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SHORT COMMUNICATION

Assessing the relative importance of nurse species on Mediterranean human-altered areas

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One advantageous strategy for the restoration of human-disturbed landscapes is the use of ecologically "important" species such as nurse plants. We propose a field-based approach to measure the functional importance of nurse species (i.e. their relative facilitative effects on other plant species) and to identify which species will yield more efficient revegetation programs regarding their abundance. We identified 30 nurse-beneficiary spatial associations, with the functional importance varying largely among four nurse species and three human-disturbed areas. A Mediterranean endemic palm was the most important nurse species, thus showing its potential key role in revegetation programs by promoting spatial associations with late-successional plant species. We encourage restorers to use nurse species with a disproportionate (regarding their relative abundance) impact on ecosystems to save additional resources.

Key words: beneficiary species, field-based approach, nurse relative abundance, plant–plant association, revegetation programs

Implications for Practice

- Estimating the relative strength of nurse effects (i.e. "functional importance") in restoration programs is key to identify species with a disproportionate (regarding their abundance) positive impact on the abundance and distribution of other plant species.
- We propose a straightforward approach to empirically estimate the expected occurrences of beneficiary individuals associated with nurse species (based on their relative abundance) and to compare them to the observed spatial associations.
- We expect that our approach will promote the use of nurse species with higher impact of facilitative effects (regarding their abundance in the landscape) during the early stages of revegetation programs and thus available resources will be used more efficiently.

Introduction

The United Nations declared 2021–2030 as the "Decade on Ecosystem Restoration" (UN 2019) to accelerate the Bonn Challenge, and thus the restoration of 350 million hectares of degraded ecosystems. This initiative seeks to encourage greater economic investments in ecological restoration in future decades and to efficiently use this funding during restoration actions. In fact, the design of restoration actions entailing an effective use of economic investment at early-stages could be critical for the achievement of the target aims. For instance, several techniques have been developed to enhance revegetation programs, including the use of different spatial configurations of tree plantations (Rey-Benayas et al. 2008) or the use of nurse plants (Cruz-Alonso et al. 2020).

The functional importance of nurse plants (i.e. their facilitative effects on other plant species abundance and distribution) has been exhaustively studied in the literature (e.g. Soliveres & Maestre 2014). In restoration ecology, the role of nurse plants facilitating ecosystem recovery in human-disturbed landscapes has been also extensively examined (e.g. Siles et al. 2010; Galindo et al. 2017). At early stages of decision-making, one strategy is to compare the facilitative effects of different nurse species regarding their abundance and then to choose the species yielding the most efficient revegetation outcomes. In other words, we could a priori identify those species maximizing ecosystem restoration while minimizing revegetation efforts. Thus, the use of nurse species with a disproportionate impact regarding their relative abundance (Dee et al. 2019) may be critical by saving resources for other important tasks (e.g. monitoring; Lindenmayer 2020) in the ecological restoration of human-disturbed landscapes.

Here, we illustrate a field-based approach to compare the level of functional importance of nurse species and we propose its generalized use in the early stages of revegetation programs. That is, we asked, how disproportionate regarding their relative

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abundance is the impact of different nurse species (i.e. their facilitative effects) on the abundance and distribution of other plant species? And which species are the most efficient for future revegetation programs? To this end, we examined whether the numbers of spatial associations between 4 nurse species and 10 woody beneficiary species were proportional to the relative abundance of each nurse species in three Mediterranean human-disturbed areas. Specifically, we expected species- and site-specific differences in the level of functional importance of nurse species as well as a greater functional importance of some species in sites at early stages of the (re)colonization process (Garrote et al. 2019).

Methods

Study Sites and Nurse Species

The study was conducted from September 2017 to March 2019 in three human-disturbed areas ("Matasgordas," "Reserva," and "Santa Rita"; 10–100 km apart) of the southwestern Iberian Peninsula (Fig. S1, Supporting Information). Both Matasgordas and Reserva plots were set at the Doñana National Park in Spain. The Santa Rita plot was in the Algarve area in Portugal, at Ria Formosa Nature 2000. These study areas are dominated by pastureland and scattered patches of Mediterranean scrubland. Their original state (Dehesas with Mediterranean scrubland understory) was strongly disturbed, having a well-known intense human-management history (Garrote et al. 2019). Briefly, Matasgordas was used for cow grazing and is being (re)colonized by woody native plants since 1996, Reserva was used for grazing and is being (re)colonized since 1964, and Santa Rita is being (re)colonized from the 1990s when intensive cultivations were abandoned.

We focused on four nurse species: (1) *Chamaerops humilis*, a palm endemic to the Mediterranean basin; a pioneer in the (re) colonization of disturbed areas; (2) *Genista hirsuta*, a common shrub with long thorns and low palatability that colonizes Mediterranean scrubland after episodes of disturbance (e.g. fires); (3) *Halimium halimifolium*, a characteristic pioneer species that usually shows an understory with numerous branches from the basal trunk; and (4) *Stauracanthus genistoides*, a common shrub with numerous short thorns forming a compact understory. Previous experimental studies have reported facilitative effects by these nurse species (e.g. Lloret & Granzow-de la Cerda 2013; Perea et al. 2016; Fedriani et al. 2019). However, because plant–plant interactions are often context-dependent (Callaway 2007), we do not rule out the possibility of neutral or even competitive plant–plant interactions.

Field Sampling

To quantify the functional importance of each nurse species (i.e. the relative impact of their facilitative effects on other plant species), we developed a three-step approach based on exhaustive monitoring of plant abundance and distribution in the field. First, we sampled the beneficiary species. We counted all individuals of each beneficiary plant species within the plots (*Asparagus* spp., *Cistus salvifolius*, *Daphne gnidium*, *Myrtus communis*, *Olea europaea* var. *sylvestris*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Pyrus bourgaeana*, *Quercus suber*, and *Rubus ulmifolius*; Table S1). Second, we sampled the nurse species by estimating directly or indirectly (depending on the species) the relative abundance of each nurse species as (1) the percentage of the total number of individuals within the plots and (2) the percentage of the total area occupied (see details in Data S1). We considered a nurse–beneficiary spatial association when the beneficiary species was located within 1 m radius from the nurse plant (i.e. observed occurrence; Data S1). We excluded adult trees and those individuals associated with two or more nurse species (Data S1). Finally, for each observed nurse–beneficiary pair, we estimated the expected occurrences by multiplying the total number of beneficiary individuals within the plots by the relative abundance of each nurse species (Table S1).

Statistical Analysis

We tested overall differences between observed and expected occurrences of each nurse–beneficiary pair by chi-square analysis using the software SAS (SAS Institute 2016). When the assumptions for using chi-square analysis were not met (i.e. small expected occurrences in one or more cells), then we used Fisher's exact test (SAS Institute 2016). We used Holm's sequential Bonferroni procedure in both tests. Finally, we calculated a functional importance index as the observed occurrences/expected occurrences of each nurse–beneficiary pair. Index values greater than 1 indicate greater than the expected nurse effects. Index values lower than 1 indicate lower than the expected nurse effects.

Results

Observed occurrences of nurse–beneficiary pairs differed from the expected ones based on the percentage of the total number of nurse individuals (Fig. 1A; Table 1). We found significant differences for 17 out of 27 nurse–beneficiary pairs in Matasgordas, 9 out of 19 in Reserva, and the two examined pairs in Santa Rita (Fig. 2A; Table S2). Interestingly, these differences were not necessarily in the same direction. Specifically, for *C. humilis* the observed occurrences were on average 22.4 times greater than expected (Fig. 2A; Fig. S2). For *G. hirsuta* and *H. halimifolium*, however, the observed occurrences were on average only 0.5 and 0.3 times the expected ones, respectively (Fig. 2A; Fig. S2). For *Stauracanthus genistoides* the observed occurrences were only slightly larger than the expected ones (Fig. 2A; Fig. S2).

By focusing on the percentage of total area occupied by each nurse species, we found similar trends with only minor deviations (Fig. 1B; Table 1). We found significant differences for 18 out of 27 nurse–beneficiary pairs in Matasgordas, 10 out of 21 in Reserva, as well as the 2 examined pairs in Santa Rita (Fig. 2B; Table S2). The observed occurrences of beneficiary species statistically associated with *C. humilis*, *S. genistoides*, and *G. hirsuta* were always greater than expected (Fig. 2B; Fig. S3). However, whereas for *C. humilis* the observed

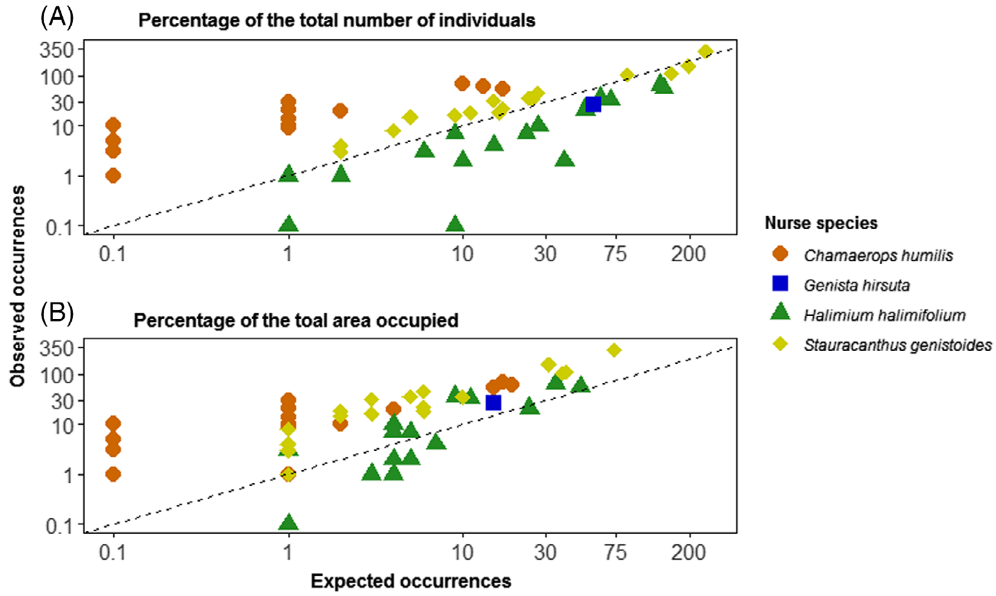

Figure 1. Comparison between observed and expected occurrences of nurse–beneficiary pairs based on (A) the percentage of the total number of nurse individuals and (B) the percentage of total area occupied by each nurse species. The dashed line indicates equal observed and expected occurrences. Note the logarithmic scales of axes.

occurrences were on average 21.3 times higher than expected, for *S. genistoides* and *G. hirsuta* the deviations were less marked (5.7 and 1.8 times, respectively (Fig. 2B, Fig. S3). For *H. halimifolium*, we found significant differences between observed and expected occurrences in only 3 out of 17 nurse–beneficiary pairs being up to four times higher than expected (Fig. 2B; Fig. S3).

Summarizing, *C. humilis* showed the highest functional importance as nurse species in all localities regardless of the abundance approach used. *Stauracanthus genistoides* also showed high importance (especially at Matasgordas) but only when using the percentage of area as abundance proxy. In contrast, *H. halimifolium* and *G. hirsuta* showed lower functional importance.

Discussion

Nurse species showing high relative facilitative effects on the ecosystem can play a most crucial role in revegetation programs of Mediterranean human-altered areas (Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2006). Our approach shows how to measure the functional importance of nurse species through their spatial associations with beneficiary species for an efficient use of available resources. Thus, while *C. humilis* showed the greatest functional importance as nurse species regardless of the abundance approach used, *S. genistoides* was highly important for the percentage of total area occupied at Matasgordas. Interestingly, the functional importance of *C. humilis* was particularly high at early stages of the (re)colonization (i.e. when the abundance of beneficiary species is low). Indeed, we have encouraged restorers to plant late-successional species beneath *C. humilis* for triggering nucleation processes (Garrote et al. 2019).

The approach used to quantify nurse plant abundance influenced our estimates of functional importance for *G. hirsuta* and *H. halimifolium*. Only *G. hirsuta* and a few of *H. halimifolium*-beneficiary pairs showed significant but weak effects based on the percentage of total area occupied; consequently, we must consider these results carefully. Taken together, our results suggest the potential in revegetation programs of some nurse species (*C. humilis* and, to a lesser extent, *S. genistoides*) with consistently higher functional importance. Thus, the use of nurse species with a disproportionate impact (regarding their abundance in the landscape) on the ecosystem would allow saving available resources for additional tasks (e.g. monitoring; Lindenmayer 2020). However, the selection of the abundance approach to measure functional importance levels could be critical. Given the species-specific differences between both abundance approaches, we recommend its combined use as we did for our study.

The first advantage of our approach is that it is applicable under context-dependent scenarios (Callaway 2007). For instance, Fedriani et al. (2019) found contrasting effects of shrubs on *P. bourgaeana* seedling survival and recruitment depending on habitat type (i.e. positive effects in shrub-dominated habitats vs. negative effects in dense pine plantation). Our approach would easily yield useful information about the functional importance of nurse shrubs in different habitat types, which would allow formulating specific hypotheses for its validation by means of field experiments. In addition, our approach is also appropriate in relation to other ecological functions of plants such as their provision of essential trophic resources (e.g. leaves, nectar, fruits) to consumers. Thus, it can be determined whether consumers use plant resources provided by a given plant more, less, or as expected based on the plant relative abundance in the landscape. However, we must consider some limitations of our approach. First, we quantified nurse–beneficiary

Table 1. Functional importance index (in bold) calculated as the average ratio (observed over expected occurrences) of nurse–beneficiary pairs in each study area. Index values greater than 1 indicate greater than expected nurse effects. Index values lower than 1 indicate lower than expected nurse effects. Beneficiary species significantly associated with each nurse species are shown below functional importance indices. The observed and expected number of individuals is indicated inside the parentheses, respectively.

	Matasgordas		*Reserva*		*Santa Rita*	
	% Individuals	*% Area*	*% Individuals*	*% Area*	*% Individuals*	*% Area*
Chamaerops humilis	**26.5** *Asparagus aphyllus* (60/13) *Cistus salvifolius* (56/17) *Daphne gnidium* (21/1) *Olea europaea sylvestris* (10/1) *Pistacia lentiscus* (14/1) *Pyrus bourgaeana* (9/1) *Quercus suber* (5/0) *Rubus ulmifolius* (10/0)	**26.4** *A. aphyllus* (60/19) *C. salvifolius* (56/15) *D. gnidium* (21/1) *O. e. sylvestris* (10/0) *P. lentiscus* (14/1) *P. bourgaeana* (9/1) *Q. suber* (5/0) *R. ulmifolius* (10/1)	**9.0** *A. aphyllus* (69/10) *O. e. sylvestris* (20/2) *R. ulmifolius* (10/1)	**4.7** *A. aphyllus* (69/17) *O. e. sylvestris* (20/4) *R. ulmifolius* (10/2)	**30** *Asparagus* spp. (30/1)	**30** *Asparagus* spp. (30/1)
Halimium halimifolium	**0.3** *D. gnidium* (33/70) *O. e. sylvestris* (10/27) *P. lentiscus* (36/61) *P. bourgaeana* (2/38) *Q. suber* (0/9) *R. ulmifolius* (7/23)	**3.5** *D. gnidium* (33/11) *P. lentiscus* (36/9)	**0.4** *A. aphyllus* (66/135) *O. e. sylvestris* (56/141) *Phillyrea angustifolia* (4/15) *Q. suber* (2/10) *R. ulmifolius* (21/50)	**1.9** *A. aphyllus* (66/34)	—	—
Stauracanthus genistoides	**1.2** *A. aphyllus* (110/156) *C. salvifolius* (156/195) *P. bourgaeana* (32/15)	**6.9** *A. aphyllus* (110/39) *C. salvifolius* (156/31) *D. gnidium* (45/6) *O. e. sylvestris* (18/2) *P. lentiscus* (36/5) *P. bourgaeana* (32/3) *Q. suber* (8/1) *R. ulmifolius* (16/3)	**1.3** *O. e. sylvestris* (314/246)	**4.1** *A. aphyllus* (15/2) *D. gnidium* (18/6) *O. e. sylvestris* (314/74) *P. angustifolia* (35/10) *Q. suber* (22/6) *R. ulmifolius* (15/2)	—	—
Genista hirsuta	—	—	—	—	**0.5** *Asparagus* spp. (27/56)	**1.8** *Asparagus* spp. (27/15)

spatial associations rather than experimentally demonstrate facilitative interactions. Therefore, further experimental studies to confirm the mechanisms underlying such patterns are necessary (but see Lloret & Granzow-de la Cerda 2013; Perea et al. 2016). Second, a large number of associations between one nurse and numerous beneficiary species must not imply that it would facilitate a particular target species of revegetation programs. Therefore, we must consider such specificity and suggest a generalized use of nurse species in revegetation programs provided that it is facilitating the beneficiary target species (e.g. Castro et al. 2004; Navarro-Cano et al. 2019). Finally, the quantification of spatial associations 1 m from the nurse edge may have overestimated the results. To avoid

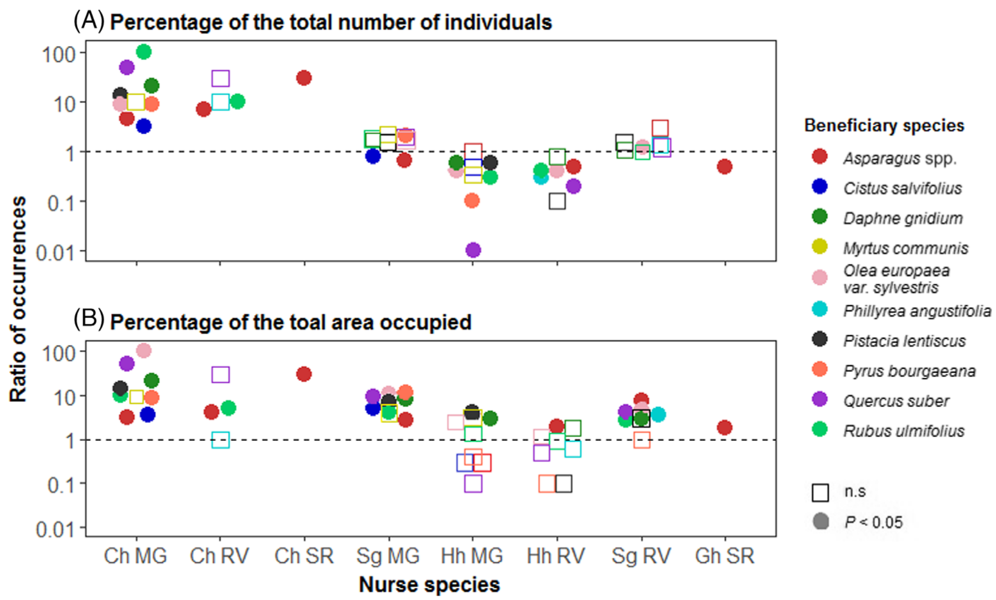

Figure 2. Ratio between observed and expected occurrences of nurse–beneficiary pairs based on (A) the percentage of the total number of nurse individuals and (B) the percentage of total area occupied by each nurse species. On *x*-axis, nurse species (Ch, *Chamaerops humilis*; Sg, *Stauracanthus genistoides*; Hh, *Halimium halimifolium*; Gh, *Genista hirsuta*) are in ascending order of relative abundance in Matasgordas (MG), Reserva (RV) and Santa Rita (SR). The dashed line indicates a ratio equal to 1. Solid circles represent statistically significant associations and open squares represent non-significant ones. Note the logarithmic scales of axes.

potential impacts on further studies, we recommend quantifying nurse–beneficiary spatial associations when there is physical contact or when beneficiaries are located up to 1 m from the base of the nurse (e.g. Joy & Young 2002).

To conclude, we propose a field-based approach to estimate the functional importance of nurse species regarding their relative abundance on an ecosystem as an additional tool for the current seeking of efficient restoration actions during early stages of decision-making (Aronson et al. 2020).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Descriptive information about beneficiary-nurse pairs at the three study plots.
Table S2. Main results from the chi-square analysis corrected by Holm's sequential Bonferroni to evaluate the differences between observed and expected occurrences of the nurse-beneficiary pairs.
Data S1. Field sampling (additional details).
Figure S1. Study areas.
Figure S2. Observed (black) and expected (gray) occurrences of nurse-beneficiary pairs at the three study areas based on the percentage of the total number of individuals of the four nurse species.
Figure S3. Observed (black) and expected (gray) occurrences of nurse-beneficiary pairs at the three study areas based on the percentage of the total area occupied by the four nurse species.

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