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Integration of exotic seeds into an Azorean seed dispersal network

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Abstract   Seed dispersal plays a central role in plant ecology. Among animals, birds are particularly important seed dispersers, often incorporating exotic plants into their diets and facilitating their integration in the communities. Network theory offers a highly informative framework to study the structural and functional attributes of complex interactions networks. We used information from bird fecal samples to build a quantitative seed dispersal network for the last fragment of native laurel forest in the island of São Miguel—Azores with three specific objectives: (1) to assess the integration of exotic seeds into seed dispersal; (2) to evaluate the impact of exotic plants in network structure; (3) to test the potential of an exotic species to reduce the seed dispersal of a co-occurring native, via competition for seed dispersers. The seed dispersal network was based on the analysis of 1,121 droppings and described 74 unique interactions between 41 plant species and 7 bird species. Exotic seeds deeply infiltrated into the seed dispersal network forming the majority (59 %) of seeds in the droppings and including those of three globally invasive plants. Overall, birds depended equally on native and exotic fruits despite the lower abundance of the latter in the study area. In an experiment, birds did not show a preference for fruits of the exotic *Leycesteria formosa* over the native *Vaccinium cylindraceum* consuming them equally. However, the presence of the exotic plant negatively affected the number of native seeds dispersed, by diverting some of the consumers of the native fruits. Taken altogether the results reveal an alarming invasion level of seed dispersal systems in one of the last remnant native forests of the Azores.

Keywords   Azores · Ecosystem services ·
Exotic plants · Laurel forest · Plant invasions ·
Seed rain

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Introduction

Seed dispersal is a key process that, to a great extent, determines plant spatial structure, population dynamics and long-term species persistence (Nathan and Muller-Landau 2000). However, seed dispersal is not only important for the regeneration of natural vegetation but it can also facilitate the spread of exotic plant species (Traveset and Richardson 2011). Indeed, it is frequently documented that the incorporation of exotic plant seeds into the diet of frugivores can be an

important step in that species becoming invasive (e.g. Bartuszevige and Gorchov 2006; Buckley et al. 2006; Williams 2006). Given the impact of plant invasions throughout the world (e.g. Vitousek et al. 1996), understanding seed dispersal can give an important contribution for planning effective wildlife conservation strategies, particularly those involving the conservation of rare plants and the control or eradication of fleshy-fruited weeds (Gosper et al. 2005; Buckley et al. 2006). The growing recognition that species-interactions patterns, and not only species-lists, are particularly important for the understanding of many ecosystem functions (MEA 2005; Duffy et al. 2007; Memmott et al. 2007), has lead ecologists to invest a considerable amount of effort in documenting the interactions between plants and their animal dispersers. However, these efforts focus mainly on the identification of the plants dispersed by specific introduced animals (e.g. Williams 2006; Milton et al. 2007; Kawakami et al. 2009; Linnebjerg et al. 2010), or on the identification of the dispersers of focal invasive plants (e.g. Stansbury 2001; Cordeiro et al. 2004; Bartuszevige and Gorchov 2006). The quantification of the whole seed dispersal processes in naturally occurring communities native and exotic plants being simultaneously dispersed by a complex assemblage of frugivores has been rarely attempted (Buckley et al. 2006), despite some notable efforts (e.g. Aslan and Rejmánek 2010; Heleno et al. 2012b). This lack of knowledge contrasts with the much better understanding of the disruptive effect of exotic plants on pollination networks, the other important reproductive mutualism for flowering plants (e.g. Memmott and Waser 2002; Olesen et al. 2002; Carvalheiro et al. 2008; Traveset and Richardson 2011).

It is now widely recognized that the disruption of these species-interaction networks can have a profound impact on the communities' response to environmental disturbance and ecological restoration (Dunne et al. 2002; Estrada 2007; Heleno et al. 2010). Knowledge on the structure and function of such mutualisms is particularly urgent on oceanic islands where recently introduced species are rapidly eroding communities which typically evolved under relaxed competitive pressure (MacArthur and Wilson 1967; Whittaker and Fernández-Palacios 2007). In this study we use seed dispersal networks to evaluate the dispersal of exotic seeds in one of the last fragments of native forest in the archipelago of the Azores.

This study has three specific objectives: (1) To evaluate the extent to which exotic plants infiltrate the seed dispersal network, and the importance of native and exotic fruits and seeds as resources for birds. We predict that in this remnant native forest frugivorous birds will depend mostly on native fruits, however given the generalized nature of most plant-frugivores interactions (Jordano 1987; Berlow 1999), we expect that exotic fruits will be easily integrated by foraging birds which will disperse their seeds (2) To determine how exotic plants change the structure of a seed dispersal network. Many exotic species are particularly attractive to many frugivores (Renne et al. 2002), thus the consumption of their fruits is likely to increase network-level parameters which are directly related to the number of interactions established by species within a community, such as linkage density, connectance and robustness. (3) To use a field experiment to test whether an exotic plant species can reduce the seed dispersal of a co-occurring native plant. If the integration of exotic fruits into seed dispersal networks occurs by diverting some of the services previously allocated to disperse native seeds, we expect that the number of native fruits dispersed is reduced when native and exotic plants with similar fruit traits and phenology are in direct competition for dispersers.

Methods

Study site

The study was conducted in *Serra da Tronqueira*, a mountainous district in the East of the Island of São Miguel, Azores, Portugal which holds the last fragment (c. 815 ha; SPEA 2005) of native forests in the archipelago—the Laurel forest (Fig. 1). The laurel forests of the Atlantic islands are considered relics of the Palaeotropical vegetation composed by broad-leaved, evergreen trees and shrubs with a relatively low canopy and dense understory of shrubs and ferns (Schaeffer 2002; Dias et al. 2007; Fernandez-Palacios et al. 2011). In the Azores the most representative species are endemic to the archipelago: *Laurus azorica*, *Juniperus brevifolia*, *Ilex perado* spp. *azorica*, *Erica azorica* and *Vaccinium cylindraceum* (Schaeffer 2002; Dias et al. 2007). The Azores have a temperate oceanic climate, with high relative humidity

Fig. 1 Location of field sites. *Open circles* indicate field sites where bird fecal samples were collected. *Closed circles* indicate field sites where fecal samples were collected and plant abundance and bird density was estimated
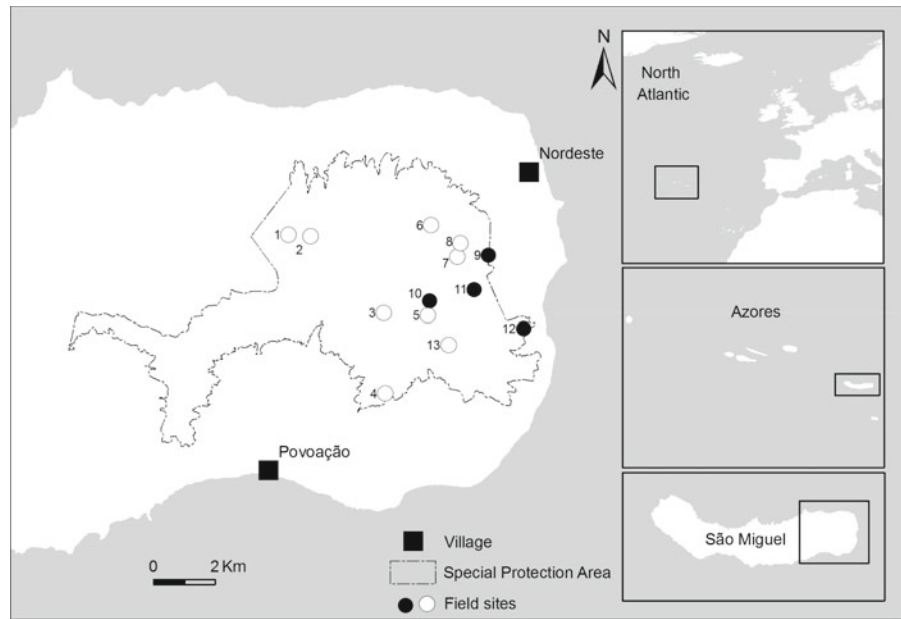
Map code	Name	Geographic coordinates
1	Bardinho	37°48'54,428"N; 25°14'13,126"W
2	Algarvia	37°48'52,314"N; 25°13'43,834"W
3	Trilhos Novos	37°47'30,230"N; 25°12'08,870"W
4	Pico da Feteira	37°46'05,587"N; 25°12'08,843"W
5	Estrada da Tronqueira	37°47'26,891"N; 25°11'10,470"W
6	Malhada	37°49'01,658"N; 25°11'03,751"W
7	Grotas Fundas	37°48'27,797"N; 25°10'29,913"W
8	Fajã do Rodrigo	37°48'41,913"N; 25°10'25,218"W
9	Outeiro Alto	37°48'28,981"N; 25°09'48,398"W
10	Miradouro da Tronqueira	37°47'42,060"N; 25°11'07,350"W
11	Cancela do Cinzeiro	37°47'53,178"N; 25°10'07,846"W
12	Lombo Gordo	37°47'11,134"N; 25°09'03,496"W
13	Pico Bartolomeu	37°46'55,387"N; 25°10'43,313"W

and small temperature range (Tutin 1953). Native vegetation in São Miguel has been largely converted to pastures and replaced by plantations of *Cryptomeria japonica*, the remaining forest has been greatly invaded by aggressive weeds such as *Pittosporum undulatum* (Australian cheesewood), *Hedychium gardnerianum* (Kahili ginger), and *Clethra arborea* (Lilly-of-the-valley-tree) (Silva 2001).

Building the quantitative seed dispersal networks and estimating fruit abundance

A seed dispersal network was built for the *Serra da Tronqueira*, quantifying each seed–bird interaction (dispersal event) by analyzing bird fecal samples collected over 3 years. Due to their high mobility and frugivorous habits, birds are in many ecosystems, the most important seed dispersers (Herrera 1995) and they are likely the only relevant seed-dispersers in the Azorean native forests, due to the absence of reptiles and native mammals. Fecal samples were collected over the course of 3 years: April 2005 to November 2007 in 13 sites across the Special Protected Area of *Serra da Tronqueira* and Ribeira do Guilherme (Fig. 1). These sites were representative of the actual gradient of plant invasion of the native laurel forest in the study area. The decision of building a single network for the whole forest was based primarily in the objective of having a detailed and realistic characterization of the seed dispersal system at the landscape-unit that is managed by practitioners. All sites are imbedded in the same forest patch and are thus not fully independent as most bird species in the area are present throughout the study area and move

frequently between sites (R. Heleno, unpublished data). Furthermore, the sampling effort allocated to each site was not uniform but proportional to the relative importance of each habitat class in the whole mountain range, with some sites receiving little effort, which would hinder any direct comparison of site-specific networks. Given that this area contains the last remaining patch of native habitat on the island, using multiple forest patches was not an option.

The collection of fecal samples was conducted during ringing sessions with mist nets. In each session, mist nets were opened at sunrise and remained open for five consecutive hours. Mist nests (c. 60 m) were erected approximately 6 times per month during the study period resulting in 193 ringing sessions (87, 45 and 61 in 2005, 2006 and 2007, respectively). Birds were kept inside ringing bags to defecate for a maximum of 30 min and droppings were stored in 70 % ethanol for later analysis. All entire seeds in the droppings were identified under a dissecting microscope by comparison with a reference collection.

Dispersal effectiveness was visually incorporated into the networks by weighing the presence of intact seeds in bird droppings by the abundance of the disperser. This was calculated by multiplying the frequency of occurrence of intact seed species in the fecal samples (an important component of the quality of seed dispersal), by independent estimates of bird abundance (a measure of the quantitative component of seed dispersal) (Schupp et al. 2010). Because there are other factors affecting the quality of seed dispersal, such as the quality of the deposition site, which we have not considered, the measure proposed here is best considered as a proxy of the real dispersal effectiveness of each disperser. Bird abundance was obtained by recording birds with 8-min point-counts, at 3 weeks intervals in four sites representative of the main levels of plant invasion (Fig. 1), from 1 May to 26 November 2005. The description of these sites and methods for estimating bird abundance are described in Heleno et al. (2011). The seed dispersal network was visualized using software written in Mathematica® (Wolfram Research 1999). In order to quantify fruit availability for dispersers, fruit production was estimated in the same four sites as bird abundance. Fruit production were sampled by counting all ripe standing fruits and seeds (hereafter collectively referred to as fruits) within a swathe of vegetation 1 m either side of 100 m linear transects. Fleshy fruits were individually counted while seeds from dry-fruited families (e.g. Asteraceae, Cyperaceae) were quantified in terms of flower/seed-heads (e.g. Evans et al. 2011). When high fruit abundance made counting prohibitive, the number of fruits in smaller areas was assessed and extrapolated for the whole transect. Forest height did not pose a problem for fruit counts as most trees in the study sites were bellow 4 m. Ten transects were run at each site at 3 weeks intervals from 1 May to 26 November 2005, this time interval incorporating the fruiting season of most plant species (Schaeffer 2002).

In order to evaluate the importance of native or exotic fruits for the bird community we evaluated plant species strength, i.e. the sum of each bird species relative dependencies on native or exotic plant species (Bascompte et al. 2006). The effect of plant abundance and origin on plant species strength (square root transformed) was evaluated with a General Linear Model. The frequency of occurrence of intact seeds on bird droppings was used as a proxy of bird dependency on each plant species.

Evaluating network structure

We tested the effect of the integration of exotic plants on five commonly used network descriptors which are likely to be influenced by species generalism. The following five descriptors were calculated for the whole seed dispersal network and for the alien and native sub-networks: (1) Connectance, i.e. the proportion of links that are realized among all possible links; (2) the mean number of dispersers per plant; (3) Linkage density, i.e. the mean number of interactions per species weighted by interaction frequency; (4) Interaction evenness, i.e. the Shannon's evenness of interaction frequencies (Bersier et al. 2002); and (5) Robustness, i.e. the effect of species loss on the network, measured in terms of linked extinctions (Dunne et al. 2002). All parameters were calculated using the R package Bipartite 1.16 (Dormann et al. 2008) and are described in Dormann et al. (2009); the first four descriptors are quantitative, i.e. incorporate a measure of interaction frequency, while robustness analysis is based on qualitative, i.e. presence only, data.

Because all of these indices are, to some extent, dependent on network size (Dormann et al. 2009), the direct comparison of parameter values is not fully informative. Thus, the results are also presented and

discussed in terms of a "standardized" percentage of the observed value for each parameter relatively to the bench-mark value of the same parameter for randomly generated networks of the same size. Such randomly generated networks were created using the algorithms implemented by method "*r2dtable*" under function "*nullmodel*" in the package Bipartite (Dormann et al. 2008) for R (R Development Core Team 2010), and replicated 1,000 times. Observed values were considered to be significantly different from random if they were outside of the 95 % confidence interval around the mean of each parameter (see Gibson et al. 2011; Montesinos-Navarro et al. 2012, and references therein).

Evaluating competition for seed dispersers

In order to evaluate if an exotic plant can appropriate the dispersers of native plants, thereby reducing the dispersal of native seeds, we compared the dispersal efficiency of the exotic *Leycesteria formosa* (Caprifoliaceae) and the native *Vaccinium cylindraceum* (Ericaceae). We focused on this particular pair of species because both are endozochorous producing berries with many small seeds, their fruits have similar size (6–9 mm), similar colour (dark purple when ripe) and similar caloric content (Mean $\pm$ SD = 4,468 $\pm$ 51 cal g^{-1} and 4,737 $\pm$ 403 cal g^{-1} for *L. formosa* and *V. cylindraceum* respectively; R. Ceia, unpublished data). Both species are abundant and ubiquitous in the study area (Fig. 2), their fruit display is very similar and they have overlapping fruiting phenologies, all suggesting that both species might directly compete for seed dispersers.

We quantified fruit removal from *V. cylindraceum* trees when isolated (i.e. pre-invasion) and when adjacent (<2 m) to *L. formosa* (i.e. post-invasion). The initial fruit load of each plant (both the native and the exotic) was reduced to 300 ripe fruits, and all flowers and flower buds were manually removed. Fallen fruits were collected with a net circling each plant, which was inspected every other day for 3 weeks, at which time the number of fruits remaining on each plant was counted. While this approach is unlikely to catch every single berry, the number of berries lost should be very similar for both species of plant. The experiment consisted of five blocks of two plant arrangements: (1) an isolated *V. cylindracem* and (2) a *V. cylindraceum* standing adjacent to a *L.*

formosa. Within a block the solitary and the paired *V. cylindracem* were at least 30 m apart and all groups were at least 100 m apart. The number of fruits removed from each tree at the end of the experiment was calculated as:

$$\text{Fruit}_{\text{removed}} = \text{fruit}_{\text{initial}} - (\text{fruit}_{\text{final}} + \text{fruit}_{\text{fallen}})$$

The number of fruit removed by birds from each plant was explored via repeated measures General Linear Model with the experimental groups of trees included as subjects. Post hoc pairwise comparisons between treatments were performed with paired *t* tests, applying a Bonferroni correction.

Results

Fruit abundance

Overall, 837,101 fruits of 68 plant species were counted or estimated on the four sampled plots in 2005. Regarding the diversity of fruiting species, 34 (50 %) were exotic, while 32 species (47 %) were native and two species (3 %), *Fragaria vesca* and *Prunella vulgaris,* were of uncertain origin. Regarding the number of fruits available, the majority were from native species (511,598 fruits, representing 61 % of all produced fruits), most of these being from endemic trees, chiefly *Ilex perado*, *Juniperus brevifolia* and *Viburnum treleasei*, and comprising 54 % of all fruits. Among exotic species, which together formed 39 % of the fruits displayed (324,703 fruits), the more important species were *C. arborea*, *H. gardnerianum* and *L. formosa* (Fig. 2).

Integration of exotic seeds into seed dispersal networks

Overall 1,121 droppings were collected from nine bird species during 965 trapping hours. A total of 1,423 intact seeds were found in 274 droppings (24 %) and were produced by seven of the nine bird species present in the study area (Fig. 2). Blackcap (*Sylvia atricapilla*) and Blackbird (*Turdus merula*), were the main seed dispersers followed by Robin (*Erythacus rubecula*). Each bird that consumed fruit dispersed a large proportion of exotic seeds (usually present in more than 50 % of the droppings). Droppings contained entire seeds from 41 plant species, these being
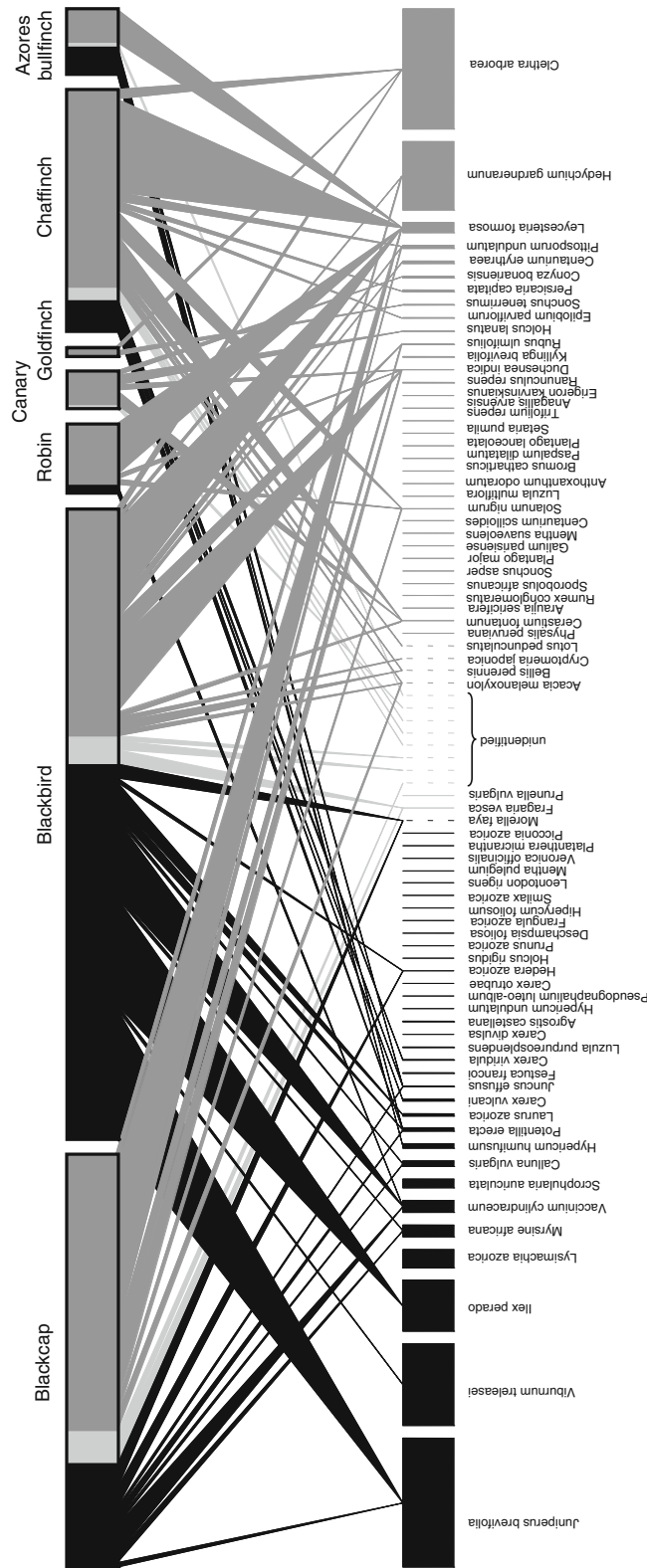
Fig. 2 Quantitative seed dispersal network of Serra da Tronqueira - Azores. Species are represented by *boxes*, plants on the *lower row* and birds in the *upper row*. Plant taxonomy and origin follows Silva et al. (2010). The width of each *box* is proportional to that species abundance within each trophic group (Birds: birds/ha; Plants: Number of fruits). The *triangles* linking the two *rows* represent seed dispersal effectiveness of each bird-seed interaction with the width of the *triangle* being proportional to its importance as seed dispersers (frequency of occurrence of intact seeds in bird droppings × bird abundance). Native seeds and their interactions are shown in *black* and exotic seeds in *dark grey*, *light grey* represent species of unknown origin (Silva et al. 2010). The *color of boxes* in the *upper row* (birds) is proportional to the consumption of native, unidentified and exotic fruits/seeds by each bird species. *Dotted lines* indicate seeds recovered from droppings that were not detected in the fruit census

linked to dispersers by 74 unique interactions (Fig. 2). Overall, the seed dispersal web indicates that the local seed dispersers have integrated exotic fruits into their diets, to the extent that almost two-thirds of all seeds dispersed are exotic. The seed dispersal network was generalized with most bird species dispersing several seed species (mean 10.6; range 2–24) and most seeds being dispersed by more than one bird species (mean 1.8; range 1–5).

From the 32 seed species that could be identified, 14 were native, 18 were exotic, and the origin of 10 species (which together comprised only 4 % of the seed recovered) could not be ascertained. Among the droppings that contained seeds, 46 % contained seeds of native species while 65 % contained exotic seeds and 11 % of the droppings contained both native and exotic seeds. Considering the absolute number of individual seeds recovered from the droppings, 843 seeds (59 %) were exotic while 521 seeds (37 %) were native and 4 % could not be identified to species level (morphotypes). These proportions reflect a bias towards the dispersal of exotic seeds, in relation to their relative abundance ($G = 20.6$; $df = 1$; $P < 0.001$). This result is largely influenced by a few highly attractive species found in the droppings; *L. formosa* and *Duchesnea indica* among the most common exotic species dispersed. Whereas neither *L. formosa* and *D. indica* are considered among the most serious invasive species in the Azores (Silva et al. 2008), seeds of several highly invasive plants were found in the bird droppings, namely seeds of *H. gardnerianum* were found in four droppings (1.6 %), seeds of *Acacia melanoxylon* in five droppings (1.8 %), *Pittosporum undulatum* in nine droppings (3.3 %) and *Clethra arborea* in five droppings (1.8 %).

The strength of fruits as resources for birds was not affected by their origin ($F = 2.01$; $df = 1$; $P = 0.164$), abundance ($F = 0.12$; $df = 1$; $P = 0.728$), or the interaction between these factors ($F = 0.86$; $df = 1$; $P = 0.362$).

Evaluating the consequences for network structure

Our predictions that the exotic sub-web will have higher linkage density, mean number of dispersers per plant, and interaction evenness than the native sub-web were correct (Table 1). The robustness of the exotic sub-web was marginally, but not significantly higher than in the native sub-web. For all the above

parameters except linkage density (which is additive), the values of the whole network were between the values obtained for the native and the exotic sub-webs. Only network connectance was affected in the opposite way, being higher in the native sub-web and lower in the whole network.

Evaluating competition for seed dispersers

Birds showed no preference for fruits of *L. formosa* or *V. cylindraceum*, consuming them equally (mean $\pm$ SE $= 96 \pm 15$ and 102 ± 23, respectively; $t_{(4)} = -0.20$; $P = 0.854$; Bonferroni corrected $\alpha = 0.025$) when both species were presented side by side in similar fruit displays (Fig. 3). However, significantly fewer fruits (56.7 % fewer) were removed from *V. cylindraceum* plants standing next to the exotic *L. formosa* than from isolated plants (mean $\pm$ SE $= 102 \pm 23$ and 180 ± 20, respectively; $t_{(4)} = -4.41$; $P = 0.012$; Bonferroni corrected $\alpha = 0.025$).

Table 1 Quantitative network descriptors for the Azores seed dispersal network (see "Methods" for parameter descriptions)

Parameter	Whole network	Exotic sub-web	Native sub-web
Connectance			
Observed	0.258	0.325	0.333
Standardized (% M_0)	73.5*	77.5*	79.1*
Linkage density			
Observed	6.26	4.23	3.46
Standardized (% M_0)	73.8*	84.4*	71.4*
Mean number of dispersers per plant			
Observed	2.61	3.35	1.56
Standardized (% M_0)	77.1*	84.0*	73.0*
Interaction evenness			
Observed	0.84	0.84	0.79
Standardized (% M_0)	98.0*	100.4	94.5*
Robustness			
Observed	0.51	0.54	0.46
Standardized (% M_0)	95.5	108.8	82.6*

For each parameter the real or "observed" value is presented as well as its "standardized" measure in the form of a percentage in relation to the same descriptor for 1,000 randomly generated networks of the same size. This latter "standardized" measure facilitates the comparison across the three networks, which would otherwise be hindered by their different sizes. Observed values outside the 95 % confidence limits around the mean of the null models are marked with *

Discussion

Although native fruits are more common in the study area, the seed dispersal network was dominated by exotic seeds (59 %). The proportion of exotic seeds dispersed in this Azorean forest is higher than in other archipelagos; for example, birds consumed on average 19 % of exotic fruits in New Zealand (Williams and Karl 1996), 15 % in Hawaii (Foster and Robinson 2007), and 5 % in the Galápagos (Heleno et al. 2012b). The level to which exotic plants have infiltrated seed dispersal network in one of the last native forests in the Azores is alarming as it is to the point that the network is no longer characterized by native seeds.

Integration of exotic seeds into seed dispersal networks

Contrary to our expectations, and despite being less abundant in the study area, exotic species were as important as native species for dispersers. This result suggests that exotic plants might be disproportionally attractive to birds, which will consume their fruits and disperse their seeds. Seeds of highly invasive species: *H. gardnerianum*, *P. undulatum* and *A. melanoxylon* were found in droppings of Blackcaps, Blackbirds and Chaffinches. These three plant species are included in the list of the World's worst invasive species (Global Invasive Species Database 2010) and are directly threatening the native laurel forest (Ramos 1996; Heleno et al. 2010) and consequently also threatening the last remaining population of the Azores bullfinch
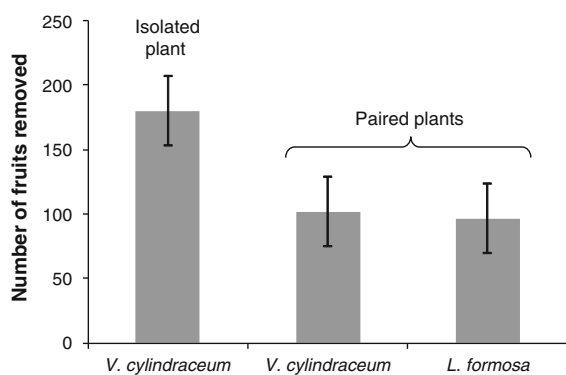
which is found at this site (Ceia et al. 2011). We recorded entire seeds of *P. undulatum* and *A. melanoxylon* in droppings of birds captured more than 300 m away from the nearest adult tree. Even though the proportion of seeds from highly invasive species was low, there is evidence that long distance dispersal events can be critically important at accelerating the invasion process (Nathan and Muller-Landau 2000). Several studies reported the facilitation of plant invasions by mutualistic interactions, for example Williams (2006) suggested that Blackbirds make a major contribution to the spread of woody weeds in New Zealand, and several native and exotic dispersers facilitate the spread of *Opuntia* spp. in the Mediterranean region and in the Canary islands among others (Padrón et al. 2011). To date, the vast majority of seed dispersal research has focused on particular species or a small component of the seed dispersing fauna. Alternatively, to consider the more typical situation of multiple invasive and native plant species, simultaneously interacting with seed dispersers, is likely to further advance our understanding and managing of plant invasions (Gosper et al. 2005).

Evaluating the consequences for network structure

An ideal experimental design to evaluate the effect of invasion on seed dispersal networks would consist of comparing independent site-specific networks along a gradient of invasion. This design has not yet been used though as it is logistically very challenging and necessitates a gradient, unconfounded by other factors, to be available for use. Such gradients are extremely difficult to find in many islands and virtually do not exist in the Azores. The difficulty in planning robust designs to statistically test changes in replicated networks is extremely difficult as a result of the large sampling effort needed to build representative and well-resolved networks. This limitation is frequently circumvented by running simulations with null models like the ones presented here (e.g. Fortuna and Bascompte 2006), by conducting meta-analysis of networks (e.g. Thébault and Fontaine 2010) or focusing on species-level interaction patterns instead of emergent network properties (e.g. Memmott and Waser 2002). Although the first steps have been given towards statistically evaluate the effect of invasion on pollination networks (Padrón et al. 2009) and for comparing patterns of seed dispersal between islands and

Fig. 3 Number of fruits removed from *Leycesteria formosa* and *Vaccinium cylindraceum* trees under two treatments: *L. formosa* side by side with *V. cylindraceum*, and an isolated tree of *V. cylindraceum*. *Error bars* represent the standard error

continents (González-Castro et al. 2012), we are aware of a single study reporting the effects of plant invasions on seed dispersal networks, that of Heleno et al. (2012b) in the Galápagos.

Our study revealed that exotic plants attracted on average more seed dispersers than native plants, and thereby their integration increased linkage density, the mean number of dispersers, and the network robustness. For these descriptors, the whole network exhibited values that are between the values of the native (more specialist) and the exotic (more generalist) subwebs, reflecting a tendency of exotic plants to inflate such descriptors. The initially counter-intuitive result that exotic plants tend to increase the robustness of plants to the loss of dispersers is caused by an increase in the linkage level, and thus on a lower probability of any individual plant losing all its dispersers. The integration of exotic plants increased interaction evenness, this is consistent with the generalism of many exotic species which attract a diverse array of frugivores and thus act as stabilizing the distribution of interaction frequencies. Connectance, which is largely related to the average generalisation of species in the network (Warren 1994; Heleno et al. 2012a), decreased with exotic plants integration. In pollination studies, exotic plants have been shown to reduce connectance (e.g. Memmott and Waser 2002) or have no effect over it (e.g. Padrón et al. 2009; Vilà et al. 2009). Our expectation of increased connectance was based on the assumption that many invasive plants tend to be highly attractive to frugivores (Renne et al. 2002). The reduction in network connectance, could be due to the abundance of naturalized herbs (e.g. *Sonchus asper*, *Plantago major*, *Anthoxanthum odoratum*, etc.; Fig. 1), which largely increase the number of possible interactions (network size) but attract few dispersers, thereby reducing the proportion of realized links.

Evaluating competition for seed dispersers

Our results suggest that most frugivorous birds do not discriminate between fruits of the native *V. cylindraceum* and the exotic *L. formosa*, consuming them equally when these are simultaneously presented. However, while the presence of the exotic plant did not seem to attract more frugivores, the presence of this exotic plant resulted in a net negative effect of the removal of the native plants that had to share the

dispersers of their fruits. Thus significantly fewer (56.7 %) *V. cylindraceum* were removed by birds when in close range to an exotic plant. Similar negative interactions between native and exotic species mediated by mutualists have been documented in pollination systems with exotic plants reducing pollinator visitation and thereby seed set of co-occurring native and alien plants (e.g. Chittka and Schurkens 2001). Few studies evaluated the influence of adjacent fruiting plants on the seed dispersal effectiveness of focal trees, and these had mostly contrasting results (e.g. Carlo 2005; Saracco et al. 2005; Blendinger and Villegas 2011). While on a relatively small scale our experiment is, to our knowledge, the first to document a negative effect of an invasive plant in the seed dispersal performance of co-occurring native plants. This results support the prevalence of competition, rather than facilitation between these two plant species. In our experiment it is not possible to conclude that competition is specifically related to the exotic status of *L. formosa* and to exclude the hypothesis of similar effects between co-occurring pairs of native species. Nevertheless, the expected range expansion of this and other exotic species is likely to increase the prevalence of exotic-native competing pairs of plants at the landscape level. The equal importance (i.e. strength) of exotic and native species, despite the higher abundance of the latter, further supports the idea that exotic plants are superior competitors than natives.

While our study is illustrative of the importance of birds for the spread of intact exotic seeds in Serra da Tronqueira, we could not quantitatively link seed dispersal with the dynamics of native and exotic plant populations (i.e. dispersal effectiveness). Previous studies in this area suggest that exotic seedlings are more competitive in early life-stages than seedlings from native species (Heleno et al. 2010), and that monotonic stands of exotic plants can have negative effects on plant, insect and vertebrate diversity and biomass (Ramos 1996; Ceia et al. 2009; Heleno et al. 2009). However, the relationship between seed dispersal and changes in the adult plant populations deserves further attention (Côrtes et al. 2009; Calviño-Cancela 2011). Furthermore, future studies that simultaneously consider the facilitation versus competition between whole natural assemblages of native and exotic plants will be important to confirm the generality of these results.

The Azores seed dispersal network is highly generalized as is typical of seed dispersal systems (Malmborg and Willson 1988). The fact that seed dispersal is such a generalized process is both positive and negative news for habitat conservation: on one hand the redundancy of dispersers is likely to confer some degree of robustness for animal-dispersed native plants to the local extinction of dispersers; while on the other hand it provides invasive plants with a suite of well established mutualists (Gosper et al. 2005; Buckley et al. 2006). In this sense, birds are part of the solution and part of the problem and the challenge facing conservation ecologists is to study possible mechanisms that allow us to increase the former and reduce the latter.

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