

 Open access • Journal Article • DOI:10.1111/J.1365-2664.2006.01210.X

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Published on: 01 Oct 2006 - Journal of Applied Ecology (Blackwell Publishing)

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Management of plant invasions mediated by frugivore interactions

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Summary

1. Some of the most damaging invasive plants are dispersed by frugivores and this is an area of emerging importance in weed management. It highlights the need for practical information on how frugivores affect weed population dynamics and spread, how frugivore populations are affected by weeds and what management recommendations are available.

2. Fruit traits influence frugivore choice. Fruit size, the presence of an inedible peel, defensive chemistry, crop size and phenology may all be useful traits for consideration in screening and eradication programmes. By considering the effect of these traits on the probability, quality and quantity of seed dispersal, it may be possible to rank invasive species by their desirability to frugivores. Fruit traits can also be manipulated with biocontrol agents.

3. Functional groups of frugivores can be assembled according to broad species groupings, and further refined according to size, gape size, pre- and post-ingestion processing techniques and movement patterns, to predict dispersal and establishment patterns for plant introductions.

4. Landscape fragmentation can increase frugivore dispersal of invasives, as many invasive plants and dispersers readily use disturbed matrix environments and fragment edges. Dispersal to particular landscape features, such as perches and edges, can be manipulated to function as seed sinks if control measures are concentrated in these areas.

5. Where invasive plants comprise part of the diet of native frugivores, there may be a conservation conflict between control of the invasive and maintaining populations of

the native frugivore, especially where other threats such as habitat destruction have reduced populations of native fruit species.

6. Synthesis and applications. Development of functional groups of frugivore-dispersed invasive plants and dispersers will enable us to develop predictions for novel dispersal interactions at both population and community scales. Increasingly sophisticated mechanistic seed dispersal models combined with spatially explicit simulations show much promise for providing weed managers with the information they need to develop strategies for surveying, eradicating and managing plant invasions. Possible conservation conflicts mean that understanding the nature of the invasive plant–frugivore interaction is essential for determining appropriate management.

Key-words: fruit traits, frugivore traits, functional groups, landscape fragmentation, conservation conflict, dispersal

Journal of Applied Ecology (2006) **43**, 848–857
doi: 10.1111/j.1365-2664.2006.01210.x

Introduction

The proportion of invasive species that are animal dispersed is unknown; estimates range from 8% of the naturalized flora of Victoria, Australia (Carr 1993) to 40% of ‘representative invasive species’ (Cronk & Fuller 1995). Of the 20 species of weeds of national significance in Australia, five are fleshy fruited with known vertebrate dispersers (Brunner, Harris & Amor 1976; Liddy 1985; Stansbury 2001; Setter *et al.* 2002; Gosper 2004), one is ant dispersed (Richardson & Hill 1998) and three receive some dispersal by livestock (Lonsdale, Miller & Forno 1989; Brown & Carter 1998; Kriticos *et al.* 1999; van Klinken & Campbell 2001). Frugivore-mediated dispersal of invasive plants is therefore an area of emerging importance in the weed management sector, highlighting a need for information on how frugivores affect weed population dynamics and spread, how frugivore populations are affected by weeds, and what management recommendations are available. Research on frugivory and weed management could benefit from a closer synthesis of the two fields.

The kind of dispersal vector is a determinant of the resulting seed shadow (the distribution of seeds in space around the parent), with animal-dispersed species having longer mean dispersal distances than wind-dispersed species (Clark *et al.* 2005). Furthermore, invasions where dispersal is mediated by frugivores have distinctive ecological features. (i) Dispersal depends on the presence of suitable frugivores, thus the variation in frugivore assemblages between regions and habitats potentially places a variable filter on the success of invasive plant species. (ii) Mutualism imparts a reciprocal positive effect on each partner’s rate of population increase. (iii) Plant or frugivore species may be simultaneously involved in interactions with multiple species. There will therefore be both community- and population-level consequences of the invasive plant–frugivore interaction.

Two recent reviews of invasive plant–frugivore interactions (Richardson *et al.* 2000; Gosper, Stansbury & Vivian-Smith 2005) have covered the extent and functions of this mutualism among invasive plant species. We discuss how a deeper understanding of the function of the invasive plant–frugivore interaction can influence management of invasive plant populations. While it has proved difficult to find traits that correlate with invasiveness generally across taxa and widely different functional groups (Kolar & Lodge 2001), we argue that the assessment of how plant and disperser traits influence dispersal and demographic processes can be used to rank risks of invasion, guide surveillance and detection, assess indirect positive or negative effects and manage invasions. We focus on six areas of research from functional group traits to landscape-scale and community processes that we believe can be integrated and used to improve management of plant invasions: fruit traits, frugivore traits, plant establishment, landscape structure, models of spread and community interactions.

Fruit traits

The success of invasive plant species is partly attributed to fruit traits that favour effective seed dispersal (Panetta & McKee 1997; Baret, Le Bourgeois & Strasberg 2005). One valuable but surprisingly rarely applied approach to assessing the role of fruit traits in promoting invasion is to compare the fruit traits and dispersal performance of co-occurring native and invasive plants (Daehler 2003). Two studies have shown that invasive species in their exotic range are superior to native congeners in terms of traits influencing fruit removal and in both cases the invasives had higher removal rates (Sallabanks 1993; Vila & D’Antonio 1998). In contrast, three other comparisons showed no clear differences (Montaldo 2000; Greenberg, Smith & Levey 2001; Drummond 2005).

With so few studies it is difficult to generalize; however, evidence from the frugivory literature indicates

that fruit traits do influence frugivore choice, and fruit preference rankings remain relatively consistent across sites and time (Herrera 1998; Carlo, Collazo & Groom 2003). Therefore, highly preferred species would be expected to be more invasive than others. We describe fruit traits that, together with frugivore preferences, form the basis for that ranking. It may be possible to use fruit and crop traits to predict reliably fruit removal rates. Using such information, if removal rate is a determinant of dispersal and establishment success, pre-import weed risk assessment (WRA) procedures could be improved.

The clearest fruit–frugivore relationship is that between fruit size and frugivore gape size, particularly in birds (Jordano 1995). Generally, larger fruits have fewer dispersal agents and the largest may depend on one or a few species (Corlett 1998; Kitamura *et al.* 2002). In human-dominated landscapes where most invasions start, frugivore size and gape size ranges tend to be truncated; there are abundant potential dispersal agents for smaller (< 15 mm) fruits but few or none for larger (> 20 mm) fruits (Corlett 2002). We might therefore expect invasives with small fruits to be more successful than those with large fruits; this prediction has not, to our knowledge, been tested. There are large fruited exceptions, dispersed by large birds or mammals (Engel 2000; Setter *et al.* 2002; Cordeiro *et al.* 2004). Other exceptions are mostly species with relatively soft, multiseeded fruits (e.g. *Passiflora* spp., *Psidium* spp., *Ficus* spp.) from which small frugivores can disperse seed-containing pieces.

Plants relying on frugivory for dispersal face a trade-off between attraction of frugivores that disperse their seeds and defence against frugivores that destroy seeds. This trade-off between frugivore attraction and defence may be a major factor underlying observed fruit preference rankings. The rate of fruit removal across species is positively related to nutrient levels and negatively to chemical defences (Schaefer, Schmidt & Winkler 2003). We therefore predict that defensive traits, such as the presence of a thick, inedible peel, are likely to limit invasiveness. This is a characteristic typically associated with fruits targeted at large mammals, although a range of smaller mammals (e.g. fruit bats, rodents and birds) can process such fruits. In contrast, fruit colour, although often correlated with fruit choice in the field, has not yet been shown to have a consistent effect on fruit preferences in any frugivore (Willson & Whelan 1990).

Although rarely quantified, many studies suggest that successful invaders have larger crop sizes than co-occurring natives (Sallabanks 1993; Meyer 1998; Vila & D'Antonio 1998). Even more common are reports that invaders have a longer fruiting season than natives and/or fruit during seasonal lows in native fruit production (Meyer 1998; Cordeiro *et al.* 2004; Gosper 2004). For dispersers, a gap-filling phenology not only reduces competition with equally attractive native fruits (Gosper 2004) but may also allow the persistence of frugivore populations year-round in areas that could not otherwise support them (Parry-Jones & Augee 2001).

The susceptibility of fruit to insect attack may influence frugivore preferences. Both positive and negative interactions between insect infestation and fruit consumption by birds have been reported (Sallabanks & Courtney 1992; Garcia *et al.* 1999). The potential exists for the use of fruit-spoiling biological control agents to reduce the attractiveness of fleshy fruited invaders (Gosper, Stansbury & Vivian-Smith 2005; Vivian-Smith *et al.* 2006). However, the amount of fruit in the neighbourhood (*sensu* Sargent 1990) can influence seed dispersal. In a field study of the seed- and fruit-damaging fly, *Ophiomyia lantana*, released to control *Lantana camara* (Vivian-Smith *et al.* 2006), significantly fewer damaged than undamaged fruits were removed by frugivores, indicating that frugivores selected against larva-infested fruits. However, as there were many undamaged fruits available, the agent could have altered patterns of fruit choice rather than quantity of fruits eaten and seeds dispersed.

Frugivore traits

The interaction of an invader's fruit traits with the suite of potential frugivores in the exotic range determines the nature of the dispersal received. This leads to a rapidly escalating number of combinations of plant and potential frugivore to consider when assessing the risk of introduction or prioritizing surveillance and control. However, common processing or dispersal outcomes within functional groups of dispersers may allow approximate prediction of dispersal and establishment patterns in invasive plants (Westcott & Dennis 2003; Moran *et al.* 2004; Gosper, Stansbury & Vivian-Smith 2005).

Frugivore traits determine the quantity and quality of dispersal provided to a plant (Schupp 1993); they affect which, when and how many seeds are dispersed, dispersal distances and seed germination. The quantity of fruits being dispersed depends mainly on fruit size, availability, competition, number of dispersers, gape size and dietary constraints of the frugivore. Quality of dispersal is the effect of frugivores' treatment on seed shadow and germination, and is determined by the length of time a seed remains in the digestive tract, physical and chemical effects on the seed and movement patterns of the disperser. We outline how groupings may be based on similar functional properties of dispersers.

Fruit-processing methods by frugivores differ widely across taxonomic groups but can be classed according to the degree and outcomes. Before ingestion seeds may be dropped or cached, after ingestion seeds may be chewed and then either expelled before swallowing, regurgitated or defecated. Non-ingested seeds will usually be dispersed shorter distances than ingested seeds and will receive reduced processing effects.

Gut passage time (GPT) has a strong but variable influence on seed dispersal patterns and distances. There can be a large range from first to last defecated seeds in the same species (Whitney *et al.* 1998; Holbrook &

Smith 2000) and mean GPT can also vary for different fruit species through the same frugivore (Fukui 2003; Westcott *et al.* 2005). Gut passage time in birds and primates (Karasov 1990; Remis 2000) and consequent dispersal distance in birds (Westcott & Graham 2000) have been reported to increase with body mass. However, gut passage effects can also depend on differences in diet and digestive physiology (Tedman & Hall 1985; Lambert 2002). Opportunistic frugivores and seed predators tend to retain seeds for a longer time period (Lambert 1988) than more specialist avian frugivores, which often have short gut passage times. Changes in diet can cause short-term digestive adaptations in insectivore–frugivores (Levey & Martinez del Rio 2001; Herrera 2002). Despite this variation, size could provide a means of classifying dispersers into groups because of its influence on gut passage times, as well as home range, and therefore seed-dispersal distances.

Another aspect of dispersal quality depends on the generated seed shadow. This is a function of a frugivore's movement pattern and is invariably right-skewed with a long tail. It can also be affected by the frugivore's seed deposition behaviour and the number of seeds per fruit. Large numbers of seed per fruit and infrequent deposition may lead to stochasticity in seed shadows, with clumps of seeds at long time intervals or distances. Because of the importance of rare long-distance dispersal events for population spread, migratory species and those with large home ranges may contribute disproportionately to the rate of spread given the number of seeds they consume (White & Stiles 1992; Vellend 2002; Mouissie, Lengkeek & Van Diggelen 2005). In some instances this may be a useful focus for management. Disperser movement is also influenced by habitat structure. Enhanced establishment of the invasive *Myrica faya* in intermediate light and low litter environments in Hawaii is typically associated with avian seed dispersal away from dense forest to perches in disturbed, open forest habitats (Walker 1990). Despite the importance of frugivore movement, there are areas that require further investigation, such as whether learned behaviour or conditioning to a new food source affects invasion.

Plant establishment

Plant establishment is a key component of dispersal effectiveness. Disperser movement patterns determine the deposition environment (Schupp 1993). Habitat characteristics influencing the successful invasion of fleshy fruited species predominantly relate to the vegetation structure (Ferguson & Drake 1999) that influences microsite conditions. Invasive plant species may further facilitate establishment via the development of canopy cover that provides more suitable microsite conditions for subsequent recruits (Gleadow 1982).

The disperser also determines whether seeds are deposited singly or in clusters (Schupp 1993). Clustered deposition may result in density-dependent seed or

seedling mortality (Clevenger 1996; Rey & Alcantara 2000), with the result that reductions in the numbers of seeds per cluster may not reduce population growth rate or spread if the number of clusters remains the same (Buckley & Metcalf 2006). Contagious deposition of multiple species, as a result of feeding on simultaneously fruiting species, can result in suites of plant species being dispersed and establishing together (Herrera 1988; Clark *et al.* 2004), which may accelerate the accumulation of additional fleshy fruited species, termed 'bird-made fruit orchards' (Lazaro, Mark & Olesen 2005).

In a meta-analysis of gut passage effects on 200 plant species, Traveset (1998) found that 50% experienced a change in germination rate or proportion of seeds germinating. Of these 50%, enhanced germination occurred in two-thirds of the species vs. one-third that experienced inhibited germination. Different animal groups had similar effects on germination, although non-flying mammals influenced germination slightly more often. Retention time influenced germination, as did the types of food ingested along with the seed, but differences in seed traits, such as size and fruit type, had little effect.

Another consequence of gut passage is that seeds are deposited in microbial- and nutrient-rich faeces that may affect germination. Documented effects include enhanced growth of seedlings because of the fertilization effect (Dinerstein & Wemmer 1988), shelter from desiccation (Engel 2000), an increased probability of secondary dispersal (Andresen & Levey 2004; Martinez-Mota, Serio-Silva & Rico-Gray 2004) and increased seed predation (Wehncke, Valdez & Domínguez 2004). These factors have been investigated less thoroughly for bird-dispersed species. However, germination success did not differ with regurgitation and defecation for several bird-dispersed shrub species, but the presence of faecal material reduced success because of greater susceptibility to pathogens (Meyer & Witmer 1998). Moreover, for bird-dispersed species, the influence of faecal material may be short-lived in relation to other factors influencing seed and seedling fates (White & Stiles 1992).

Landscape structure

Landscape heterogeneity strongly influences animal movement (Ims 1995) and commonly generates heterogeneity in the conditions suitable for plant establishment (Nathan & Muller-Landau 2000). The effects of habitat fragmentation on plant distribution will vary depending on dispersal abilities, habitat preferences and the pattern of fragmentation (With 2002). Although less disturbed habitats have greater recruitment of some invasive species (Hutchinson & Vankat 1998), many invasives are able to disperse and recruit in the disturbed matrix between fragments. Consequently, caution is needed in extrapolating results from fragmentation studies on species that cannot survive in the matrix to those which can.

In general, fragmentation results in an overall reduction in effective colonization rate for native plant species, particularly below a threshold of habitat availability for frugivores (With 2002). Smaller habitat fragments may suffer a decline in fleshy fruited plants (Tabarelli, Mantovani & Peres 1999) and the disproportionate loss of certain frugivores (Santos & Telleria 1994; Silva & Tabarelli 2000) compared with large fragments, and this can contribute to lower rates of fruit consumption, seed arrival and seedling establishment at fragmented sites for native species (Santos & Telleria 1994; Galetti, Alves-Costa & Cazetta 2003). Theoretically, however, a degree of fragmentation could increase the movement of species as frugivores would need to move further to find food, with fragments acting as stepping stones across the landscape and foci of frugivore activity and seed deposition (With 2002). In this way invasive plants spread across fragmented landscapes, dispersed by species that cross habitat boundaries (Williams & Karl 1996). Fragmentation could also result in invasives being spread into the matrix surrounding the frugivores' preferred habitat if that frugivore has to travel between patches.

Fragments may become dominated by edges (Tabarelli, Mantovani & Peres 1999) and movement across edges may be less restricted for frugivorous birds than for other feeding guilds (Laurance, Stouffer & Laurance 2004). The edges of habitats, within forest gaps and at forest boundaries, often have more fruits (Restrepo, Gomez & Heredia 1999), attract more frugivorous birds (Malmborg & Willson 1988; but cf. Restrepo, Gomez & Heredia 1999) and hence have greater rates of fruit consumption (Galetti, Alves-Costa & Cazetta 2003) and seed arrival (Hoppe 1988). Edges may therefore enhance invasions (Cordeiro *et al.* 2004).

Seeds dispersed to habitat fragments can be strongly influenced by the composition of the surrounding matrix (Anderson, Heiss-Dunlop & Flohr 2006) and seed dispersal may be significantly reduced when connectivity falls below a certain level (With 2002). Habitat corridors can enhance seed dispersal between patches (Levey *et al.* 2005; but cf. Norton, Hobbs & Atkins 1995) and are used to restore connectivity in fragmented landscapes, but may also improve the dispersal of invasive species (Hutchinson & Vankat 1998).

Directed dispersal, which results in the non-random arrival of seeds and survival of plants in predictable locations (Wenny 2001), is affected by landscape structure. Seeds can be deposited in disproportionate abundance by frugivores beneath perches, such as on gap edges (Wenny & Levey 1998), in agricultural and successional landscapes (McClanahan & Wolfe 1993) and under heterospecific fruiting trees (Kwit, Levey & Greenberg 2004). While artificial perches are used to enhance bird-dispersed seed input in restoration, simultaneous deposition of invasive plant seeds can also be high beneath these perches (Ferguson & Drake 1999; Dean & Milton 2000) and these may become foci of invasive spread (With 2002).

Potential management interventions using manipulations of landscape structure are described in detail by Gosper, Stansbury & Vivian-Smith (2005) and With (2002). These include using perches to capture seeds, reducing connectivity between suitable invasive plant habitats and targeting the main sources of dispersed seed for control. The potential for invasion can be used in prioritizing areas for restoration activities at a landscape scale (Borgman & Rodewald 2005; Anderson, Heiss-Dunlop & Flohr 2006).

Models of spread

Computer models constitute powerful tools for guiding management decisions concerning invasion threats in general (Trakhtenbrot *et al.* 2005). Recent advances in modelling the spatial spread of organisms (Levin *et al.* 2003; Hastings *et al.* 2005) have been motivated largely by the substantial implications of biological invasions, along with other threats, for which the process of spatial spread plays a critical role.

Spatial models of spread include two basic terms: the first accounts for processes regulating population growth, the second for dispersal and other processes that govern the redistribution of individuals (Kot, Lewis & van den Driessche 1996). A more detailed approach incorporates stage-specific demography and dispersal (Neubert & Caswell 2000; Neubert & Parker 2004). While both demography and dispersal play important roles in determining the rate of invasion, the shape of the redistribution (or dispersal) kernel is a key determinant of the rate of spread (Kot, Lewis & van den Driessche 1996; Neubert & Caswell 2000). Information about dispersal, while necessary, is not sufficient for estimating the realized redistribution kernel because this also depends on pre- (seed production) and post- (seedling establishment and growth to reproductive maturity) dispersal processes.

Among spatial models of invasive spread, Higgins & Richardson (1996) distinguished between phenomenological and mechanistic models. Phenomenological models have been commonly used to estimate redistribution kernels for plant species (Higgins & Richardson 1996; Kot, Lewis & van den Driessche 1996; Nathan *et al.* 2003). These models use some functional forms, calibrated against observed data, to describe the distribution of distances of progeny from the seed source. Because model parameters are fitted from observed dispersal data, the identity of the dispersal agent(s) is unimportant, thus relaxing the need to identify and quantify the role of different dispersal agents. However, this approach entails several disadvantages, including the high sensitivity of the fitted functions to variation not only in dispersal data but also in data collection procedures (Hastings *et al.* 2005). The variation in dispersal processes between species, sites and times implies that this modelling approach is best used for a posteriori analysis of invasions (Higgins & Richardson 1999; Higgins, Richardson & Cowling 2001), which

can also be achieved by models that correlate the observed patterns of spatial spread of invasive species with climatic, edaphic or other environmental variables (Foxcroft *et al.* 2004). In both cases, models parameterized in one site/region and over a certain time period may not be accurate, and even misleading, for the same species in another place or time.

Mechanistic models use data on factors influencing dispersal processes to predict dispersal kernels, where a dispersal kernel is a probability distribution function of a seed landing at a particular distance from the parent. Mechanistic models of seed dispersal by frugivores, in their simplest form, calculate dispersal distances as the product of the seed handling time and the rate of frugivore displacement (Murray 1988; Westcott & Graham 2000). More complex models incorporate other relevant aspects of disperser behaviour (Westcott *et al.* 2005) and responses to landscape structure. It is reasonable to assume that, at least in early stages of invasions, frugivore movements are not significantly affected by the presence and spatial distribution of the invasive species itself. Thus, *a priori* predictions of the spread of frugivore-dispersed, potentially invasive, species can be based on existing data on the foraging movements of local frugivores and data on gut passage time.

The need for incorporating spatial heterogeneity in models of invasions has only recently been highlighted (With 2002, 2004). This motivates the development of models that are capable of incorporating spatially explicit representation of the invaded landscape and that can account for the effects of spatial heterogeneity on the dispersal and establishment of the invader. Several spatially explicit simulations have been developed and tested for seed dispersal by frugivorous animals (Johnson *et al.* 1981; Lavorel, Smith & Reid 1999; Tews, Moloney & Jeltsch 2004). Yet we are unaware of any empirical evaluation of these models, or any other published mechanistic spatially explicit simulation of seed dispersal by frugivores. Encouraged by the recent progress in modelling movements of animals in heterogeneous environments (Turchin 1998; Revilla *et al.*

2004), we envision extension of these animal movement models to predict dispersal and establishment of frugivore-dispersed plant species in spatially heterogeneous landscapes.

Community interactions

Mutualistic seed–dispersal interactions are typically generalized and diffuse, with each plant species being consumed and dispersed by a range of different frugivores, and vice versa (Herrera 2002). This appears to hold for relationships between invasive plants and their dispersers, whether in their native or introduced range (Richardson *et al.* 2000; Gosper, Stansbury & Vivian-Smith 2005), with two important consequences. First, many potential plant invaders will encounter a diverse disperser community that will readily shift its diet to include the introduced plant. Secondly, positive feedbacks and secondary effects are likely to involve a wide range of native and invasive species, and to be complex, variable and context-specific (Gosper, Stansbury & Vivian-Smith 2005; Richardson *et al.* 2000). This will complicate attempts to predict the community outcomes of invasions by frugivore-dispersed plants. The ecological literature is largely silent about the possibility of making such predictions, because research into plant invasions has mainly focused on the success of the invader population, rather than on multiple interacting species (Gosper, Stansbury & Vivian-Smith 2005; but see Traveset & Richardson 2006).

There is a wide range of possible trajectories for communities following invasion, resulting in negative ‘degradation and meltdown’ and positive ‘rescue and recovery’ scenarios (Table 1). These sometimes reflect contrasting perspectives on the same data. For example, while native frugivores are agents in the spread of exotic plants, these plants can also support native frugivores (Table 1, A1 and B1). This is particularly significant for conservation in landscapes, where most of the native vegetation has been cleared followed by declines in native biota. In these situations, invasive frugivores may become useful dispersers of native plants

Table 1. Community effects of frugivore-mediated plant invasion. Unless otherwise specified, ‘plant’ implies ‘frugivore-dispersed’. Note that many scenarios, especially those in B, involve landscapes greatly affected by anthropogenic disturbance. A complete table with additional references is in Appendix S1 in the supplementary material

A.	Degradation and meltdown scenarios
1.	Native frugivores often assist the spread of exotic plants (Cordeiro <i>et al.</i> 2004)
2.	Native plants in frugivore diets may be usurped by exotics (Vila & D’Antonio 1998)
3.	Multispecies dispersal complexes may develop, incorporating exotic frugivores and exotic plants; these may support further invasions by exotic frugivores and plants (Bourgeois <i>et al.</i> 2005)
4.	Higher order dysfunctions may follow interactions with species outside the disperser mutualism (Fulton & Ford 2001)
B.	Rescue and recovery scenarios
1.	Exotic plants often subsidise native frugivore populations, both common and threatened species (Setter <i>et al.</i> 2002)
2.	Exotic dispersers may assist the movements and recruitment of native plants (Dungan <i>et al.</i> 2002)
3.	Multispecies dispersal complexes may develop, incorporating native and exotic frugivores and plants; these may facilitate native plant recruitment (Neilan <i>et al.</i> 2006)
4.	Presence of exotic plant cover on cleared or disturbed land may facilitate recovery of, or prevent loss of, native biodiversity (Crome, Isaacs & Moore 1994)

Table 2. High- and low-risk scenarios for each stage in the invasion process with associated management options

	High risk	Low risk	Management
Introduction	Small fruit, large crop size, long fruiting season, gap-filling phenology	Large fruit (unless large frugivores available or soft and multiseeded), thick inedible peel, highly defended	Pre-import weed risk assessment
Naturalization	Directed dispersal to suitable habitat	Destructive processing by frugivore	Eradication, prioritization for management
Local population growth	Non-ingested seeds, specialist frugivores, clumped deposition	As above	Fruit-spoiling biocontrol, prevention of fruit-set (herbicide spray-topping), exclusion of terrestrial frugivores
Spread	Large, opportunistic, or migratory frugivores. Fragmented habitat, proximity to sources	Small frugivores confined to fragments	As above. Minimize edges, use perches as managed seed sinks

(Table 1, B2), or invasive plants may facilitate disperser-mediated colonization by native plants (Table 1, B3) or provide habitat for fauna (Table 1, B4). On the other hand, disturbed landscapes may also support expanding complexes of exotic plants and exotic frugivores that assist each other's establishment (Table 1, A3). This would be enhanced by differences in interaction characteristics that favour exotic partners over native partners, such as frugivore preferences for exotic species (Table 1, A2). Conservation conflicts can result when both positive and negative community interactions are perceived (D'Antonio & Meyerson 2002; Dungan *et al.* 2002). Should the invasive plant or animal be eliminated, with the result that native biota may decline (or fail to recover), or should it be tolerated or actively managed as an agent of ecological sustainability, but with the risk of adverse outcomes for native biota?

Conclusions

Information on frugivory can be considered at all stages of weed management, including pre-entry risk assessment, prioritization of 'sleepers weeds', delimitation of areas for surveillance and eradication and area-wide management of established invasions. To manage effectively a frugivore-dispersed weed, we need to know what suites of dispersers exist, what weed species they are spreading, and the distances and directions of dispersal involved. While we are building up this suite of knowledge for a few case studies, a functional group approach based on fruit and frugivore traits and their interaction with the landscape could lead to more useful generalizations. These can be applied to new weed threats at an early stage, facilitating quicker and cheaper control. In Table 2 we present some rules of thumb that can be used by managers when considering plant invasions at different stages from pre-introduction to widespread invasions.

We need better knowledge of the patterns of interaction between plant and frugivore species, both native and exotic. This needs to be combined with knowledge of the extent to which these patterns are the result of the attributes of the species, or to other situation-specific

factors, such as the opportunities available for the interaction and the spatial context at local and landscape scales. Modelling, long-term monitoring and experimental manipulations should be used to test and identify community outcomes. Generalized predictions may be more feasible if useful criteria for grouping species functionally could be identified and shown to predict patterns of interaction in new situations.

Although invasive species frequently have detrimental impacts on ecosystems, it could be erroneous for managers to assume that removal of frugivore-dispersed exotic plants will always enhance conservation outcomes, especially if the invasions have occurred in areas where land has been cleared and developed and if there is poor knowledge of local plant–frugivore interactions. Management responses to invasive plants need to be sensitive to the multiple ecological roles that frugivore-dispersed exotics play in human-dominated landscapes. Interventions may need to be gradual, to target ecosystem components in addition to the plant itself (Zavaleta, Hobbs & Mooney 2001; Gosper, Stansbury & Vivian-Smith 2005), and to be accompanied by monitoring of the consequences for other biota.

Acknowledgements

We acknowledge the following support: RN-National Science Foundation (NSF-DEB-0453665), Israeli Science Foundation (ISF-FIRST 1316-05), International Arid Land Consortium (ILAC-03R-25) and CRG-CRC for Australian Weed Management. Thanks to Don Butler, Wendy Neilan and Cath Moran for helpful discussions and comments and the organisers of the Fourth International Symposium on Frugivores and Seed Dispersal.

References

- Anderson, S., Heiss-Dunlop, S. & Flohr, J. (2006) A moving feast: bird dispersal of weeds into conservation areas. *Proceedings of the 15th Australian Weeds Conference* 25–29 September 2006. Australian weeds conference Secretariat, Adelaide.
- Andresen, E. & Levey, D.J. (2004) Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, **139**, 145–154.

- Baret, S., Le Bourgeois, T. & Strasberg, D. (2005) How would *Rubus alceifolius*, an intrusive exotic species, progressively colonize the entirety of a humid tropical forest. *Canadian Journal of Botany*, **83**, 219–226.
- Borgman, K.L. & Rodewald, A.D. (2005) Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. *Restoration Ecology*, **13**, 334–340.
- Bourgeois, K., Suehs, C.M., Vidal, E. & Medail, F. (2005) Invasional meltdown potential: facilitation between introduced plants and mammals on French Mediterranean islands. *Ecoscience*, **12**, 248–256.
- Brown, J.R. & Carter, J. (1998) Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology*, **13**, 93–102.
- Brunner, H., Harris, R.V. & Amor, R.L. (1976) A note on the dispersal of seeds of blackberry (*Rubus procerus* P.J. Muell.) by foxes and emus. *Weed Research*, **16**, 171–173.
- Buckley, Y.M. & Metcalf, J. (2006) Density dependence in invasive plants: demography, herbivory, spread and evolution. *Conceptual Ecology and Invasions Biology* (eds M.W. Cadotte, S.M. McMahon & T. Fukami), pp. 109–123. Springer, Berlin.
- Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119–131.
- Carr, G.W. (1993) Exotic flora of Victoria and its impact on indigenous biota. *Flora of Victoria. Volume 1. Introduction* (eds D.B. Foreman & N.G. Walsh), pp. 256–297. Inkata Press, Melbourne, Australia.
- Clark, C.J., Poulsen, J.R., Bolker, B.M., Connor, E.F. & Parker, V.T. (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, **86**, 2684–2694.
- Clark, C.J., Poulsen, J.R., Connor, E.F. & Parker, V.T. (2004) Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia*, **139**, 66–75.
- Clevenger, A.P. (1996) Frugivory of *Martes martes* and *Genetta genetta* in an insular Mediterranean habitat. *Revue d'Ecologie-la Terre et la Vie*, **51**, 19–28.
- Cordeiro, N.J., Patrick, D.A.G., Munisi, B. & Gupta, V. (2004) Role of dispersal in the invasion of an exotic tree in an East African submontane forest. *Journal of Tropical Ecology*, **20**, 449–457.
- Corlett, R.T. (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biological Reviews*, **73**, 413–448.
- Corlett, R.T. (2002) Frugivory and seed dispersal in degraded tropical east Asian landscapes. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 451–465. CAB International, Wallingford, UK.
- Crome, F., Isaacs, J. & Moore, L. (1994) The utility to birds and mammals of remnant riparian vegetation and associated windbreaks in the tropical Queensland uplands. *Pacific Conservation Biology*, **1**, 328–343.
- Cronk, Q.C.B. & Fuller, J.L. (1995) *Plant Invaders. The Threat to Natural Ecosystems*. Chapman & Hall, London, UK.
- D'Antonio, C. & Meyerson, L.A. (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology*, **10**, 703–713.
- Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology and Systematics*, **34**, 183–211.
- Dean, W.R.J. & Milton, S.J. (2000) Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments*, **15**, 305–311.
- Dinerstein, E. & Wemmer, C.M. (1988) Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. *Ecology*, **69**, 1768–1774.
- Drummond, B.A. (2005) The selection of native and invasive plants by frugivorous birds in Maine. *Northeastern Naturalist*, **12**, 33–44.
- Dungan, R.J., O'Cain, M.J., Lopez, M.L. & Norton, D.A. (2002) Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. *New Zealand Journal of Ecology*, **26**, 121–128.
- Engel, T.R. (2000) *Seed Dispersal and Natural Forest Regeneration in a Tropical Lowland Biocoenosis (Shimba Hills, Kenya)*. Logos, Berlin, Germany.
- Ferguson, R.N. & Drake, D.R. (1999) Influence of vegetation structure on spatial patterns of seed deposition by birds. *New Zealand Journal of Botany*, **37**, 671–677.
- Foxcroft, L.C., Rouget, M., Richardson, D.M. & MacFadyen, S. (2004) Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. *Diversity and Distributions*, **10**, 427–437.
- Fukui, A. (2003) Relationship between seed retention time in a bird's gut and fruit characteristics. *Ornithological Science*, **2**, 41–48.
- Fulton, G.R. & Ford, H.A. (2001) The pied currawong's role in avian nest predation: a predator removal experiment. *Pacific Conservation Biology*, **7**, 154–160.
- Galetti, M., Alves-Costa, C.P. & Cazetta, E. (2003) Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biological Conservation*, **111**, 269–273.
- García, D., Zamora, R., Gómez, J.M. & Hódar, J.A. (1999) Bird rejection of unhealthy fruits reinforces the mutualisms between juniper and its avian dispersers. *Oikos*, **85**, 536–544.
- Gleadow, R.M. (1982) Invasion by *Pittosporum undulatum* of the forests of Central Victoria. II. Dispersal, germination and establishment. *Australian Journal of Botany*, **30**, 185–198.
- Gosper, C.R. (2004) Fruit characteristics of invasive bitou bush, *Chrysanthemoides monilifera* (Asteraceae), and a comparison with co-occurring native plant species. *Australian Journal of Botany*, **52**, 223–230.
- Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions*, **11**, 549–558.
- Greenberg, C.H., Smith, L.M. & Levey, D.J. (2001) Fruit fate, seed germination, and growth of an invasive vine: an experimental test of 'sit and wait' strategy. *Biological Invasions*, **3**, 363–372.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. & Thomson, D. (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters*, **8**, 91–101.
- Herrera, C.M. (1988) Habitat-shaping, host plant use by a hemiparasitic shrub, and the importance of gut fellows. *Oikos*, **51**, 383–386.
- Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs*, **68**, 511–538.
- Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant-Animal Interactions: An Evolutionary Approach* (eds C.M. Herrera & O. Pellmyr), pp. 186–187. Blackwell Science, Oxford, UK.
- Higgins, S.I. & Richardson, D.M. (1996) A review of models of alien plant spread. *Ecological Modelling*, **87**, 249–265.
- Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, **153**, 464–475.
- Higgins, S.I., Richardson, D.M. & Cowling, R.M. (2001) Validation of a spatial simulation model of a spreading alien plant population. *Journal of Applied Ecology*, **38**, 571–584.

- Holbrook, K.M. & Smith, T.B. (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, **125**, 249–257.
- Hoppes, W.G. (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology*, **69**, 320–329.
- Hutchinson, T.F. & Vankat, J.L. (1998) Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist*, **139**, 383–390.
- Ims, R.A. (1995) Movement patterns related to spatial structures. *Mosaic Landscapes and Ecological Processes* (eds L.A. Hansson, L. Fahrig & G. Merriam), pp. 85–109. Chapman & Hall, London, UK.
- Johnson, W.C., Sharpe, D.M., DeAngelis, D.L., Fields, D.E. & Olson, R.J. (1981) Modeling seed dispersal and forest island dynamics. *Forest Island Dynamics in Man-Dominated Landscapes* (eds R.L. Burgess & D.M. Sharpe), pp. 215–239. Springer-Verlag, New York, NY.
- Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *American Naturalist*, **145**, 163–191.
- Karasov, W.H. (1990) Digestion in birds. Chemical and physiological determinants and ecological implications. *Avian Foraging: Theory, Methodology, and Applications* (eds M.L. Morrison, C.J. Ralph, J. Verner & J.R. Jehl), pp. 391–415. Allen, Lawrence, Kansas.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, **133**, 559–572.
- van Klinken, R.D. & Campbell, S.D. (2001) The biology of Australian weeds. 37. *Prosopis* L. species. *Plant Protection Quarterly*, **16**, 2–20.
- Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.
- Kot, M., Lewis, M.A. & van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.
- Kriticos, D., Brown, J., Radford, I. & Nicholas, M. (1999) Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biological Control*, **16**, 230–239.
- Kwit, C., Levey, D.J. & Greenberg, C.H. (2004) Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos*, **107**, 303–308.
- Lambert, F.R. (1988) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis*, **131**, 521–527.
- Lambert, J.E. (2002) Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, **23**, 1169–1185.
- Laurance, S.G.W., Stouffer, P.C. & Laurance, W.F. (2004) Effects of road clearings on movement patterns of understorey rainforest birds in central Amazonia. *Conservation Biology*, **18**, 1099–1109.
- Lavorel, S., Smith, M.S. & Reid, N. (1999) Spread of mistletoes (*Amyema preissii*) in fragmented Australian woodlands: a simulation study. *Landscape Ecology*, **14**, 147–160.
- Lazaro, A., Mark, S. & Olesen, J.M. (2005) Bird-made fruit orchards in northern Europe: nestedness and network properties. *Oikos*, **110**, 321–329.
- Levey, D.J. & Martinez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *Auk*, **118**, 819–831.
- Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146–149.
- Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology Evolution and Systematics*, **34**, 575–604.
- Liddy, J. (1985) A note on the associations of birds and *Lantana* near Beerburum, south-eastern Queensland. *Corella*, **9**, 125–126.
- Lonsdale, W.M., Miller, I.L. & Forno, I.W. (1989) The biology of Australian weeds. 20. *Mimosa pigra* L. *Plant Protection Quarterly*, **4**, 119–131.
- McClanahan, T.R. & Wolfe, R.W. (1993) Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology*, **7**, 279–288.
- Malmborg, P.K. & Willson, M.F. (1988) Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. *Condor*, **90**, 173–186.
- Martinez-Mota, R., Serio-Silva, J.C. & Rico-Gray, V. (2004) The role of canopy ants in removing *Ficus perforata* seeds from howler monkey (*Alouatta palliata mexicana*) feces at Los Tuxtlas, México. *Biotropica*, **36**, 429–432.
- Meyer, J.Y. (1998) Observations on the reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). *Biotropica*, **30**, 609–624.
- Meyer, G.A. & Witmer, M.C. (1998) Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *American Midland Naturalist*, **140**, 129–139.
- Montaldo, N.H. (2000) Reproductive success of bird-dispersed plants in a subtropical forest relict in Argentina. *Revista Chilena de Historia Natur*, **73**, 511–524.
- Moran, C., Catterall, C.P., Green, R.J. & Olsen, M.F. (2004) Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. *Oecologia*, **141**, 584–595.
- Mouissie, A.M., Lengkeek, W. & Van Diggelen, R. (2005) Estimating adhesive seed-dispersal distances: field experiments and correlated random walks. *Journal of Functional Ecology*, **19**, 478–486.
- Murray, K.G. (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, **58**, 271–226.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. & Cain, M.L. (2003) Methods for estimating long-distance dispersal. *Oikos*, **103**, 261–273.
- Neilan, W., Catterall, C.P., Kanowski, J. & McKenna, S. (2006) Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia? *Biological Conservation*, **129**, 393–407.
- Neubert, M.G. & Caswell, H. (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.
- Neubert, M.G. & Parker, I.M. (2004) Projecting rates of spread for invasive species. *Risk Analysis*, **24**, 817–831.
- Norton, D.A., Hobbs, R.J. & Atkins, L. (1995) Fragmentation, disturbance, and plant distribution: mistletoes in woodland remnants in the western Australian wheatbelt. *Conservation Biology*, **9**, 426–438.
- Panetta, F.D. & McKee, J. (1997) Recruitment of the invasive ornamental, *Schinus terebinthifolius*, is dependent upon frugivores. *Australian Journal of Ecology*, **22**, 432–438.
- Parry-Jones, K.A. & Augee, M.L. (2001) Factors affecting the occupation of a colony site in Sydney, New South Wales by the grey-headed flying-fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecology*, **26**, 47–55.
- Remis, M.J. (2000) Initial studies on the contributions of body size and gastrointestinal passage rates to dietary flexibility among gorillas. *American Journal of Physical Anthropology*, **112**, 171–180.
- Restrepo, C., Gomez, N. & Heredia, S. (1999) Anthropogenic

- edges, treefall gaps, and fruit–frugivore interactions in a neotropical montane forest. *Ecology*, **80**, 668–685.
- Revilla, E., Wiegand, T., Palomares, F., Ferreras, P. & Delibes, M. (2004) Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. *American Naturalist*, **164**, E130–E153.
- Rey, P.J. & Alcantara, J.M. (2000) Recruitment dynamics of a fleshy fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622–633.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000) Plant invasions: the role of mutualisms. *Biological Reviews*, **75**, 65–93.
- Richardson, R.G. & Hill, R.L. (1998) The biology of Australian weeds. 34. *Ulex europaeus* L. *Plant Protection Quarterly*, **13**, 46–58.
- Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madroño*, **40**, 108–116.
- Sallabanks, R. & Courtney, S.P. (1992) Frugivory, seed predation, and insect–vertebrate interactions. *Annual Review of Entomology*, **37**, 377–400.
- Santos, T. & Tellería, J.L. (1994) Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera*. *Biological Conservation*, **70**, 129–134.
- Sargent, S. (1990) Neighbourhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology*, **71**, 1289–1298.
- Schaefer, H.M., Schmidt, V. & Winkler, H. (2003) Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, **102**, 318–328.
- Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107/108**, 15–29.
- Setter, M., Bradford, M., Dorney, B., Lynes, B., Mitchell, J., Setter, S. & Westcott, D. (2002) Pond apple: are the endangered cassowary and feral pig helping this weed to invade Queensland's wet tropics? *Thirteenth Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 173–176. R.G. & F.J. Richardson, Melbourne, Australia.
- Silva, J.M.C. & Tabarelli, M. (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, **404**, 72–74.
- Stansbury, C.D. (2001) Dispersal of the environmental weed bridal creeper *Asparagus asparagoides* by silvereyes *Zosterops lateralis* in south-western Australia. *Emu*, **101**, 39–45.
- Tabarelli, M., Mantovani, W. & Peres, C.A. (1999) Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation*, **91**, 119–127.
- Tedman, R.A. & Hall, L.S. (1985) The morphology of the gastrointestinal tract and food transit times in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Australian Journal of Zoology*, **33**, 625–640.
- Tews, J., Moloney, K. & Jeltsch, F. (2004) Modeling seed dispersal in a variable environment: a case study of the fleshy-fruited savanna shrub *Grewia flava*. *Ecological Modelling*, **175**, 65–76.
- Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181.
- Traveset, A. (1998) Effect of seed passage through vertebrate frugivore's guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, **1/2**, 151–190.
- Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology and Evolution*, **21**, 208–216.
- Turchin, P. (1998) *Quantitative Analysis of Movement*. Sinauer, Sunderland, MA.
- Vellend, M. (2002) A pest and an invader: white-tailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). *Natural Areas Journal*, **22**, 230–234.
- Vila, M. & D'Antonio, C.M. (1998) Fruit choice and seed dispersal of invasive vs. noninvasive *Carpobrotus* (Aizoaceae) in coastal California. *Ecology*, **79**, 1053–1060.
- Vivian-Smith, G., Gosper, C.R., Wilson, A. & Hoad, K. (2006) *Lantana camara* and the fruit- and seed-damaging fly, *Ophiomyia lantanae* (Agromyzidae): seed predator, recruitment promoter or dispersal disrupter? *Biological Control*, **36**, 247–257.
- Walker, L.R. (1990) Germination of an invading tree species (*Myrica faya*) in Hawaii. *Biotropica*, **22**, 140–145.
- Wehnecke, E.V., Valdez, C.N. & Dominguez, C.A. (2004) Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: consequences for seed dispersal effectiveness. *Journal of Tropical Ecology*, **20**, 1–9.
- Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3**, 51–74.
- Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences USA*, **95**, 6204–6207.
- Westcott, D. & Dennis, A.J. (2003) The ecology of seed dispersal in rainforests: implications for weed spread and a framework for weed management. *Weeds of Rainforests and Associated Ecosystems* (eds A.C. Grice & M.J. Setter), pp. 19–23. Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns, Australia.
- Westcott, D.A. & Graham, D.L. (2000) Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, **122**, 249–257.
- Westcott, D.A., Bentrupperbaumer, J., Bradford, M.G. & McKeown, A. (2005) Incorporating disperser movement and behaviour patterns into models of seed dispersal. *Oecologia*, **146**, 57–67.
- White, D.W. & Stiles, E.W. (1992) Bird dispersal of fruits of species introduced into eastern North-America. *Canadian Journal of Botany*, **70**, 1689–1696.
- Whitney, K.D., Fogiel, M.K., Lamperti, A.M., Holbrook, K.M., Stauffer, D.J., Hardesty, B.D., Parker, V.T. & Smith, T.B. (1998) Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, **14**, 351–371.
- Williams, P.A. & Karl, B.J. (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology*, **20**, 127–145.
- Willson, M.F. & Whelan, C.J. (1990) The evolution of fruit color in fleshy-fruited plants. *American Naturalist*, **136**, 790–809.
- With, K.A. (2002) The landscape ecology of invasive species. *Conservation Biology*, **16**, 1192–1203.
- With, K.A. (2004) Assessing the risk of invasive spread in fragmented landscapes. *Risk Analysis*, **24**, 803–815.
- Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*, **16**, 454–459.

Received 4 December 2005; final copy received 23 May 2006
Editor: Rob Freckleton

Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix S1. Community effects of frugivore-mediated plant invasion.