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Tiptoeing between restoration and invasion: seed rain into natural gaps within a highly invaded relic forest in the Azores

Sandra Hervías Parejo · Ricardo S. Ceia ·
Jaime A. Ramos · Hugo L. Sampaio ·
Ruben H. Heleno

Abstract The last remains of native laurel forest in the Azores are highly threatened by the spread of invasive plants. Because landslides are very frequent in these islands, conservation of native laurel forest requires knowledge of the patterns of bird-dispersed seed rain into forest gaps. We monitored 78 seed traps over 1 year to investigate (1) the role of perches in attracting avian dispersers into gaps, (2) temporal patterns in the dispersal of exotic and native seeds, (3) how seed rain affects vegetation establishment in gaps at different distances from the native forest and (4) whether the caloric content of fruits could explain the number of seeds dispersed. Perches were highly effective in concentrating avian seed dispersal. While some native fruits are produced all year-round, most exotic plants set fruits during the main peak of the native fruit production (August–November). Most seeds recovered from the traps were native, and native seed rain inside the native forest was higher than in gaps. However, deposition of exotic seeds was not affected by distance from native forest. Seed dispersal frequencies monitored by seed traps and by faecal analysis were correlated with each other, but not with fruit caloric content, suggesting that other factors are more important that the nutritional value in predicting avian fruit choice. Forest restoration activities should take into consideration that seed dispersal decreases sharply beyond 100 m from native forest and the attractive potential of perches to direct natural seed dispersal into forest gaps.

S. H. Parejo (✉)
Animal Health Department, Faculty of Veterinary, Regional Campus of International Excellence "Campus Mare Nostrum", University of Murcia, 30100 Espinardo, Murcia, Spain
e-mail: shparejo@gmail.com

R. S. Ceia · J. A. Ramos
Department of Life Sciences, Marine and Environmental Research Center (IMAR/CMA), University of Coimbra, Coimbra, Portugal

H. L. Sampaio
Portuguese Society for the Study of Birds (SPEA), Avenida João Crisóstomo, 18-4°Dto., 1000-179 Lisbon, Portugal

R. H. Heleno
Department of Life Sciences, Centre for Functional Ecology, University of Coimbra, Coimbra, Portugal

Introduction

Natural disturbances such as landslides open areas in the canopy of a forest (hereafter gaps), exposing the soil to plant colonization but also erosion (Walker 1994). Vegetation gaps accelerate species turnover, especially if most of the top soil layer containing the seed bank is dragged off (Garwood 1989; Vazquez-Yanes and Orozco-Segovia 1996). Therefore, such disturbances might facilitate exotic plant invasions because competition with native species is reduced in gaps (Hooper 1992). The conservation of native forests where landslides are frequent requires knowledge of whether seed dispersal into gaps tends to facilitate either native forest re-establishment or exotic plant invasions (McClanahan 1986; Aide and Cavelier 1994).

Birds are the main seed dispersers in many temperate ecosystems and particularly in oceanic archipelagos where mammals are frequently absent (Nogales et al. 2005; Arteaga et al. 2006; Whittaker and Fernández-Palacios 2006).

Exotic plants often produce large fruit crops of nutritious berries and hence are particularly attractive to birds (Heleno et al. 2013), which may disproportionately disperse seeds from fruits with a higher calorific content. Patterns of fruit preference by birds frequently result in non-random seed deposition, likely affecting plant composition and abundance in the context of succession (Manasse and Howe 1983; Wenny and Levey 1998; Schupp et al. 2002).

The Macaronesian laurel forest persists in the archipelagos of the Canaries, Madeira and Azores (Fernández-Palacios et al. 2011). In the Azores, cattle grazing, agriculture and forestry activities have caused serious damage to the laurel forest since the human colonization in the fifteenth century (Ramos 1996). Since the 1940s, many areas were planted with Japanese red cedar (*Cryptomeria japonica*), and presently native laurel forest is restricted to high altitudes and is mostly threatened by plant invasions, particularly Australian cheeswood (*Pittosporum undulatum*), Kahili ginger (*Hedychium gardneranum*) and Lily-of-the-valley-tree (*Clethra arborea*), which are outcompeting the native plants (Ramos 1996; Heleno et al. 2010). This scenario motivated European financed programmes of laurel forest restoration (three consecutive LIFE projects coordinated by the Portuguese Society for the Study of Birds, 2003–2013) through invasive plant clearance in São Miguel, the largest island of the archipelago. Due to their geographical location (at the end of the North Atlantic hurricanes highway), high humidity and geological setting with steep cliffs of relatively recent age, São Miguel has a high risk of landslides (Valadão et al. 2002). Exotic plant invasion into native forest gaps may cause the fragmentation of the last remains of Azorean laurel forest, jeopardizing the efforts of restoring this valuable ecosystem which sustains the endemic Azores Bullfinch (*Pyrrhula murina*) (Ceia et al. 2011).

This study was aimed at assessing differences in patterns of bird-dispersed seed rain (hereafter seed rain) into forest gaps at different distances from the native forest. It focused on four specific objectives: (1) to test whether the introduction of perches can assist seed rain into gaps by attracting frugivorous birds (Howe and Smallwood 1982); (2) to investigate temporal patterns on the dispersal of exotic and native seeds, in order to examine potential competitive advantages for exotic seeds; (3) to measure seed rain into gaps inside the native laurel forest and in gaps formed within plantations of the exotic Japanese red cedar at different distances from native forest. Because afforested areas are effective barriers to bird movement (Vergara and Simonetti 2006), we expect that seed rain and hence the rate of native forest establishment are likely to decrease with increasing distance from remnant forest patches (Schupp 1990; Clark 1998); and (4) to evaluate whether fruit caloric content can explain the relative number of bird-dispersed seeds, by directing fruit choice.

Methods

Study area

This study was carried out in the eastern part of São Miguel Island (37°47′N, 25°13′W; Fig. 1) within an European Union Natura 2000 protected area due to the exclusive occurrence of the Azores bullfinch (Special Protection Area *Pico da Vara/Ribeira do Guilherme*). This area encompasses one of the largest remnants of native laurel forest in the archipelago which is surrounded by dense extensive plantations of Japanese red cedar. The incidence of heavy rainfall (above 3,000 mm year^{-1}) and storms (Tutin 1953) in association with the extremely mountainous terrain often results in the formation of forest gaps, as a consequence of landslides (Marques et al. 2008).

Seven bird species disperse native and exotic seeds in the study area, and Blackcap (*Sylvia atricapilla*), Blackbird (*Turdus merula*) and Robin (*Erithacus rubecula*) are the main seed dispersers (Heleno et al. 2013). Among native fruits, birds feed mainly on a high variety of trees and shrubs (*Juniperus brevifolia*, *Ilex perado* spp. *azorica*, *Laurus azorica*, *Viburnum treleasei*, *Myrsine africana* and *Vaccinium cylindraceum*) and some herbaceous species (*Lysimachia azorica*, *Scrophularia auriculata*, *Hypericum humifusum*, *Potentilla erecta*). The most consumed exotic species are two tree species (*Clethra arborea* and *Pittosporum undulatum*), two shrubs or sub-shrubs (*Leycesteria formosa* and *Hedychium gardneranum*) and two herbs (*Conyza bonariensis* and *Centaurium erythraea*). Most species in the study area produce seeds annually.

Seed rain into forest gaps

Seed traps were placed inside selected landslides according to the following treatments: (1) gaps inside the native laurel forest (also approximately 100 m from the edge), (2) gaps within plantations of Japanese red cedar at approximately 100 m from native laurel forest edge and (3) gaps within plantations of Japanese red cedar at approximately 300 m from native laurel forest edge. Each treatment was replicated in three different gaps at least 300 m apart. All nine gaps were similar in area (0.5–1 ha), altitude (550–760 m), age (5–10 years) and dominant vegetation (only herbaceous stratum). Apart from the large plantations of Japanese red cedar around the gaps we studied, there are no other relevant vegetation patches that could differentially

Fig. 1 Spatial distribution of the nine gaps where bird-dispersed seed rain was estimated: within native laurel forest (*dark grey squares*), 100 m (*light grey squares*) and 300 m (*open squares*) from native laurel forest; and of the nine sites used to collect bird droppings with mist-nets (*circles*). The area dominated by native laurel forest is *shaded light grey*. *Squares* represent the centre of each gap, but *square* size is not proportional to gap size (*squares* are larger, for increased visibility)
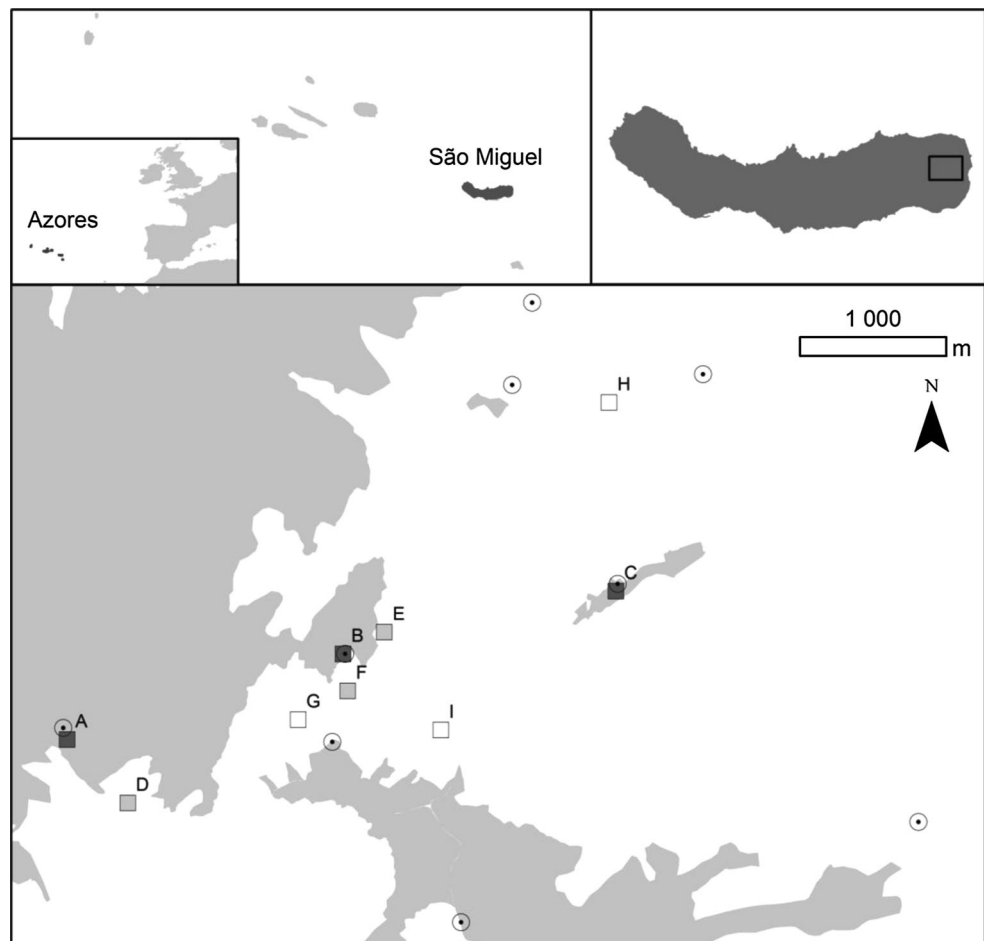

Table 1 Characterization of the nine sampled forest gaps, including plot code (Fig. 1), altitude, number of seed traps and number of seeds and species recovered in each gap

Treatment	Gaps (Fig. 1)	Altitude (m)	Number of seed traps		Number of seed (number of species)	
			Perch	No perch	Perch	No perch
(1) Gaps inside native forest	A	760	6		102 (13)	
	B	660	6		131 (7)	
	C	590	6		109 (13)	
(2) Gaps 100 m away from native forest edge	D	750	6		72 (9)	
	E	620	6	6	71 (11)	3 (1)
	F	690	6	6	73 (10)	0 (0)
(3) Gaps 300 m away from native forest edge	G	620	6		67 (7)	
	H	550	6	6	61 (11)	6 (1)
	I	680	6	6	46 (10)	1 (1)

influence seed rain. The location of each gap is shown in Fig. 1 and their altitudes in Table 1.

In each gap, six traps were randomly placed (i.e. independently of any habitat cues, but no less than 5 m apart) to evaluate seed rain. Traps consisted of a 75 cm × 75 cm cloth, suspended 30 cm above ground, and a small stone was placed in the centre of the trap to ensure a concave surface and thus prevent seed run-off. Perches were erected over each trap to increase the

frequency of seed dispersal by birds (Shiels and Walker 2003). All perches were approximately 3 m high and made from small exotic trees stripped of leaves, flowers and fruits. In addition, 24 seed traps without any perch were installed in four gaps (two within treatment 2 and two within treatment 3) in order to compare seed rain in traps with and without perches. All seed traps were visited weekly to collect bird droppings for one complete year (August 2006 to July 2007).

In the laboratory, entire seeds found in the droppings were identified under a dissecting microscope by comparison with a reference collection, and counted. Wind-dispersed seeds not clearly inside bird droppings were excluded from the analysis as they were not bird dispersed and they would artificially increase the number of seeds inside the native forest (i.e. under trees).

Seed dispersal and fruit caloric content

Based on the likely effect of caloric content on fruit choice (e.g., Stiles 1980; Vilà and D'Antonio 1998), we evaluated whether the caloric content of fruits could explain the number of seeds dispersed by birds. The caloric content of fruits of dispersed species was assessed together with that of other fruiting plants common in the study area. Results were compared with the abundance of seeds collected both on the seed traps (this study) and on droppings of mist-netted birds from Heleno et al. (2013). In that study, the authors built a quantitative seed dispersal network by identifying entire seeds in the droppings of birds, collected during ringing sessions with mist-nets over 3 years at nine different sites within the study area (Fig. 1). Overall, 274 of the 1121 analysed droppings contained entire seeds from seven bird species.

Caloric content was measured using a Semimicro bomb calorimeter (Parr Instrument Company, model 1425). Fruits were collected, dried at 60 °C until weight became stable and then ground into powder. For each plant species, a minimum of three samples of dry pulp were measured, and the mean was used for the analysis (Paiva et al. 2006).

Statistical analysis

To test the null hypothesis of no difference in the number of seeds collected in seed traps with and without perch, we used a one-way ANOVA, as the data were normally distributed and had homogeneous variance.

Differences in the number of native and exotic seeds collected from traps with perches were tested among treatments with a univariate general linear model followed by Tukey HSD tests. 'Seed origin' (native vs. exotic) and 'distance from native forest' were used as fixed factors, and an interaction between 'seed origin' and 'distance' was also included in the model based on the hypothesis that the consumption of native and exotic seeds by birds would vary with distance from native forest. Due to the small number of seeds collected in seed traps without a perch, these seeds were not included in this analysis.

To test the null hypothesis of no difference in the caloric content between native and exotic fruit species, we used a one-way ANOVA. As data did not meet the assumptions of parametric correlation, we used Kendall's correlation coefficient (τ) to assess the relationship between the

number of seeds collected by seed traps and the number of seeds in droppings collected during the mist-netting sessions. Kendall's rank-order correlations were also used to test the relationship between fruit caloric content and the number of seeds recovered from seed traps and from droppings collected during the mist-netting sessions.

All tests were performed with SPSS 20.0 to a significance level of $\alpha < 0.05$. Except when mentioned, results are presented as mean ± SE.

Results

Seed rain into landslides

A total of 683 seeds were recovered from the seed traps, 30.6 % of which were herbaceous, 34.4 % shrub and 35.0 % tree species (Table 1). The presence of perches significantly increased seed rain ($F_{1,4} = 57.1$, $p = 0.002$); only 10 seeds were collected from the 24 seed traps without perches while 251 seeds were recovered from the 24 paired traps with perches. Overall, seed rain beneath the perches was estimated at 24.1 ± 3.8 seeds m^{-2} year^{-1} and 3.3 ± 2.6 seeds m^{-2} year^{-1} on seed traps without perches.

Almost 90 % of the seeds were recovered between July and November which coincides with the fruiting season of most exotic and native plants in the Azorean laurel forest (Heleno et al. 2009). Nevertheless, seeds of native plants were found in the seed traps throughout the year with a minimum in March (1 seed) and a maximum in September (85 seeds) (Fig. 2).

Most seeds recovered in the seed traps were native ($F_{1,17} = 47.1$, $p < 0.001$; Fig. 3). The number of native seeds decreased with distance to the native forest (85.0 ± 18.7, 52.7 ± 6.9 and 36.0 ± 2.6 seeds,
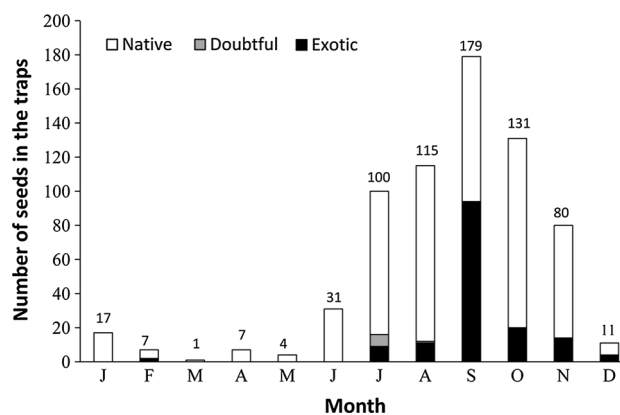

Fig. 2 Total number of seeds from bird droppings collected in seed traps with perch over a 1-year period, from August 2006 to July 2007 (months where re-ordered according to a full calendar year for clarity), in the eastern part of São Miguel Island, Azores. Seeds of doubtful origin include unidentified seeds
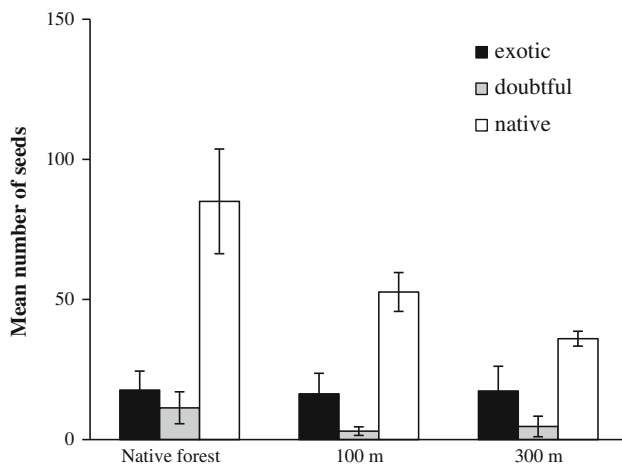
Fig. 3 Mean number of seeds collected from seed traps with perch placed in gaps inside native laurel forest and in two gaps within plantations of Japanese red cedar that varied in their distance to the closest native forest patch: 100 m and 300 m. *Error bars* represent the standard error

respectively, for treatments 1, 2 and 3; $F_{1,17} = 6.0$, $p = 0.016$), and significantly fewer seeds were recovered in treatment 3 than in treatments 1 and 2 (Tukey HSD; $p = 0.035$), but no differences were found between the latter two treatments. On the other hand, the number of exotic seeds recovered in the seed traps showed no differences concerning the distance to native forest (17.7 ± 6.8, 16.3 ± 7.3 and 17.3 ± 8.8 seeds, respectively, for treatments 1, 2 and 3) In the native forest, 84 % of the seeds were from native and doubtful-origin species, but this percentage dropped to 78 % in the treatment 2 and to 71 % in the treatment 3 ($F_{\text{origin} \times \text{distance} \ 2,17} = 5.7$, $p = 0.018$; Fig. 3).

Seed dispersal and fruit caloric content

A total of 683 entire seeds belonging to 21 plant species were collected from the traps, 73 % of which were native, 26 % exotic and 1 % of doubtful-origin (Table 2). Bird droppings collected in the mist-netting sessions contained 305 entire seeds belonging to 33 plant species (39 % native, 59 % exotic and 2 % of doubtful-origin species). Two-thirds of the exotic seeds (67 %) recovered (both from seed traps and mist-netted birds) were of species considered invasive in the Azores.

There was no significant differences between the caloric content of native and exotic fruits (native = 4,757 ± 117 cal. g^{-1}; exotic = 4,779 ± 96 cal. g^{-1}; $F_{1, 10} = 0.1$, $p = 0.761$). The number of seeds of each species found in seed traps was positively correlated with that recovered from droppings during the mist-netting sessions ($\tau = 0.56$, $p = 0.015$), but none of these was significantly correlated with fruit caloric content ($\tau = -0.32$, $p = 0.149$ and $\tau < 0.01$, $p = 1.000$, respectively).

Discussion

This study characterizes seed rain in a highly invaded laurel forest in the Azores and reveals that most seeds dispersed into forest gaps at different distances from the native forest are native, thus likely contributing to forest regeneration. Although the most problematic invaders in the study area, i.e. Australian cheesewood, Kahili ginger and blackwood (*Acacia melanoxylon*) were also dispersed by birds, none of these species was highly attractive to dispersers, in contrast to other invasive species in other studies (e.g. Gosper and Vivian-Smith 2006).

Factors influencing seed rain into forest gaps

As expected, the use of perches significantly increased the arrival of seeds to the seed traps. However, it is not clear how the seed rain might change at an increasing density of perches. The attractive potential of perches can be used to direct dispersal to suitable recruitment sites, thus helping to overcome the demonstrated barrier effect of dense Japanese red cedar stands to bird movement (Ceia et al. 2009). Perch manipulations in the field in order to direct seed dispersal have showed a clear increase in seed deposition (Wenny 2001; Shiels and Walker 2003). However, because other factors can affect plant recruitment in natural conditions, such as seed predation or low seed germination (e.g. Shepherd and Chapman 1998), perches should be used integrated with other management techniques.

Our estimate of seed rain below perches (24.1 seeds m^{-2} year^{-1}) is at the lower end of estimated bird-dispersed seed rain from other studies, spanning from 10 seeds m^{-2} year^{-1} (Zanini and Ganade 2005) to 340 seeds m^{-2} year^{-1} (McClanahan and Wolfe 1993). This is likely a reflection of the relatively small number of seed dispersers in the Azores (Heleno et al. 2013). The frequency of occurrence of seeds in the seed traps and in the droppings of mist-netted birds was positively correlated, suggesting that both methods accurately quantify seed dispersal. Birds did not show a preference for either native or exotic fruits during the period both were simultaneously available (July–November). In accordance, no differences were found between the caloric content of native and exotic fruits. However, fruit caloric content alone did not explain the different number of native and exotic seeds dispersed by birds in the studied system. Effective competitive advantage results from the interaction of several drivers, such as seed size, plant chemical defences and resource location, nevertheless here we focus exclusively on the number of seeds dispersed as this sets the template for seedling establishment.

As predicted, native seed deposition decreased with distance of the gap from the closest native forest patch,

Table 2 Number and diversity of seeds recovered from the seed traps with perch and from the droppings of mist-netted birds

Origin	Species	Number of seeds		Fruit caloric content (mean ± SE cal. g^{-1})
		Seed traps	Mist-netting	
Exotic				
Trees	*Pittosporum undulatum**	0	9	5,557 ± 41
	*Acacia melanoxylon**	0	5	
	Clethra arborea	0	5	
	Cryptomeria japonica	4	1	
Shrubs	*Hedychium gardneranun**	2	4	5,757 ± 49
	*Leycesteria formosa**	114	87	4,468 ± 25
	Rubus ulmifolius	11	12	4,307 ± 11
	*Conyza bonariensis**	0	1	
Herbaceous	*Duchesnea indica**	0	26	4,031 ± 98
	Solanum nigrum	0	8	4,558 ± 55
	Holcus lanatus	24	2	
	Persicaria capitata	17	1	
	Cerastium fontanum	0	11	
	Kyllinga brevifolia	5	0	
	Bellis perennis	0	3	
	Centaurium erythraea	0	1	
	Lotus pedunculatus	0	2	
	Epilobium parviflorum	0	1	
	Paspalum dilatatum	1	0	
	Sonchus tenerrimus	0	1	
Doubtful				
Herbs	*Fragaria vesca*	4	7	4,472 ± 16
	Prunella vulgaris	4	0	
Native				
Trees	*Juniperus brevifolia*	151	29	4,784 ± 49
	Ilex perado	75	23	3,856 ± 21
	Morella faya	0	8	4,429 ± 17
	Laurus azorica	9	4	
	Persea indica	0	0	7,870 ± 90
	Picconia azorica	0	0	4,759 ± 19
	Prunus azorica	0	0	4,497 ± 112
	Frangula azorica	0	0	4,166 ± 16
Shrubs	*Viburnum tinus*	6	1	4,856 ± 24
	Hedera azorica	0	5	4,823 ± 43
	Vaccinium cylindraceum	97	24	4,737 ± 201
	Myrsine africana	0	3	4,637 ± 25
	Calluna vulgaris	5	2	
	Smilax canariensis	0	0	3,670 ± 126
Herbaceous	*Juncus effusus*	65	4	
	Hypericum humifusum	48	3	
	Potentilla erecta	21	9	
	Scrophularia auriculata	17	0	
	Luzula azorica	3	0	
	Carex viridula	0	2	
	Carex vulcani	0	1	
Total		683	305	

The caloric content of fruits of bird-dispersed species is shown as well as that of other fruiting plants common in the study area

Invasive species in the Azores are marked with an asterisk

with significantly fewer seeds arriving to traps located 300 m from the native forest. In contrast, deposition of exotic seeds was not affected by distance from native forest probably because these are more available to birds than native seeds outside the laurel forest. Native seeds were also recovered from gaps away from the native forest and surrounded by dense Japanese red cedar plantations, showing that frugivorous birds can fly over Japanese red cedar stands and increase native seed rain into newly available areas. Therefore, this finding suggests that seed dispersal by birds is likely to play an important role in assisting the recovery of native laurel forest in Azores. However, because most exotic plants will do extremely well in the Azores favourable climate (Heleno et al. 2010), longer-term information on the vegetation that will dominate these gaps throughout the ecological succession is desirable.

Concluding remarks

Over the past 10 years, LIFE projects have guaranteed the preservation of one of the largest native laurel forest fragments in the Azores. However, given that invasive exotic species are very aggressive competitors, laurel forest safeguard will depend on restoration measures over a much longer time period. Based on the results presented here, we recommend to: (1) prioritize areas for recovery activities within 100 m from native forest edge, (2) increase the active plantation of native species in weeded areas further away from the native forest, as the number of native seeds arriving at larger distances is significantly reduced and (3) use perches to direct avian seed dispersal into forest gaps near the native forest.

Japanese red cedar has been economically explored in the Azores for 150 years. On the absence of active management, exotic species seem to outcompete native species in the colonization of recently logged Japanese red cedar stands (authors personal observation). The lack of perching structures might hinder the arrival of native seeds into logged areas. Furthermore, because root structures help to prevent erosion, logged areas have higher risk of landslides. Therefore, landslide mitigation measures should be considered in restoration strategies to accelerate the ecological succession process. Further studies contributing to the design of a laurel forest management plan as well as spatial information of seed dispersers are critical to improve protocols which allow the economic activity to be compatible with nature conservation.

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