## chapter ten

# Invasive plants and mutualistic interactions between fleshy fruits and frugivorous animals

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### Contents

## 10.1 Introduction

Plant–animal interactions are important for invasion success in many plant species, often determining patterns of recruitment and establishment in a new area. Frugivory and associated seed dispersal are among the most important of such interactions. In fact, most of the world's worst invasive plants are dispersed by animals, and some of the most aggressive weeds, *Miconia, Psidium*, and *Ardisia*, produce seeds in fleshy fruits that are dispersed by frugivores (Lowe et al. 2000). Frugivores not only disperse seeds, but the passage through the gut often has a positive effect on germination success, which can be crucial to the process of colonization. However, the efficacy of this relationship depends on both plant characteristics and animal behavior.

The relationship between frugivores and fleshy-fruited invasive plants is highly variable and deserves attention as such interactions can be the key to understanding how invasive plants spread so successfully. Invasion of fleshy-fruited plants may be facilitated by either native or invasive frugivores, and the consequences for native flora and fauna may vary from beneficial to devastating. In this chapter, we review the current literature on invasive plant species that bear fleshy fruits and the role of frugivorous animals in their establishment and spread in novel habitats. First and foremost, we will review the interactions between fleshy-fruit plants and frugivorous animals to elucidate the mechanisms involved under Section 10.2, “Frugivory in fleshy-fruit plants.” Second, in Section 10.3, “Animals as seed dispersal vectors,” we will examine the consequences for invasive plants after their fruit is consumed by frugivores and how animals transport seeds both internally and externally. Third, we will address why invasive plants are attractive to frugivores in Section 10.3, “Invasive plants as source of food.” In Section 10.4, “Management of fleshy fruited invasive plants,” we outline current strategies for control and management of the invasive plants that bear fleshy fruits.

## 10.2 Frugivory in fleshy-fruit plants

Seed dispersal in fleshy-fruited species begins with fruit maturation and display and ends with dispersal of seeds to appropriate sites for germination (Wang and Smith 2002, Schupp et al. 2010, Blendinger et al. 2011). A wide variety of vertebrates act as frugivores and seed dispersers, primarily mammals (e.g., monkeys, bats, ungulates) and birds (Clark et al. 2001), but occasionally lizards on islands (Valido and Nogales 1994) and fish in seasonally flooded tropical forests (Anderson et al. 2011). Plants signal frugivores with their fruit color (Lomascolo and Schaefer 2010) and sometimes odor (Sánchez et al. 2004), and the frugivores also make choices depending on fruit size and nutritional quality of the pulp, which may involve traits such as sugar, water, lipid, and protein content (Schaefer et al. 2003, Muñoz et al. 2007, Floerchinger et al. 2010). Considerable interspecific variation in fruit presentation strategies exists. Some plant species produce large fruit crops once a year and other species mature fewer fruits but with multiple fruiting peaks through the year (Genini et al. 2009). These fruiting phenology patterns influence frugivore diet choice, visitation rates, and foraging behavior (McCarty et al. 2002, Prasad and Sukumar 2010, Blendinger and Villegas 2011).

Frugivory is not always mutualistic; rather, it spans a continuum of possible plant–animal interactions. At one extreme is exploitation by animals, such as parrots, curassows, and deer mice that not only consume fruits but often destroy seeds as well (Santamaria and Franco 2000, Lobo et al. 2009, Villaseñor-Sánchez et al. 2010). At the other extreme is food deception, whereby fruits or seeds are mimetic, they appear nutritious but lack nutritional value, or are indigestible (Peres and Roosmalen 1996, Foster and Delay 1998, Galetti 2002, Herrera 2002, Cazetta et al. 2008).

When frugivores do not entirely destroy the seeds they ingest, their performance as dispersers may vary considerably. There are two components to effective seed dispersal. The first is quality, which includes dispersal distance to suitable places for seed germination, and the second is quantity, involving fruit removal rates and the number of seeds dispersed (Schupp et al. 2010). Effective seed dispersal not only involves plant traits but also frugivore characteristics such as body size, home range, seed passage time, seed passage treatment, or attachment to fur or feathers. All these are important determinants of seed movement across the landscape (Traveset et al. 2001, Luck and Daily 2003, Schupp et al. 2010, Blendinger et al. 2011, Holbrook 2011). Nevertheless, dispersal may not end after the initial transport from parent plant. Secondary dispersers such as ants, small rodents, and dung beetles are well known for their roles in moving seeds beyond frugivore deposition sites (Passos and Oliveira 2004, Vander Wall et al. 2005, Ponce-Santizo et al. 2006). Thus, seedling recruitment in fleshy-fruited plant populations is often closely tied to animal interactions: frugivores foraging fruits, removing pulp from their seeds, and effectively dispersing them. Throughout the next section of this chapter, we will look into how frugivores affect each stage of the dispersal cycle of invasive plants.

## *10.3 Animals as seed dispersal vectors*

### *10.3.1 Gut treatment*

The main consequence of frugivory is seed movement, a strategy upon which many plant species depend (Jordano 2000). When seeds are removed and transported from the parent tree, they have a better chance to find suitable places for germination and growth; new habitats are colonized, distributional area is expanded, and escape from pathogens and herbivores is enhanced (Howe and Smallwood 1982, Augspurger 1983, Wenny 2001, Wang and Smith 2002). Besides dispersal, frugivores can have effects on post-dispersal processes (Table 10.1). Seeds of many species have a higher percent germination or germination rate after passage through the gut of a frugivore (Traveset 1998, Heer et al. 2010, Reid and Armesto 2011), through scarification of the seed coat (Carpinelli et al. 2005, Bradford and Westcott 2010), or by removal of the inhibitory fruit or seed pulp (Yagihashi et al. 1998, Wenny 2000, Westcott et al. 2008). While others may not be affected by ingestion, there can be adverse consequences as some frugivores can destroy seeds in the gut or inhibit seed germination after defecation (Janzen et al. 1985, Traveset 1998).

Most dispersers of invasive plants are birds and mammals (Figure 10.1), and many of these animals have a positive effect on seed germination through scarification. Across a broad geographical sampling, invasive or exotic species have been shown to have higher percent seed germination after consumption by avian frugivores (Greenberg et al. 2001, Bartuszevige and Gorchov 2006, Linnebjerg et al. 2009), rats and rabbits (D'Antonio 1990, Bourgeois et al. 2005), jackrabbits (D'Antonio 1990), ungulates (Shiferaw et al. 2004, Vavra et al. 2007), and lizards (Padrón et al. 2011).

Sometimes the role of frugivores is indispensable to increase seed germination, although the effect on the seeds depends on the identity of the frugivores. Many plant species either cannot germinate or suffer much reduced germination when fruit pulp remains around the seeds. In Australia, seed germination of the invasive Brazilian pepper tree, *Schinus terebinthifolius*, is minimal without pulp removal, a task that is effectively accomplished by the native Silvereye, *Zosterops lateralis* (Panetta and McKee 1997). After fruit consumption, the seed germination increases to 87%–100%, reflecting how important this native bird is to this exotic plant. However, one cannot generalize from this. After gut passage through the native Cedar Waxwing, *Bombycilla cedrorum*, seed germination in the invasive plant *Lonicera maackii* is reduced to less than 50%, whereas the native American Robin, *Turdus migratorius*, had a positive effect on the same invasive species by improving germination to more than 80% (Bartuszevige and Gorchov 2006). Thus, the effect that frugivores have on seed germination can vary considerably.

Frequently, where there are invasive fleshy-fruited plants, invasive frugivores co-occur. Do invasive plants do better with native frugivores or are they most successful when paired with invasive frugivores? Although it is difficult to forecast future relationships among species, available data suggest that there are several possible components to consider. In the Canary Islands, frugivorous birds, mammals, and reptiles consume invasive cacti fruits (*Opuntia* spp.), but their performances varied. Only two of seven native frugivorous species enhanced germination: Western Canaries lizard (*Gallotia galloti*) and Stone Marten (*Martes foina*) (Padrón et al. 2011). The three exotics that also consumed the fruits (Hermann's tortoise, *Testudo hermanni*; Pine Marten, *Martes martes*; European rabbit, *Oryctolagus cuniculus*) had no effect on cactus seed germination. On the other hand, on the Canary Island of Fuerteventura, a comparison of frugivory by one native and two exotic frugivores found that the native, a lizard (*Gallotia atlantica*), was an effective disperser

***Table 10.1*** Invasive Plants and Consequences of Fruit Consumption by Frugivores

| Invasive plant | Family | Locality | Seed dispersal process | Local dispersers | Exotic dispersers | Reference |
|---|---|---|---|---|---|---|
| *Annona glabra* | Annonaceae | Australia | Neutral effect after gut passage | 1 | | Westcott et al. (2008) |
| *Carpobrotus edulis* | Aizoaceae | France | Positive effect after gut passage | | 4 | Bourgeois et al. (2005) |
| *Carpobrotus acinaciformis* | Aizoaceae | France | Positive effect after gut passage | | 4 | Bourgeois et al. (2005) |
| *Carpobrotus edulis* | Aizoaceae | U.S.A. | Positive effect after gut passage | 2 | | Vila and D'Antonio (1998) |
| *Carpobrotus edulis* | Aizoaceae | U.S.A. | Positive effect after gut passage | 4 | | D'Antonio and Vila (1990) |
| *Celastrus orbiculatus* | Celastraceae | U.S.A. | Positive effect after gut passage | 1 | | Greenberg et al. (2001) |
| *Clidemia hirta* | Melastomataceae | Mauritius | Positive effect after gut passage | | 1 | Linnebjerg et al. (2009) |
| *Clidemia hirta* | Melastomataceae | U.S.A. | Positive effect after gut passage | 1 | 2 | Smith (1992) |
| *Lonicera maackii* | Caprifoliaceae | U.S.A. | Neutral effect after gut passage | 4 | 1 | Bartuszevige and Gorchov (2006) |
| *Ligustrum robustum* | Oleaceae | Mauritius | Neutral effect after gut passage | | 1 | Linnebjerg et al. (2009) |
| *Maesopsis eminii* | Rhamnaceae | Tanzania | Neutral effect after gut passage The greatest dispersion 3.97 km | 3 | | Cordeiro et al. (2004) |
| *Opuntia maxima* | Cactaceae | Canary Islands | Positive effect after gut passage | 1 | 2 | Lopez-Diaz and Nogales (2008) |
| *Opuntia spp.* | Cactaceae | Canary Islands | Two species have a positive effect after gut passage/nine species have a negative effect | 9 | 3 | Padron et al. (2011) |
| *Opuntia sp.* | Cactaceae | South Africa | Positive effect after gut passage | 1 | | Dean and Milton (2000) |
| *Prunus serotina* | Rosaceae | Belgium | Spatial clustering of perching birds | 18 | | Deckers et al. (2008) |
| *Schinus terebinthifolius* | Anacardiaceae | Australia | Neutral effect after gut passage | 1 | | Panneta and McKee (1997) |

The potential effect was divided by three categories: neutral (any effect), positive (increase percent germination), and negative (seed damage or reduction on percent germination) effect.

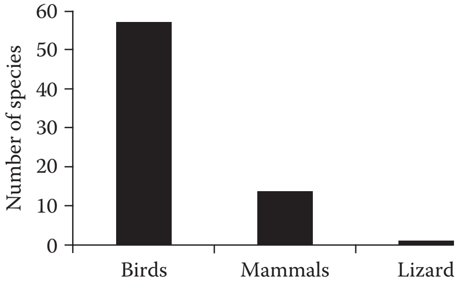

***Figure 10.1*** Frugivorous species reported as consumers of exotic plant species. We grouped the species per category based on a review of 17 articles published after 1996. Mammals include cats, hares, rabbits, deer, monkeys, mice, rabbits, and squirrels. Only one species of lizard was reported as a frugivore of exotic plants.

for three native species and one exotic plant on the island. Conversely, the exotic rabbit (*O. cuniculus*) preyed on all the seeds consumed including native and exotic plants, but the other exotic (Barbary ground squirrel, *Atlantoxerus getulus*) was an effective disperser of the exotic cactus, *Opuntia*. Seed germination was faster in one of the native plant species when the lizard ate the fruits than when the squirrel did (López-Darias and Nogales 2008). The former study suggests that exotic frugivores can have a negative effect on seed germination of the native plant species, and the exotic plant (*Opuntia*) has native and exotic frugivorous species facilitating its spread in the island.

One would not expect that all frugivores, native or exotic, would have the same effects on seed germination of a particular plant species. And by the same token, we would not expect the same frugivore to have the same effect on different invasive plant species. In Mauritius, the exotic frugivorous Red-whiskered Bulbul, *Pycnonotus jocosus*, had different mean gut passage times for seeds of two exotics *Clidemia hirta* (12.71 minutes) and *Ligustrum robustum* (15.49 minutes). Both exotic plants depend on frugivorous birds to remove pulp from the seeds, but the two species differed in their dependence on frugivores for seed germination. *C. hirta* seeds may not germinate without first passing through the gut of bulbuls, and they are more successful when they do. On the other hand, success of *L. robustum* is completely dependent on the bulbuls for germination (Linnebjerg et al. 2009).

Although our focus has been on frugivory and invasive plant species, exotic frugivores can have as wide ranging effects on native plant species as they do on exotic ones. Nogales et al. (2005) found that the endemic plant Tasiago (*Rubia fruticosa*) is well dispersed by native fauna such as lizards (*Gallotia atlantica*), warblers birds (*Sylbia* sp.), raven (*Corvus corax*), and the Yellow-legged Gull (*Larus cachinnans*), but the exotic rabbit (*O. cuniculus*) and the squirrel (*A. getulus*) damaged a great proportion of the seeds after fruit consumption and reduced seed germination compared to the positive effect of the native dispersers.

The consequences of differential effects of frugivores on native and exotic plant species can alter community structure and composition by facilitating invasion success while at the same time diminishing fitness of native species. In California, the ice plant, *Carpobrotus chilensis* (Aizoaceae) is becoming displaced by both the non-native *C. edulis* and the hybrid between the two. If the fruits are not consumed, seed germination of *C. chilensis* is almost 80%, whereas germination in the exotic *C. edulis* and their hybrids is less than 13%. However, the advantage is lost when native jackrabbits (*Lepus californicus*) and mule deer (*Odocoileus hemionus*) eat the fruits and disperse the seeds. Seed germination drops to 31% for the native *C. chilensis*, whereas germination improves to almost 40% for the exotic *C. edulis* and to 16% for the hybrid, which partially accounts for the invasive behavior of the two (Vilá and D'Antonio 1998). In Hawai'i, a recent study found that the Black Rat (*Rattus rattus*) consumes fruits of both native and invasive species, sometimes destroying seeds in the process. Although some species in both plant categories had high seed predation, 5 of 8 native species suffered, and the rat negatively affected only one of four invasive plants species (Shiels and Drake 2011). Such differential seed predation may facilitate invasion success of exotic plants. Considering the variation in performance of native and exotic frugivores on seed germination of either native or invasive plant species, it is clear that roles of frugivore are context dependent. Thus, a first step in the control of fleshy-fruited invasive plant species is to determine the role of each frugivore along the continuum of possible interactions.

### 10.3.2 Dispersion to habitats

Seed dispersal by frugivorous animals is usually directed, nonrandom. Frugivores often carry seeds to particular places such as nest sites, feeding roosts, and perch sites (Dean and Milton 2000, Corlett 2005, Deckers et al. 2008). They can move seeds among habitats such as ecotonal edges, wooded corridors, spurs, and open areas (Bartuszevige and Gorchov 2006; Linnebjerg et al. 2009). Seedling recruitment is also associated with disperser movements (Deckers et al. 2008) and the capacity of the seeds to germinate under tree canopies where the dispersers stay (Milton et al. 2007). When frugivorous animals forage from fleshy-fruited invasive plants, they may deposit seeds of many other species, even native species, and improve the general recruitment of seedlings in the forest (Tecco et al. 2006). Some birds with the ability to use human structures such as telegraph poles and wire fences have dispersed seeds along these structures and extended the distribution of invasive plants (Dean and Milton 2000). Other frugivorous species that feed on fruits of ornamental plants have been responsible for their escape from gardens, moving seeds to other anthropogenic areas as well as to native forests and savannas where the invasives may form dense stands (Lavergne et al. 1999, Koop 2004, Mack 2005, Milton et al. 2007, Foxcroft et al. 2008, Linnebjerg et al. 2009). Even though exotic frugivores can disperse high numbers of seeds of exotic plant species, in Hawai'i, they can also be important dispersers of native plants, helping in the restoration of the native forests (Foster and Robinson 2007). Thus, a first approach to predict the spatial patterns of invasive plant species with fleshy fruits is to identify which animals consume the fruits and where these animals travel.

### 10.3.3 Dispersal distances

Large animals usually have the capacity to move more seeds and over longer distances than small animals, which generally produce a smaller seed shadow. One of the largest frugivorous birds is the endangered Southern Cassowary, *Casuarius casuarius*, which can weigh 50 (male) to 70 kg (female). In Australia, these birds move seeds of an invasive species (Pond Apple; *Annona glabra*, L.) an average distance of 605 m, but 17% of the seeds were dispersed more than 1000 m, promoting the spread of the invasive plant (Westcott et al. 2008). Likewise, other large dispersers such as ungulates are very effective in moving seeds of invasive plants due to their wide home ranges. A comparative study of native elk (*Cervus elaphus*) and deer (*Odocoileus* sp.) found that these species can disperse both native and exotic species (Bartuszevige and Endress 2008). Over a 1 year period, the white-tailed deer (*Odocoileus virginianus*) can move seeds of approximately 70 exotic and native species. With a digestion time of 15–20 h and a range of 1–50 km depending on the season (Vellend 2002), these deer may be a significant dispersal vector of invasive species (Myers et al. 2004).

The estimate for seed dispersal distance by Mule deer, *Odocoileus hemionus*, is not quite significant, 10 to 800 m and some seeds to 1 km distance (D'Antonio 1990).

In contrast, small animals promote short seed dispersal distances. Bourgeois et al. (2005) estimated that on the French Mediterranean islands, rats move seeds an average of 40 m and rabbits may transport seeds for an average distance of 160 m. Brush rabbits (*Sylvilagus bachmani*) in the United States move seeds for even shorter distances, just an average of 10 m (D'Antonio 1990). In the case of small birds, the Silvereye retains seeds for 25 minutes after fruit consumption, but we have no estimate of the potential seed dispersal range for this species (Panetta and McKee 1997). Other small birds have a gut retention range for exotic fruits of 10–70 minutes and therefore their dispersal distance is short (Bartuszevige and Gorchov 2006). Additionally, McAlpine and Jasson (2008) reported that birds in New Zealand can move seeds of the invasive Darwin's barberry (*Berberis darwinii*) 100–450 m, but 65%–76% of the ingested seeds fell beneath the parental tree. On the other hand, migratory birds such as ducks (*Anas crecca*) may carry intact exotic seeds in their gut for distances up to 1000 km, helping to spread many exotic species across Europe (Brochet et al. 2009). So, much variation exists in dispersal distances of fleshy-fruited invasive species and this depends on which frugivores are involved.

### 10.3.4 Seed movement by epizoochory

Animals commonly disperse seeds through either frugivory (endozoochory) or epizoochory, which is when seeds or fruits are attached to hair, fur, feathers, or feet. Plants with this type of dispersal mechanism often have fruits or seeds with mucus, barbs, hooked hairs, or spines that attach the propagule to the animal's body. These can travel long distances and remain attached for a long time (Sorensen 1986, Manzano and Malo 2006, Couvreur et al. 2008). Epizoochory as a means of dispersal for invasive plants is not well known; however, some authors have suggested that exotic plant species have the tendency to adhere to a variety of mammal fur types, indicating flexibility for dispersal (Kulbaba et al. 2009). On Santa Catalina Island, off the coast of California, non-native species have spread across the island by becoming attached to the hair of another non-native, the American bison (*Bison bison*) (Constible et al. 2005). Likewise, horses (*Equus ferus caballus*) disperse seed of non-native species in their hooves (Gower 2008). Recently, migratory birds in Korea were observed dispersing propagules of the invasive weed, *Achyranthes japonica*. Choi et al. (2010) found that 3 of 3947 birds had seeds attached to the nape, back, or crural feathers. On one occasion, seeds were discovered on the lore and tail feathers. Although the authors did not know the origin of the seeds, they did note that these birds fly long distances. Thus, epizoochory is another means by which invasive species may be dispersed, though documentation is currently scant.

## 10.4 Invasive plants as source of food

### 10.4.1 Fruit crop attractiveness

The great advantage of fleshy-fruited invasive plants is that they can offer an alimentary resource for local fauna, contributing significantly to the portion of the total fruit available for frugivorous animals. Fruit abundance, fruit size, and pulpiness are used as cues by frugivores to select fruits (Sallabanks 1993). When invasive species have large fruit crops, they should be competitive, particularly where dispersal is frugivore-limited. Yet the spread of invasive species may simply occur through high fruit production, whether the plant–frugivore relationship is fruit- or frugivore-limited. Propagule pressure is expected to be greater for such plants. There are two key components of propagule pressure: (1) propagule size, which is the number of individuals in a propagule, and (2) propagule number, which is the rate at which propagules arrive per unit time (Simberloff 2009). Invasive plants generally have large fruit crops, and in many cases they produce numerous small fruits with bright and intense colors (Williams and Karl 1996, Shiferaw et al. 2004, Gosper and Vivian-Smith 2010). For example, in Australia, the most frequent color for fruits of invasive plants was purple to black, red, orange, and yellow (Gosper and Vivian-Smith 2010). And one of the most productive trees is *Miconia calvescens*, an aggressive invasive in Hawai'i, where these small trees average 45,000 fleshy berries per tree per year (Meyer 1998). Additionally, this tree can produce fruit for 6 months, with three major peaks, providing a steady resource for frugivores. *Chromolaena odorata* in South Africa can produce 2000 seeds/m$^2$/year (Witkowski and Wilson 2001). *Ardisia elliptica* in Puerto Rico produces an average of 2841 fruits per tree, with just one crop per year (Muñoz and Ackerman 2011). Fruit production by the same species in Florida varied across years and sites. However, the highest average number of seeds per tree was 929 (Pascarella 1998). *Carpobrotus* species (*C. edulis* and *C.* aff. *acinaciformis*), which is invading various localities in France, produces an estimated 25 fruits/m$^2$. The fruits are larger than the average for the region (6–10 mm vs. 19 mm) and have high energy and water content. Consequently, during drought and starvation periods, the fruits of these plants are highly desirable, attracting a number of different frugivores (Bourgeois et al. 2005). In California, Vilá and D'Antonio (1998) found that clones of the invasive *C. edulis* produce more fruits (average = 497) with a higher energy content than the native *C. chilensis*, which produces only 13 fruits per clone. As a consequence, fruits of the invasive species were preferred and removed more quickly by frugivores than those of the native *Carpobrotus*.

### *10.4.2 Fruiting phenology*

Fruiting phenologies of local and exotic plants often differ (e.g., Gosper 2004, Tecco et al. 2006), which can facilitate the success of exotic plant species. In Hong Kong, fruit traits of native and exotic species are similar; however, there are differences between the two groups in fruiting phenologies. Fruits of native species are available only in February–April, whereas those of exotic species are available throughout the whole year, facilitating their establishment by native frugivores (Corlett 2005). In Australia, *Chrysanthemoides monilifera* produces fruit throughout the year, but with a peak in autumn to winter, when few native plants have fruits (Gosper 2004). This invasive species also has small fruits, which nearly all frugivorous birds in the region are able to manipulate and consume (Gosper et al. 2006). In Argentina, Tecco et al. (2006) found that native species are dispersed in the warmer months, whereas exotic species fruit in the cooler months. Likewise, in New Zealand, two exotic species are available in June and July, when no native fruits are available (Williams and Karl 1996). In the Canary Islands, local plants have their maximum fruit production in the winter and spring, but exotic species peak in autumn, thereby extending the period of fruit availability for frugivorous animals (López-Darias and Nogales 2008). Thus, exotic plants frequently fruit for longer periods than native species or fruit when native fruits are rare, providing reliable, long-term resources for both native and invasive frugivores.

Both native and invasive frugivores will incorporate exotic fruits in their diets (Williams and Karl 1996, Foster and Robinson 2007); when fleshy-fruited invasive plants occur with other fleshy fruited species in the same habitat, competition for frugivores may ensue. The presence of the invasive *C. monilifera* in Australia reduced fruit removal rates of three native plant species with fleshy fruits (Gosper et al. 2006). However, facilitation may occur if frugivores are in short supply, but respond positively to increased fruit availability. In the United States, where invasive *Lonicera maackii* and *L. morrowii* occur in high densities, fruit-removal rates for a native plant species increased (Gleditsch and Carlo 2011). In another case, Drummond (2005) conducted food choice experiments in Maine and found that birds ate similar proportions of the native *Viburnum opulus* and the invasive *Rosa multiflora* without discriminating between them. Similarly, field observations of the invasive *Lonicera tatarica* and the native *Cornus amomum* showed that they had the same fruit removal rates by local frugivores. Should populations of these invasive species increase, then seed dispersal of native species might be overwhelmed, negatively affecting mutualistic relationships (Drummond 2005), but this topic warrants more research. Additional evidence comes from the exotic *Celastrus orbiculatus* and the native *Ilex opaca*, two sympatric vines in the eastern United States whose fruit removal rates over a 7-month period were statistically similar (Greenberg et al. 2001). So, competition, facilitation, or no apparent effect on fruit removal may occur between fleshy-fruited invasive and native plant species in the first phase of seed dispersal. However, we need more comparative studies to detect whether there are indeed consequences of apparent neutrality to population growth of native and invasive frugivores and the native and invasive plant species that they disperse.

Invasive species are generally considered to be detrimental to native communities and ecosystems. However, under certain circumstances, invasive species may be beneficial, particularly in poorly managed, severely degraded ecosystems. Fleshy-fruited invasive species may become important resources for native frugivores whose original food resources have declined (Foster and Robinson 2007). Such substitution may actually benefit the depauperate populations of native plants if frugivores are limiting and they respond to increased food densities as discussed in Section 10.4.2. Another possibility is that invasive trees and shrubs may be able to penetrate abandoned agricultural lands thick with non-native grasses, setting the stage for native, animal-dispersed species to become established (Ewel and Putz 2004, Lugo 2004, Abelleira Martínez 2010). Thus, before devising eradication, control, or management strategies, one needs to know not only the relationship between fleshy-fruited invasive species and their frugivores, but also whether or not the invasive plants are actually detrimental to species richness, composition, or ecosystem function.

## 10.5 Management of fleshy-fruited invasive plants

There are three common types of management to control or eradicate invasive species, and the cost, efficacy, and collateral damage of each depends on particular situations. The first type of control is physical removal. This is done through felling, pulling, digging out stumps and saplings, and burning areas (Hobbs and Humphries 1995). Moreover, for fleshy-fruited plants, physical removal should be timed before their fruits mature (Cheplick 2010). The second method is chemical control, using toxic formulations or herbicides such as tripclopyr, glyphosate, picloram/2,2,4-D amine or Tordon (Hobbs and Humphries 1995, Simberloff 2003, Munniapan et al. 2005). The third one is biological control, which is one of the most controversial strategies because of negative impacts on the environment and non-target species, both plants and animals (Hobbs and Humphries 1995). Nevertheless, there are natural enemies such as beetles (Bruchidae, Carabidae, Chrysomelidae, Curculionidae), isopods (Oniscidea), and slugs and snails (Mollusca: Pulmonata) that consume seeds or seedlings, which may be manipulated to increase mortality in invasive plants. Such a strategy to control invasive species is in its infancy (Honek et al 2009, Maguire et al. 2011).

In addition to the three conventional mechanisms to eradicate invasive plants, additional measures are recommended for control of fleshy-fruited plants. Because naturalized fruit-bearing plants vary widely in their invasiveness, risk assessment is critical. Buckley et al. (2006) categorized fleshy-fruited species as at either high or low invasion risk based on fruit traits. High-risk species are those with small fruits, large crop size, long fruiting season, and gap-filling phenology. Moreover, the risk stays high if these fruits are dispersed by large, opportunistic, or migratory frugivores. Low-risk species have large fruits, a thick inedible peel, and are highly defended. Exceptions are when large frugivores are involved or when fruits are soft and multiseeded. Risk stays low when frugivores destructively process fruits during ingestion or digestion or when dispersers are confined to small habitat fragments. Natural resource managers should be able to effectively classify the type of risk simply with a sound knowledge of both plants and frugivorous animals.

Thus, the main objective in management of fleshy-fruited invasive species is to minimize the impact of seed dispersal. Gosper et al. (2005) suggested that managers should focus on four points: (1) reduce fruit production or fruit quality; (2) direct seed deposition; (3) identify and remove major sources of seed spread; and (4) provide alternative resources for frugivorous animals. Strategies to minimize seed dispersal of fleshy fruited invasive species may include the following: (1) create barriers around weed infestations; (2) after using an infested pasture, pen livestock for 48 hours before moving them; (3) deter or prevent animal use or movement through weed infestations when plants are fruiting; (4) do not feed livestock hay that is contaminated with seeds of invasive species in uninfected locations (Davies and Sheley 2007); (5) minimize habitat edges because they help frugivore movements; (6) create perches as managed seed sinks (Buckley et al. 2006); and (7) cultivate native plants that may compete with invasive fruit-bearing species or substitute as resources for frugivores where invasives are to be exterminated (Gosper and Vivian-Smith 2006).

Gosper and Vivian-Smith (2006) developed a methodology to determine which native species should substitute as replacements for invasive plants in restoration programs, garden settings, parks, and urban environments. All fruit-bearing species are assigned scores based on phenology, morphology, conspicuousness, and accessibility. Native species with scores similar to that of invasive species are targeted as potential substitutes. The main idea is to identify native species that might compete with invasives for seed dispersal services and seedling recruitment sites (Gosper and Vivian-Smith 2009).

For the success of any invasive species management program, one needs the support of those that live within or close to infected areas. Multifaceted educational strategies can be developed to raise public awareness of the consequences of a plant invasions and how everyone can help control the problem with simple measures, such as avoiding invasive plants as ornamentals or removing such species from gardens (Foxcroft et al. 2008).

## 10.6 Conclusions

Establishment and colonization of many invasive plant species is greatly facilitated by resident animals, whether they are native or invasive themselves. Many invasive plants with fleshy fruits have large, colorful fruit crops that are often available to frugivores at time periods different from those of local species, thus either avoiding competition or facilitating the maintenance of frugivore populations. Although recent attention has been given to the role of native and exotic frugivores, it appears that their performance is very much context-dependent, and so much remains unknown of the interaction, from differential effects on seed germination to seed dispersal distances. Despite gaps in our knowledge of the particulars of cases involving frugivores and invasive species, methods for invasive species risk assessments show some degree of success. These need to be implemented to target invasive plants for further study, and if they are determined to be detrimental to local communities, then strategies to control them can be developed.

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