

A modelling approach to estimate the effect of exotic pollinators on exotic weed population dynamics: bumblebees and broom in Australia

Kate E. Stokes^{1*}, Yvonne M. Buckley^{2,3} and Andrew W. Sheppard¹

¹CSIRO Entomology, Black Mountain Laboratories, Clunies Ross St, GPO Box 1700, Canberra, ACT 2601, Australia, ²The Ecology Centre, School of Integrative Biology, University of Queensland, St. Lucia, Queensland 4072, Australia, ³CSIRO Sustainable Ecosystems, Queensland Bioscience Precinct, 306 Carmody Road, St. Lucia, Queensland 4067, Australia

ABSTRACT

The role of mutualisms in contributing to species invasions is rarely considered, inhibiting effective risk analysis and management options. Potential ecological consequences of invasion of non-native pollinators include increased pollination and seed set of invasive plants, with subsequent impacts on population growth rates and rates of spread. We outline a quantitative approach for evaluating the impact of a proposed introduction of an invasive pollinator on existing weed population dynamics and demonstrate the use of this approach on a relatively data-rich case study: the impacts on *Cytisus scoparius* (Scotch broom) from proposed introduction of *Bombus terrestris*. Three models have been used to assess population growth (matrix model), spread speed (integrodifference equation), and equilibrium occupancy (lattice model) for *C. scoparius*. We use available demographic data for an Australian population to parameterize two of these models. Increased seed set due to more efficient pollination resulted in a higher population growth rate in the density-independent matrix model, whereas simulations of enhanced pollination scenarios had a negligible effect on equilibrium weed occupancy in the lattice model. This is attributed to strong microsite limitation of recruitment in invasive *C. scoparius* populations observed in Australia and incorporated in the lattice model. A lack of information regarding secondary ant dispersal of *C. scoparius* prevents us from parameterizing the integrodifference equation model for Australia, but studies of invasive populations in California suggest that spread speed will also increase with higher seed set. For microsite-limited *C. scoparius* populations, increased seed set has minimal effects on equilibrium site occupancy. However, for density-independent rapidly invading populations, increased seed set is likely to lead to higher growth rates and spread speeds. The impacts of introduced pollinators on native flora and fauna and the potential for promoting range expansion in pollinator-limited 'sleepier weeds' also remain substantial risks.

Keywords

Biological invasions, *Cytisus scoparius*, dispersal, invasive plant, mutualism, pollination efficiency, seed limitation, weed.

*Corresponding author. Kate E. Stokes, CSIRO Entomology, Black Mountain Laboratories, Clunies Ross St, GPO Box 1700, Canberra, ACT 2601, Australia. E-mail: kate.stokes@csiro.au

INTRODUCTION

The importance of bumblebees (*Bombus* spp.) in enhancing pollination of commercial glasshouse crops has led to their introduction from native ranges in the northern hemisphere to countries around the globe, resulting in non-native bee species recently establishing in the wild. Examples include the establishment of *Bombus terrestris* (Hymenoptera, Apidae) in Japan (Inari *et al.*, 2005) and Israel (Dafni & Schmida, 1996), following escape from commercial glasshouse colonies, and additionally in

Tasmania (Hingston *et al.*, 2002), where wild populations of *B. terrestris* were initially recorded in 1992, originating from introduced populations in New Zealand (Semmens *et al.*, 1993). The ecological consequences of exotic bee invasions are largely unknown (see Goulson, 2003a for a review) but could include competition with native organisms for floral resources or nest sites (Butz Huryn, 1997; Hingston & McQuillan, 1999; Paini, 2004; Thomson, 2004), transmission of parasites or pathogens to native organisms (Goka *et al.*, 2001), increases or decreases in seed set of native plants (Goulson, 2003a), and pollination of

exotic weeds (Hanley & Goulson, 2003). Population level consequences of increased weed pollination are relatively unexplored (cf. Parker, 1997), but potential risks include increases in both population growth rate and speed of spread.

In Australia and New Zealand, the spread of exotic weeds has been particularly acute in both agricultural and native systems, resulting in an estimated cost to agricultural industries of \$A 4 billion per annum in control measures and lost yields (Sinden *et al.*, 2004). It has been argued that the majority of weeds do not rely on insect pollination; either because they are anemophilous, self-pollinating, apomictic, or reproduce vegetatively (Butz Huryn, 1997). Relatively little quantitative information is available regarding the pollination communities of invasive plants. Carr (1993) describes the alien flora of Victoria, Australia, stating that many species are entomophilous and utilize a wide range of insects; including natives (predominantly Hymenoptera, Lepidoptera, and Diptera), aliens (honeybees, *Apis mellifera*), and recent immigrants (*Syrphid* spp.). Several weed species in Australia are self-incompatible and reliant on pollinator mutualisms to set seed; examples include woody shrubs such as *Lupinus arboreus*, *Cytisus scoparius*, and *Ulex europaeus* (all Fabaceae). Pollen limitation in introduced species can exist; a well-documented case is the failure of red clover (*Trifolium pratense*) to set seed in New Zealand before bumblebees were introduced (Hopkins, 1914). There are also cases of alien plants acquiring novel pollinators in the new environment. Plants that are pollinated by hummingbirds (Trochilidae) and sunbirds (Nectarinidae) in their native ranges have developed facultative mutualisms with native Australian nectarivores, primarily the honeyeaters (Meliphagidae); examples include *Aloe saponaria*, a garden escape, and *Cotyledon orbiculata*, both native to South Africa (Carr, 1993).

Introduced bees from a similar region of origin as an introduced plant have the potential to act as a catalyst for weed spread in new environments (Hanley & Goulson, 2003). Unlike the introduced honeybee, *A. mellifera*, *B. terrestris* is able to 'buzz-pollinate' species with poricidal anthers (Buchmann, 1983). A few native Australian bees are also capable of buzz-pollination, such as blue-banded bees (*Amegilla*), but *B. terrestris* is larger and heavier than most native Australian bees, and is initially likely to be a superior pollinator of northern temperate plant species that are specifically adapted for pollination by large hairy bees. The ecological importance of an absolute increase in seed set at the population level will depend on the role of seeds in population dynamics (Harper, 1977). This has implications for 'sleepers' plants that have naturalized in new environments but failed to expand their populations exponentially (Groves, 1999). By definition, sleeper weeds are present at low densities in the environment, making it difficult to assess the number of susceptible weed species at risk.

Costs and benefits of exotic pollinator importation

Motivation to introduce *B. terrestris* to mainland Australia is given by perceived economic benefits to the horticultural industry, as greenhouse growers currently pollinate their crops

using mechanical, hand-held vibrators, at high labour, equipment, and maintenance cost (Hogendoorn *et al.*, 2000), whereas competing overseas producers, in particular New Zealand, have access to low-cost bumblebee technology (Hogendoorn *et al.*, 2000). Importation applications from the Australian Hydroponics and Greenhouse Association have generated concern, due to the potential for increased abundance of exotic weeds and negative impacts on native pollinators (Hergstrom *et al.*, 2002).

Threats to native biota resulting from invasive exotic pollinators remain largely unknown. In Tasmania, *B. terrestris* has displaced two native bee species from floral resources (Hingston & McQuillan, 1999). Additional concern exists regarding pollinator competition with the swift parrot, *Lathamus discolor*, an endangered species largely dependent on blue gum trees (*Eucalyptus globulus*) for both nesting sites and as a nectar food source (MacNally & Horrocks, 2000; Hingston *et al.*, 2004).

The risk of accidental introduction of *B. terrestris* to mainland Australia is considerable. Climatic differences exist between Tasmania, which currently hosts established *B. terrestris* populations (Hingston *et al.*, 2002), and southern Australia, principally a reduction in annual precipitation. Within its native northern hemisphere *B. terrestris* is restricted to non-arid regions within the latitudinal range of 28–58° (Dafni & Schmida, 1996). Based on this information, Hingston *et al.* (2002) predict that *B. terrestris* could potentially colonize non-arid regions in Australia as far north as southern Queensland.

Risk management forecasting related to pollinator importation is inhibited by lack of quantitative data and predictive knowledge regarding impacts, one of which is the potential impact increased seed set may have on weed population dynamics. In this paper, we provide a synthesis of the current status of invasive *C. scoparius* populations in Australia and describe a modelling protocol to address the potential threat posed by the introduction of *B. terrestris*. In particular, the impacts of increased pollination on population growth rate (λ), invasion wave speed (c^*), and equilibrium site occupancy of the weed are explored.

DEVELOPMENT OF POPULATION MODELS FOR INVASIVE SPECIES

The demography of invasive populations in new environments can differ from that observed in the native range, requiring collection of field data on plant performance in the invaded region (Grigulis *et al.*, 2001; Paynter *et al.*, 2003). Scotch broom, *C. scoparius*, is a shrub native to western and central Europe and considered an exotic invader in Australia, New Zealand, and the USA. Several studies have examined the dynamics of broom in both the native (Memmott *et al.*, 1993; Paynter *et al.*, 1998, 2000, 2003; Buckley *et al.*, 2003) and the exotic ranges (Williams, 1981; Smith & Harlen, 1991; Bossard & Rejmánek, 1994; Fowler *et al.*, 1996; Rees & Paynter, 1997; Paynter *et al.*, 1998, 2000, 2003; Downey & Smith, 2000; Parker, 2000; Sheppard *et al.*, 2000, 2002; Buckley *et al.*, 2003), providing one of the most comprehensive data sets of an invasive weed species to date.

Cytisus scoparius has no clonal growth and relies entirely on seed set for reproduction (Parker, 1997). It has an explosive

pollination mechanism; flowers remain closed until an insect of sufficient weight alights on the wings and triggers the opening of the keel, which remains open thereafter. This releases the style and anthers, which then spring up to contact the back of the pollinator in an explosive motion, depositing pollen on both the dorsal and the ventral surfaces of the visitor (Parker, 1997; Stout, 2000). These floral traits tend to preclude pollination by native visitors; bumblebees are most efficient at triggering the pollination mechanism of *C. scoparius* in its native range, especially the heavier species such as *B. terrestris*, which is bigger than *A. mellifera* (Stout *et al.*, 2002). Currently, the major pollinator of *C. scoparius* on mainland Australia is the introduced honeybee, *A. mellifera* (Simpson *et al.*, 2005).

Is the invasive plant population pollinator limited?

Limitation of seed production by insufficient pollinator visitation is a common phenomenon in plants (Burd, 1994). Additionally, pollination efficiency of an introduced pollinator may be lower than that of a native pollinator (Freitas & Paxton, 1998). In south-east Australia, field experiments conducted at Barrington Tops National Park (NSW) using hand out-cross pollination treatments imply pollinator limitation of individual *C. scoparius* plants: 84% of bagged flowers allowed a single honeybee visit set fruit; whereas only 35% of open-control flowers set fruit (Simpson *et al.*, 2005). In addition, mean fruit to flower ratios of bagged hand out-crossed plants were higher than open-flower controls (Simpson *et al.*, 2005).

Broom plants are prolific seeders, accumulating large seed banks under resident populations (Rees & Paynter, 1997). Established populations are unlikely to be seed limited, it is more probable that limitation at the population level results from availability of colonization sites (Rees & Paynter, 1997), implying that pollinator limitation is unlikely to impact upon population growth rate in mature populations. However, in sites undergoing expansion of *C. scoparius*, no established seed bank exists and increased seed set could potentially contribute to greater spread rates in newly invasive populations.

A comparison of invasive *Cytisus scoparius* populations using matrix population models

Parker (2000) used sensitivity and elasticity analysis of matrix population models in an attempt to identify ecologically appropriate targets to reduce the population growth rate (λ) of invasive *C. scoparius* populations in the USA. Sensitivity of λ to model parameters (e.g. fecundity) measures how a small additive change in the parameter affects λ , whereas elasticity measures how a proportional change in the parameter affects λ (Caswell, 2001). For populations at the leading edge of an invasion front, elasticity analysis indicated alterations to survival in the seed bank would have the greatest impact on λ (Fig. 1b), although elasticities were relatively comparable across all life-history stages (Parker, 2000). We parameterize a matrix population model for invasive low-density broom populations in Australia to provide a comparative indication of the vital rates (e.g. fecundity and the

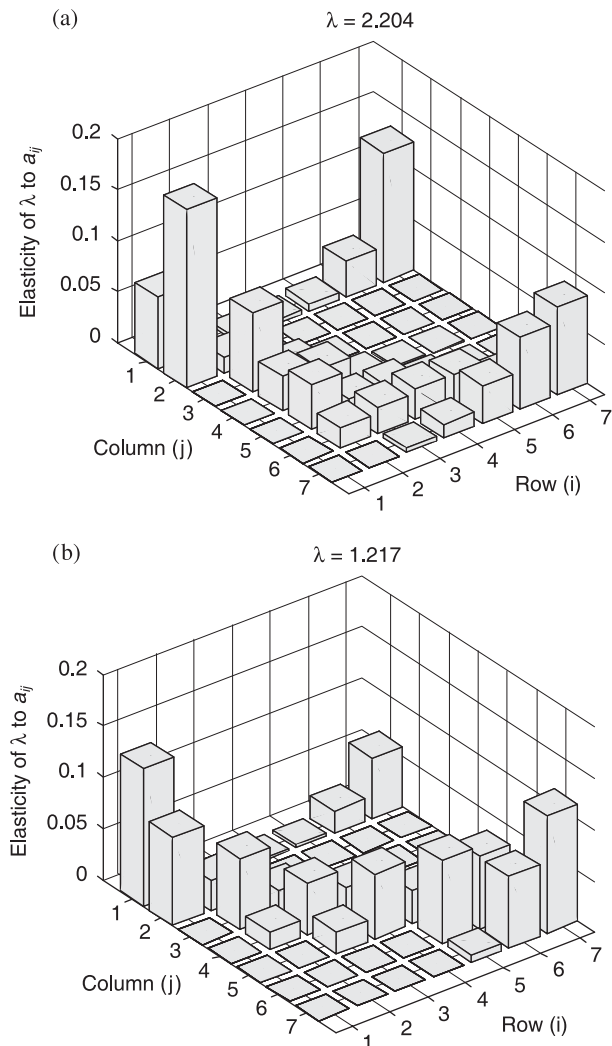


Figure 1 Elasticity of population growth rate (λ) to demographic parameters (a_{ij} matrix entries) for invasive *Cytisus scoparius* populations in (a) SE Australia and (b) Washington, USA (Parker, 2000).

probabilities of stasis, growth, and survival) influencing λ . Our matrix is constructed with an annual time step using height (Paynter *et al.*, 2003) to define the stage categories. Demographic data were obtained from immature broom populations (i.e. vegetation cover < 50%), located along the Shoalhaven River in the southern tablelands of New South Wales (Sheppard *et al.*, 2002). Field estimates (Sheppard *et al.*, 2002) describe annual probabilities for the following parameters: survival of seed in the seedbank, proportion of the seedbank germinating, transition from seed to seedling, transitions between juvenile and adult size classes, and adult mortality. In common with many other studies, there are little data available on adult mortality. Following Buckley *et al.* (2005), we assumed that all plants have the same probability of survival from year to year. Assuming that the proportion of adult plants alive at some maximum age, u , was 0.05 and that the maximum age approximates 23 years (from Table 5 in Rees & Paynter, 1997), therefore $S_a^u = 0.05$, where s_a is the

$$A = \begin{bmatrix} .630 & 0 & 9.3 & 26.9 & 78.1 & 502.2 & 2002.2 \\ .060 & .173 & .032 & .020 & 0 & 0 & 0 \\ 0 & .220 & .298 & .040 & 0 & 0 & 0 \\ 0 & .039 & .274 & .120 & .042 & .032 & 0 \\ 0 & .031 & .097 & .300 & .125 & .032 & 0 \\ 0 & .008 & .089 & .340 & .458 & .194 & 0 \\ 0 & 0 & .008 & .080 & .292 & .677 & .890 \end{bmatrix}$$

$$B = \begin{bmatrix} .741 & 0 & 3.4 & 47.1 & 108.7 & 1120 & 3339 \\ .00105 & .310 & 0 & 0 & 0 & 0 & 0 \\ 0 & .350 & .310 & .024 & 0 & 0 & 0 \\ 0 & .038 & .290 & .390 & 0 & 0 & 0 \\ 0 & 0 & .069 & .440 & .320 & 0 & .091 \\ 0 & 0 & 0 & 0 & .440 & .530 & .091 \\ 0 & 0 & 0 & 0 & .029 & .400 & .730 \end{bmatrix}$$

Figure 2 Transition matrices for immature *Cytisus scoparius* populations in (A) SE Australia and (B) Washington, USA (Parker, 2000) showing the probabilities of stasis, growth and survival between the different stage classes (a_{ij}).

yearly adult survival probability and u is the maximum age. Yearly survival probability, s_a , is then calculated as $s_a = 0.05^{1/u}$, which in this case is 0.89.

Fecundity estimates were obtained on an individual basis from a low-density Shoalhaven River population. Sixty plants of flowering age, encompassing a range of plant sizes, were monitored on a yearly basis to obtain plant height, number of flowers per shoot, number of pods per shoot, and number of seeds per pod (A. W. Sheppard, unpublished data). Mean seed number per pod was not affected by stand maturity and averaged 7.75 ± 0.25 (SE) (Sheppard *et al.*, 2002). Pod production per plant was regressed against plant size, enabling an estimate of annual seed production per individual to be derived for each size class ($N = 60$, $R^2 = 0.4$, $P < 0.001$). This value was multiplied by seed number per pod to obtain a final value for seed production per plant.

The estimates of λ obtained for invasive broom populations in Australia are higher ($\lambda = 2.204$) than those obtained for the North American populations ($\lambda = 1.217$), indicating that the Australian populations are increasing at a faster rate (Fig. 1). It is probable that this difference is due to the higher probability of seedling establishment observed in Australia (0.060), in comparison to North America (0.001) (Fig. 2).

Projecting rates of spread for invasive species

A framework for calculating asymptotic invasion speed from stage-specific data on demography and dispersal is presented by Neubert and Caswell (2000). This method couples structured matrix population models with integrodifference (discrete time)

equations for dispersal. Perturbation analysis explores how sensitive model conclusions are to changes in both demographic vital rates (i.e. the entries in the matrix) and dispersal parameters, and can be used to calculate the sensitivity and elasticity of invasion wave speed (c^*), which is the asymptotic rate of spread in metre per year, to these changes. Close correlation has been observed between the sensitivity and the elasticity of c^* and of λ to changes in the vital rates (Neubert & Caswell, 2000).

Development of stage-structured dispersal kernels

Sensitivity and/or elasticity of invasion wave speed has been shown to be greatest to long-distance dispersal parameters (Neubert & Caswell, 2000; Buckley *et al.*, 2005). Scotch broom plants have two dispersal mechanisms (Parker, 2000): first, ballistic dispersal, resulting from explosive dehiscence of pods and, second, ant-mediated dispersal, as ants are attracted to elaiosomes, lipid-rich bodies attached to the seeds. A lack of information regarding secondary ant dispersal of *C. scoparius* prevents us from parameterizing the integrodifference equation model for Australia. However, this information exists for invasive broom populations in the USA: Neubert and Parker (2004) estimated dispersal kernels for a *C. scoparius* population at the leading edge of an invasion front. Field data on dispersal distances were manipulated to obtain a composite dispersal kernel from estimates of ant-mediated and ballistic dispersal kernels (Neubert & Parker, 2004). Elasticity analysis of the demographic parameters reveals that the largest proportional changes in c^* result from changes in the survival of seeds in the seed bank and germination rate (Neubert & Parker, 2004); implying that germination rate could be a management target for slowing speed of spread in the USA populations.

Increased pollination scenarios

Short time-scale simulations (10–30 years) of the USA populations demonstrated that increased pollination could potentially increase λ (Parker, 1997); however, elasticity of c^* to fecundity is not particularly high (Neubert & Parker, 2004), indicating that a relatively large increase in fecundity would be necessary to increase spread speed substantially. Incorporating a 10% increase in fecundity values of the Australian matrix model also results in a small increase in population growth rate ($\lambda = 2.241$), but in the Australian case, the elasticity of λ to fecundity is less than the elasticity of λ to seedling establishment (Fig. 1a).

Spatially-explicit *C. scoparius* lattice population model

A spatially-explicit model was developed by Rees and Paynter (1997) to explore which population parameters influence the area occupied by broom. The model incorporates spatially local competition, asymmetric competition between seedlings and established plants, local seed dispersal, a seed bank, and an age-structured established plant population (Rees & Paynter, 1997). The model uses a coupled map lattice formulation with sites arranged in a square lattice with wrap-around margins. This ensures that seed dispersed on one edge of the plot will land on

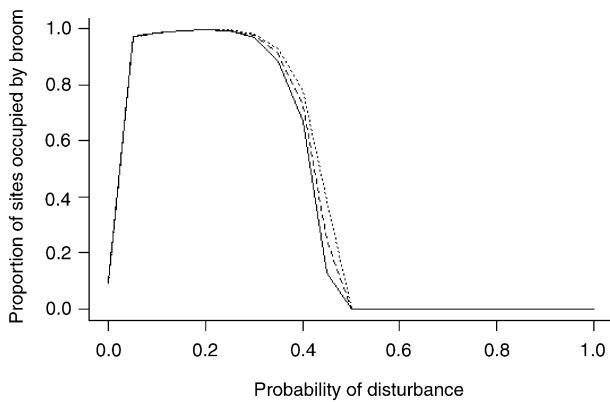


Figure 3 Output from the *Cytisus scoparius* lattice model (Rees & Paynter, 1997) showing the impact of increased seed set on the proportion of sites occupied by *C. scoparius* varying the probability of disturbance. The solid line was calculated from the simulation model using parameters obtained from Fig. 10 (a) in Sheppard *et al.* (2002). The dashed lines were derived from the model incorporating increasing amounts of seed set (25% — long dashes and 50% — short dashes).

the opposite side; therefore, all sites within the lattice are equivalent. Site size is based on the approximate size of an adult broom plant. Model analysis indicated that the fraction of sites occupied by broom was largely determined by three parameters: the probability a site is disturbed, the probability a site becomes suitable for colonization following plant senescence, and maximum longevity (Rees & Paynter, 1997). We parameterized the Rees and Paynter model (1997) for the Shoalhaven River populations in Australia (Sheppard *et al.*, 2002).

The lattice model has been used to explore biological control scenarios of the potential for seed-feeding insects to decrease the area occupied by broom in Australia (Rees & Paynter, 1997; Sheppard *et al.*, 2002). We ran the model for the Shoalhaven River populations, examining the converse perspective of whether increased seed set resulting from enhanced pollination translates to increased occupancy levels of the weed under differing probabilities of disturbance. Model simulations incorporating proportional increases in fecundity show little impact on the equilibrium proportion of sites occupied by broom under a range of probabilities of disturbance (Fig. 3). Even during the early stages of an invasion when initial occupancy levels are low, local colonization processes rapidly saturate.

DISCUSSION

The comparative modelling approach we use here demonstrates that increased seed set of an exotic weed due to arrival of an exotic pollinator has negligible effect on equilibrium site occupancy if broom populations are microsite- rather than seed-limited, as appears to be the case in Australia (Figs 1 & 3). In density-independent stage-structured models, increased seed set will lead to increases in population growth rate (λ) and spread speed (c^*) because the models do not incorporate microsite limitation. However, the elasticities and sensitivities of λ and c^*

to fecundity are not particularly high, suggesting a large increase in fecundity would be required to increase λ and c^* substantially.

While this case study is specific to one weed species, we believe that our results can be generalized to other scenarios. The risk of increasing λ and c^* due to increased seed set will be highest for populations where suitable habitat for germination is not limiting. If germination is microsite limited, or density dependence is operating at the seed establishment stage (Buckley & Metcalf, 2006), increased seed set may not translate to higher equilibrium populations.

Exotic pollinators have been shown to increase seed set in a variety of exotic weeds. Establishment of *B. terrestris* in Tasmania has increased seed set in *L. arboreus*, the tree lupin, a major weed in New Zealand (Stout *et al.*, 2002), and additionally Greater trefoil, *Lotus uliginosus* (Hergstrom *et al.*, 2002), but decreased seed set of Scotch thistle, *Onopordum acanthium*, attributed to nectar robbing (Hergstrom *et al.*, 2002). In mainland Australia, *A. mellifera* has increased seed set of a woody weed, *Lantana camara* (Goulson & Derwent, 2004). In North America, honeybees increase seed set of the yellow star thistle, *Centaurea solstitialis* (Barthell *et al.*, 2001). Our case-study example highlights that future research requires the extension of these studies to quantify the impacts of increases and decreases in seed set at the population level. Seed addition experiments are a simple means of demonstrating seed or microsite limitation for particular populations.

A further factor likely to control pollinator performance is aggregation of floral structures (Roberston & Macnair, 1995; Kunin, 1997), resulting in subsequent effects on pollination and seed production (Klinkhamer & de Jong, 1990; Kato & Hiura, 1999). Larger, denser populations could attract a higher number of pollinators than low-density populations invading new areas. In addition, low plant density can lead to reduced delivery of compatible outcross pollen (Kunin, 1993). Therefore, even when pollinator visitation is maintained at a high level, reduced plant density and increased isolation from a source of outcrossed pollen can result in substantial declines in the probability of outcrossing (Duncan *et al.*, 2004). As a result of this process plants will either develop reduced seed set or increased inbreeding, depending on the mating system, even when pollinator abundance and behaviour are unaffected (Duncan *et al.*, 2004).

Bumblebees also exhibit a high degree of floral constancy (Goulson, 2003b), although this effect has been reported to decrease at low density in some *Bombus* species (Kunin, 1993), further complicating the probability of fertilization success. In addition, introduced plants may attract pollinators, reducing flower visitation and pollination of native flora (Chittka & Schürkens, 2001).

Pollinator limitation is rarely a constraint to the spread of introduced weeds because most alien plants are either well served by generalist pollinators or capable of asexual propagation (Richardson *et al.*, 2000). Tightly co-evolved pollination systems are rare (Waser *et al.*, 1996; Pellmyr, 2002) and many alien species, including *C. scoparius*, are capable of successful establishment in new environments in the absence of their dominant pollinator. While species invasions are remarkably idiosyncratic, and therefore difficult to predict, mutualisms involving animal-mediated

pollination and seed dispersal, and symbioses between plant roots and microbiota, are often implicated in the establishment and spread of alien plant species in novel environments (see Richardson *et al.* (2000) for a review). The global prevalence of these mutualisms led Richardson *et al.* (2000) to conclude that propagule spread of insect-pollinated, fleshy-fruited plants with small seeds should be expected almost wherever such species are introduced. Such plants are often introduced as garden exotics, where they attract dispersers that later migrate out of urban areas. The consequences of an increasing flow of propagules from areas of high human density to less urbanized areas are likely to lead to a higher prevalence of successful invasions, with the potential for 'awakening' of current sleeper weeds. In comparison, threats to already established environmental weeds are likely to be less significant, either because current pollinator services are sufficient to enable the weed to achieve pest status, or because increased seed set does not translate to an increase in growth rate or speed of spread at the population level.

In conclusion, this study demonstrates the importance of integrating modelling approaches in quantitative risk assessments of pollinator importations. A focus on identifying sleeper weed populations where rates of population growth and spread are limited by pollinator availability and seed abundance provides an initial step towards effective risk forecasting approaches.

ACKNOWLEDGEMENTS

We thank Saul Cunningham for insightful comments on the manuscript.

REFERENCES

- Barthell, J.F., Randall, J.M., Thorp, R.W. & Wenner, A.M. (2001) Promotion of seed set in yellow star-thistle by honeybees: evidence of an invasive mutualism. *Ecological Applications*, **11**, 1870–1883.
- Bossard, C.C. & Rejmánek, M. (1994) Herbivory, growth, seed production, and resprouting of an exotic invasive shrub *Cytisus scoparius*. *Biological Conservation*, **67**, 193–200.
- Buchmann, S.L. (1983) Buzz pollination in angiosperms. *Handbook of experimental pollination biology* (ed. by C.E. Jones and R.J. Little), pp. 73–113. Van Nostrand Reinhold, New York, USA.
- Buckley, Y.M. & Metcalf, J. (2006) Density dependence in invasive plants: demography, herbivory, spread and evolution. *Conceptual ecology and invasions biology: reciprocal approaches to nature* (ed. by M.W. Cadotte, S.M. McMahon and T. Fukami), pp. 109–123. Springer, Dordrecht, the Netherlands.
- Buckley, Y.M., Downey, P., Fowler, S.V., Hill, R., Memmott, J., Norambuena, H., Pitcairn, M., Shaw, R., Sheppard, A.W., Winks, C., Wittenberg, R. & Rees, M. (2003) Are invasives bigger? A global study of seed size variation in two invasive shrubs. *Ecology*, **84**, 1434–1440.
- Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H. & Rees, M. (2005) Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, **42**, 1020–1030.
- Burd, M. (1994) Bateman principle and plant reproduction — the role of pollen limitation in fruit and seed set. *Botanical Review*, **60**, 83–139.
- Butz Huryn, V.M.B. (1997) Ecological impacts of introduced honeybees. *Quarterly Review of Biology*, **72**, 272–297.
- Carr, G.W. (1993) Exotic flora of Victoria and its impact on indigenous biota. *Flora of Victoria, vol. 1. introduction* (ed. by D.B. Foreman and G.B. Walsh), pp. 256–297. Intaka Press, Melbourne, Australia.
- Caswell, H. (2001) *Matrix population models: construction, analysis and interpretation*, 2nd edn. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Chittka, L. & Schürkens, S. (2001) Successful invasion of a floral market. *Nature*, **411**, 653.
- Dafni, A. & Schmida, A. (1996) The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt Carmel, Israel. *The conservation of bees* (ed. by A.C. Matheson), pp. 183–200. The Linnean Society of London and the International Bee Research Association, London, UK.
- Downey, P.O. & Smith, J.M.B. (2000) Demography of the invasive shrub scotch broom (*Cytisus scoparius* (L.) Link) at Barrington Tops, NSW: insights for management. *Austral Ecology*, **25**, 477–485.
- Duncan, D.H., Nicotra, A.B., Wood, J.T. & Cunningham, S.A. (2004) Plant isolation reduces outcross pollen receipt in a partially self-compatible herb. *Journal of Ecology*, **92**, 977–985.
- Fowler, S.V., Harman, H.M., Memmott, J., Paynter, Q., Shaw, R., Sheppard, A.W. & Syrett, P. (1996) Comparing the population dynamics of broom *Cytisus scoparius*, as a native plant in the UK and France, and as an invasive alien weed in Australia and New Zealand. *Proceedings of the IX international symposium on biological control of weeds* (ed. by V.C. Moran and J.H. Hoffmann), pp. 19–26. University of Cape Town, Cape Town, South Africa.
- Freitas, B.M. & Paxton, R.J. (1998) A comparison of two pollinators: the introduced honey bee *Apis mellifera* and an indigenous bee *Centric tarsata* on cashew *Anacardium occidentale* in its native range of NE Brazil. *Journal of Applied Ecology*, **35**, 109–121.
- Goka, K., Okabe, K., Yoneda, M. & Niwa, S. (2001) Bumblebee commercialization will cause worldwide migration of parasitic mites. *Molecular Ecology*, **10**, 2059–2099.
- Goulson, D. (2003a) Effects of introduced bees on native ecosystems. *Annual Review of Ecology and Systematics*, **34**, 1–26.
- Goulson, D. (2003b) *Bumblebees; their behaviour and ecology*. Oxford University Press, Oxford, UK.
- Goulson, D. & Derwent, L.C. (2004) Synergistic interactions between an exotic honeybee and an exotic weed: pollination of *Lantana camara* in Australia. *Weed Research*, **44**, 195–202.
- Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves, R.H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281–290.

- Groves, R.H. (1999) Sleeper weeds. *Proceedings of the 12th Australian weeds conference* (ed. by A.C. Bishop, M. Boersma and C.D. Barnes), pp. 623–636. Tasmanian Weed Society, Hobart, Tasmania, Australia.
- Hanley, M.E. & Goulson, D. (2003) Introduced weeds pollinated by introduced bees: cause or effect? *Weed Biology and Management*, **3**, 204–212.
- Harper, J.L. (1977) *Population biology of plants*. Academic Press, London, UK.
- Hergstrom, K., Buttermore, R., Seman, O. & McCorkell, B. (2002) Environmental research on the impact of bumblebees in Australia and facilitation of national communication for/against further introductions. *Horticulture Australia project No. VG99033*. The Tasmanian Museum and Art Gallery, Tasmania, Australia.
- Hingston, A.B. & McQuillan, P.B. (1999) Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee, *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Australian Journal of Zoology*, **47**, 59–65.
- Hingston, A.B., Marsden-Smedley, J., Driscoll, D.A., Corbett, S., Fenton, J., Anderson, R., Plowman, C., Mowling, F., Jenkin, M., Matsui, K., Bonham, K.J., Iowski, M., McQuillan, P.B., Yaxley, B., Reid, T., Storey, D., Poole, L., Mallick, S.A., Fitzgerald, N., Kirkpatrick, J.B., Febey, J., Harwood, A.G., Michaels, K.F., Russell, M.J., Black, P.G., Emmerson, L., Visoiu, M., Morgan, J., Breen, S., Gates, S., Bantich, M.N. & Desmarchelier, J.M. (2002) Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral Ecology*, **27**, 162–172.
- Hingston, A.B., Potts, B.M. & McQuillan, P.B. (2004) The swift parrot, *Lathamus discolor* (Psittacidae), social bees (Apidae) and native insects as pollinators of *Eucalyptus globulus* ssp. *globulus* (Myrtaceae). *Australian Journal of Botany*, **52**, 371–379.
- Hogendoorn, K., Steen, Z. & Schwarz, M.P. (2000) Native Australian carpenter bees as a potential alternative to introducing bumblebees for tomato pollination in greenhouses. *Journal of Apicultural Research*, **39**, 67–74.
- Hopkins, I. (1914) History of the bumblebee in New Zealand: its introduction and results. *Bulletin of the New Zealand Department of Agriculture (New Series)*, **46**, 1–28.
- Inari, N., Nagamitsu, T., Kenta, T., Goka, K. & Hiura, T. (2005) Spatial and temporal pattern of introduced *Bombus terrestris* abundance in Hokkaido, Japan, and its potential impact on native bumblebees. *Population Ecology*, **47**, 77–82.
- Kato, E. & Hiura, T. (1999) Fruit set in *Styrax obassia* (Styracaceae): the effect of light availability, display size, and local floral density. *American Journal of Botany*, **86**, 495–501.
- Klinkhamer, P.G.L. & de Jong, T.J. (1990) Effects of plant size, plant density and sex differential nectar reward on pollinator visitation in the protandrous *Echium vulgare* (Boraginaceae). *Oikos*, **57**, 399–405.
- Kunin, W.E. (1993) Sex and the single mustard: population density and pollinator behaviour effect seed set. *Ecology*, **74**, 2145–2160.
- Kunin, W.E. (1997) Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology*, **85**, 225–234.
- MacNally, R. & Horrocks, G. (2000) Landscape-scale conservation of an endangered migrant: the Swift Parrot (*Lathamus discolor*) in its winter range. *Biological Conservation*, **92**, 335–343.
- Memmott, J., Fowler, S.V., Syrett, P. & Hosking, J.R. (1993) What makes broom a major problem? *Proceedings of the Brighton crop protection conference*, pp. 753–758. British Crop Protection Council, Farnham, UK.
- Neubert, M.G. & Caswell, H. (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1623.
- Neubert, M.G. & Parker, I.M. (2004) Projecting rates of spread for invasive species. *Risk Analysis*, **24**, 817–831.
- Paini, D.R. (2004) Impact of the introduced honeybee (*Apis mellifera*) Hymenoptera: Apidae) on native bees: a review. *Austral Ecology*, **29**, 399–407.
- Parker, I.M. (1997) Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. *Ecology*, **78**, 1457–1470.
- Parker, I.M. (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications*, **10**, 726–743.
- Paynter, Q., Downey, P.O. & Sheppard, A.W. (2003) Age structure and growth of the woody legume weed *Cytisus scoparius* in native and exotic habitats: implications for control. *Journal of Applied Ecology*, **40**, 470–480.
- Paynter, Q., Fowler, S.V., Memmott, J., Shaw, R.H. & Sheppard, A.W. (2000) Determinants of broom (*Cytisus scoparius* (L.) Link) abundance in Europe. *Plant Protection Quarterly*, **15**, 149–155.
- Paynter, Q., Fowler, S.V., Memmott, J. & Sheppard, A.W. (1998) Factors affecting the establishment of *Cytisus scoparius* in southern France: implications for managing both native and exotic populations. *Journal of Applied Ecology*, **35**, 582–595.
- Pellmyr, O. (2002) Pollination by animals. *Plant–animal interactions: an evolutionary approach* (ed. by C.M. Herrera and O. Pellmyr), pp. 157–184. Blackwell Science Ltd, Oxford, UK.
- Rees, M. & Paynter, Q. (1997) Biological control of scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology*, **34**, 1203–1222.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000) Plant invasions — the role of mutualisms. *Biological Reviews of the Cambridge Philosophical Society*, **75**, 65–93.
- Roberston, A.W. & Macnair, M.R. (1995) The effects of floral display size on pollinator services to individual flowers of *Myosotis* and *Mimulus*. *Oikos*, **72**, 106–114.
- Semmens, T.D., Turner, E. & Buttermore, R. (1993) *Bombus terrestris* (L.) (Hymenoptera, Apidae) now established in Tasmania. *Journal of the Australian Entomological Society*, **32**, 346.
- Sheppard, A.W., Hodge, P. & Paynter, Q. (2000) Factors affecting broom regeneration in Australia and their management implications. *Plant Protection Quarterly*, **15**, 156–161.

- Sheppard, A.W., Hodge, P., Paynter, Q. & Rees, M. (2002) Factors affecting the persistence of broom *Cytisus scoparius* in Australia. *Journal of Applied Ecology*, **39**, 721–734.
- Simpson, S., Gross, C.L. & Silberbauer, L. (2005) Broom and honeybees in Australia: an alien liaison. *Plant Biology*, **7**, 541–548.
- Sinden, J., Jones, R., Hester, S., Odum, D., Kalisch, C., James, R. & Cacho, O. (2004) *The economic impact of weeds in Australia*. CRC for Australian Weed Management, Technical Series no. 8, Adelaide.
- Smith, J.M.B. & Harlan, R.L. (1991) Preliminary observations on the seed dynamics of broom (*Cytisus scoparius*) at Barrington Tops, New South Wales. *Plant Protection Quarterly*, **6**, 73–78.
- Stout, J.C. (2000) Does size matter? Bumblebee behaviour and the pollination of *Cytisus scoparius* L. (Fabaceae). *Apidologie*, **31**, 129–139.
- Stout, J.C., Kells, A.R. & Goulson, D. (2002) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation*, **106**, 425–434.
- Thomson, D. (2004) Competitive interactions between the invasive European honey bee and native bumblebees. *Ecology*, **85**, 458–470.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996) Generalizations in pollination systems, and why it matters. *Ecology*, **77**, 1043–1060.
- Williams, P.A. (1981) Aspects of the ecology of broom (*Cytisus scoparius*) in Canterbury, New Zealand. *New Zealand Journal of Botany*, **19**, 31–43.