The effects of an exotic palm on a native palm during the first demographic stages: contributions to ecological management

Ana Luisa T. Mengardo[1,*] and Vânia R. Pivello[1]

ABSTRACT

Biological invasions have negative impacts on native biota and consequently on biodiversity. In patches of Atlantic Forest in Brazil, the Australian palm tree *Archontophoenix cunninghamiana* has become invasive, whereas the endemic palm *Euterpe edulis* is threatened with extinction. The two species occupy parts of the same functional niche within the forests, which raises a question: Does the invasive species interfere with the recruitment of the native one when the two co-occur? We compared the initial demographic stages of these palms, and assumed that *A. cunninghamiana* would present better performance (higher rates of germination and seed viability) and would feature allelopathic properties that could influence the recruitment of the native species. We investigated indirect and direct allelopathic interference, respectively, by watering *E. edulis* seeds with aqueous leachate solutions of *A. cunninghamiana* fruits and leaves and by conducting combined germination experiments. The leachate solutions neither inhibited germination nor affected the size of *E. edulis* seedlings. In the direct interference experiments, depulped *A. cunninghamiana* seeds had higher viability and germination rates than did *E. edulis* seeds. In *E. edulis*, exposure to *A. cunninghamiana* seeds did not affect germination nor seedling development but slightly decreased germination speed. In conclusion, *A. cunninghamiana* presented no significant allelopathic impediment to *E. edulis* establishment. However, because *A. cunninghamiana* seeds are usually depulped when dispersed by birds, the potential of the species to establish itself in the community surpasses that of *E. edulis*. We propose management strategies to enhance *E. edulis* performance and to restrict the spread of *A. cunninghamiana*.

Key words: allelopathy, Arecaceae, biological invasion, germination, palm heart

Introduction

The rapid disappearance of tropical forests worldwide is a result of direct and indirect human activities (Turner 1996). Intentional or accidental introduction of exotic species has become one of the greatest threats to the balance of ecosystems and the maintenance of native species in their habitats. When such introduction results in biological invasion, negative impacts may be observed at the individual, population, community or ecosystem level (Pyšek *et al.* 1995; Lockwood *et al.* 2007; Simberloff & Rejmánek 2011). Therefore, biological invasions have received increasing attention from conservation biologists (Davis 2006) and are currently considered one of the major threats to biodiversity on a global scale (Perrings *et al.* 2005; Petenon & Pivello 2008).

Several hypotheses have been proposed to explain the process of biological invasion. The novel weapons hypothesis adds a new mechanism to explain the success of invasive species in the habitats into which they have been introduced (Hierro & Callaway 2003). The novel weapons hypothesis is based on the negative interaction with native organisms through the release of allelopathic substances in the environment (Callaway & Aschehoug 2000; Schaffner *et al.* 2011). Hierro & Callaway (2003) argued that many invasive species are not dominant competitors in their natural habitats but can successfully outcompete their new neighbors by releasing phytotoxins that inhibit or eliminate the surrounding organisms, providing an alternative explanation for the ability of invaders to become more abundant and competitively dominant in the invaded sites (Inderjit *et al.* 2008).

Direct competition for resources and indirect interference such as allelopathic impediment are both decisive for the establishment of plant populations (Gurevitch *et al.* 2009). Allelopathy could compromise the initial demographic stages of a plant, which are vital for maintaining plant populations, because germination, seedling survival and growth are crucial stages of the recruitment process in plants (Kitajima & Fenner 2000).

The palm tree *Archontophoenix cunninghamiana* H. Wendl. & Drude (Arecaceae), native to tropical Australian forests, was introduced into southeastern Brazil for

ornamental purposes as early as the 1950s, and its establishment in urban areas led to its invasion of nearby remnants of Atlantic Forest (Dislich *et al.* 2002; Dislich & Pivello 2002; Zenni & Ziller 2011). This species had been described as invasive in other countries, such as New Zealand, and even in regions to which it is not native within Australia (Global Invasive Species Database 2005). A six-year study conducted in an Atlantic Forest fragment inside an urban area within the city of São Paulo, Brazil, showed that the population of invasive species presented an ongoing positive growth rate, whereas the native arboreal community presented negative annual growth (Silva-Matos & Pivello 2009). In addition, the species comprised almost one third of all the adult individuals in that forest, the highest density observed among more than one hundred native tree species recorded (Dislich *et al.* 2002; Silva-Matos & Pivello 2009).

The palm tree *Euterpe edulis* Martius (Arecaceae) is native and endemic to the Atlantic Forest Biome, once having been one of the most common species in the dense rain forests (Queiroz 2000; Reis *et al.* 2000). However, it is now extinct in many regions (Galetti & Fernandez 1998). Extensive populations of *E. edulis* are found only in a few large protected reserves (Galetti & Aleixo 1998), whereas individuals of this species are rarely found in smaller forest patches, even those protected as reserves (Reis *et al.* 2000; Dislich & Pivello 2002).

Euterpe edulis is very important to the native frugivorous fauna because it is one of the few Atlantic Forest species that provide nutritious fruits for frugivorous fauna during the winter (Galetti & Aleixo 1998; Silva-Matos & Watkinson 1998; Mantovani & Morellato 2000). Within the forests it has invaded, *Archontophoenix cunninghamiana* fructifies during the same period (Mengardo & Pivello 2012). Both species are prolific, their fruits are of the same size, and the fruits of both are dispersed by generalist frugivorous birds (Galetti *et al.* 1999; Christianini 2006; Mengardo & Pivello 2012). Therefore, it is probable that the niches of *A. cunninghamiana* and *E. edulis* overlap to some extent (Dislich 2002). Forest fragments in which *E. edulis* is now extinct or has populations that are quite small could present favorable conditions for the establishment of *A. cunninghamiana*, given that their fruits are consumed and dispersed by the same animal assemblage that previously used the once abundant native palm as a primary resource.

The re-establishment of *Euterpe edulis* has been recommended as a management strategy for the invaded patches of Atlantic Forest (Dislich 2002; Christianini 2006), in an attempt to restore the original abundance of the native palm tree and to provide food for the local frugivorous community. To support this approach, it is essential to evaluate the ability of the invasive palm species to interfere with the early demographic stages of the native one. Otherwise, management actions such as *E. edulis* re-introduction or enrichment could be jeopardized, efforts and funding being expended without achieving the expected goals.

Considering the establishment phase as a bottleneck for plant population recruitment (Gurevitch *et al.* 2009), we aimed to compare the native and exotic palm species in their first demographic stages—germination and seedling development—in the laboratory. We also investigated a possible allelopathic effect of *Archontophoenix cunninghamiana* on *Euterpe edulis* germination or development in the laboratory, while attempting to simulate natural conditions. We had three main hypotheses: that the viability and germination rates of the seeds of *A. cunninghamiana* are higher than are those of *E. edulis*, and that the native species would therefore be at a disadvantage in the establishment phase; that *A. cunninghamiana* fruits and seeds could interfere directly with the early establishment of *E. edulis* when the two species co-occur, due to allelopathic effects; and that the fruits and dry leaves of *A. cunninghamiana* can also release allelopathic substances onto the forest floor, inhibiting the germination of *E. edulis* and thus reducing the likelihood of its establishment in the forest. The data generated here could inform decisions regarding management strategies to restore *E. edulis* populations in Atlantic Forest patches and to control the *A. cunninghamiana* invasion.

Material and methods

Species studied

Archontophoenix cunninghamiana H. Wendl. & Drude (Arecaceae) is a solitary palm tree with green pinnate leaves and pendant inflorescences (i.e., bunches; Lorenzi *et al.* 2004). In southeastern Brazil, it shows a generalized dispersal system and produces abundant, round red drupes throughout the year (Mengardo & Pivello 2012). The drupe itself is large, fibrous, hard, and lumpy, and the pulp contains small amounts of nutrients (Mengardo & Pivello 2012). The species shows rapid growth in full sun or half shade and has adapted well to the subtropical climate of the region (Lorenzi *et al.* 2004).

Euterpe edulis Martius (Arecaceae) is native to the Atlantic Forest Biome, originally occurring along the eastern and southeastern coast of Brazil. Its palm hearts are widely appreciated as food for humans. It has therefore been extensively exploited and is now extinct in most of its original area of distribution (Galetti & Aleixo 1998; Galetti & Fernandez 1998). The fruits (black drupes) are available from December to September (Silva-Matos & Watkinson 1998). It is considered a keystone species for frugivorous fauna (Galetti & Aleixo 1998; Silva-Matos & Watkinson 1998) and contributes to the maintenance and restoration of forest remnants (Reis *et al.* 2000).

Sampling and processing

We removed drupes (hereafter generically referred to as seeds, although the endocarp attached to the seed is also

included) from intact mature fruits of both species. The fruits of *Archontophoenix cunninghamiana* were collected in gardens on the campus of the Universidade de São Paulo, in the city of São Paulo, Brazil (23°33'57"S; 46°43'43"W). *Euterpe edulis* fruits were collected at random in the native forest at Neblinas Park, in the nearby city of Mogi das Cruzes (23°44'07"S; 46°11'05"W).

The fruits of both species were processed and depulped immediately after collection, because their seeds neither show dormancy nor tolerate desiccation (Martins *et al.* 2000; 2003). In experiments in which the depulped fruits (seeds) were used, fruits were soaked in water at room temperature for 24 h to facilitate the removal of the mesocarp. Subsequently, the pulp was mechanically removed and the seeds were dried in the shade. In other experiments, the whole fruits of *A. cunninghamiana* were used immediately after collection.

Seed viability

Before conducting germination experiments, we tested a random selection of 100 seeds from each of the two species evaluated (*Archontophoenix cunninghamiana* and *Euterpe edulis*), to determine the mean viability. Seeds were opened longitudinally to expose the embryo and then soaked in a solution of 0.5% tetrazolium salt (2,3,5-triphenyltetrazolium chloride) in the dark for 5 h at 30°C (test for *E. edulis* according to Brasil 1992). Seeds were considered viable when showing a light reddish color in more than 50% of the embryo (Biagioni & Godoy 2005). Seeds that were physically deformed or that showed colorless or intensely red embryos after the tetrazolium test were considered unviable (Ferreira *et al.* 2007). The same viability tests were performed on the remaining ungerminated and intact seeds.

Interference experiments

We conducted experiments to check for both direct and indirect allelopathic effects of fruits and leaves of the invasive palm species (*Archontophoenix cunninghamiana*) on *Euterpe edulis* germination. The direct effects were defined as seed-to-seed or fruit-to-seed interaction in combined germination experiments; the indirect effects included the possible release of allelopathic substances by *A. cunninghamiana* organs (leaves and fruits) when washed by rain.

To test for direct allelopathic effects of *Archontophoenix cunninghamiana* seeds and fruits on *Euterpe edulis* germination, we applied four treatments: *A. cunninghamiana* seeds only (control); *E. edulis* seeds only (control); seeds of both species (Gs); and seeds of *E. edulis* and fresh fruits (seed + pulp) of *A. cunninghamiana* (Gf). Seeds were placed in germination boxes containing vermiculite substrate and watered with distilled water sufficiently to maintain the substrate constantly moist. All tests followed a randomized

design, with nine replications of 12 seeds or fruits per treatment. The experiment was performed in a germination chamber (25±2°C, relative air humidity = 80%), and the seeds were monitored for 20 weeks or until 15 consecutive days passed with no seeds germinated.

Seeds were considered germinated when coleoptiles were visible; they were kept in the germination box until primary leaves emerged (seedling formation). The following variables were measured: percentage of germination; germination velocity index—a measure of the number of days taken for seed germination (Borghetti & Ferreira 2004); and total seedling length.

To test for indirect allelopathic effects, we attempted to simulate natural forest conditions. Therefore, rather than preparing extracts of crushed material, we used aqueous leachate solutions of *Archontophoenix cunninghamiana* fruits and leaves, applying those solutions to *Euterpe edulis* seeds to mimic the washing of forest litter by rainfall. In an invaded patch of urban forest (23°33'44"-23°34'02"S; 46°43'38"-46°43'49"W), we observed the volumes of fruits and leaves on the forest floor near the base of *A. cunninghamiana* individuals to determine ecologically relevant concentrations (Dietz *et al.* 1996). On the basis of these observations, we used freshly collected fruits at a proportion of 80 g of fruit to 120 ml of distilled water (67% w/v), and the mixture was shaken for 24 h. From that, diluted solutions were prepared to concentrations of 33% w/v and 17% w/v. Following the same procedure, we prepared aqueous solutions of dry leaves, the initial (and highest) concentration being 11% w/v. Subsequent dilutions were to 5.5% w/v and 2.7% w/v. All solutions were filtered and stored at 8°C until the beginning of the experiment.

We established seven treatments to test for indirect effects of *Archontophoenix cunninghamiana*: one involving irrigation of *Euterpe edulis* seeds with distilled water (control); three involving irrigation with fruit leachate solutions (at concentrations of 67%, 33%, and 17%, respectively); and three involving irrigation with leaf leachate solutions (at concentrations of 11%, 5.5%, and 2.7%, respectively). The test design and analyses performed were the same as those described above.

In our analysis of the direct interference experiments we used the non-parametric Kruskal-Wallis test, followed by Dunn's test for multiple comparisons, to check for intraspecific differences among treatments (control, Gs, and Gf). To verify interspecific differences in the variables measured (*Archontophoenix cunninghamiana* versus *Euterpe edulis*) in the same treatments (control, Gs, and Gf) we used a Student's t-test. In our analysis of the indirect allelopathic effects of *A. cunninghamiana*, we used two-way ANOVA, followed by Tukey's *a posteriori* test (for normally distributed data), to assess differences among treatments according to the factors (fruit or leaf solution and different concentrations).

Results

In the control conditions of the direct interference experiment, the mean germination rate was much lower for the *Euterpe edulis* seeds than for the *Archontophoenix cunninghamiana* seeds (38.9% vs. 93.5%), the first being approximately half of and the latter being close to the initial seed viability (df=1, t=11.9, *p*<0.0001), whereas seed germination of *E. edulis* was unaffected by the Gs or Gf treatments (H=2.7, *p*=0.3). We found it surprising that the *A. cunninghamiana* germination rate was lower in the Gf condition than in the Gs condition (H=18.1, *p*<0.001, Fig. 1A). In isolation (control condition), *E. edulis* germination was much slower than was that of *A. cunninghamiana* (t=7.6, *p*<0.0001). However, the two species showed similar germination speeds in the Gs condition (t=-8.0, *p*<0.01). In addition, the germination speed of *A. cunninghamiana* decreased significantly in the Gf condition (H=23.21, *p*<0.0001). Nevertheless, exposure to the seeds and fruits of *A. cunninghamiana* decreased the germination speed of *E. edulis* (H=8.59, *p*=0.01, Fig. 1B). The *A. cunninghamiana* seedlings were shorter than were those of *E. edulis* in all conditions (t=−4.9, *p*=0.0001) and were even shorter in the Gf condition (H=15.95, *p*<0.001, Fig. 1C). After the end of the Gf treatment, 30.6% of *A. cunninghamiana* seeds remained viable, whereas none of the *E. edulis* seeds did.
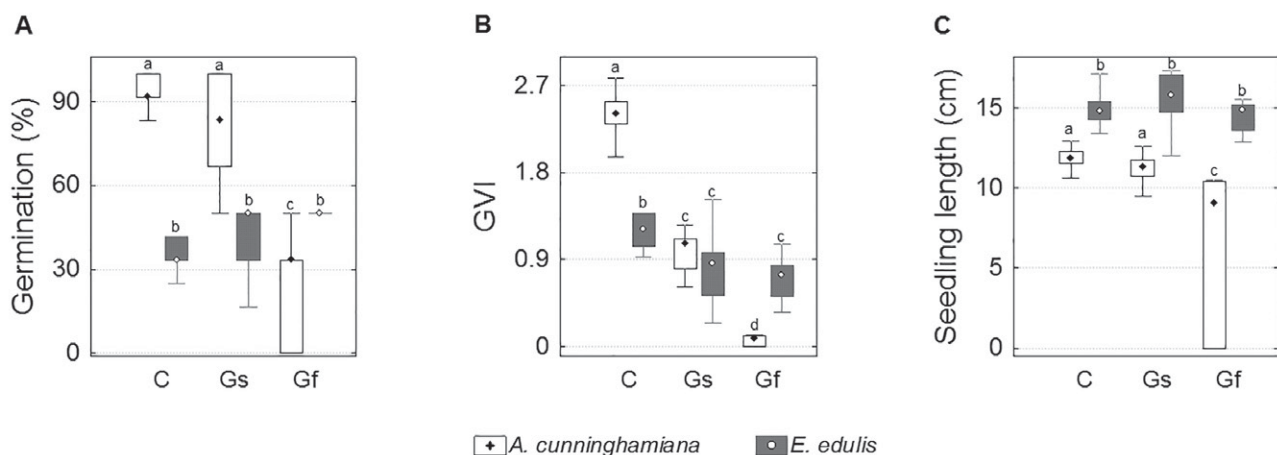
Our results show that there was no statistical effect of *Archontophoenix cunninghamiana* leaf or fruit leachate solutions on *Euterpe edulis* germination rate or speed, regardless of the leachate solution concentration (Tab. 1; Figs. 2A and 2B). The average germination rate for the control sample was 38.9%, compared with 40.4% for seeds treated with leachate solutions (Fig. 2A), although the initial viability test indicated that 73.1% of the seeds had the potential to germinate. All *E. edulis* seeds classified as ungerminated

at the end of the experiment were not viable. In addition, treatment with the leachate solutions of *A. cunninghamiana* did not affect the length of *E. edulis* seedlings (Tab. 1). The average seedling length was 14.4±1.55 cm (Fig. 2C).

Discussion

Our first hypothesis was confirmed, because *Archontophoenix cunninghamiana* showed higher germination and viability rates compared with *Euterpe edulis*. Other authors have already reported low germination rates (of approximately 55%) for *E. edulis* seeds under controlled conditions (Bovi & Cardoso 1975; Silva-Matos & Watkinson 1998). In the field, Reis & Kageyama (2000) reported an even lower *E. edulis* germination rate (26%) and Mengardo *et al.* (2012) reported very low post-germination survival (< 5%) for *E. edulis* when growing side-by-side with *A. cunninghamiana* seedlings. However, because some studies have reported better establishment of *E. edulis*, seed quality must be considered a potential limitation of our study. Martins *et al.* (2000) showed how seed quality may significantly alter experimental results.

In addition to the better performance of *Archontophoenix cunninghamiana* seeds in isolation, exposure to its fruits and seeds decreased the speed of *Euterpe edulis* germination. However, we cannot state categorically that the invasive palm has an advantage over the native palm in the establishment phase, because the slowed germination of *E. edulis* seeds was not reflected in its germination rate or seedling length; therefore, recruitment was not completely hampered after all. In addition, the seedlings of the native palm tree were taller in all treatments, so in this parameter *E. edulis* actually performed better, although Mengardo *et al.* (2012) showed that after the first demographic stages, *A. cunninghamiana* does perform better. One possible expla-
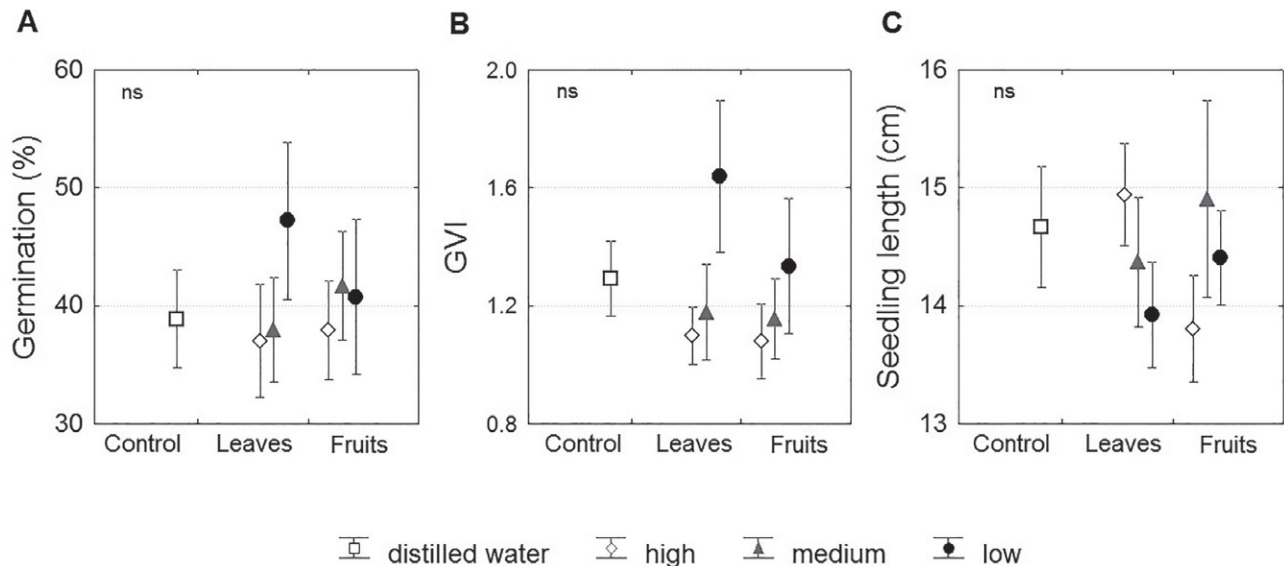

Figure 1. Box plots of germination rates (**A**), germination velocity index (**B**), and seedling length (**C**) of *Euterpe edulis* and *Archontophoenix cunninghamiana* (greenhouse experiments). Different letters indicate significant differences (*p*≤0.05).
GVI – germination velocity index; C – control (seeds of *A. cunninghamiana* or *E. edulis* only); Gs – seeds of both species; Gf – seeds of *E. edulis* and fresh fruits (seed + pulp) of *A. cunninghamiana*.

Table 1. ANOVA of the allelopathic effects of *Archontophoenix cunninghamiana* leaf and fruit aqueous leachates at different concentrations (11%, 5.5%, and 2.75% for leaf leachates; and 66%, 33%, and 16.5% for fruit leachates) on *Euterpe edulis* germination rate, germination velocity index, and seedling length. GVI – germination velocity index.

Factor	Germination rate		GVI		Seedling length	
	F	**p**	**F**	**p**	**F**	**p**
Organ (leaf or fruit)	0.02	0.89	0.623	0.43	0.008	0.93
Leachate concentration	0.765	0.47	2.81	0.07	0.383	0.68
Organ X leachate concentration	0.49	0.61	0.421	0.66	1.55	0.22

Figure 2. *Euterpe edulis* germination rate (**A**), germination velocity index (**B**), and seedling length (**C**) in tests for allelopathic effects of *Archontophoenix cunninghamiana* (mean±SE, $p \geq 0.05$). The control seeds were irrigated with distilled water only and untreated. Other seeds were treated with high, medium, or low concentrations of leachate solutions of *A. cunninghamiana* dry leaves (11%, 5.5%, and 2.75%, respectively) or of leachate solutions of *A. cunninghamiana* fruits (66%, 33%, and 16.5%, respectively). ns – not significant.

nation for the differences in performance between the two palm species is that the native palm has not been domesticated and therefore has no history of artificial selection (Nodari & Fantini 2000). In contrast, of *A. cunninghamiana* has been used as an ornamental, and it has probably undergone artificial selection for specific desirable traits such as vigorous individuals that could reproduce more efficiently (Kitajima *et al.* 2006).

The high performance of *Archontophoenix cunninghamiana*, which enhances the probability of its successful establishment, is due to intrinsic qualities, such as its viability rates, as demonstrated in our germination experiments, in which the observed germination rates were higher than those predicted by the initial tests (90% and 85%, respectively). High survival rates derived from high performance at the early stages increase population fitness, one of the five biological attributes responsible for plant invasiveness (Rejmánek 2011). However, one major, unexpected result was the low germination rate of *A. cunninghamiana* when the whole fruit was used. This probably occurred because of

the barrier effect of the pulp, which affects water absorption by the seed (Corner 1966). According to Corner (1966), pulp tissue may inhibit or delay germination, and seeds only begin to germinate when the pulp starts to decompose and parts of the endocarp are exposed. That was noticed in another experiment with *Euterpe edulis*, in which less than 10% of the pulped seeds germinated, compared with 50% of the depulped seeds in the same lot (Leite *et al.* 2012). Such a delay in germination can have additional consequences; for example, the resulting seedlings would be shorter than those grown from depulped seeds, as was observed in the present study. This fact highlights the importance of pulp removal by the frugivorous community to the success of those palms germination.

Our hypothesis that *Archontophoenix cunninghamiana* fruits and dry leaves would release allelopathic substances onto the forest floor, thus inhibiting *Euterpe edulis* germination, was rejected. Allelopathic substances are not commonly described in palms, although Lima *et al.* (2011) reported an allelopathic effect of *E. edulis* fruits on *Lactuca*

sativa L. (Asteraceae). In another study, we conducted similar allelopathic tests, applying the same leachate solutions of *A. cunninghamiana* leaves and fruits on seeds of *L. sativa* cv. Grand Rapids, *Lycopersicon esculentum* Mill. (Solanaceae), and *Pterogyne nitens* Tul. (Fabaceae). None of those were affected by the leachate solutions of *A. cunninghamiana* (Mengardo, unpublished data). Here, we only checked a plant-to-plant approach (Inderjit *et al.* 2008), which revealed no indirect effect of the invasive on the native species. However, the novel weapons hypothesis is not limited to native-invasive plant interactions and can involve microorganisms or even generalist herbivores (Schaffner *et al.* 2011). It must also be borne in mind that factors other than allelopathy might be operating in the rapid establishment of *A. cunninghamiana*, such factors including high physiological performance, as was tested in our study.

Contribution to management

The information obtained in this study is relevant to guiding decisions regarding management procedures in Atlantic Forest patches invaded by *Archontophoenix cunninghamiana*, especially in terms of its interaction with *Euterpe edulis*, a threatened endemic species. The interactive approach is considered better than the "single-species management" approach, when the objective is to re-establish an endangered native species in invaded communities (Mack *et al.* 2000). Our results indicate that strategies for the re-introduction or enrichment of *E. edulis* in the forest must be implemented in concert with measures aimed at inhibiting the establishment of *A. cunninghamiana* seedlings and enhancing the opportunities for *E. edulis* regeneration.

In invaded patches of Atlantic Forest, a first and obvious management measure would be the felling of all *Archontophoenix cunninghamiana* individuals. However, that would be labor-intensive and costly, not only in monetary terms—because the topography in most of the region is very hilly, making it difficult to access the individuals and to use certain tools—but also in ecological terms, because the felling of large *A. cunninghamiana* individuals would damage the forest floor and the seedlings of the native species (Pivello & Mauro, unpublished data). Instead, the cutting of the leaves and meristem (leaving the trunk standing) would kill the individuals and cause less damage to the forest floor. The removal of *A. cunninghamiana* bunches is highly recommended in order to avoid the consumption of fruits and dispersal of seeds by frugivorous birds.

Here, we showed that *Archontophoenix cunninghamiana* leaves and fruits have no allelopathic effect on *Euterpe edulis* germination, and it would therefore be unnecessary to remove them from the forest floor after cutting. Also, *A. cunninghamiana* fruits (but not seeds) could be left on the forest soil after the bunches had been removed, given that

the germination rate and speed were found to be quite low for the seeds contained within whole fruits.

The planting of *Euterpe edulis* fruits and seeds is known to be an effective method of re-introducing the species in degraded areas (Queiroz 2000), although the success of such efforts may be limited by variations in local conditions of soil moisture and shade during the germination phase (Tavares *et al.* 2008). The primary obstacle to *E. edulis* re-establishment is the natural reproductive bottleneck that the species shows at its early demographic stages (Reis *et al.* 2000). However, we found was that the low germination performance of *E. edulis* was not due to any allelopathic effect of *A. cunninghamiana*, and the two species can therefore co-exist. Consequently, an alternative approach proposed is to sow large quantities of *E. edulis* seeds in the invaded fragments throughout the year, either manually or from the air, thereby enhancing the production of seedlings (Nodari *et al.* 2000).

Acknowledgments

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