Biol Invasions (2018) 20:1719–1734
https://doi.org/10.1007/s10530-017-1656-1

ORIGINAL PAPER

A spatially explicit analysis of *Paysandisia archon* attack on the endemic Mediterranean dwarf palm

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Received: 30 March 2017 / Accepted: 21 December 2017 / Published online: 27 December 2017

Abstract Autochthonous plant species are heavily threatened by the increasing spread of invasive insects. The spatial distribution of invasive species' hosts is likely to play a pivotal role in the establishment and further expansion of the invading species; more specifically, distance and density dependent (DDD) processes linked to plant spatial arrangement are crucial in determining susceptibility to attack, but they have usually been overlooked in invasive research. We take a spatially explicit approach to evaluate potential DDD processes in the interaction between *Paysandisia archon*, a tropical lepidopteran recently introduced in Spain, and the endemic Mediterranean dwarf palm (*Chamaerops humilis*) in Mallorca (Balearic Islands). Specifically, we used spatial marked point pattern analyses, which allowed testing whether DDD processes affect attack probability and intensity on three dwarf palm populations corresponding to three different invasion phases (i.e., infestation core, early expansion, and expansion front). Our approach also allowed evaluation of whether and how intrinsic palm traits (size, sex) alter the proneness to *P. archon* attack over a range of spatial scales. The occurrence and nature of DDD effects on *C. humilis* performance varied largely among localities. At the infestation core, our analyses revealed positive density dependence, i.e., reduced damage at high densities or proximity to conspecific neighbors. By contrast, the early expansion locality showed negative density dependence of *C. humilis* performance, whereas at the expansion front, there was no evidence of DDD effects. Larger palms were consistently more prone to *P. archon* attack than small ones up to scales of 50 m. We found no evidence that palm sex altered the probability of attack by *P. archon*. Our results highlight the importance of spatially explicit analyses for assessing invasive events and point to the need of early interventions and prioritizing management efforts on larger palms in order to guarantee the conservation of autochthonous dwarf palm populations.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-017-1656-1) contains supplementary material, which is available to authorized users.

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Keywords Biological invasions · *Chamaerops humilis* · *Paysandisia archon* · Distance and density dependence · Spatial point pattern analysis

Introduction

Biological invasions, driven by the increasing globalization of human societies, pose one of the greatest problems biodiversity has to tackle in recent times (Bellard et al. 2016). The unprecedented magnitude of merchandise trade of countless plant and animal species, paired to the augmented disturbances on most ecosystems, have allowed for the establishment of many alien species (Meyerson and Mooney 2007; Hulme 2009). Nevertheless, the vast majority of species that are introduced remain rare, with only a small fraction becoming widespread and dominating local communities (Colautti et al. 2014). Several intrinsic and extrinsic factors markedly impinge the success of invasive species. Whereas intrinsic factors (high dispersal ability, generalist habits, rapid life cycles, etc.) make some species inherently good invaders, invasions are sometimes largely facilitated by extrinsic factors such as the release from natural enemies, high availability of resources, or hybridization (Colautti et al. 2014). Given that the occurrence and strength of such extrinsic factors are likely to vary spatially, a full understanding of the impact of invasive species on native populations requires spatially replicated studies that seek to identify and quantify the attack patterns and discern the underlying ecological mechanisms that give rise to such invasion events.

Autochthonous plant communities are heavily threatened by the ever-growing spread of invasive insects, with more than 1300 potentially invasive alien species established just in Europe (Roques et al. 2009). The international plant trade in Europe constitutes the main cause of this alarming issue, more specifically the trade of ornamentals, which usually constitute the main pathway of invasion (ranging from 50 to 90% of the instances (Kenis et al. 2007; Inghilesi et al. 2013; Smith et al. 2007). Plant trade thus allows numerous alien insects to avoid biogeographical constraints and reach suitable environments that may lack natural enemies or host coevolved defensive capabilities. To efficiently establish themselves in the invaded habitats, as widely documented for plant-natural enemy interactions (Sullivan 2003; Jones and Comita 2010; Mezquida and Olano 2013), the distribution and density of introduced insects' hosts constitutes a critical extrinsic factor, though seldom evaluated in a spatially explicit manner (but see Bell et al. 2006). The number and impact of specialized herbivores tend to increase with host plant density since high-density patches are most easily detected and exploited (i.e., negative density dependence of plant performance; Root 1973; Hambäck and Englund 2005). Also, mainly in tropical forests, high density of or proximity to conspecific neighbors results in distance- and density-dependent (hereafter referred to as "DDD") seed and seedling mortality driven by host-specific seed predators or pathogens (Sullivan 2003; Bell et al. 2006; Freckleton et al. 2006; Jones and Comita 2010). Nonetheless, the possibility also exists that high plant density promotes predator satiation or some sort of associational resistance, thus attenuating the *per capita* chances of predation, and leading to positive density-dependent effects (i.e., positive relationship between host density and fitness; Augspurger 1981; Callaway 2007; Fedriani et al. 2015).

In this study, we aim to unravel potential DDD processes operating in the recent invasion of *Paysandisia archon* (Lepidoptera: Castniidae), a palm borer introduced in the Iberian Peninsula and the Balearic Islands (Alario 2004; Sarto i Monteys and Aguilar 2005) inside ornamental palms imported from Argentina in the early 1990s. Larvae feed inside the trunk of numerous palm species (*Arecaceae*), causing severe damage as a result of the galleries they bore in the stems as well as secondary infections by fungi and other microorganisms (Sarto i Monteys and Aguilar 2005). This damage creates a serious risk to the conservation of the Mediterranean endemism *Chamaerops humilis* (MAGRAMA 2013), a charismatic dwarf palm of high ecological, cultural, and economic value (Merlo et al. 1993; López 2004; Fedriani and Delibes 2009, 2011) that has been intensively cultivated in various regions of the world with ornamental purposes due to its sturdiness and tolerance (del Cañizo 2002).

There have been a handful of studies concerning the incidence of insect pests on *C. humilis* (Sarto i Monteys and Aguilar 2005; Rodríguez et al. 2014; Cangelosi et al. 2016). Surprisingly, and despite the fact that *P. archon* can eventually cause death to many adult individuals of *C. humilis*, we still lack proper information about the spatial patterns and ecological correlates of its attack; in particular, whether and how *C. humilis* population density, aggregation level, and distance among conspecific palms alter the probability and intensity of attack by *P. archon* remains a puzzle. Given the inherent spatial nature of these DDD processes, assessing them in detail requires the application of spatially explicit analyses (e.g., Fedriani et al. 2015). In particular, spatial marked point pattern analyses (Illian et al. 2008; Wiegand and Moloney 2014) constitute a powerful, albeit seldom used approach in invasion ecology (but see Call and Nilsen 2003). This technique deals with the statistical analysis of mapped point patterns (e.g., plants), which comprise the coordinates as well as additional features of ecological objects (e.g., size, sex), technically called "marks." Such approach allows, for example, to disentangling how the spatial distribution of *C. humilis* individuals affects the invasion behavior of *P. archon*.

Paysandisia archon attack may depend not only on the spatial distribution of *C. humilis* individuals, but also on their specific traits. Spatial point pattern analyses allow us to assess whether intrinsic factors of palms play some role in the spatial pattern of *P. archon* attack. *C. humilis* size and sex may be important determinants of the spatial arrangement of *P. archon* attack as both factors could influence host selection. Some *P. archon* larvae have been found within the fruits of *C. humilis* (Sarto i Monteys and Aguilar 2005), which could favor selection of female hosts by *P. archon* as they offer more resources for their larvae to feed on, also alleviating overcrowding of larvae inside the palm trunks. Host size plays an important role in host selection in many other systems, and thus this could be well the case of *P. archon*. The Plant Vigor Hypothesis (Price 1991) postulates that herbivores are more abundant on hosts that are larger or display a more vigorous growth. While a number of studies have found support for this hypothesis (Smith and Story 2003; Cornelissen et al. 2008), others have not (Santos et al. 2010, 2011). Whether *P. archon* selects larger and more vigorous *C. humilis* at any spatial scale is an intriguing possibility. As mentioned above, spatial marked point pattern analyses allow us to spatially test these hypotheses so as to fully characterize this interaction.

The present study investigates for the first time DDD processes in the interaction between the invasive lepidopteran *P. archon* and its host *C. humilis*. To identify potential spatial variations in this interaction, we considered three localities of Mallorca (Balearic Islands, Spain) where *P. archon* exists in three different invasion phases, from oldest to youngest: "infestation core" (where *P. archon* was first discovered in 2002), "early expansion" (the pest has been known to exist since 2006), and "expansion front" (Alcúdia, where the pest has been only recently detected and has potential to spread to unaffected populations) and estimated qualitative and quantitative measurements of attack (i.e., palm attacked/non-attacked and intensity of attack, respectively). Our goal was to answer the following three specific questions: (1) Does *C. humilis* experience DDD processes in its interaction with *P. archon*? (2) If so, are those processes consistent in magnitude, sign, and spatial scale across study localities? and (3) Do palm traits such as size and sex alter the probability of interaction between the palm and the invasive insect and, if so, at what spatial scales?

Methods

Study species

Paysandisia archon (Burmeister 1880), or palm borer, is a member of the family Castniidae (Lepidoptera) comprised of diurnal moths of neotropical origin. It is the only Castniid representative in Europe and is considered to be the largest accidentally introduced insect in the continent (Alario 2004). The native distribution of this species is limited to the northeast of Argentina, Paraguayan Chaco, the western area of Uruguay, and the southern part of Brazil (Sarto i Monteys and Aguilar 2005), not causing major damage there due, probably, to the presence of natural enemies such as birds (Corvidae, Mimidae) or parasitoid wasps (Ichneumonidae; Sarto i Monteys and Aguilar 2005). In Europe, it has reached pest status in Spain (Aguilar et al. 2001), Italy (Espinosa et al. 2003), and France (Drescher and Dufay 2001). This moth was first detected in the Iberian Peninsula inside *Trachycarpus fortunei* palm trees in Catalonia, being probably introduced around 1992–1993 when large imports of *T. fortunei* individuals from Argentina began in this area (Alario 2004; Sarto i Monteys and Aguilar 2005), though it remained undetected until 2000. It is expanding throughout the Mediterranean coastline from Girona to Almería, reaching also Madrid, Canary Islands, and Balearic Islands (MAGRAMA 2013). The pest is registered in the Spanish Catalogue of Invasive Exotic Species and the EPPO and DAISIE lists, being also regulated in the European Phytosanitary Legislation. It causes notorious economic loss in ornamental gardening and poses a profound threat to the conservation of the autochthonous species *Phoenix canariensis* and *Chamaerops humilis* (MAGRAMA 2013).

Chamaerops humilis is a dwarf palm (~ 1.5 m high), shrub-like, widely distributed throughout the Iberian Peninsula as well as Mallorca and mainly associated with coastal and subcoastal areas on the south and the east regions because of its thermophilic nature, either in the form of shrublands or being part of diverse forests understory from sea level to mountain ranges up to 1200 m (Herrera 1989; Merlo et al. 1993; Galán and Castroviejo 2007). This species is considered the only autochthonous palm of continental Europe (Guzmán et al. 2017). This palm has had various traditional usages (Merlo et al. 1993; López 2004), and it has been used for ornamental purposes in many parts of the world. Nevertheless, it also plays a crucial role in the ecosystem as it provides food to animals such as badgers, foxes, ungulates, and rabbits (Fedriani and Delibes 2009, 2011). Because of its vigorous sprouting, *this species* is highly tolerant to disturbance (Herrera 1989), which added to its ample distribution throughout the Iberian Peninsula makes *C. humilis* an ideal candidate for Mediterranean xeric cover regeneration interventions (Merlo et al. 1993). Furthermore, they act as "nurse plants" as they can facilitate establishment and development of other less tolerant species under their canopy, providing microhabitats that can alleviate harsh environmental conditions (e.g., Saiz and Alados 2012).

Study localities

Field work was carried out during the spring of 2016 in Mallorca. The first detection of *P. archon* was in 2002 at the north of the island, in the gardens of Hotel Formentor, and the moth has expanded to other locations afterward likely due to the sale of affected palms from nurseries. Based on the information collected by the Government of the Balearic Islands since 2004, we selected three localities for this study. The first study locality, a holm-oak forest, was located close to the Formentor Hotel parking lot (39° 55′ 56.3982″N, 3° 8′ 10.536″E). This was the source of outbreak of the infestation ("infestation core" locality, hereafter). The second study locality was at Ses Cases Velles (39° 56′ 31.2504″N, 3° 9′ 7.3866″E, 1.8 km away from source), a mixed holm-oak/pine forest where the influence of *P. archon* has been tracked since 2006, counting up to 435 dead individuals (Núñez Vázquez 2015; "early expansion" locality, hereafter). Lastly, the third study locality was a pine forest located at La Victòria campsite in Alcúdia (39° 52′ 5.4726″N, 3° 9′ 33.84″E, 7.3 km away from source); this is a more recently infested region with potential for widespread of the pest ("expansion front" locality, hereafter). All three areas were human-influenced landscapes as a result of their proximity to urban or recreational settlements, presenting an understory dominated by *C. humilis* and *Pistacia lentiscus* to a lesser extent, with lower presence of other Mediterranean shrubs such as *Cistus spp.*, and a few Poaceae species. In these areas, the climate is Mediterranean, characterized by hot summers (reaching mean temperatures above 25 °C during summer) and mild winters, with scarce or nonexistent frosts which assures the survival of overwintering larval populations (Sarto i Monteys and Aguilar 2005). Mean annual rainfall reaches values above 650 mm, with most rain falling during the winter/autumn seasons (data obtained from AEMET).

Sampling

We established three 100 × 10 m plots, one per locality. In these plots, all *C. humilis* individuals (palm hereafter) were geo-referenced. To characterize the intrinsic palm traits which may lead to differences in vulnerability to attack, we recorded the following variables from each palm: size (i.e., the number of stems per individual), gender, and the number of stems attacked by *P. archon* as a measure of intensity of attack. Individuals were marked with security tape for future monitoring purposes.

Spatial analysis

Spatial marked point pattern analysis deals with the statistical analysis of mapped point patterns (e.g., plants), which comprise the coordinates as well as additional features of ecological objects (e.g., size, sex), technically called "marks." We used different techniques of spatial marked point pattern analysis (Diggle 2003; Illian et al. 2008; Wiegand and Moloney 2014) to investigate the spatial patterns of *P. archon* attack in the three localities (Fig. 1). In addition to their spatial location, palms were characterized by qualitative (e.g., attacked vs. non-attacked) and quantitative "marks" (e.g., size) which were used in different analyses (Table 1). We calculated empirical test statistics that were contrasted to appropriate null models (see below), which represent a "benchmark" point process with known structure adapted to our questions. We used a Monte Carlo approach for construction of simulation envelops of a given null model and test statistic. Each of the 199 simulations of the point process underlying the null model generates a test statistic, and simulation envelopes with an approximate $\alpha = 0.05$ were calculated for the test statistic using its 5th highest and 5th lowest values. Note that we cannot interpret the simulation envelopes as confidence intervals because we tested the null hypothesis at several scales of r simultaneously, which could cause type I error. To test overall departure of the data from the null model without type I error inflation, we used a goodness-of-fit (GoF) test that collapses the scale-dependent information contained in the test statistics into a single test statistic u_i which represents the total squared deviation between the observed pattern and the theoretical result across the scales of interest. The u_i were calculated for the observed data ($\mathrm{i} = 0$) and for the data created by the $\mathrm{i} = 1, \ldots, 199$ simulations of the null model, and the rank of u_0 among all u_i is determined. If the rank of u_0 is larger than 190, there is a significant departure from the null model with $\alpha = 0.05$ over the scales of interest (i.e., 0–50 m). All point pattern analyses were conducted with the software *Programita* (Wiegand and Moloney 2014), freely available at http://programita.org.

Detailed descriptions of procedures used for estimation of summary statistics are provided in Supplementary Information. Briefly, we evaluated the null hypothesis that attacked palms were a random sample of all the palms by using techniques of qualitatively marked patterns (i.e., dead vs. live) and the random labeling null model to represent the absence of spatial structure (e.g., Fedriani and Wiegand 2014). Mark connection functions (e.g., Jacquemyn et al. 2010; Fedriani and Wiegand 2014) were used as summary statistics to quantify such spatial patterns. Specifically, to evaluate whether attacked palms tended to be aggregated or segregated at a certain spatial scales, we used the mark connection function $p_{11}(r)$ which indicates spatial association or segregation for observed values above the top or below the bottom of the simulation envelops, respectively. To evaluate whether attacked palms tended to associate or segregate from non-attacked ones, we used the bivariate mark connection function $p_{12}(r)$ which indicates spatial association or segregation for observed values above the top or below the bottom of the simulation envelops, respectively. Finally, to evaluate whether attacked palms tended to associate or segregate from conspecific clusters (attacked + non-attacked), we used the test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ which indicates spatial association or segregation to conspecific clusters for observed values above the top or below the bottom of the simulation envelops, respectively. On the other hand, to evaluate potential DDD of the intensity of *P. archon* attack on the *C. humilis* (i.e., fraction of infested stems per palm), we used techniques of quantitatively marked point pattern analysis, with mark correlation functions as summary statistics (e.g., Fedriani et al. 2015). We calculated three test functions to address different questions: (1) To evaluate whether the presence of conspecific neighbors at certain spatial scale from a target individual was associated with higher or lower attack intensities, we used the r-mark correlation function k_m, which indicates higher- or lower-than-expected attack intensities for observed values above or below the simulation envelops, respectively; (2) to evaluate whether the intensities of attack of conspecific neighbors tended to be positively or negatively correlated at certain spatial scale, we used the Schlather's I_mm correlation function (Schlather et al. 2004) which indicates significant positive or negative correlations in attack intensities for observed values above or below the simulation envelops, respectively; and (3) to evaluate whether the intensity of attack of target palms was correlated—and is so, in what direction—with the density of conspecifics at certain spatial scales, we

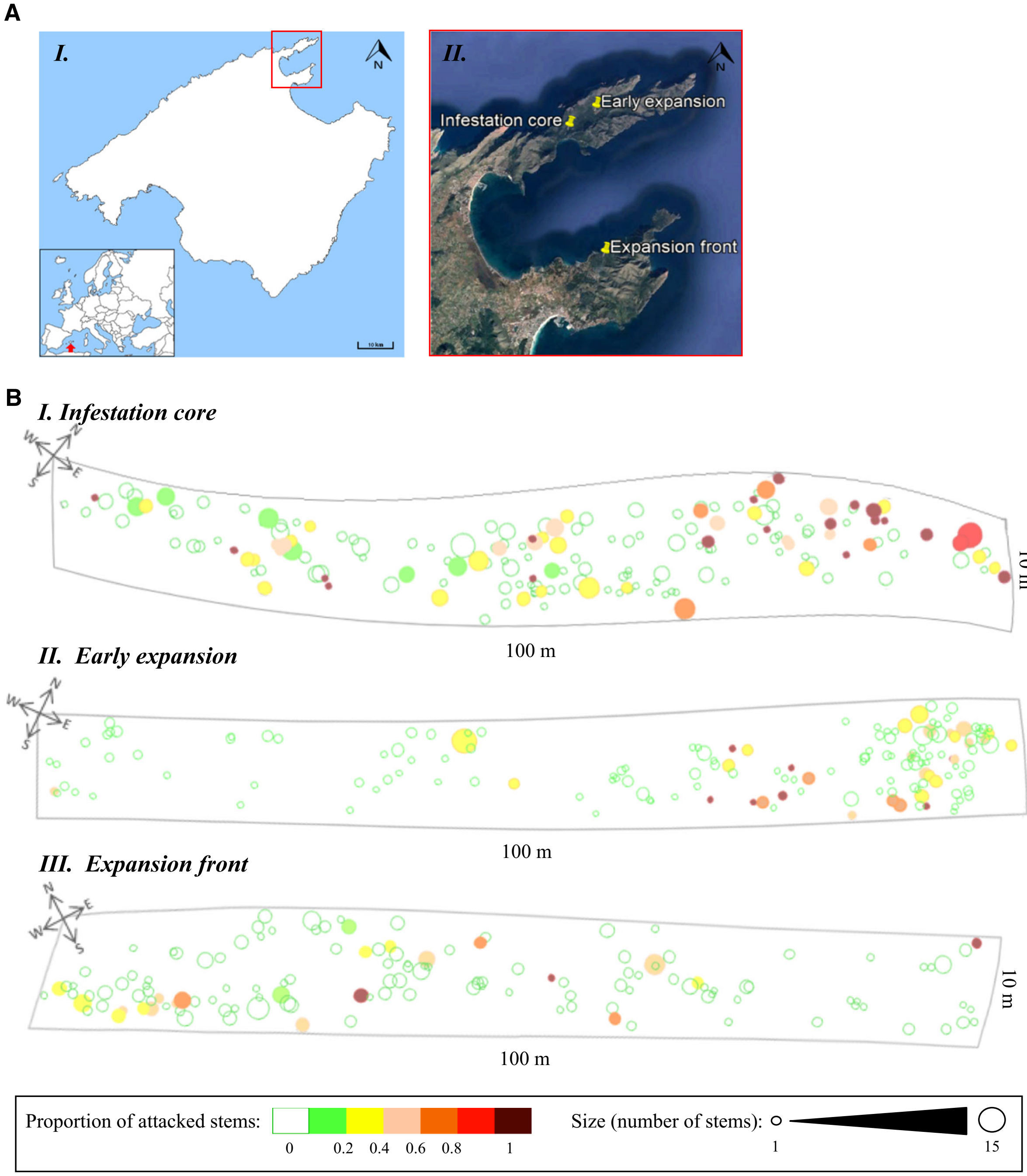

Fig. 1 **a** Map of the study area. (I) Location of Mallorca, Spain (red arrow, bottom left corner). The location of the three study localities is shown in (II) (close-up view of area delimited by a red square in I). **b** Bubble scatterplots representing the UTM coordinates location of palms in (I) infestation core, (II) early expansion and (III) expansion front localities. The size of the bubbles indicates palm size (i.e., the number of stems). Open green circles indicate no symptoms of attack (i.e., proportion of attacked stems = 0.0), and closed circles represent increasing values of attack (i.e., percentage of attacked stems; 6-leveled scale, ranging from light green—proportion of attacked stems = (0.0, 0.2)—to dark red—proportion of attacked stems = 1.0—, with color range in between representing open intervals of 0.2).The solid line represents the approximate limits of the 100 × 10 m plots

Table 1 Descriptive statistics of qualitative (percentage of attacked individuals) and quantitative (proportion of attacked stems per individual and number of stems per individual) marks, as well as sex ratio at the different study sites

	Infestation core Formentor (n = 177)	Early expansion Ses cases velles (n = 152)	Expansion front La Victòria (n = 135)
Descriptive variables			
Attacked individuals (%)	36.16%	21.71%	16.30%
Proportion of attacked stems/individual			
Mean ± SE	0.208 ± 0.025	0.123 ± 0.021	0.081 ± 0.018
Median	0.0	0.0	0.0
Range	0.0–1.0	0.0–1.0	0.0–1.0
Size (number of stems)			
Mean ± SE	3.096 ± 0.172	2.158 ± 0.145	2.578 ± 0.146
Median	2	2	2
Range	1–14	1–15	1–10
Sex ratio			
Males/females/undetermined	8/29/140	13/23/116	26/36/73
Ratio (male/female)	1:3.6	1:1.8	1:1.4

used the density correlation function $C_{m,K}$ which indicates positive or negative correlations (i.e., negative or positive density dependence, respectively) for observed values above or below the simulation envelops, respectively (Fedriani et al. 2015).

Even though specific functions are better tailored to unravel specific processes (density correlation function and the r-mark correlation tend to point, respectively, to density and distance dependence), both processes cannot be completely dissected (Fedriani et al. 2015). Hence, to increase clarity we consistently refer to density dependence throughout the results. Note, however, that the direction of results under the distance dependence approach would be the opposite to that of density dependence, as density scales with 1/distance.

Finally, we evaluated whether *P. archon* selected individual palms based on their sizes at a range of spatial scales. This question requires a null model where the qualitative marks (i.e., attacked and non-attacked) are fixed, but the size of the quantitative mark (palm size measured as the total number of stems) is randomly shuffled over all points (i.e., attacked and non-attacked palms). The test statistics used for this data structure and their interpretation are analogous to those used for the univariate mark correlation functions described above (see Wiegand and Moloney 2014 for details).

Gender could not be identified in a large proportion of the individuals, either because they were not yet reproductive (i.e., juveniles), because they had not flowered the study year, or because inflorescence remains from previous seasons were not found. Because the low number of palms that could be readily sexed did not allow for a robust spatial point pattern analysis, differences on attack rates between the two sexes were evaluated using Chi-square tests.

Results

Overall patterns

The three localities showed noticeable differences regarding the percentage of attacked individuals (Table 1), being highest in the source of *P. archon* infestation (i.e., the “infestation core” locality) and showing a decreasing trend as infestation time decreases. The number and density of palms and the proportion of attacked stems per individual followed the same trend (i.e., highest and lowest values at the “infestation core” and the “expansion front” localities, respectively; Table 1). Palm size (i.e., the number of stems) was relatively constant across localities (see Table 1), but was highly variable within each location, ranging from one to 15 stems per individual. Female palms were more abundant than males in all three locations (Table 1), although this may be due to female inflorescences enduring longer than male ones, which could skew the proportions of detected individuals of each gender.

Spatial pattern of *P. archon* attack on *C. humilis*

In either the "infestation core" or "expansion front" localities, *P. archon* attack did not show any spatial aggregation or segregation at any scale (Fig. 2a–c, g–i, respectively). As an exception to such general pattern, the probability that an attacked palm in the "infestation core" had a non-attacked palm at a distance of

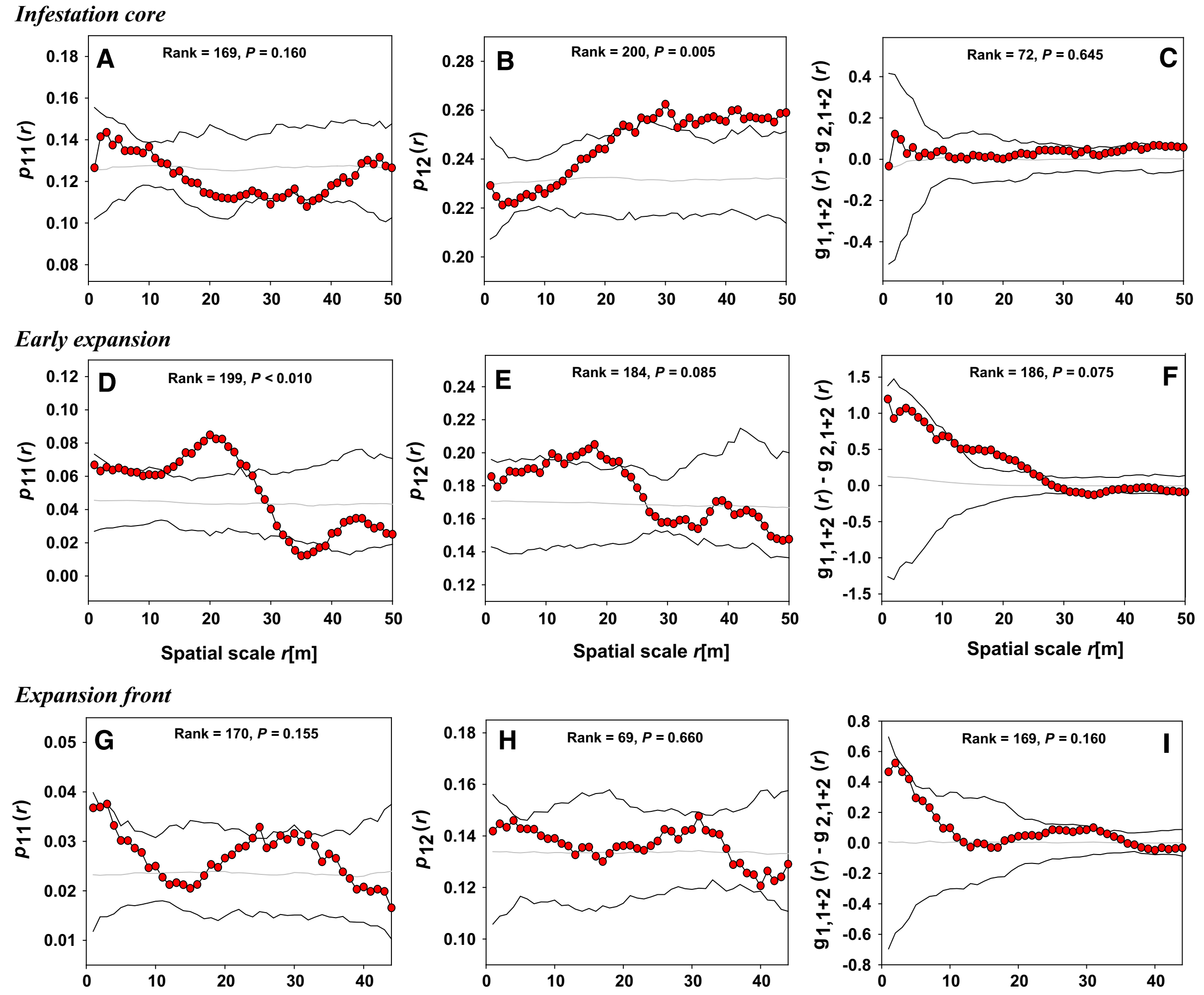

Fig. 2 Analysis of *P. archon* attack using mark connection functions as summary statistics in the three studied localities (**a**–**c**, infestation core; **d**–**f**, early expansion; **g**–**i** expansion front). **a**, **d**, **g** The mark connection function $p_{11}(r)$ gives the conditional probability that, for two dwarf palms separated by distance *r,* both are type 1 (i.e., attacked). **b**, **e**, **h** The mark connection function $p_{12}(r)$ gives the conditional probability that, for two dwarf palms separated by distance *r,* the first is type 1 (i.e., attacked) and the second type 2 (i.e., non-attacked). **c**, **f**, **i** The test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ compares the density of palms (i.e., 1 + 2) around attacked palms (i.e., type 1) with the density of palms (i.e., 1 + 2) around non-attacked palms (i.e., type 2). The expected value of this test statistics is zero under random labeling, but if *P. archon* attack tends to occur in palm clusters, then we expect positive values (i.e., $g_{1,1+2} > g_{2,1+2}$). The observed mark connection functions (closed disks), the expected function under the null model (gray solid line), and the corresponding simulation envelops (solid lines), being the 5th lowest and highest values of the functions created by 199 simulations under the null model, are shown. A rank larger than 190 shows a significant departure from the null model with $\alpha = 0.05$ over the scales of interest (see text for details)

30–50 m ($p_{12} = 0.257 \pm 0.002$; mean ± 1SE) was, on average, 10.8% higher than under the null hypothesis of absence of spatial structure (i.e., random labeling null model; 0.232 ± 0.001; Fig. 2b). In the "early expansion" locality, however, there was strong evidence of *P. archon* attack aggregation leading to negative density-dependent plant performance (Fig. 2d–f). For instance, the probability that two palms separated by a distance of 15–25 m were both attacked individuals ($p_{11} = 0.077 \pm 0.006$) was, on average, 76.3% higher than under the expectation of random labeling (0.043 ± 0.001; Fig. 2d). The bivariate $p_{12}(r)$ showed only a marginal departure from random labeling, suggesting that attacked palms tended to associate with non-attacked ones at scales 14–22 m (Fig. 2h). Finally, the test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ showed marginal evidence that *P. archon* probability of attack was higher at palm clusters. Specifically, attacked palms had a higher density of conspecific neighbors (attacked + non-attacked) than expected by random labeling for distances of 12–24 m.

Spatial patterns in the intensity of *P. archon* attack on *C. humilis*

Interestingly, the mark correlation functions for attack intensity (i.e., proportion of attacked stems) revealed rather contrasting DDD of *C. humilis* performance in each of the three localities (Fig. 3a–i). In the "infestation core" locality (the one with the highest proportion of attacked stems; Table 1), the r-mark correlation function indicated that the attack intensity was significantly lower for palms with conspecific neighbors within 10–35 m (Fig. 3a; $P < 0.005$). For example, a palm that had other conspecific at 25 m had an intensity of attack about 15% smaller than the mean of all palms in the plot, with such differences declining rapidly above 36 m (Fig. 3a). At this locality, Schlather's I_{mm} correlation function showed that attack intensities of palms separated by less than 18 m were positively correlated (Fig. 3b; $P < 0.005$). The density correlation function $C_{m,K}$ in the "infestation core" locality indicated a highly significant and negative correlation between density of conspecifics and the intensity of attack (i.e., positive density dependence) at scales > 14 m ($P < 0.005$; Fig. 3c) with a peak at 39 m [$C_{m,K}(r) = 0.289$]. In contrast, the attack intensity in the "early expansion" locality was significantly higher for palms with conspecific neighbors within 10–23 m (Fig. 3d; $P < 0.010$). For example, a palm that had another conspecific at distance 10–23 m had an intensity of attack about 40% higher than the mean of all palms in the plot (Fig. 3d). At this locality, Schlather's I_{mm} correlation function showed no correlation in attack intensities of palms at any spatial scale (Fig. 3e; $P < 0.210$). Again, as opposed to the "infestation core," the density correlation function $C_{m,K}$ depicted a significant and positive effect of density on attack intensity at distances above 16 m, leading to negative density dependence of palm performance (Fig. 3f; $P < 0.010$). Data from the "expansion front" (i.e., the lowest intensity of attack) exhibited a very different pattern, with no evidence of DDD (Fig. 3g–i).

Effect of palm size and sex on the spatial pattern of *P. archon* attack

At the "infestation core," the *r*-mark correlation function $km_{1}.(r)$, which estimates the mean size of attacked palms that had another attacked conspecific at distance *r*, indicates that the size of attacked palms located at distance up to 50 m from other attacked palms was significantly larger than expected (Fig. 4a; $P < 0.005$). Furthermore, the mean size of attacked palms that had a non-attacked conspecific at distance up to 50 m was also significantly larger than expected (Fig. 4b; $P < 0.005$). The mark "bivariate" variogram, which estimates the mean-squared size difference between the size of an attacked palm and that of an intact one at distance *r*, shows that attacked palms tend to be larger than non-attacked conspecifics at medium (17–25 m) and large (40–50 m) spatial scales (Fig. 4c; $P < 0.050$). In the "early expansion" locality, the trend was similar but more marked than in the other two localities, particularly at larger scales. For example, the *r*-mark correlation function $km_{1}.(r)$ indicated that the size of attacked palms that had another attacked conspecific at distance *r* was up to threefold larger than expected (Fig. 4d; $P < 0.005$). Similarly, the size of attacked palms that had a non-attacked conspecific at distance *r* was up to 2.2-fold larger than expected (Fig. 4e; $P < 0.005$). The mark variogram shows that attacked palms tend to be much larger than non-attacked conspecifics for scales > 30 m (Fig. 4f; $P < 0.005$). Finally, at the "expansion front," we also found that the size of attacked palms located at

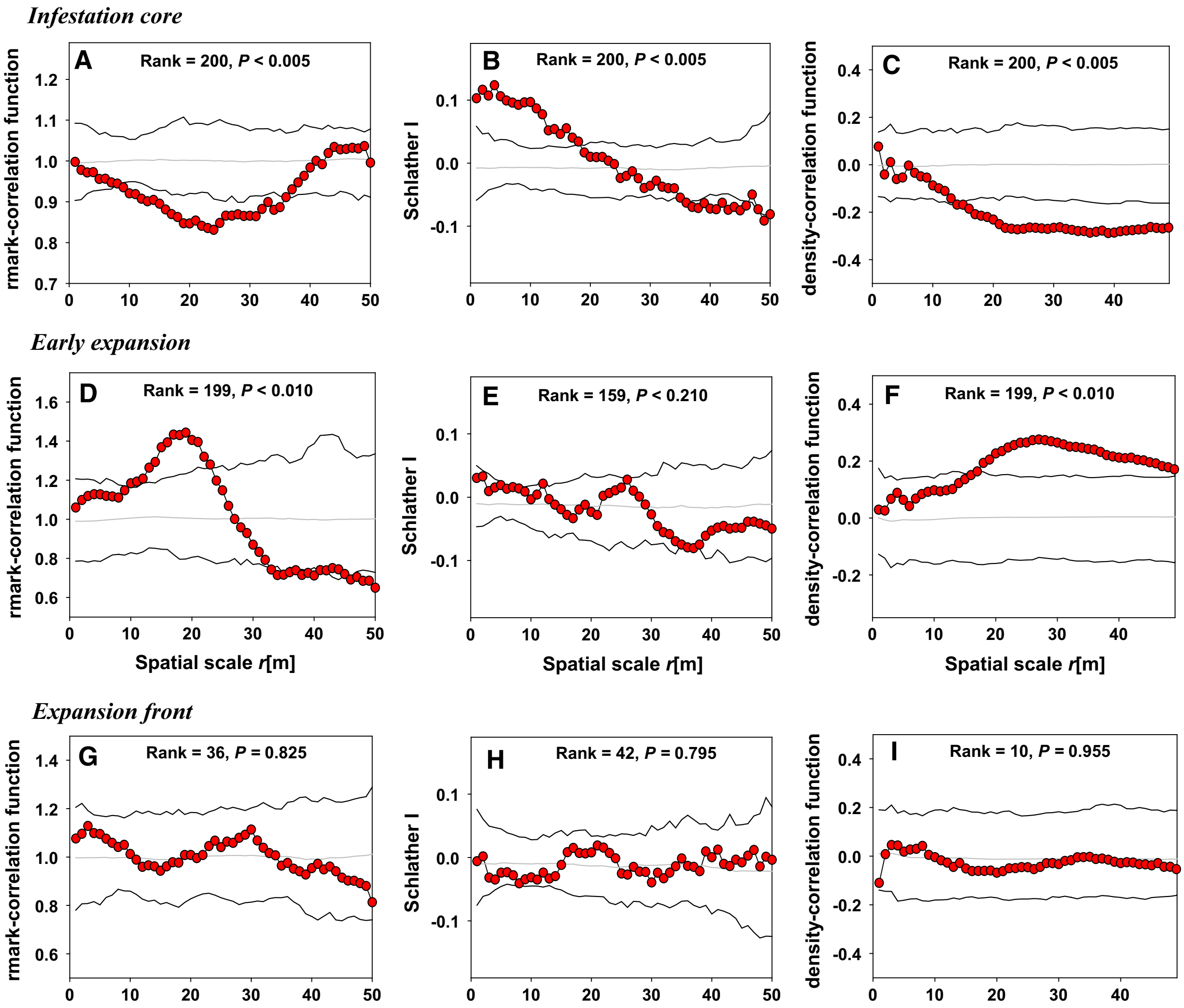

Fig. 3 Analyses with mark correlation functions to evaluate potential DDD of *P. archon* attack intensity on dwarf palms performance in the three studied localities (**a**–**c**, infestation core; **d**–**f**, early expansion; **g**–**i** expansion front). The r-mark correlation function is the mean attack intensity m_i (measured as the proportion of attacked stems) of a palm at distance r of another palm, Schlather's I_{mm} correlation function is the correlation between the attack intensities m_i and m_j of two palms i and j separated by distance r, respectively, and the neighborhood correlation function $C_{mK}(r)$ is the correlation between the mark m_j and the number of conspecific neighbors within distance r. The observed mark correlation functions (closed disks), the expected function under the null model (gray solid line), and the corresponding simulation envelops (solid lines), being the 5th lowest and highest values of the functions created by 199 simulations under the null model, are shown. A rank larger than 190 shows a significant departure from the null model with $\alpha = 0.05$ over the scales of interest (see text for details)

distance up to 50 m from either other attacked (Fig. 4d; $P < 0.005$) or non-attacked (Fig. 4e; $P < 0.005$) palms was significantly larger than expected. The mark variogram shows that attacked palms tend to be larger than non-attacked conspecifics at distances > 35 m (Fig. 4f; $P < 0.010$).

The percentages of individual palms that could be readily sexed in the three localities, from the oldest to youngest infestation, were 20.9, 23.7, and 45.9%, respectively (Table 1). The proportion of attacked individuals did not differ between sexes neither considering a pooled sample of all individuals across localities ($\chi^2 = 0.331$, $df = 1$, $P = 0.565$) or when considering each locality separately ($\chi^2 \leq 2.60$, $df = 1$, $P > 0.107$). Thus, we did not find any

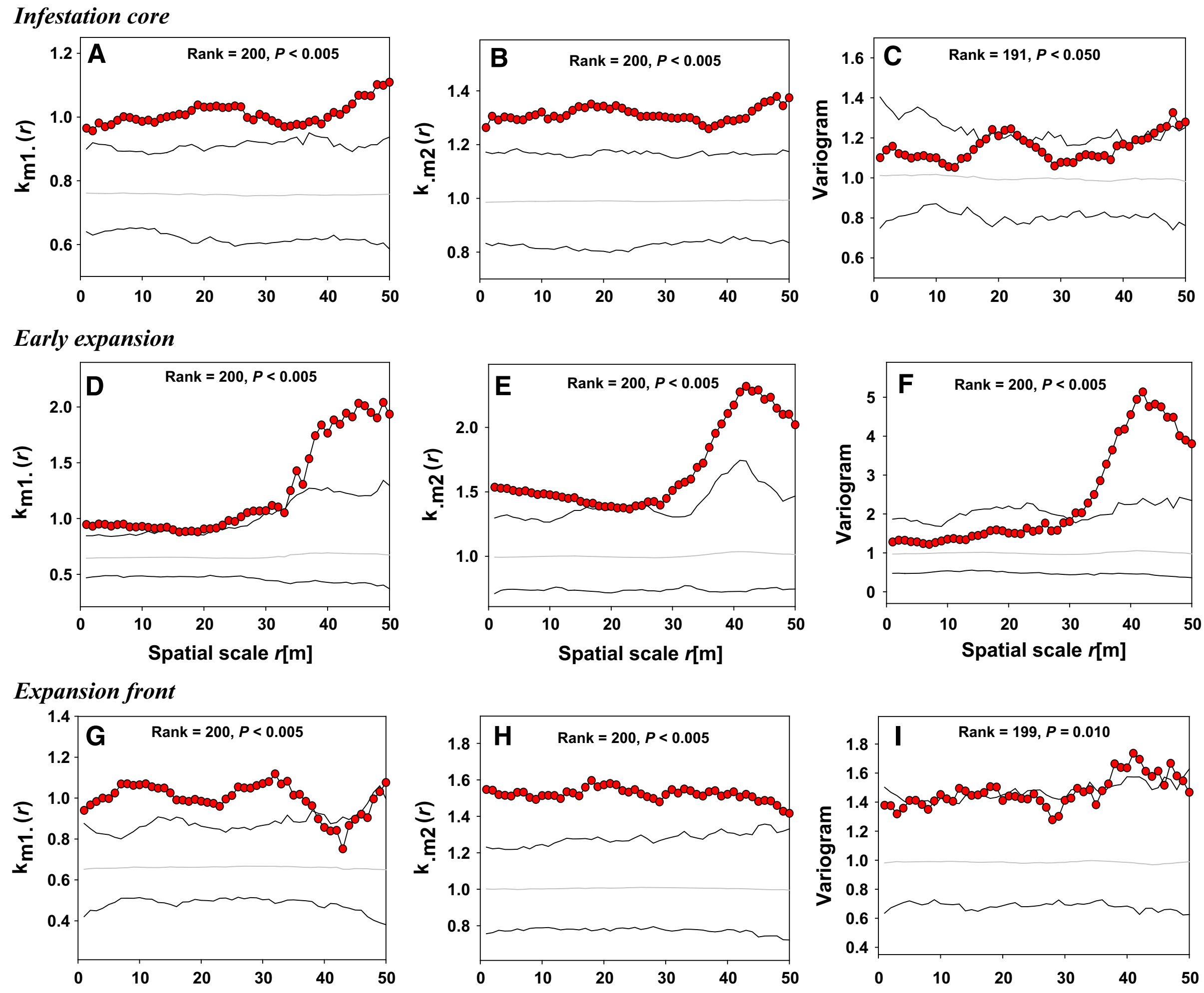

Fig. 4 Mark correlation functions analyzing potential *P. archon* palm selection based on their size in the three study localities (**a**–**c**, infestation core; **d**–**f**, early expansion; **g**–**i** expansion front). The "univariate" *r*-mark correlation function $k_{m1}.(r)$ estimates the mean size of attacked palms (type 1) that have another attacked palm at distance *r*. The "bivariate" *r*-mark correlation function $k_{m2}.(r)$ estimates the mean size of an attacked palm (type 1) that have a non-attacked palm (type 2) at distance *r*. The "bivariate" mark variogram γmm(r) estimates the mean-squared size difference between pair of attacked and non-attacked palms located at distance *r*. The observed mark correlation functions (closed disks), the expected function under the null model (gray solid line), and the corresponding simulation envelops (solid lines), being the 5th lowest and highest values of the functions created by 199 simulations under the null model, are shown. A rank larger than 190 shows a significant departure from the null model with $\alpha = 0.05$ over the scales of interest (see text for details)

evidence that *C. humilis* sex affected the attack by *P. archon*.

Discussion

We evaluated whether *C. humilis* experiences DDD processes on its interaction with *P. archon* at three localities as well as whether palm traits (size, sex) alter the probability of *P. archon* infestation. We found that *C. humilis* did experience DDD on its interaction with *P. archon*, but with contrasting directions between localities: At the "infestation core," we revealed strong evidence of positive density dependence of palm performance (i.e., lower infestation as palm density increases), whereas the opposite trend was found at the "early expansion" locality. The "expansion front" locality, by contrast, showed no evidence of density dependence. Our findings also revealed a strong correlation between palm size and attack probability, with larger palms showing more evidence of attack at a wide range of spatial scales in the three localities. Such results therefore shed light on the factors and spatial scales impinging the invasive behavior of this exotic lepidopteran, which should give rise to more effective monitoring and control methods to prevent further damage on the dwarf palm populations.

Contrasting DDD in the interaction between *P. archon* and *C. humilis*

In herbivore–host plant interactions, negative density-dependent effects on survival or performance of host plant seem to be the norm, regardless of the region considered (see meta-analysis from Comita et al. 2014), which agrees with our results found in the "early expansion" locality, but not in the other two locations. In the "early expansion" locality, individuals close to or surrounded by high densities of other palms had both higher attack probability and intensity. These negative density-dependent effects have been widely documented, especially in tropical forests and including stem-boring species (e.g., Sullivan 2003; Moravie et al. 2006; Freckleton et al. 2006). Sullivan (2003), from experiments and field observations during 3–4 years in Costa Rica, revealed that *Cromarcha stroudagnesia*—a shoot-boring lepidopteran—herbivory was higher when densities of host trees measured in a 50-m radius were also high. Moreover, Moravie et al. (2006) using the nearest neighbors' analysis and logistic regressions proved that *Apion onopordi,* a stem-boring weevil that preferentially attacks previously rust fungus-infected thistles, selects hosts for oviposition based not only upon whether it is rust-infected, but rather based on the density of rusted shoots within the neighborhood.

When considering the intensity of attack, the "infestation core" and "expansion front" localities showed positive and nonsignificant density-dependent effects, respectively. It is possible that such marked differences in the direction of DDD processes are, at least partially, related to differences between sites in invasion phase. In the "early expansion" locality, palms that are aggregated seem to be those most easily detected and exploited, as also found in other studies (Root 1973; Hambäck and Englund 2005). The "expansion front" locality shows the lowest attack intensity with just slightly over 20 individuals infested (Table 1), and it may be only a matter of time before DDD effects become similar to those found in the "early expansion" locality. At initial stages of the invasion process, palms selected by *P. archon* might be more randomly distributed; in fact, according to Sarto i Monteys and Aguilar (2005), *P. archon* seems to have a rather variable oviposition behavior (sometimes laying eggs in clumped palms, in other instances flying tens of meters away until the next oviposition) which may not result in an appreciable spatial pattern in attack in the short term. However, positive density dependence in *C. humilis* performance observed in the "infestation core" locality is an intriguing, seldom observed pattern (but see Augspurger 1981; Callaway 2007), as opposed to the more common negative DDD. Specific processes operating in this locality could account for these opposing DDD effects: The higher palm density in this locality could give rise to some kind of resource dilution effect (Kunin 1999; Otway et al. 2005) or predation satiation (Augspurger 1981). Positive density dependence of plant performance may also arise from habitat heterogeneity (Zhu et al. 2010; Bagchi et al. 2011; Piao et al. 2013). For instance, factors such as light (which is known to alter *P. archon* activity; Sarto i Monteys and Aguilar 2005; Liégeois et al. 2016) or potential associational resistance exerted by nearby vegetation cover (Barbosa et al. 2009) could offset any negative effect exerted by palm aggregation. Alternatively, it could also be that high infestation rates in the "infestation core" induce shifts in *P. archon* behavior, making the moths move further distances before ovipositing compared to when infestation rates are lower, therefore alleviating attack on clumped palms. In summary, our results support the conclusion that DDD processes are highly context dependent (e.g., Fedriani and Wiegand 2014; Fedriani et al. 2015), and future studies should pay more attention to habitat heterogeneity and to possible changes in DDD processes as infestation time/intensity increases, using for that a replicated, wider range of invasion time.

Interestingly, there was spatial aggregation of attacked with non-attacked individuals at medium (15–25 m, as in the case of the "early expansion" locality; Fig. 2e) to large scales (> 25 m, see the "infestation core" locality; Fig. 2b). "Attraction" of attacked and non-attacked individuals is typical of one-sided competition, since suppressed (attacked) individuals, or "losers," will be near superior rivals

(Kenkel 1988). As far as herbivore attack is concerned, to our knowledge there are no previous studies revealing such pattern. It might be possible that females of *P. archon* could eventually detect palms with symptoms of infection by other moths and avoid them in order to reduce intraspecific competition of larvae (i.e., food depletion by excess of larvae on the same palm stem). This might encourage moths to oviposit elsewhere, resulting in some healthy palms "escaping" moth attack when being close to attacked ones. This could be especially true in the "infestation core" and "early expansion" localities, where intensity of attack is higher. In fact, *P. archon,* as well as other castniid species, usually lay eggs singly despite palm fibers may contain several eggs very close to each other (Sarto i Monteys and Aguilar 2005). However, a study with the insect *Eutreta diana* (Wetzel and Strong 2015) does point out that females select host plants in a density-independent manner and do not avoid infested palms. It is nonetheless important to note that *E. diana* is not host specific and did select rare host plants that mediate only weak larval density dependence. Also, preliminary results from the "early expansion" locality point to a positive relationship between the number of eggs laid on the palms and the degree of infestation of individuals (unpublished data), so further research on this issue is needed to elucidate this behavior.

P. archon selects larger palms

In all three locations, large palms experienced stronger negative density dependence compared to small ones. The attacked individuals were in all cases larger than their neighbors over a wide range of scales, irrespectively of the attack status of their neighbors. Previous monitoring of *P. archon* attack on the "early expansion" locality also suggested the pest tended to select taller (3–4 m) palms, which remained true even after the eradication of numerous affected palms in the area (Núñez Vázquez 2015), further supporting the Plant Vigor Hypothesis (Price 1991). Moreover, this might be especially true in stem-borer insects (e.g., Price 1991; Solomon 1995; Solis et al. 2003; Moravie et al. 2006). *Paysandisia archon* mating behavior relies on visual cues (Sarto i Monteys et al. 2012; Delle-Vedove et al. 2014). Males mainly adopt a perching behavior, resting in highest, and therefore more visible places to locate mates (Sarto i Monteys et al. 2012; Delle-Vedove et al. 2014), and females lay their eggs not long after copulation (Sarto i Monteys and Aguilar 2005) which may further point to the importance of palm size in the whole life cycle of this invasive lepidopteran.

Conclusions and management implications

Our study constitutes one of the first attempts to characterize an invasive organism attack pattern in a spatially explicit manner. Furthermore, studies that analyze these DDD processes at localities at different infestation stages are rare. By studying three localities at different stages of infection and applying the same analytical approach, we obtained comparable results that help us understand how *P. archon* attacks *C. humilis* populations in relation to their spatial distribution and traits and how such spatial patterns are, in turn, spatially variable.

Some limitations of our study need to be noted for future investigations. Though one sampling study season provides a static snapshot pattern, such pattern is the result of a dynamic temporal process accumulated over the years (i.e., attacked palms survive for several years). Also, the locations studied here impose constraints regarding how spatial point pattern analyses operate. Palm individuals affected by *P. archon* are located in highly humanized areas, as this pest expands through cultivation from nurseries (Núñez Vázquez 2015), and therefore their spatial location is somewhat non-random (i.e., adjacent to roads, etc.), which influenced the selection of 10 × 100 m plots as opposed to more evenly dimensioned ones. Long narrow observation windows may constrain the power of point pattern analyses because many points could have unobserved neighbors outside the window (Wiegand and Moloney 2014) and thus might have reduced the statistical power in some of our analyses. Also, the availability of only one sampling plot for each of the invasions phases only allows for cautious conclusions, and more localities need to be studied so as to fully understand the characteristics of each invasion phase.

In spite of these constrains, our study has direct implications in *P. archon* management. The intensity of attack by *P. archon* appears to increase over time, which suggests managers should early intervene to ensure the conservation of attacked *C. humilis* populations. We have also shown that larger palms are preferentially selected, and therefore conservation efforts should prioritize these individuals. Nurseries and private properties, main sources of this pest, logically feature more vigorous (and, therefore, visually attractive) palms, and such factors could play a pivotal role in the high invasion success of *P. archon* in heavily managed areas, and therefore monitoring interventions should prioritize these locations. Our study has also shown that DDD effects of *P. archon* attack are highly variable and might depend on several factors such as local heterogeneity and degree of infestation, which calls for management strategies that account for specific features of each affected locality.

To attain a most complete picture of how *P. archon* invasion process develops over time, future studies should expand the analyses undertaken here over several consecutive years, also considering the entire life cycle of this pest, which will be certainly useful for future control efforts of this lepidopteran. Our study, and those to come, opens promising possibilities in the management of this and others exotic pests and will further contribute to the successful conservation of the endemic Mediterranean dwarf palm.

Acknowledgements We are very grateful to Luis Núñez, Caterina Amengual and Sandra Closa, from the Conselleria de Medi Ambient of the Balearic Government, for their support during all the phases of this study and for sharing their previous knowledge. We also thank a number of people who helped in the field: Miguel Ángel González, María Martín and Julieta Benítez-Malvido, and Tòfol Borràs, gardeners' foreman at Ses Cases Velles, who facilitated the work at this property. Special thanks go to Miguel González Calleja, from the GIS department at IMEDEA, for preparing the software to precisely georeference the palms in our GPS. This work was financed by the Conselleria de Medi Ambient of the Balearic Government and coordinated by AT. AL was supported by a postdoctoral contract co-funded by the Regional Government of the Balearic Islands and the European Social Fund 2014–2020. JMF was funded by a Portuguese FCT Grant (IF/00728/2013).

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