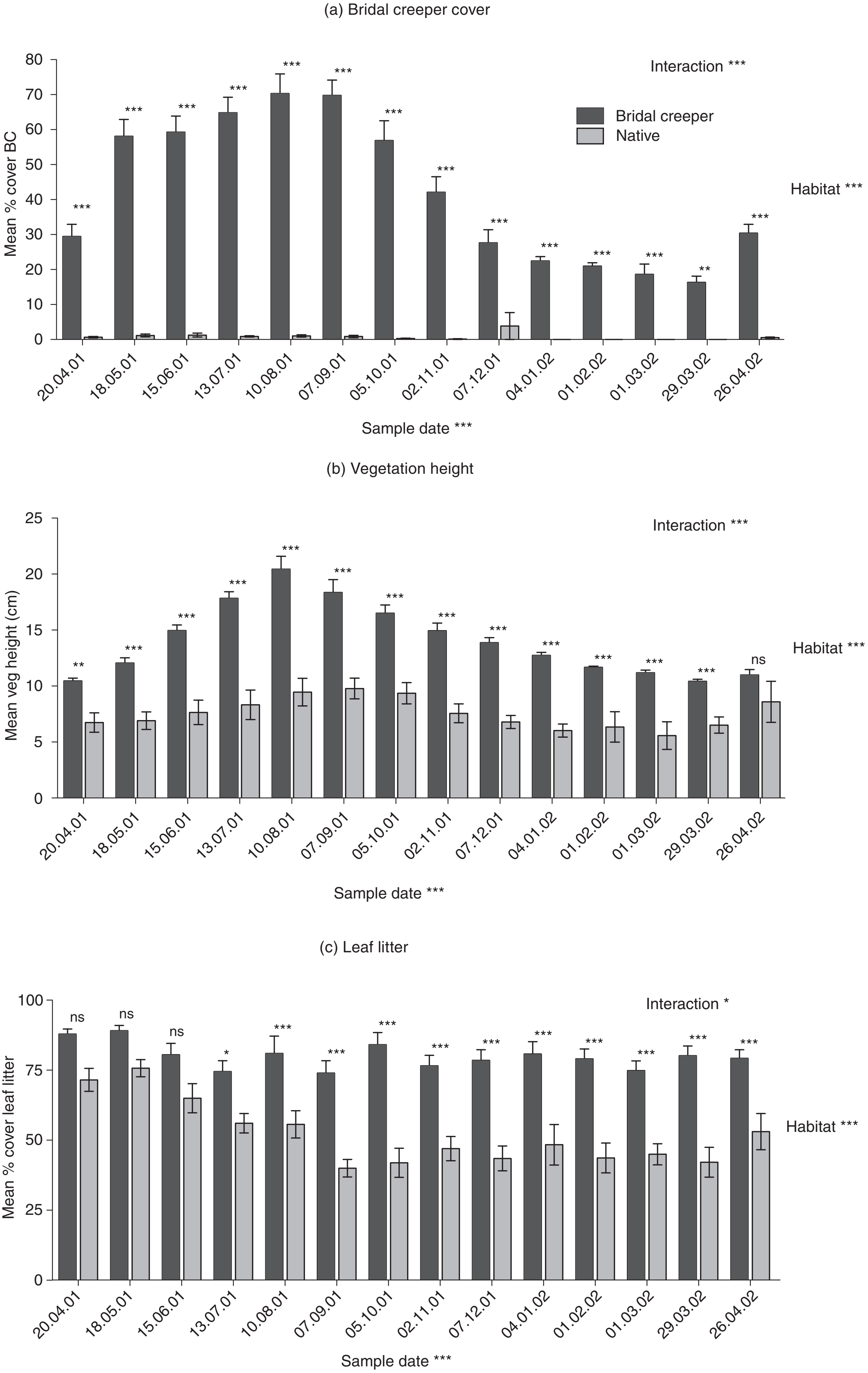

Figure 6. Mean (±SE) (a) per cent cover of bridal creeper, (b) maximum vegetation height, and (c) per cent cover of leaf litter over time from bridal creeper (*n* = 8) and native (*n* = 8) transects. ns: not significant, * P <0.05, ** P <0.01, ***P <0.001.

negative effect on vegetation influencing factors such as germination rates, light levels and herbivory (Facelli 1994, Foster and Gross 1998) and is considered to be one of the fundamental factors controlling plant community structure (Xiong and Nilsson 1999). In particular, the higher levels of *Eucalyptus* leaf litter in bridal creeper invaded areas could have a considerable impact on native plant species due to the leaching of allelopathic chemicals that inhibit seedling growth (May and Ash 1990, Florentine and Fox 2003).

Typically, leaf litter is not equally distributed across a habitat and litter patchiness is common in forests, woodlands and other habitats with plant canopies (Facelli and Carson 1991). Litter is frequently redistributed by wind and water, often accumulating beneath understorey plants, thus having large impacts on resource distribution, plant productivity and animal activity (Facelli and Pickett 1991, Todd *et al.* 2000, Boeken and Orenstein 2001). Dighton (2000) showed that leaf litter accumulation was related to the density of shrub stems, i.e. the more ground-cover shrubs (and hence stems), the greater amount of litter on the ground. Thus, it is likely that the dense structure of bridal creeper stems and leaves have a similar effect in invaded habitat. Further evidence for litter accumulation around bridal creeper is the temporal comparison that showed over autumn and early winter that there was little difference in leaf litter cover between habitats, but as the season progressed, litter cover in native areas was reduced while remaining constant across invaded sites (Figure 6c). As this coincides with bridal creeper's autumn re-growth, it is possible that when wind and water redistribute leaf litter it becomes trapped by the weed's twinning stems and accumulates under the thick foliage. Another investigation of bridal creeper at Mt Billy CP also indicates greater litter accumulation in invaded habitat. Holt (2005) found that litter depth was also greater under bridal creeper due to a deeper, more decomposed litter layer than in native areas, suggesting that bridal creeper does 'trap' and accumulate leaf litter under its thick foliage.

Determining the impacts of weed invasion by comparing locations differing in the presence or absence of weeds is often problematic because of confounding effects of other site factors (Adair and Groves 1998). Thus, there are alternative explanations for the higher accumulation of litter under bridal creeper. Firstly, bridal creeper may preferentially grow where there is a greater cover of litter. Raymond (1999) showed that litter cover enhanced the germination of bridal creeper seeds. However, this effect was somewhat confounded, as sites with greater litter cover were also under tree canopies and, once established, canopy cover did not affect seedling survivorship. In addition, the invasion points of bridal creeper are typically under trees (Stansbury 1996), where more leaf litter may be expected. The age of invasion at Mt Billy CP (>20 years, R. Taylor personal communication 2000) is such that the weed had spread out from the base of large trees so the invaded areas that were measured had similar canopy cover as native ones. This careful selection of sites with similar slope and canopy cover, and the obvious 'open' type of ground-level habitat in non-invaded areas, does suggest that the extent of leaf litter was not as great prior to invasion.

If the presence of bridal creeper results in greater litter accumulation in invaded areas, then the weed not only has a direct negative impact on native plant diversity, but is likely to change ecosystem processes such as decomposition of organic matter, and nutrient and soil dynamics. Decomposition rates are influenced by litter quality and composition, and site microclimate (Köchy and Wilson 1997). Several invasive species have been shown to have such effects, such as tamarisk trees (*Tamarix aphylla*) in northern Australia, which produce a more densely packed litter layer with lower cover than the native eucalypt woodland they displace (Griffin *et al.* 1989). Invasive species can also change the timing of decomposition and thus nutrient release into invaded systems, e.g. *Lythrum salicaria* in North America (Blossey *et al.* 2001). Because bridal creeper had not changed the woodland canopy (although it may eventually by impacting on recruitment), the composition of leaf litter was the same between invaded and non-invaded habitats, consisting of *Eucalyptus* and *Acacia* leaves, bark and twigs. However, there may be fine-scale changes in the litter produced by the monoculture of bridal creeper compared to that from a diverse community of native herbs and grasses that was not measured. The significant shading effects of bridal creeper (Raymond 1999) may also modify the temperature and moisture of the litter microclimate and thus, decomposition rates (Köchy and Wilson 1997, Standish *et al.* 2004). Litter may also have complex effects on different species. For example, under dry conditions it may enhance seedling establishment, whereas under wetter conditions it may reduce survivorship because of increased herbivory or pathogen activity (Facelli 1994, Facelli *et al.* 1999). Therefore, based on the preliminary findings from the current study, a more targeted investigation into bridal creeper growth and its effects on litter accumulation, and associated decomposition and nutrient cycles, is required. In particular, a comparison of stem density, litterfall and litter depth, composition, quality and nitrogen content between native and invaded habitat would be valuable in determining both community- and ecosystem-level effects.

Conclusion

Invasive species that constitute a large proportion of an ecosystem's biomass at one trophic level can alter ecosystem structure and processes (Dukes and Mooney 2004) and this study suggests that bridal creeper can do this. By increasing both the above- and below-ground plant biomass and transforming an open, species-rich ground-cover habitat into a closed, homogenous one, bridal creeper has a deleterious effect on the native plant community. In addition to reducing native plant diversity, bridal creeper may also change ecosystem processes such as nutrient and soil dynamics and decomposition via litter accumulation that, in turn, may affect processes such as seedling establishment and growth. Invaders that modify ecosystems by changing the availability or quality of resources (e.g. food, living space, water, heat or light) have been shown to cause cascading effects for associated plants and animals (Crooks 2002). Accordingly, one prediction from the significant decrease in plant diversity and considerable habitat changes due to bridal creeper invasion is that it causes flow-on changes in the associated faunal communities, such as plant- and litter-associated arthropods, in this woodland and other invaded habitats.

Acknowledgments

We thank Ron Taylor (Friends of Mt Billy Conservation Park) for his assistance with field site selection and plant surveys and identifications; Nicholas Stevens and Elise Head for fieldwork assistance; and two anonymous reviewers for their helpful comments on the manuscript. This research was funded by a University of Adelaide Postgraduate Scholarship and a Supplementary Scholarship from the Cooperative Research Centre (CRC) for Australian Weed Management.

References

Adair, R.J. and Groves, R.H. (1998). Impact of environmental weeds on biodiversity: a review and development of a methodology. National Weeds Program, Environment Australia, Canberra.

Agriculture and Resource Management Council of Australia and New Zealand, Australian and New Zealand Environment and Conservation Council and Forestry Ministers (2001). Weeds of National Significance: bridal creeper (*Asparagus asparagoides*) strategic plan. National Weeds Strategy Executive Committee, Launceston.

Allen, M.F., Morris, S.J., Edwards, E. and Allen, E.B. (1995). Microbe-plant interactions in Mediterranean-type habitats: shifts in fungal symbiotic and saprophytic functioning in response to global change. *In* 'Global change and Mediterranean-type ecosystems', eds. J.M. Moreno and W.C. Oechel, p. 287. (Springer-Verlag, New York).

Bickerton, D. (2001). Draft recovery plan for *Pterostylis bryophila* (Hindmarsh Valley greenhood). National Parks and Wildlife SA, Adelaide.

Blossey, B., Skinner, L.C. and Taylor, J. (2001). Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation* 10, 1787-1807.

Boeken, B. and Orenstein, D. (2001). The effect of plant litter on ecosystem properties in a patchy Mediterranean semi-arid shrubland. *Journal of Vegetation Sciences* 12, 825-32.

Braithwaite, R.W., Lonsdale, W.M. and Estbergs, J.A. (1989). Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation* 48, 189-210.

Carson, W.P. and Root, R.B. (2000). Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70, 73-99.

Clouse, R. (1999). Leaf-litter inhabitants of a Brazilian pepper stand in Everglades National Park. *Florida Entomologist* 82, 388-403.

Crooks, J.A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97, 153-66.

Dighton, J., Bonillas, A.S.M., Jimînez-Nûnez, R.A. and Martînez, N. (2000). Determinates of leaf litter patchiness in mixed species New Jersey pine barrens forest and its possible influence on soil and soil biota. *Biology and Fertility of Soils* 31, 288-93.

Dukes, J.S. and Mooney, H.A. (2004). Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural* 77, 411-37.

Facelli, J.M. (1994). Multiple indirect effects of plant litter affect the establishment of woody seedlings on old fields. *Ecology* 75, 1727-1735.

Facelli, J.M. and Carson, W.P. (1991). Heterogeneity of plant litter accumulation in successional communities. *The Bulletin of the Torrey Botanical Club* 118, 62-6.

Facelli, J.M. and Pickett, S.T.A. (1991). Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* 53, 12-35.

Facelli, J.M., Williams, R., Fricker, S. and Ladd, B. (1999). Establishment and growth of seedlings of *Eucalyptus obliqua*: interactive effects of litter, water and pathogens. *Australian Journal of Ecology* 24, 484-94.

Florentine, S.K. and Fox, J.E.D. (2003). Allelopathic effects of *Eucalyptus victrix* on *Eucalyptus* and grasses. *Allelopathy Journal* 11, 77-84.

Foster, B.L. and Gross, K.L. (1998). Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology* 79, 2593-602.

Goodwin, J. (1992). The role of mycorrhizal fungi in competitive interactions among native bunchgrass and alien weeds: a review and synthesis. *Northwest Scientist* 66, 251-60.

Griffin, G.F., Stafford Smith, D.M., Morton, S.R., Allan, G.E., Masters, K.A. and Preece, N. (1989). Status and implications of the invasion of Tamarisk (*Tamarix aphylla*) on the Finke River, Northern Territory, Australia. *Journal of Environmental Management* 29, 297-315.

Groves, R.H. and Willis, A.J. (1999). Weeds and loss of native plant biodiversity: some Australian examples. *Australian Journal of Environmental Management* 6, 156-63.

Holt, V. (2005). The impact of bridal creeper (*Asparagus asparagoides*) on ground-dwelling and leaf litter insect biodiversity. Honours thesis, School of Earth and Environmental Sciences, The University of Adelaide, Adelaide.

Jones, D.L. (1988). 'Native orchids of Australia'. (Reed Books, Frenches Forest).

Köchy, M. and Wilson, S.D. (1997). Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology* 78, 732-9.

Lyons, K.G. and Schwarta, M.W. (2001). Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters* 4, 358-65.

May, F.E. and Ash, J. (1990). An assessment of the allelopathic potential of *Eucalyptus*. *Australian Journal of Botany* 38, 245-54.

McCune, B. and Grace, J.B. (2002). 'Analysis of ecological communities'. (MJM Software Design, Oregon).

Morin, L., Batchelor, K.L. and Scott, J.K. (2006). The biology of Australian weeds. 44. *Asparagus asparagoides* (L.) Druce. *Plant Protection Quarterly* 21, 46-62.

Raymond, K.L. (1999). Ecology of *Asparagus asparagoides* (bridal creeper), an environmental weed of southern Australia. PhD thesis, Department of Biological Sciences, Monash University, Clayton.

Schowalter, T.D. (2000). 'Insect ecology: an ecosystem approach'. (Academic Press, San Diego).

Simberloff, D. and Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1, 21-32.

Sorensen, B. and Jusaitis, M. (1995). The impact of bridal creeper on an endangered orchid. *In* 'Weeds of conservation concern' eds. D. Cooke and J. Choate, p. 27. (Department of Environment and Natural Resources and Animal and Plant Control Commission, South Australia, Adelaide).

Standish, R.J., Williams, P.A., Robertson, A.W., Scott, N.A. and Hedderley, D.I. (2004). Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants. *Biological Invasions* 6, 71-81.

Stansbury, C. (1996). Observations of birds feeding on bridal creeper (*Asparagus asparagoides*) fruits within Yanchep National Park, Western Australia. *Plant Protection Quarterly* 11, 59-60.

Todd, M.C.L., Grierson, P.F. and Adams, M.A. (2000). Litter cover as an index of nitrogen availability in rehabilitated mine sites. *Australian Journal of Soil Research* 38, 423-33.

Turner, P.J. and Virtue, J.G. (2006). An eight year removal experiment measuring the impact of bridal creeper (*Asparagus asparagoides* (L.) Druce) and the potential benefit from its control. *Plant Protection Quarterly* 21, 79-84.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. and Westbrooks, R. (1997). Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21, 1-16.

Xiong, S. and Nilsson, C. (1999). The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology* 87, 984-94.