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ORIGINAL ARTICLE

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Assessing the accuracy of paired and random sampling for quantifying plant–plant interactions in natural communities

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Abstract

Plant interactions in extreme environments are often inferred from spatial associations and quantified by means of paired sampling. Yet, this method might be confounded by habitat-sharing effects. Here, we address whether paired and random sampling methods provide similar results at varying levels of environmental heterogeneity. We quantified spatial associations with the two methods at three sites that encompass different micro-environmental heterogeneity and stress levels: Mediterranean environments in Canary Islands, Spain, and Sardinia, Italy, and a cold alpine environment in Hokkaido, Japan. Then, we simulated plant communities with different levels of species micro-habitat preferences, environmental heterogeneity, and stress levels. We found that differences in species associations between paired and random sampling were indistinguishable from zero in a homogeneous space. When simulating codispersion over a decreasing abundance gradient, both sampling methods correctly identified facilitation and distinguished it from codispersion. Yet, the pairwise method provided higher facilitation estimates than the random one. At each site, there were strong differences between beneficiary species in their spatial association with nurse species, and associations

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Richard Michalet and Gianalberto Losapio contributed equally to this work.

became more positive with increasing stress in Spain. Most importantly, there were no differences in results yielded by the two methods at any of the different stress levels at the Spanish and Japanese sites. At the Italian site, although microenvironmental heterogeneity was low, we found weakly significant differences between methods that were unlikely due to habitat-sharing effects. Thus, the paired sampling method can provide significant insights into net and long-term effects of plant interactions in spatially conspicuous environments.

KEYWORDS

Canary Islands, facilitation, field experiments, Hokkaido, Sardinia

1 | INTRODUCTION

The interplay between competition and facilitation in shaping plant communities has been intensively studied for more than three decades (Callaway et al., 2002; Goldberg & Barton, 1992; Losapio et al., 2021). Most empirical studies assessing these two ecological processes in natural communities have focused on the net outcome of pairwise interactions by comparing the performance of a target species (or dependent community) with and without neighbors often by means of pairwise comparison. This method, sometimes called the observational method (Kershaw & Looney, 1964; Maestre et al., 2005), compares the performance of the target species between spatially proximate locations within the same community that are naturally with and without neighbors. It avoids artificial modifications of environmental conditions that could confound the results. However, it can only be applied in situations where the clear and conspicuous presence and absence of a target species (i.e., nurse or competitor) can be determined unambiguously, and this method would be preferable in habitats where vegetation cover is patchy (Liancourt & Dolezal, 2020). Consequently, this method has been used mostly for assessing facilitation rather than the competition because facilitation has been described more frequently in conditions of low biomass and vegetation cover (Cavieres et al., 2014).

Two sampling methodologies have been used for the observational method. The random sampling method is based on a unique set of randomly chosen locations sampled within the same area, some of which contain plants and some do not (Kikvidze et al., 2005). On the other hand, the paired sampling method involves deliberately identifying pairs of samples, one randomly including a nurse plant (or a competitor) or vegetation patch and a random, nearby sample from an adjacent area where the facilitator or competitor species under study is absent (Cavieres et al., 2014). The facilitator and beneficiary species can be associated in space in the absence of interactions (i.e., the "oasis effect" often observed in arctic or alpine ecosystems, Muc et al., 1989) if both share the same abiotic requirements, such as deeper soil patches or rock shelters. Consequently, important requirements of the method are that sampled vegetation patches and open areas must be located in similar microhabitats. However, the paired sampling method may be statistically biased towards over-estimating facilitation (Steinbauer et al., 2016). A point of argument is that microhabitat heterogeneity may lead to facilitation overestimation because the probability to have better spots for a beneficiary species is higher in vegetated patches than in open areas if nurse species have a preference for those better spots. Nevertheless, it is important to keep in mind that environmental heterogeneity is itself created by long-term feedback mechanisms between vegetation and the abiotic environment (Bera et al., 2021). In other words, the better spots could have been created by the nurse itself, although microenvironmental heterogeneity did not exist before the colonization of the nurse.

Ecosystem-engineering effects generate positive, reciprocal feedback processes "that operate by modifying any of several features of the environment, including water, pH, soil elements, light, temperature, wind, fire, or allelopathic toxins" (Wilson & Agnew, 1992). These biophysical interactions then produce a stable vegetation mosaic, with environmental conditions now differing between areas with and without vegetation in what otherwise was previously a uniform environment. Yet, it is important to note that, if microenvironmental heterogeneity within plant communities is biotically driven through long-term ecosystem engineering, they should not be considered as pre-existing differences in environmental conditions between open and vegetated areas that could confound the results but as an outcome of plant interactions.

Consequently, there is a need for the paired sampling method to focus on accounting—if possible—for what might be termed pre-existing (i.e., pre-vegetation development) small-scale environmental heterogeneity and eventually disentangling that component from ecosystem-engineering effects. Addressing this point will enable us to draw important conclusions from the results of paired sampling studies. For example, Michalet, Brooker, et al. (2015) and Noumi et al. (2016) proposed disentangling short- from long-term effects of neighbors using both the paired sampling and removal procedures (i.e., experimental elimination of the neighbors from a vegetated area) in the same community. They argued that short-term effects could be quantified using the removal method (with neighbors vs. removed-neighbors conditions) and long-term effects by comparing target responses in removed-neighbors versus naturally open conditions without neighbors (Noumi et al., 2016). Thus, the net neighbor effects (i.e., the sum of short- and long-term effects) are those quantified by the paired sampling method.

The crucial point is how to separate pre-existing micro-environmental heterogeneity from ecosystem-engineering effects. This is important because both pre-existing spatial environmental heterogeneity and facilitation are expected to increase with increasing environmental harshness (Steinbauer et al., 2016). Indeed, Bertness and Callaway (1994) have proposed that facilitation should increase with increasing stress (the stress gradient hypothesis [SGH]). Co-analyzing environmental factors, as suggested by Steinbauer et al. (2016), is one route to address this problem, but it is not always easy to determine whether differences between vegetated and bare patches are pre-existing or due to ecosystem engineering effects, as explained above. However, we suggest that by focusing on conspicuous micro-topographic variations that occur in both vegetated and bare patches within the same community, ecologists can account for the likely pre-existing environmental heterogeneity using the paired sampling method, thus overcoming its drawbacks.

The main goal of our article was to test the accuracy of the paired sampling method for quantifying spatial associations in stressful environments. Specifically, we aim at addressing whether paired and random sampling methods provide similar results at varying levels of environmental heterogeneity by using both a modeling approach and field measurements of spatial associations using the two methods. We first used a modeling approach assessing the effects of different environmental and biotic factors on spatial association as quantified with the paired and random sampling methods. In particular, we tested the role of within-community habitat heterogeneity, abundance, and ecological preferences of nurse (i.e., the potential facilitator species) and beneficiary species (i.e., the species facilitated by the nurse). We also applied these two methods (i.e., random and paired sampling methods) in three different real-world ecosystems subjected to varying stress levels and exhibiting contrasting soil heterogeneities. In this empirical test of the paired sampling method our goal was not to separate preexisting environmental heterogeneity from ecosystem engineering effects but to assess if the paired sampling and random sampling methods provide similar results when the sampling is conducted such as that obvious preexisting environmental heterogeneity is considered during the paired sampling procedure. We posed two main questions in both the modeling study and the field systems: (i) are spatial associations detected with the two methods significantly different when preexisting within-community environmental heterogeneity is high? (ii) are spatial associations detected with the two methods affected by species preferences and stress level?

2 | MATERIALS AND METHODS

2.1 | Modeling study

2.1.1 | Plant–plant and plant–environment interaction model

The plant community simulation consisted of two modeling approaches. The first modeling approach assumed a homogeneous space, while the second modeling approach used a gradient over a spatial grid. Our rationale, here, is to simplify the community including few, basic biotic components and to focus on the differences between the two methods. We do not aim at reproducing every and each community assembly process or spatial pattern.

In the homogeneous space model (Wiegand & Moloney, 2014), we simulated a plant community composed of nurse (α) and beneficiary (β) plant species. We considered the following abiotic and biotic factors: (i) habitat availability (q), (ii) nurse abundance (i.e., landscape cover) (a_α), (iii) beneficiary abundance (i.e., landscape cover) (a_β), (iv) nurse habitat preference (h_α), (v) beneficiary habitat preference (h_β), and (vi) beneficiary affinity to nurse ($\alpha \rightarrow \beta$). A given plant community was characterized by a set of spatial units x ($n = 500^2$). We adopted a presence–absence assembly model where the occurrence y of nurse plants α and beneficiary plants β is given by $y = 1$ for species presence and $y = 0$ for species absence.

Nurse occurrence y_α was calculated as the geometric mean of nurse abundance (a_α) and habitat suitability (hs_α), such that $y_\alpha = \sqrt{a_\alpha \times hs_\alpha}$. The factor habitat suitability (hs_α) was calculated as $hs_\alpha = 1 - |q - h_\alpha|$, where we considered the differences between habitat availability (q) and nurse habitat preference (h_α). This way, habitat suitability is given by a combination of abiotic factors (habitat availability q) and intrinsic species-specific habitat preferences (nurse habitat preference h_α). For instance, a stressful environment would be less unsuitable to a stress-resistant plant rather than to a demanding plant, and vice versa. Furthermore, habitat availability was expressed in a homogeneous environment (heterogeneity $= 0$) or homogeneous ($q = 0.1$ or 0.9). Nurse abundance (a_α) was considered as relative cover and ranged from 0.05 (5%) to 0.3 (30%); nurse habitat preference (h_α) ranged from 0.2 to 0.9. The occurrence probability of a nurse plant was drawn from those values y_α following a binomial distribution. The probability of drawing 1 from this binomial distribution was drawn according to the equation for y_α reported above from 250,000 observations (i.e., a 500×500 sampling grid).

Beneficiary occurrence y_β is drawn from a distribution of values resulting from the geometric mean between beneficiary abundance (a_β) and habit suitability (hs_β) with a nurse–beneficiary matching factor (m_β), such that, $y_\beta = \sqrt{\sqrt{a_\beta \times hs_\beta} \times m_\beta}$. This way, we weighted the contribution between beneficiary niches ($a_\beta \times hs_\beta$) and a nurse–beneficiary effects (m_β) in equal parts. The nurse beneficiary matching factor (m_β) was calculated as $m_\beta = 1 - |y_\alpha - y_{\alpha\to\beta}|$, where we considered the combination of nurse occurrence (y_α) and beneficiary affinity to nurse ($y_{\alpha\to\beta}$). This matching factor m_β entails nurse effects on beneficiary species, depending on the presence of nurse plants in the community (i.e., nurse occurrence, y_α) and on the dependency of beneficiary species on the nurse ($y_{\alpha\to\beta}$). Weighing among beneficiary abundance (a_β), habit suitability (hs_β), and nurse–beneficiary effects (m_β) by considering the geometric mean among these three factors ($\sqrt{a_\beta \times hs_\beta \times m_\beta}$) would produce similar outcomes (see Supporting Information [SI]). Beneficiary abundance a_β was considered as relative cover and ranged from 0.01 (1%) to 0.20 (20%); habit suitability hs_β ranged between 0.2 and 1.0.

Simulation model parameters were set as follows: $q = 0.0$, 0.1, 0.9; $a_\alpha = 0.050$, 0.133, 0.217, 0.300; $a_\beta = 0.010$, 0.073, 0.137, 0.200; $h_\alpha = 0.200$, 0.467, 0.733, 1.000; $hs_\beta = 0.200$, 0.467, 0.733, 1.000; $\alpha \to \beta = 0.000$, 0.333, 0.667, 1.000. In the simulation, habitat availability q is first treated as binary (i.e., 0 or higher than 0), then we considered two heterogeneity levels (0.1 and 0.9) for values of q different than zero. Each factor combination was replicated in a fully-factorial experiment, resulting in $n = 3 \times 4 \times 4 \times 4 \times 4 \times 4 = 3072$ communities. Sampling efforts (i.e., number of sampled plots) were equal to 5% and 10% of the spatial units.

2.1.2 | Simulation of and sampling over homogeneous space

We proceeded with sampling the community according to the random or pairwise approaches in this homogeneous space.

In the random approach, a set of plots is sampled randomly from a uniform distribution, that is, with constant probability for each spatial unit. In the pairwise approach, a set of plots is sampled randomly from a uniform distribution of plots in which the nurse is present (i.e., for those spatial units where $y_\alpha = 1$), while a second set of plots is sampled randomly from a uniform distribution of plots in which the nurse is absent (i.e., for those spatial units where $y_\alpha = 0$). Pairwise plots are generated from randomly sampling plots where the nurse is present or absent, as opposed to random plots where nurse presence is not considered a priori. Then, we recorded whether the nurse α and the beneficiary β plants were present or absent in each plot for each of the two sampling methods (see also the R code in SI).

We addressed the influence of sampling methods (i.e., random vs. paired) on the estimated facilitation effects. Facilitation effects were calculated as the dependency of beneficiary species β on nurse occurrence α. We used a generalized linear model of the form $\text{logit}(\psi(\beta|\alpha)) \sim b_0 + b_1(\alpha)$, where beneficiary occurrence β was the response variable, nurse occurrence α the explanatory variable, and b_0 (intercept) and b_1 (slope) are the estimated parameters indicating occurrence probability of beneficiary in the absence of nurse plants and the facilitation effects of nurse plants on beneficiary species.

Then, we looked at the impact of gabiotic and biotic factors on facilitation effects. To compare relative facilitation effects regardless of model context, we considered the normalized b_1 parameters (i.e., z-score) for each sampling method in conjunction (see SI). This was accomplished by running linear models with facilitation effects (i.e., z-score of b_1) as response variable and the following variables as predictors: habitat availability, nurse abundance, beneficiary abundance, nurse habitat preference, beneficiary habitat preference, beneficiary affinity to nurse, and sampling effort; sampling method (random vs. paired) was included as predictor, alone and in interactions with all these previous factors (see SI), to test its effects on facilitation.

Finally, we considered the differences in facilitation effects b_1 between pairwise and random sampling as $\delta = b_1\text{pairwise} - b_1\text{random}$. We tested how these values δ change among abiotic and biotic factors using a linear model that follows the same syntax as explained above (see SI). The model intercept indicates if differences in estimated facilitation effects between the two methods δ are significantly different from zero. The model parameters indicate an effect of environmental homogeneity, nurse abundance, beneficiary abundance, nurse habitat preference, beneficiary habitat preference, beneficiary affinity to nurse, and sampling effort on relative differences in facilitation.

2.1.3 | Simulation of and sampling over gradient patterns

In the second approach, we assumed a heterogeneous space simulating community with a different spatial structure of environmental variation (Buckley et al., 2016). Instead of a homogeneous space as in the first simulated community, we generated a bivariate spatial pattern in an inhomogeneous space. We did so, using the codispersion model proposed by Buckley et al. (2016). We used this spatial pattern as it previously showed the best codispersion accuracy (Buckley et al., 2016).

Species abundance decreased along a single gradient direction (the y-axis for convention) for both nurse and beneficiary species. This way, nurse and beneficiary plants covary, showing similar species–environment relationships. Yet, as their covariation is anisotropic, they show no change with codispersion but constant covariation along the gradient. Species association (i.e., significant co-occurrence beyond covariation) can thus be attributed to other factors than the specificity of species–environment relationships. The community is created by simulating a set of abundance values n for nurse n_a and beneficiary n_b species. Plant abundance was generated as $n = 100 + (2 \times \mathrm{c})^{-1} \pm \rho$, where c is the y-axis coordinate values, which ranges from 1 to 500, and ρ is a random noise with mean 5 and SD 1 (Buckley et al., 2016; see SI). This way, abundance values decrease linearly with increasing y-axis coordinates (see also the R code SI). We simulated species co-occurrence patterns as a raster of 250,000 grid points over an area of 500 × 500 spatial units. The simulation pattern was replicated 50 times for each species (see also the R code in SI). Results do not qualitatively change with changing the number of replicates as demonstrated in the sensitivity analysis (see SI, pages 29–32).

Species in each pattern were sampled either randomly or pairwise. Notice that this second approach differs from the first one in that species, rather than plots, were sampled randomly or pairwise (i.e., the same grid point). The reason is that the codispersion pattern fills the whole spatial grid and has abundance values in each grid point (i.e., the nurse and the beneficiary species are present everywhere with different abundance, that is there are no grid points without nurse plants). Each nurse and beneficiary species pattern was sampled from a uniform distribution 500 times.

2.1.4 | Statistical inference

For each pattern, we computed the facilitation effect looking at the dependency of beneficiary species on nurse species by means of Generalized Least Square (GLS) models (Pinheiro & Bates, 2000). Each GLS fits beneficiary abundance data as response variable and nurse abundance data as predictor. Linear spatial correlation along the y-axis was included as error correlation structure. Then, we compared the GLS model parameters (beta and t-value) between the two methods using linear mixed models (Pinheiro & Bates, 2000). Two separate models were run for beta and t-value, including spatial pattern replicate as a random effect. Finally, we calculated the type-II (i.e., false negative) error rate for each method by looking at the amount of misidentified, unsignificant (i.e., t-value lower than 1.96) cases.

Simulations and analyses were done in R environment version 4.0.2 (R Core Team, 2020).

2.2 | Field communities

2.2.1 | Study sites, communities, and species

We aimed to compare the association between nurse and beneficiary species using paired sampling and random sampling methods in different natural conditions of pre-existing environmental heterogeneity and stress. We selected two summer-dry Mediterranean-type systems and an alpine-type system, as dry and cold ecosystems are considered as the most likely to exhibit facilitation effects by nurse plants. The dry site with greater within-community pre-existing environmental heterogeneity due to high physical disturbance was located in the Gran Canaria Island (Spain; Agaete, 28°05′20″ N, 15°42′18″ W). A dry site in Sardinia Island (Italy; Dorgali, 40°18′58″ N, 09°32′09″ E) and a wet alpine site in Japan were our homogeneous sites (43°40′2″ N, 142°55′16″ E).

The Spanish site was located at sea level in a climate with a long summer drought (10 months) due to its very low latitude for a Mediterranean climate. Mean annual temperature is 20°C and annual rainfall is 195 mm. The Italian site was located at 180 m a.s.l. with a shorter summer drought (6 months) due its higher latitude. Mean annual temperature is 16°C and annual rainfall is 480 mm. The Japanese site was located at 2158 m a.s.l. near Mt. Koizumi (43°40′2″ N, 142°55′16″ E). Climate is temperate oceanic alpine with mean annual temperature and rainfall of −6.2°C and 2492 mm, respectively (https://www.ibbr.cnr.it/climate-dt/, 1981–2020 period).

At the Spanish site vegetation is an open shrubland dominated by *Euphorbia balsamifera*, a species abundant in the Macaronesian region (South West of Morocco and Canary Islands; Figure 1). At our site, the plant cover ranges between 30 and 70% depending on local factors. *Euphorbia* was used both as nurse and beneficiary

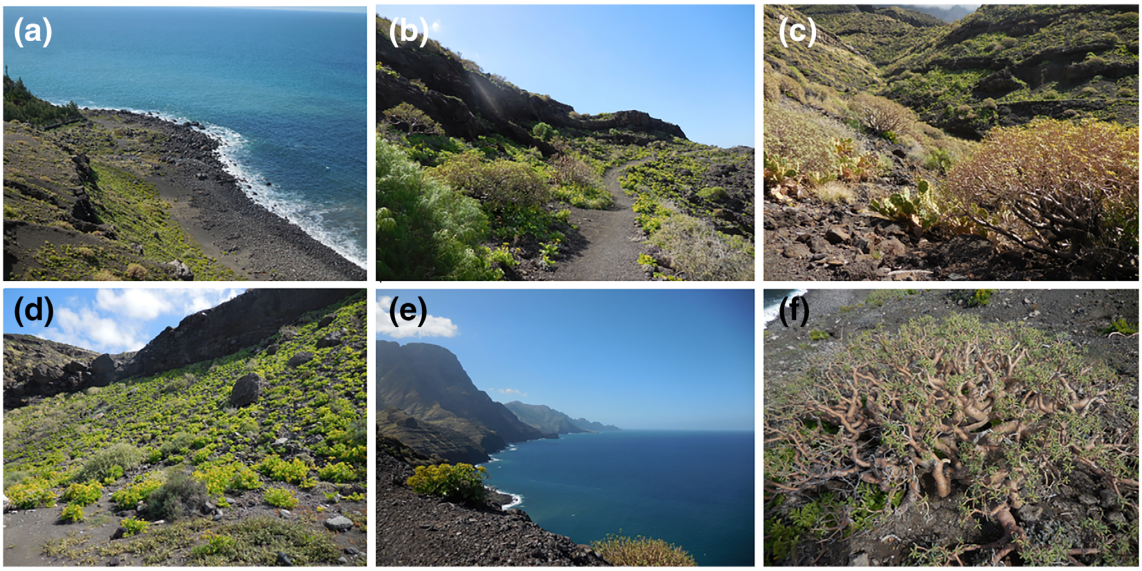


FIGURE 1 The Spanish site (Gran Canaria): (a): the least stressed subsite below the black cliff, (b): the intermediately stressed subsite, (c): the most stressed subsite on the left part of the slide (in Southern exposure, with the intermediately stressed subsite on the right side of the slide in north exposure), (d): abundance of *Astydamia* in the open in the least stressed subsite, (e): general view of the Atlantic coast at the site with *Astydamia* (left) and *Euphorbia* (right) in open conditions, (f): *Astydamia* (in green on the bottom left) below the canopy of *Euphorbia* in the most stressed subsite. Note that in all slides *Astydamia* is very easy to locate thanks to its very light green color. [Color figure can be viewed at wileyonlinelibrary.com]

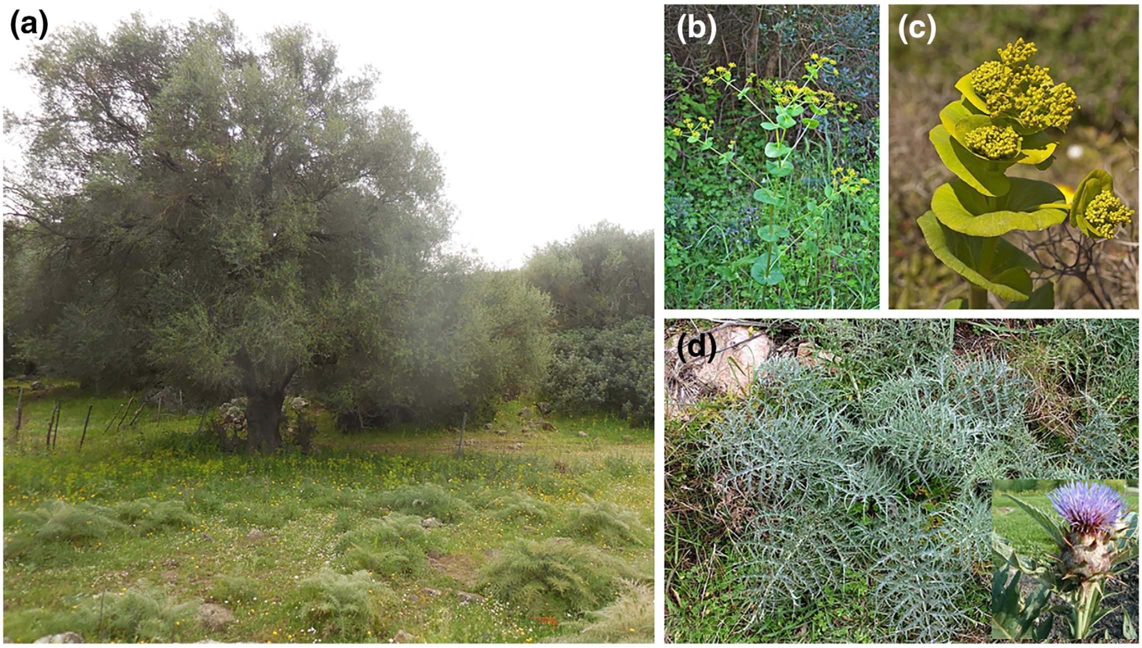


FIGURE 2 The Italian site (Sardinia): (a): the Northern position of the canopy of *Olea* with below in green *Smyrnium* and in the open (in the front) *Cynara*, (b) and (c): *Smyrnium*, (d): *Cynara*. [Color figure can be viewed at wileyonlinelibrary.com]

species, and the other beneficiary species was the forb *Astydamia latifolia*, a perennial species from the Apiaceae family. In general, in the three systems, nurse species were chosen because of their dominance and target species because of obvious patterns of association with nurses. At the Spanish site, *Astydamia* cover varied between 5% and 75% depending on local factors modifying stress levels, such as distance to the ocean and exposure.

At the Italian site, the vegetation is an old *Olea europaea* orchard plantation that was abandoned and now transformed into a savannah community used for grazing by sheep (Figure 2). Vegetation cover is approximately 50% for the trees, which are regularly spaced due to management. The associated herbaceous community cover is between 20% and 90% depending on microhabitats. It is dominated by grasses and two forb species that were selected as beneficiaries, *Smyrnium rotundifolium* and *Cynara cardunculus*, while the nurse species was *Olea europaea*.

The Japanese site was located on a mild slope (5°) near the summit of Mt. Koizumi. The vegetation was patchy, its cover reaching 75%, and was dominated by cushions of *Diapensia lapponica* and lichens. Other prominent species were *Arcterica nana, Carex stenantha var. taisetsunensis, Empetrum nigrum, Loiseleuria procumbens*, and *Salix nummularia*. Mean diameter of the cushions of the nurse species *Diapensia* was 35.5 ± 20.3 cm ($n = 70$). *Diapensia lapponica* was the nurse and the beneficiaries were species richness and *Salix nummularia*.

2.2.2 | Experimental design

In each site we sampled with the two methods—paired and random sampling. At the Spanish site, we sampled three very similar communities but having contrasting levels of stress, whereas at both the Italian and Japanese sites we sampled only one community. At the Spanish site, we selected three subsites along a complex gradient of increasing stress due to distance to the ocean and exposure. The least stressed subsite had a North-West exposure and was quite close to the ocean (less than 100 m). Thus, the lower drought stress was very likely due to the amelioration of drought by water spray, as found by Forey et al. (2008) in the French coastal dunes (Figure 1a). Close to the ocean the cover of *Astydamia* was highest (approximately 75%), with lots of individuals occurring in the open between *Euphorbia*, the latter having the lowest cover (approximately 30%) at this subsite. The intermediately stressed subsite had the same exposure but was farther from the ocean (several hundred meters). The cover of *Astydamia* and *Euphorbia* were both high (approximately 50% for each species), with no obvious spatial patterns of association or repulsion. The most stressed subsite was located at a similar distance from the ocean, but had a South West exposure. The cover of *Astydamia* and *Euphorbia* were the lowest (5%) and highest (70%), respectively, at this site, and most *Astydamia* were only observed below the canopy of the nurse. Physical disturbance was high in all three subsites, with deep ravines alternating with vegetated patches, due to the occurrence of the three subsites in slopes on volcanic scoria.

At the Italian site, pre-existing environmental heterogeneity was very low, since the site was in a dry floodplain on calcareous rock. Topography was flat and soils deep with a fine texture. We chose to assess the association of two understory (beneficiary) species with *Olea* at three canopy positions because there were obvious differences in abundance and cover of the dominant forb *Smyrnium*, between the three *Olea* canopy positions, likely due to higher stress with increasing irradiance. The other beneficiary species, *Cynara*, did not show obvious differences in abundance related to *Olea* canopy position but mostly occurred in the open where its cover can be high (approximately 70%). In contrast, *Smyrnium* was more abundant below trees, and in particular on the Northern side of the canopy (approximately 70% cover vs. 5% on the Southern side).

At the Japanese site, sampling was performed on alpine scree soils of a volcanic origin in a mature alpine community with a homogeneous matrix of cushions. Thus, the pre-existing environmental heterogeneity was apparently low, with regular action of snow on a nearly flat terrain (Figure 3).

2.2.3 | Vegetation sampling

In the Spanish site, at the three stress levels, and in the Italian site at the three canopy positions, we sampled the performances of beneficiary species with and without neighbors, using both sampling methods. At each of the three subsites in the Spanish site, for the paired sampling method we randomly selected 30 *Euphorbia* patches (as nurse plots) with a size above 1 m^2 and positioned a quadrat of 250 cm^2 on the Northern side of the canopy at mid-distance between the trunk and the edge of the canopy. Another quadrat of the same size was randomly positioned in open conditions in vicinity (1 m) to the *Euphorbia* patch and in similar environmental conditions (same microtopography and soil). In the 60 quadrats of each subsite, we visually estimated the cover of the two beneficiary species, *Astydamia* and *Euphorbia* seedlings. For the random sampling method, we randomly chose the position of 60 plots and sampled with the same quadrat the cover of the two beneficiary species. The position of each quadrat was determined by throwing the quadrat to the back and walking 10 m along transects between two quadrats to fully explore the whole community (but see Dudley, 1982 for a straightforward random approach). Thus, the number of plots per microhabitat condition at each subsite was dependent on the cover of each microhabitat. It varied between 14 for open conditions to 46 in adult *Euphorbia* patches of the most stressed site.

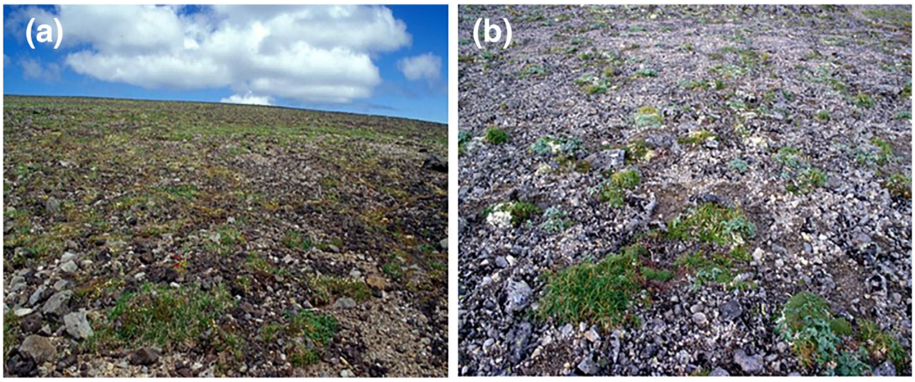


FIGURE 3 The Japanese site (Hokkaido): (a): the sampling site with low apparent pre-existing heterogeneity; (b): a typical cushion of *Diapensia lapponica*. [Color figure can be viewed at wileyonlinelibrary.com]

At the Italian site, for the paired sampling method we randomly selected 30 *Olea* individuals (as nurse plots) that were spaced at least 30 m apart from each other. The height and diameter of the canopy of selected trees varied between 3 and 8 m and 4 and 10 m, respectively. For each of the 30 tree individuals and at each position of the tree canopy (North, South, and West) we positioned a quadrat of 1 m^2 at mid-position between the trunk and the edge of the canopy. Then, we positioned the paired quadrats for the open positions at 5 m from the edge of the canopy for each individual. In each quadrat, we recorded the number of individuals of the two beneficiary species. For the random sampling method, because the cover of the tree population was approximately 50% and because the size of the trees prevented random throwing of a quadrat, we chose to separately sample tree and open plots. Tree plots and their positions were selected by the same technique as used for the paired sampling approach. For open plots, we first randomly selected 30 open areas between trees with the same technique as the one used to select tree individuals. Then, we randomly threw the quadrat three times in the 30 selected open areas for positioning the three open plots that were systematically affected by treatments (North, West, and South). Thus, for the Italian site, the number of replicates was the same in all treatments, although plots were different for the two samplings.

At the Japanese site, for the paired sampling method we haphazardly chose 70 cushions of *D. lapponica* (as nurse plots), and all plants growing within these selected cushions were identified to the species level and their abundance recorded. We measured the maximum and minimum axes of each cushion to estimate its area. To obtain comparable samples for assessing species richness in surrounding "open" areas (areas not covered by cushions), areas matching the size of each sampled cushion were surveyed at haphazardly selected paired points away from each sampled cushion. Random sampling was performed with a small wire square (10 cm on a side), which was randomly placed 100 times within the sampling area; then all established plants within the square were identified and recorded. Thus, the plot size was smaller with the random method design than with the paired-sampling one.

2.2.4 | Statistical analyses

For the Spanish site, the effects of the stress level, method (paired vs. random), neighbor (*Euphorbia* vs. open), beneficiary (*Euphorbia* vs. *Astydamia*), and all their interactions on cover of the target species was tested using a linear mixed effects model. As random terms, we included the replicate for which the two beneficiary species were quantified, and the interactions of replicate with the stress level, stress level and method, and stress level and method and neighbor to account for pseudoreplication.

For the Italian site, the effects of method (paired vs. random), neighbor (*Olea* vs. open), canopy position (three cardinal directions), beneficiary (*Cynara* vs. *Smyrnium*), and all their interactions on abundance of the beneficiary species were tested using a linear mixed effects model. As random terms, we included the replicate for which the two beneficiary species were quantified, and the interactions of replicate with method, neighbor and method, canopy position, and neighbor and method.

For the Japanese site, the effect of method (paired vs. random), neighbor (*Diapensia* vs. open) and their interaction on species richness was tested using a linear model with square-root-transformed richness data to meet model assumptions. The effect of method, neighbor and their interaction on the frequency of occurrence of the beneficiary species *Salix nummularia* was tested using a generalized linear model with presence/absence of Salix as the response variable and the corresponding binomial distribution of error terms.

The linear mixed effects model analyses were conducted with asreml for R environment version 4.1 (Butler, 2020) and the convenience functions for fitting negative variance components and for type-I analysis of

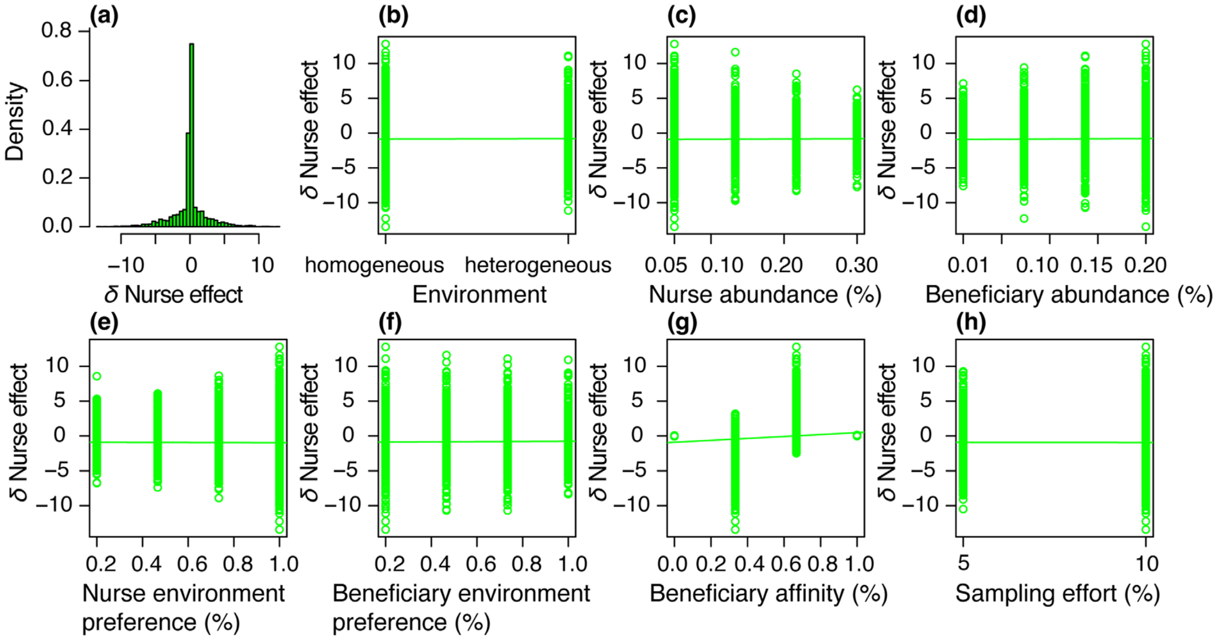


FIGURE 4 (a) Distribution of relative differences δ in facilitation effects between pairwise and random sampling. (b–h) Impact of abiotic and biotic factors on δ. Lines represent the linear regression model. [Color figure can be viewed at wileyonlinelibrary.com]

variance provided by Pascal (Niklaus, 2019). Sequential (type-I) testing of factors was justified with our hierarchical experimental designs where the two different methods were assessed with/without neighbor species and different beneficiary species growing with/without neighbor. Therefore, the general sequential order of factors following the pattern "method > neighbor > beneficiary" was followed during testing. Linear models and generalized linear models and the corresponding type-I analyses of variance were conducted with the base functions in R version 4.0.4 (R Core Team, 2020).

3 | RESULTS

3.1 | Modeling results

The results of our first-approach simulation indicate no significant differences between random and pairwise methods in estimating facilitation effects (absence of correlation as $t = -1.59$, $p = 0.113$). Looking at the effects of abiotic and biotic factors and sampling method on facilitation effect (Table S1), we found that the variance in standardized parameters (z-score) was: (i) marginally explained by nurse habitat preference h_α ($p = 0.061$); (ii) significantly explained by beneficiary habitat preference h_β ($p = 0.046$); (iii) significantly explained by beneficiary affinity to nurse $\alpha \rightarrow \beta$ alone and depending on sampling method ($p < 0.001$ and $p = 0.020$, respectively). When considering parameter estimates (Table S2), beneficiary affinity to nurse $\alpha \rightarrow \beta$ significantly increases facilitation effects quantification, both per se (estimate $= 8.02 \pm 0.42$ SE, $p < 0.001$), as reasonably expected, as well as with higher impact using the pairwise method (estimate $= 1.38 \pm 0.59$ SE, $p = 0.020$).

The estimated differences δ in facilitation effects between pairwise and random sampling were negative (mean $= -0.06$; median $= 0.03$; intercept $= -0.90$, 95% CI $= -1.26$ to -0.54, Figure 4a), indicating that facilitation effects were overall lower in pairwise sampling than in random sampling models. Among the abiotic and biotic factors, we tested, only beneficiary affinity to nurse significantly explained δ ($F_{1,4088} = 207$, $p < 0.001$). In particular, the higher the beneficiary affinity to the nurse the larger the differences in facilitation effects between the two methods (estimate $= 1.38 \pm 0.10$ SE, $p < 0.001$, Figure 4g).

The second-approach simulation, that of species codispersion over a decreasing abundance gradient, yielded qualitatively similar results. Results indicate that both sampling methods are valid for identifying facilitation. Yet, the two methods differ quantitatively as the pairwise method produced significantly higher betas (11.3%, $p = 0.021$) that were closer to one and higher t-values (65.1%, $p < 0.001$) than random ones (Figure 5). Furthermore, the variance of dependency parameter estimates was much higher for the random sampling (estimate SD = 0.30, t-value SD = 108.4) than for the pairwise sampling (estimate SD = <0.01, t-value SD = 12.6). Finally, while random sampling sometimes failed at correctly

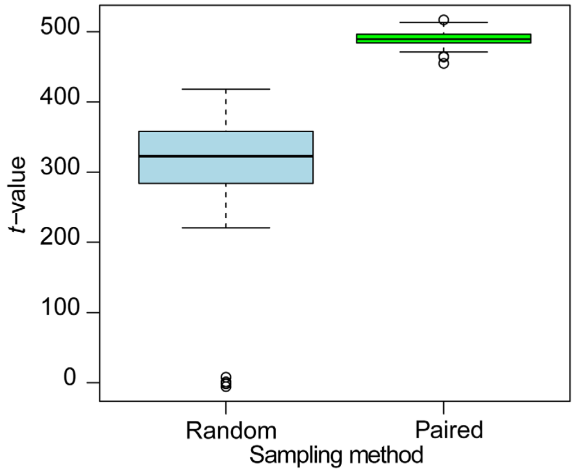


FIGURE 5 Summary data (boxplot) of model parameters (*t*-value) assessing facilitation effects in a spatial grid (abundance gradient codispersion). Plant species were sampled either randomly (blue) or paired (green). Lines represent Median, Q1, and Q3 as well as outlier range. [Color figure can be viewed at wileyonlinelibrary.com]

detecting facilitation (four false negative cases, type-II error rate of 8%), the pairwise method was correct overall 50 simulations. In summary, the two methods are qualitatively similar, but the pairwise method is more precise and accurate.

3.2 | Field results

At the Spanish site, there were highly significant beneficiary and stress level effects due to the lower cover of *Euphorbia* than of *Astydamia* and an overall decreasing cover with increasing stress, respectively (Figure 6, Table S3). However, there was a significant stress by neighbor by beneficiary interaction because the decreasing cover with increasing stress was stronger for *Astydamia* in the open than below *Euphorbia* nurses, while there was a tendency for *Euphorbia* seedlings to increase in cover in the open but not below the nurse shrub. There were no significant effects of the method either as a single factor or in interaction with other factors (Figure 6, Table S3).

At the Italian site, there were highly significant canopy position, neighbor, and beneficiary effects, due to lower cover at the sunniest (South) canopy position, in the open and for *Cynara* than at the other two canopy positions, below the tree canopy and for *Smyrnium* (Figure 7, Table S4). However, there was a highly significant canopy position by neighbor by beneficiary interaction because the lower abundance at the South position was observed for *Smyrnium* below the tree canopy while its abundance in the open was always very low and there were no differences among canopy positions for *Cynara* both under the tree canopy and in the open (Figure 7, Table S4). There was also a significant method by beneficiary interaction because the abundance of *Smyrnium* was slightly higher with the paired than random method and the reverse was observed for *Cynara*. Finally, there was a weakly significant canopy position by method by neighbor interaction (Figure 7, Table S4).

At the Japanese site, the performance of the two sampling techniques was very similar at the community level, with both methods showing more species associated with *Diapensia* cushions than colonizing open areas (Figure 8). Additionally, there was no significant method × neighbor interaction and, thus, no difference in facilitation measured by the two methods (Table S5). For an abundant beneficiary species (*Salix nummularia*), frequency of occurrence was higher within *Diapensia* cushions than in the open with both methods (highly significant neighbor effect, Table S5). Additionally, frequency of occurrence was higher with the paired than random method (significant method effect, Table S5), due to the larger plot size used in the former than the latter.

4 | DISCUSSION

Our simulation results and field surveys indicate that the two methods of sampling pairwise or randomly provide similar outcomes. Notably, the methods were robust against local environmental heterogeneity. Yet, our simulation results showed that facilitation effects were higher in random as compared to paired sampling on average, with differences increasing with increasing beneficiary affinity for the nurse. Nevertheless, all other community parameters had no effect on differences between the methods in the observed nonrandom spatial associations. Additionally, spatial associations measured in the three systems were strongly influenced by species stress_tolerances and relative environmental stress. However, neither species nor stress effects led to differences in spatial associations measured with the two methods. Overall, these results show that the paired sampling method is as accurate as the random sampling method and, thus, can be used for assessing long-term facilitation in a wide range of environmental and community conditions, a task that cannot be accomplished with the removal method.

4.1 | The validity of the paired sampling method

The results of our simulated plant community indicate that the two sampling methods produce statistically indistinguishable estimates of facilitation effects. Yet,

FIGURE 6 Means (± SE) of percent cover of *Astydamia* (a–c) and *Euphorbia* (d–f) beneficiaries with *Euphorbia* nurses and in open plots measured with the random ($n = 14–46$) and paired ($n = 30$) sampling methods, at three levels of stress (low: [a] and [d], intermediate: [b] and [e], and high: [c] and [f]) at the Spanish site. See Table S1 for the complete statistical analyses.

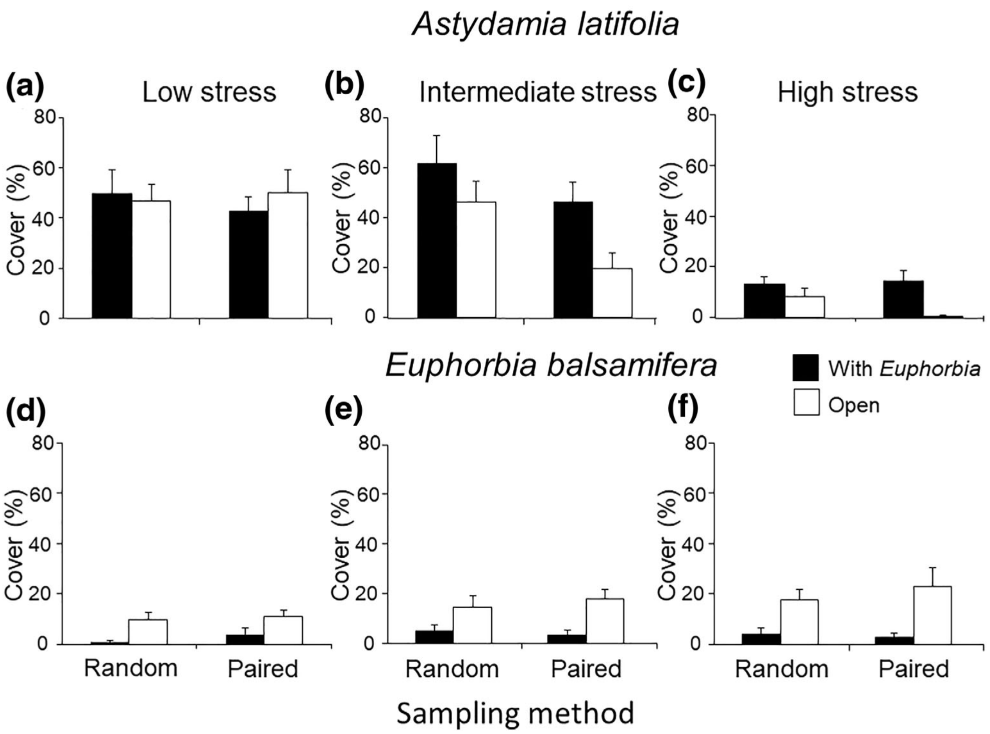
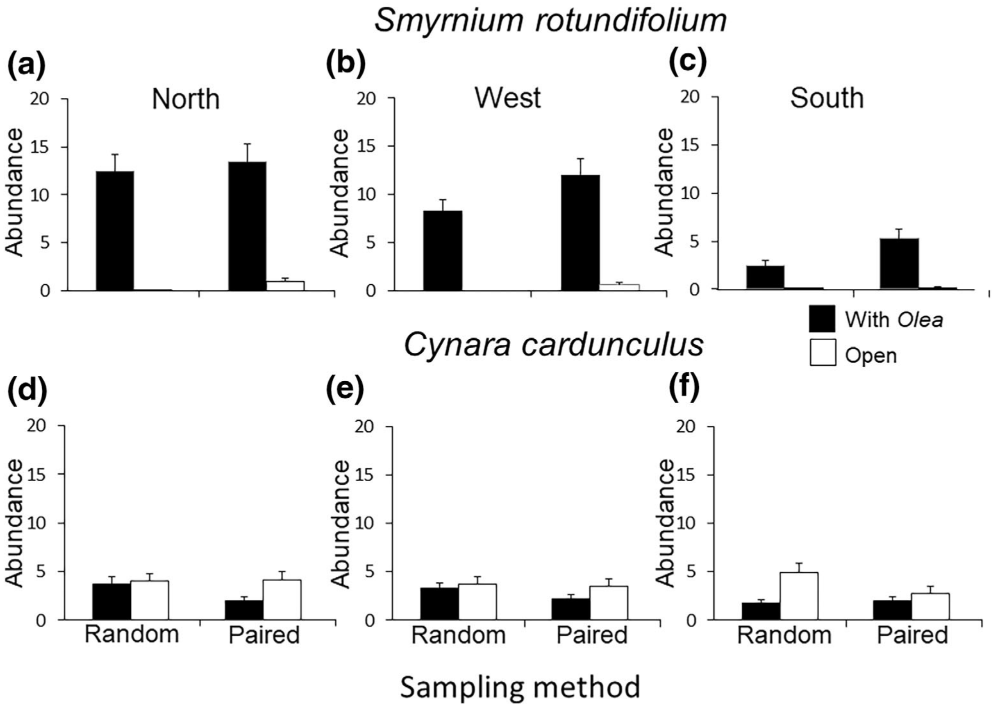


FIGURE 7 Mean (± SE, $n = 30$) abundance of *Smyrnium* (a–c) and *Cynara* (d–f) targets below *Olea* canopy and in the open measured with the random and paired sampling methods, at three canopy positions (North: [a] and [d], West: [b] and [e], and South: [c] and [f]) at the Italian site. See Table S2 for the complete statistical analyses.



when considering facilitation effects as response (i.e., model parameter b_1), we found that only beneficiary affinity for the nurse influenced estimates of nurse effects. Instead, habitat availability, species abundance, or species preferences had no significant effects. Interestingly, beneficiary affinity for the nurse mediates the effects of sampling methods. When considering differences in facilitation effects δ between the two methods, our model showed that random sampling provides higher estimates of facilitation effects as compared to paired sampling on average. Thus, within an overall picture of minimal but significant influence of sampling method on estimating facilitation, the paired sampling does a better job in excluding the effects of local

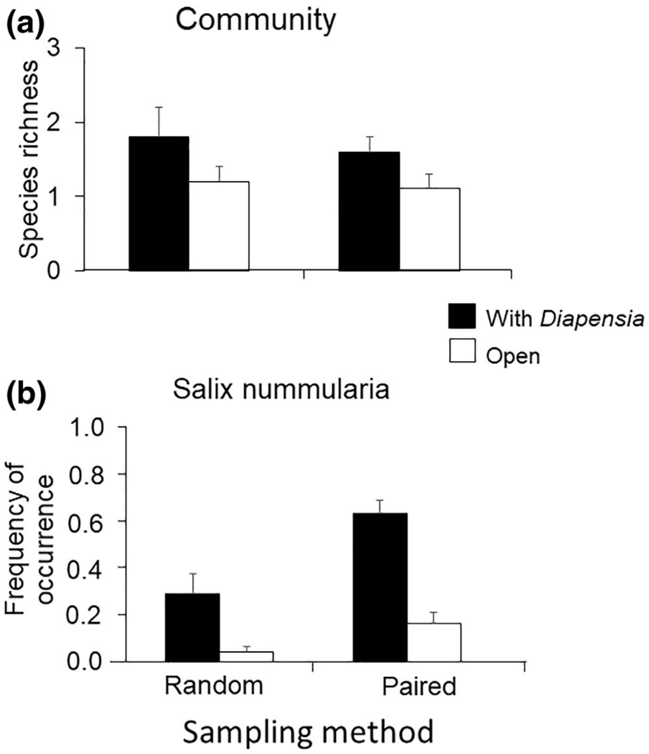


FIGURE 8 Mean (± SE, $n = 70$) species richness of the community (a) and frequency of occurrence of *Salix* (b) within the cushion canopy and in the open measured with the random and paired sampling methods at the Japanese site. See Table S3 for the complete statistical analyses.

conditions and ultimately estimating the dependency of beneficiary plants on nurse species.

Some discrepancies arise between ours and previous simulations (Steinbauer et al., 2016). A possible reason is that what was previously defined as environmental heterogeneity was actually habitat sharing. In that case, all plants respond to environmental conditions the same way as they all show the same preferences for a "better," less stressful environment. However, this assumption is not very realistic since plants respond in different ways to environmental conditions (Liancourt, Callaway, et al., 2005). In our model, we included a species-specific response to environmental conditions with contrasting preferences between plants for the environment. This way, we could separate the environmental heterogeneity component from the habitat-sharing component. Another likely explanation resides in the differences between modeling parameters. While the entire landscape is covered by plants and each cell has on average more than two plants in previous models (Steinbauer et al., 2016), we considered a more realistic stressful environment where plant cover does not exceed 50% of the landscape. Previous models also use many species, their simulation is based on individuals, and they consider species richness as the response variable (though without a Poisson or Negative Binomial distribution). On the other hand, our model considers only one beneficiary species, and species occurrence is used as the response variable (with a binomial distribution).

At the Japanese site, we did not find any difference in spatial associations measured with the two methods. However, at this site within-community environmental preexistent heterogeneity was low and we might expect no or little differences between methods. In contrast, at the Spanish field site, within-community environmental heterogeneity is very high and it would be here where results of the paired sampling method were most likely to be affected by habitat-sharing effects (Steinbauer et al., 2016). However, results showed no effects of the method. This shows that in sites with high microenvironmental heterogeneity, so long as the open and with-neighbor plots are sampled conservatively (i.e., not increasing the probability of occurrence of positive associations by sampling open plots in obviously more stressful microhabitats than with-neighbor plots) there is no impact of the method on the assessment of spatial association.

Finally, the Italian site contained low within-community environmental heterogeneity due to the flat topography. There, we found a weak but significant neighbor by canopy position by method interaction. However, since the effect was only weakly significant and occurred at the site with the lowest within-community environmental heterogeneity, processes other than habitat-sharing effects are likely to drive this effect. Finally, the significant beneficiary by method interaction could reveal habitat-sharing effects since the neighbor treatment was not involved in this interaction.

4.2 | Species preferences and stress level influences

The only parameter that influenced effects of methods on spatial associations in our modeling study was beneficiary affinity for the nurse. We also found strong differences in spatial associations with the dominants depending on the target species in both the Spanish and Italian systems. Additionally, we found strong variation in spatial associations with increasing stress in the Spanish system for *Astydamia*, the least stress-tolerant beneficiary species at this very dry site.

Plant communities include species from contrasting functional strategies with different responses to the abiotic environment and the effects of neighbors (Michalet, Chen, et al., 2015). At the Spanish site, *Euphorbia* increased in dominance with increasing stress, but the converse was observed for *Astydamia*, which is consistent with the former being present in drier conditions than the latter. In agreement with the functional tradeoffs described in several studies between physical stress- and shade-tolerance (Liancourt, Callaway, et al., 2005; Nemer et al., 2021), *Euphorbia* was outcompeted at the three stress levels, whereas *Astydamia* was increasingly facilitated with increasing stress. At the Italian site, *Smyrnium* was strongly facilitated by *Olea*, whereas *Cynara* was more abundant in the open than below the trees, thus, highlighting that the former was less tolerant to high irradiance and the latter more negatively affected by shade. The former—less stress-tolerant—species showed higher variation in the effect of neighbors with canopy position than the shade-avoiding species, with higher facilitation found in the North position where light interception was the highest.

In conclusion, our results showed that the paired sampling method is robust enough for assessing spatial associations in a wide range of environmental and community conditions. Combining the paired sampling with other approaches may help to tease out confounding, habitat-sharing effects and identify the mechanisms underlying biotic interactions. This is important given the need to use the paired sampling approach in association with the removal method to enable disentangling of short- from long-term effects of neighbors (Chaieb et al., 2021; Michalet, 2006; Michalet, Brooker, et al., 2015; Schöb et al., 2012).

AUTHOR CONTRIBUTIONS

Richard Michalet and Christian Schöb conceived the idea and wrote the first draft of the manuscript. Gianalberto Losapio made the modeling study and contributed to editing the manuscript draft, Richard Michalet made the field studies in Spain and Italy, and Zaal Kikvidze in Japan. Christian Schöb made the statistical analyses. Rob W. Brooker, Bradley J. Butterfield, Ragan M. Callaway, Lohengrin A. Cavieres, Christopher J. Lortie, and Francisco I. Pugnaire contributed critically to the writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code will be archived in Dryad.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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