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METHODOLOGICAL ARTICLE

A simulation study comparing common methods for analyzing species–habitat associations of plants

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Abstract

Question: Species-specific habitat associations are one of several processes that lead to a clustered spatial pattern of plant populations. This pattern occurs in tropical and temperate forests. To analyze species–habitat associations, four methods are commonly used when determining species–habitat associations from spatial point pattern and environmental raster data. Two of the methods randomize the spatial point pattern of plants, and two randomize the raster data of habitat patches. However, the strengths and weaknesses of the four methods have never been analyzed in detail.

Methods: We conducted a simulation study to analyze the strengths and weaknesses of the four most used methods. The methods are the gamma test, pattern reconstruction, the torus-translation test and the randomized-habitats procedure. We simulated neutral landscapes representing habitat patches and point patterns representing fine-scale plant distributions. We built into our simulations known positive and negative species–habitat associations.

Results: All four methods were equally good at detecting species–habitat associations. Detected positive associations better than negative ones. Furthermore, correct detections were mostly influenced by the initial spatial distribution of the point patterns, landscape fragmentation and the number of simulated null model randomizations.

Conclusions: The four methods have advantages and disadvantages, and which is the most suitable method largely depends on the characteristics of the available data. However, our simulation study shows that the results are consistent between methods.

KEYWORDS
gamma test, neutral landscapes, pattern reconstruction, randomized-habitats procedure, simulation study, spatial point pattern analysis, torus-translation test

1 | INTRODUCTION

Worldwide, individuals in tree and shrub populations tend to be spatially clustered. This is true in tropical forests (Condit et al., 2000; Jara-Guerrero et al., 2015), temperate forests (Getzin et al., 2006; Rubio-Camacho et al., 2023), boreal forests (Gray & He, 2009; Das Gupta & Pinno, 2018), secondary forests (Jia et al., 2016), savanna shrublands (Hesselbarth et al., 2018) or natural grasslands

(Alvarez et al., 2011; Browning et al., 2014). This clustering is caused by biotic processes, abiotic processes, or a combination of both (Cottenie, 2005; Legendre et al., 2009). For example, spatially limited seed dispersal is a biotic process that leads to clustered patterns of trees (Condit et al., 2000). By contrast, the specialization of species to specific environmental conditions (Tilman & Pacala, 1993) is an abiotic process that leads to clustered patterns of trees in suitable habitats through species–habitat associations (Harms et al., 2001; Comita et al., 2007). The study of small-scale species–habitat associations, using methods such as spatial point pattern analysis, provides insights into the importance of environmental heterogeneity in shaping the spatial pattern of tree and shrub populations (Garzon-Lopez et al., 2014). Point pattern analysis is a powerful tool for studying small-scale species–habitat associations because the pattern contains information about the processes that shaped it (Law et al., 2009; Brown et al., 2016). It is possible to infer the processes by modeling the discrete locations of all individuals within a study area (Wiegand & Moloney, 2004; Law et al., 2009).

Most studies analyzing small-scale species–habitat associations use either the gamma test (Plotkin et al., 2000) or the torus-translation test (Harms et al., 2001). Both methods have in common that they require data on the location of all individuals in the study area (the point pattern) and additionally on small-scale environmental conditions, such as topography or soil conditions, classified into discrete habitat patches as raster cells. The classification of habitats into discrete habitat patches is a great simplification because environmental conditions are usually continuous (Cushman et al., 2010). Nevertheless, using discrete habitat patches has computational advantages and allows the easy communication of results. To test the null hypothesis that there are no species–habitat associations, or in other words, that the point pattern is independent of the spatial arrangement of the habitat patches, possible spatial dependencies between the species and habitats must be broken. Whereas the gamma test randomizes the point pattern, the torus-translation test randomizes the habitat patches to simulate null model randomizations. In addition, there are two closely related approaches for detecting species–habitat associations. These are pattern reconstruction (randomizes the point pattern; Tscheschel & Stoyan, 2006; Wiegand & Moloney, 2014) and the randomized-habitats procedure (randomizes the habitat patches; Harms et al., 2001). Both methods differ in the details of the randomization algorithms compared with the gamma test and torus-translation test. It is ultimately possible to understand all four methods as being complementary to each other (Harms et al., 2001).

Although the torus-translation test (Guo et al., 2016; Du et al., 2017; Furniss et al., 2017) is more commonly used than the gamma test (Garzon-Lopez et al., 2014; Yang et al., 2016), this preference is not based on published knowledge on the strengths and weaknesses of the methods. We found only a single study analyzing expected false-positive detections for the torus-translation test (Comita et al., 2007) and very few studies comparing several methods (but see Harms et al., 2001; Garzon-Lopez et al., 2014). In addition to species characteristics and local environmental conditions,

differences between the methods may be another reason why results differ between studies for similar forest types. For example, for tropical forest, the percentage of species with habitat associations differs greatly; e.g., 30% (Plotkin et al., 2000), 64% (Harms et al., 2001), 70% (Lan et al., 2012) or 80% (Yamada et al., 2006) of the analyzed species. Thus, to be able to infer general conclusions about forest dynamics from individual case studies, we need to understand how the applied method influences the study results. We therefore conducted a simulation study to analyze the power of the different methods to identify differences.

Using simulated data with known characteristics, we compared the ability of the gamma test, pattern reconstruction, the torus-translation test and the randomized-habitats procedure to detect species–habitat associations. As well as comparing the ability of the four methods to detect species–habitat associations for different association strengths, we also explored three potential confounding factors. These factors were: (a) spatial characteristics of the point patterns, (b) the number of simulated null model randomizations, and lastly (c) landscape fragmentation.

2 | METHODS

The two dominant methods for analyzing species–habitat associations, the gamma test (Plotkin et al., 2000) and the torus-translation test (Harms et al., 2001), use randomized null model data to break possible dependencies between the individuals and the habitat patches to show species–habitat associations (Figure 1b, d). However, because individuals and habitat patches are unlikely to be independent themselves, the spatial structures of the point pattern and the habitat patches must be preserved during randomization (Plotkin et al., 2000; Wiegand & Moloney, 2014). For example, dependencies between individuals can be caused by limited seed dispersal and hence spatial clustering of plants (Lutz et al., 2014; Nguyen et al., 2016), or competition between plants leading to regular spatial patterns (Pielou, 1962; Kenkel, 1988). In addition, it is probable because of Tobler's first law of geography (Tobler, 1970) that spatial autocorrelation between the habitat patches is present, i.e., neighboring patches are more similar than distant ones. Thus, when analyzing species–habitat associations, preserving the existing spatial structure of both the point pattern and the habitat patches controls for the biotic and other abiotic processes that shape spatial structure (Plotkin et al., 2000; Harms et al., 2001).

Species–habitat associations are tested by comparing, for each habitat type, the number of individuals of the observed data with the number of individuals of randomized null model data (Plotkin et al., 2000; Harms et al., 2001). Most previous published studies test only whether species–habitat associations are present, but not the strength of the associations (but see Comita et al., 2007). Thus, we also focused only on detecting associations, but not their strength. Species–habitat associations are detected with an approximated significance of $p \approx 0.05$ for a two-tailed test if the observed stem density is above the 97.5th percentile or below the 2.5th
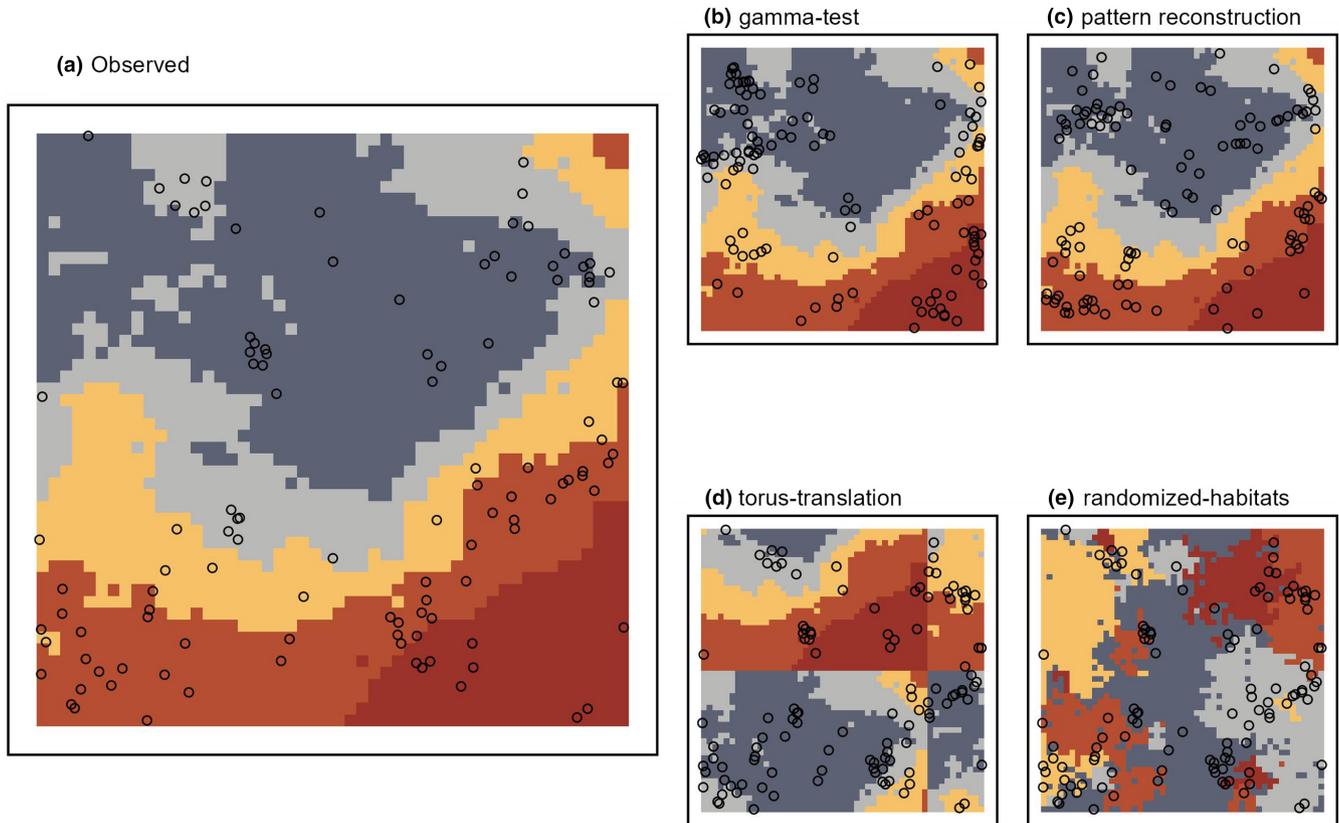
(a) Observed

(b) gamma-test

(c) pattern reconstruction

(d) torus-translation

(e) randomized-habitats

FIGURE 1 (a) Observed point pattern and discrete habitat patches and illustration of all randomization methods. (b–e) Whereas the (b) gamma test and (c) pattern reconstruction randomize the point pattern, the (d) torus-translation test and (e) randomized-habitats procedure randomize the habitat patches.

percentile of *n* iterations of the simulated null model randomizations for positive or negative associations (Harms et al., 2001). Thus, the simulation of null model randomizations is methodologically loosely related to envelope tests that are commonly applied in spatial point pattern analysis for hypotheses testing (Baddeley et al., 2014).

2.1 | The gamma test

The gamma test (Plotkin et al., 2000) randomizes the point pattern (Figure 1b). First, a suitable point process model is fitted to the observed data. Point process models simulate stochastic point patterns using mathematical descriptions of the pattern properties (Diggle, 2014; Wiegand & Moloney, 2014). For example, the Thomas point process model (Thomas, 1949) is a model commonly fitted to clustered patterns. Second, point patterns are simulated using the fitted point process model. Lastly, the simulated point patterns are superimposed on the observed habitat patches and the number of individuals within each habitat type is compared between the observed data and the null model randomizations (Plotkin et al., 2000). Thus, the gamma test is methodologically similar to a regular χ^2 test, except that the expected value is generated by a point process model (Plotkin et al., 2000; Agresti, 2007). The gamma test, however, should only be applied if the observed point pattern can be

described by a suitable point process model (Wiegand et al., 2007, 2009). For the simulation study, we used a homogenous Poisson process or a Thomas cluster process (using the minimum contrast method, Appendix S1) to simulate the null model randomizations depending on the spatial characteristics of the initial pattern.

2.2 | Pattern reconstruction

Pattern reconstruction (Tscheschel & Stoyan, 2006) randomizes the point pattern using an optimization algorithm comparable to simulated annealing (Figure 1c; Kirkpatrick et al., 1983). This has the advantage that the method does not depend on specific point process models and can be closely fitted to any point pattern (Appendix S2). First, pattern reconstruction starts with a completely random pattern with the same number of individuals as the observed point pattern. Second, the spatial characteristics of the observed pattern (denoted as φ) and reconstructed pattern (denoted as ψ) are described by one or several summary functions, namely $f_i(r, \varphi)$ and $f_i(r, \psi)$. We used the most powerful combination of two summary functions (Wiegand et al., 2013), namely the pair-correlation function $g(r)$ (Stoyan & Stoyan, 1994) and the nearest-neighbor-distribution function $G(r)$ (Illian et al., 2008; Diggle, 2014) without edge correction. Third, the difference between the patterns is described by the

energy $E^{\varphi}_{total}(\psi_t) = \frac{1}{n_i}\sqrt{\sum_{r=1}^{n_i}\left[f_i^{\varphi}(r) - f_i^{\psi_t}(r)\right]^2}$. Fourth, an individual of the reconstructed pattern ψ is relocated and the new location is kept only if $E^{\varphi}_{total}(\psi_t)$ decreases. To avoid optimizing towards a local minimum, the new location is kept with a small probability (the so-called annealing parameter) even if $E^{\varphi}_{total}(\psi_t)$ increases. The procedure is reiterated until a stopping criterion is met, i.e., a pre-set threshold of $E^{\varphi}_{total}(\psi_t)$, a maximum number of iterations t_{max} (Tscheschel & Stoyan, 2006), or a number of iterations without a reduction of energy $t_{nochange}$. Lastly, the reconstructed point pattern is superimposed on the observed habitat patches and for each habitat the number of individuals is compared between the observed data and the null model randomizations. For the simulation study, we used an annealing parameter of $a = 0.01$. The stopping criteria were an energy $E^{\varphi}_{total}(\psi_t) < 0.01$, reaching $t_{max} = 10,000$ iterations, or no reduction in energy in $t_{nochange} = 5,000$ iterations. Following Ripley's rule of thumb (Baddeley et al., 2015), we calculated $g(r)$ up to a distance of $r = 250$ m to reconstruct the null model randomizations.

2.3 | Torus-translation test

The torus-translation test (Harms et al., 2001) randomizes the habitat patches (Figure 1d). This is done by shifting the patches about a two-dimensional torus in all four cardinal directions. Whenever patches reach the border of the study plot, they are shifted to the opposite side of the plot. It is also possible to simulate further null model randomizations by rotating and mirroring the shifted habitat patches. However, this test is only possible for rectangular study plots (Harms et al., 2001) and only if no strong gradients are present in the environmental data. Finally, the observed point pattern is superimposed on the simulated habitat patches and the number of individuals for each habitat type is compared between the observed data and the null model randomizations (Harms et al., 2001). For the simulation study, we shifted the habitats in all cardinal directions using 20-m steps (the resolution of the raster data). To create the null model randomization, this was repeated until the original simulation landscape was obtained again (or in other words, until the habitat classes had passed once around the torus).

2.4 | Randomized-habitats procedure

Harms et al. (2001) also proposed a "randomized-habitats procedure" that randomizes the habitat patches and works for irregularly shaped study plots (non-rectangular; Figure 1e). At the beginning, all cells of the null model data are "empty" and a random cell is assigned to the rarest habitat type. Random, but neighboring cells are subsequently assigned to the same habitat. This is repeated until the same number of cells as in the observed data are assigned to the habitat. The assignment is repeated with the second, third, etc. to the rarest habitat. To prevent the occurrence of excessively large patches of cells for one habitat, we slightly modified the procedure. If $cells_{patch}/cells_{plot} < p; p \in [0; 1]$ the procedure jumps to a random,

non-neighboring starting cell. Thus, as patch size increases, so does the probability of jumping to a non-neighboring starting cell. The procedure stops when all cells are assigned to a habitat. Lastly, the observed point pattern is superimposed on the simulated habitat patches and for each habitat the number of individuals is compared between the observed data and the null model randomizations (Harms et al., 2001).

2.5 | Simulation study

We conducted a simulation study to analyze the four methods (Figure 2). The simulation study included three major steps: (a) simulating "observed" data with predefined (and thus known) characteristics, (b) analyzing the observed data using the four described methods, and (c) evaluating the results against the known characteristics of simulated observed data. Our simulation study was designed based on parameters used in published research; e.g., the number of discrete habitats and the spatial resolution (Table 1; Velázquez et al., 2016).

We first created neutral landscapes using the *NLMR R* package (two-dimensional fractional Brownian motion; Sciaini et al., 2018). Neutral landscapes are computer-generated landscapes without biotic or abiotic processes creating them, commonly used to test null hypotheses (With & King, 1997). The landscapes had an extent of 50×50 cells with a spatial resolution of 20 m. To simulate and test the influence of landscape fragmentation on the result, we used two values for the fractal dimension. The fractal dimension describes the correlation between values of the process, and we simulated low fragmentation with $f = 0.5$ and high fragmentation with $f = 1.65$. We classified the continuous values of the fractional Brownian motion into five discrete habitat classes using natural breaks (Fisher, 1958; Jenks & Caspall, 1971). The algorithm thereby increased between-group variability and reduced within-group variability. We used five discrete habitat classes because this was the most common number in other published research studies that apply at least one of the four methods we analyzed (Table 1). Whereas low fragmentation resulted in larger habitat patches (Figure 3a), high fragmentation resulted in rather scattered habitat patches (Figure 3b). Furthermore, the relative area of individual habitat classes differed between simulated landscapes. For low landscape fragmentation, the relative area of classes ranged from a minimum of 2.8% to a maximum of 47.5% and from a minimum of 3.8% to a maximum of 35.9% for high fragmentation (Appendix S3).

Second, we created point patterns with known habitat associations (Appendix S4) and increasing association strength α. To simulate the observed patterns, we used a homogenous Poisson process (complete spatial randomness; CSR) and a Thomas process (clustered) with 100 individuals for each pattern (also referred to as initial pattern hereafter). For the Thomas process we used a mean displacement from the cluster center of $\sigma = 40$ m and a mean number of $\mu = 5$ individuals for each cluster. These initial patterns were subsequently modified to realize different association strengths. We

FIGURE 2 Conceptual figure of the simulation study experiment. Colored boxes indicate different components (input, method, treatment) of the experiment. The numbering of each box refers to the three major steps of the simulation study.
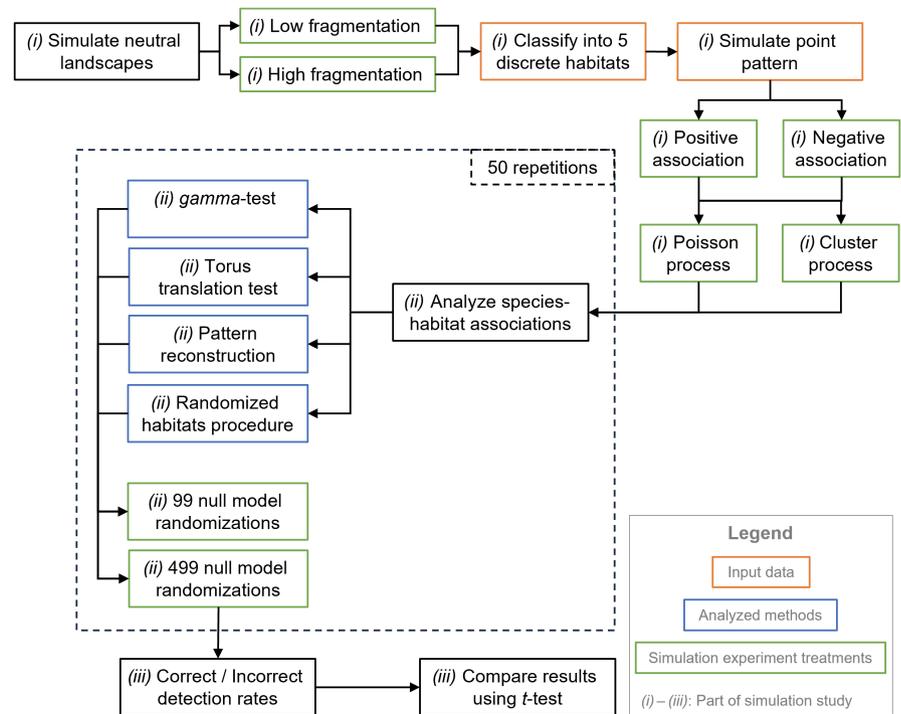
TABLE 1 Summary of published study designs for analyzing species–habitat associations.

References	Method	No. of habitats	Spatial grain (m)	Spatial extent (ha)
Comita et al. (2007)	TTT	5	20×20	50
Dalling et al. (2012)	TTT	5	20×20	50
Du et al. (2017)	TTT	4	20×20	25
Furniss et al. (2017)	χ^2, TTT	8	20×20	13.64
Garzon-Lopez et al. (2014)	GT	2, 4, 5	Various	50–1600
Gunatilleke et al. (2006)	TTT	8	20×20	25
Guo et al. (2016)	TTT	8	20×20	15
Harms et al. (2001)	χ^2, TTT, RH	5	20×20	50
Lai et al. (2009)	TTT	4	20×20	24
Lan et al. (2012)	TTT	6	20×20	20
Plotkin et al. (2000)	GT	2	25×25	50
Yamada et al. (2006)	TTT	8	20×20	52
Yang et al. (2016)	GT	7	20×20	20
Ye et al. (2011)	TTT	3	20×20	25

Abbreviations: GT, gamma-test; RH, Random habitats procedure; TTT, Torus translation test; $\chi2$, Chi-squared test.

randomly chose habitats to which the point patterns showed a positive or negative association. We increased the association strength from $\alpha=0.1$ to $\alpha=1.0$ in increments of 0.1. Where there were positive associations, we added additional individuals $\text{indiv}_{add}=\text{indiv}_{pattern}\times\alpha$ in the habitat. For CSR patterns, we also added individuals using a homogenous Poisson process. However, for clustered patterns, we used an inhomogeneous Poisson process based on the intensity of the initial pattern. Thus, there was a higher probability of adding individuals to an already existing cluster than adding them elsewhere. For negative associations, we removed individuals from the habitat using a probability of remaining of $\rho_{thin}=1-\alpha$. This resulted in a large number of individuals for positive associations and in a small number of individuals for negative associations in the corresponding habitats.

Third, we considered a correct result to be the detection of the truthful habitat association (positive or negative) of a species to the respective habitat. Because a positive association with a habitat potentially leads to a negative association to another habitat (and a negative association potentially leads to a positive association; Yamada et al., 2006), we defined a detection as incorrect whenever:
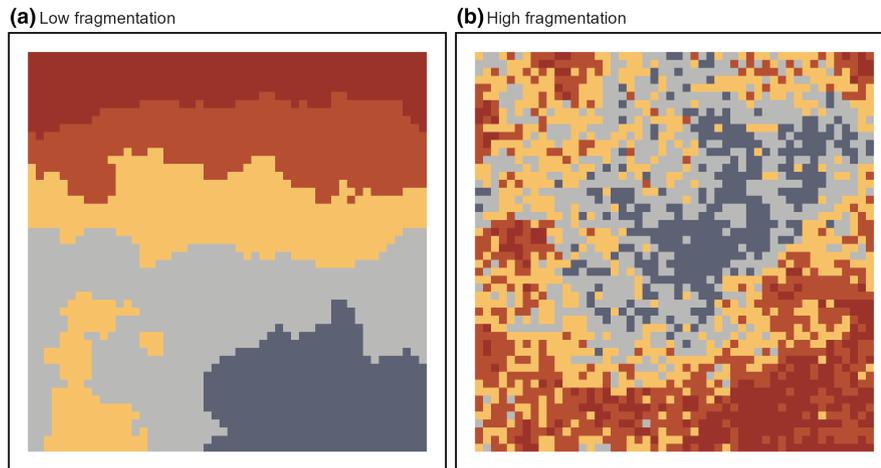
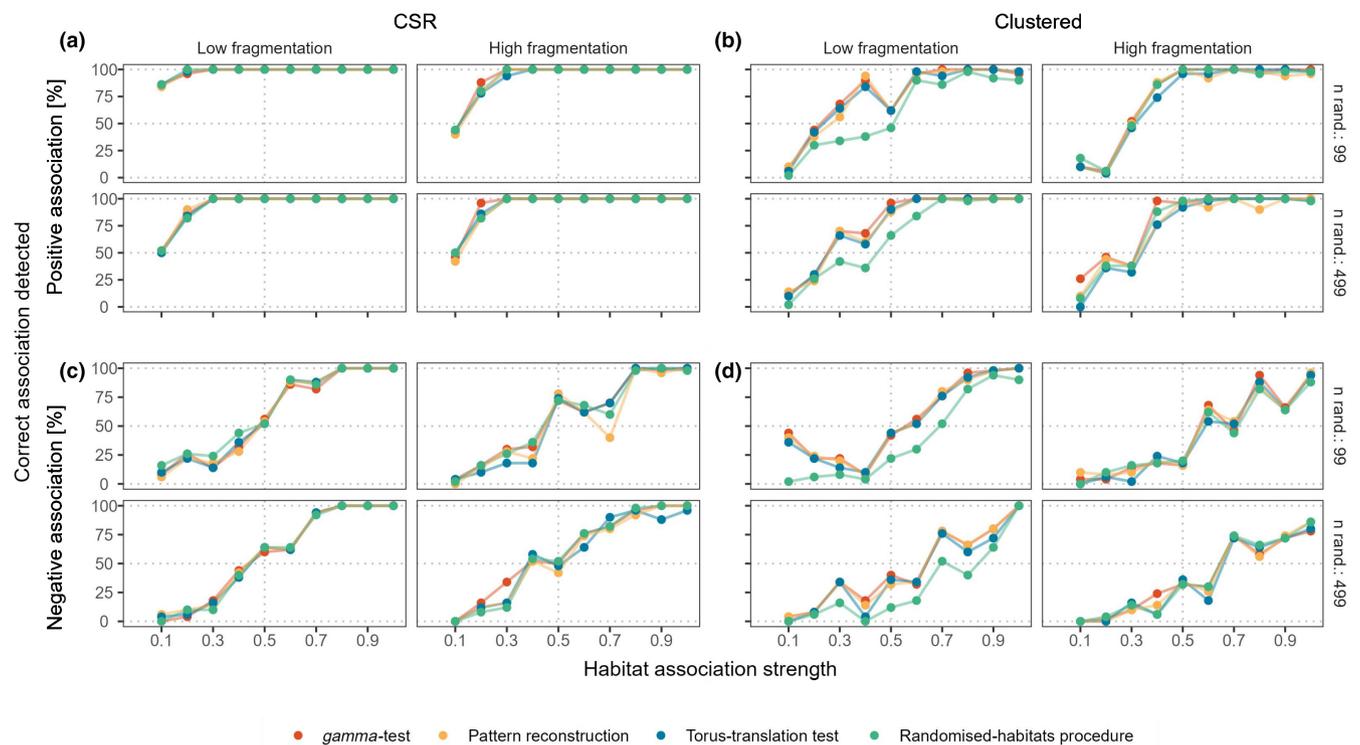**(a)** Low fragmentation **(b)** High fragmentation

FIGURE 4 Correct detection of species–habitat associations for (a, b) positive associations and (c, d) negative associations. We simulated initial patterns using (a, c) a Poisson point process model (CSR) or (b, d) a Thomas point process model (clustered). The association strength α describes the fraction of individuals in relation to the overall number of individuals that were added for positive or removed for negative associations. The detection rate summarizes 50 repetitions for each association strength, fragmentation level (columns) and number of null model randomizations (rows) and randomization approach (colors).

(a) the opposite association was detected with the habitat concerned (e.g., negative association when the known association was positive), (b) no significant association was detected with habitat, and (c) the correct association was detected with another habitat. Because we followed published methodologies (Table 1) as closely as possible, we only analyzed whether species–habitat associations were detected, but not the strength of the association itself.

To test whether the number of simulated null model randomizations influences the results of the analyses, we used two values, namely 99 and 499, for the four methods and the two fragmentation levels. These are typical values, according to a review paper on

spatial point pattern analysis in ecology (Velázquez et al., 2016). For the torus-translation test, the number of possible translations is determined by the grain and the extent of the study plot. Thus, we sampled the corresponding number of null model randomizations from the total of 2,597 possible translations.

All combinations of initial point pattern type, landscape fragmentation, null model randomizations and association strength were simulated 50 times. However, these simulations did not include the simulation of the null model data. They only included the simulations we used to investigate the four methods of analyzing species–habitat associations. To account for the stochasticity in the

simulation of the neutral landscapes and the point patterns, with a probability of $p = 0.25$ for each simulation also the observed data was simulated again. All results represent the rates of correct and incorrect detections for all repetitions (a correct detection of the corresponding species–habitat association in 35 of the 50 repetitions would be a correct detection rate of $r = 70\%$). We used t-tests to analysis the difference of detection rates between the different simulation experiment treatments. We performed the analyses and simulations using R (version 4.2, R Core Development Team, R Foundation for Statistical Computing, Vienna, AT) and the *spatstat* R package (Baddeley et al., 2015) for all spatial point pattern analyses. The methods for investigating species–habitat associations are implemented in the open-source R package *shar* (Hesselbarth, 2021).

3 | RESULTS

Overall, the gamma test, pattern reconstruction, the torus-translation test and the randomized-habitats procedure were all able to detect species–habitat associations similarly well. This included positive and negative associations, as well as correct and incorrect detections and all simulation experiment treatments (initial point pattern, fragmentation, null model randomizations). For negative associations differences between the methods were slightly more pronounced than for positive associations; however, the performance of the four methods was still very similar overall.

Positive species–habitat associations based on a Poisson point process model were detected the best by the four methods (Figure 4a). Where there were 10% additional individuals within a habitat ($\alpha = 0.1$), the four methods detected positive associations correctly in ca. 50% of all repetitions. Starting from 30% additional individuals within a habitat, the four methods detected positive associations correctly in almost all repetitions. For positive species–habitat associations based on a Thomas cluster process, the correct detection rate was slightly worse (Figure 4b). Correct detection of positive associations in 50% of all repetitions was present starting from ca. 30% to 40% of additional individuals within a habitat ($\alpha = 0.3–0.4$). Beyond 50% of additional individuals ($\alpha = 0.5$), the four methods detected positive associations correctly in almost all repetitions.

Compared with positive habitat associations, negative associations were detected less reliably. For species–habitat associations based on a Poisson point process model, the four methods detected negative associations in at least 50% of all repetitions only if more than 50% of individuals were removed from the habitat ($\alpha > 0.5$; Figure 4c). Although the detection rate increased with the strength of negative association, correct detections in almost all repetitions were achieved only if most individuals were removed from the habitat ($\alpha > 0.75$; Figure 1c). Last, negative associations based on an initial Thomas process model had overall the lowest correct detection rate (Figure 4d). A correct detection rate of 50% was only achieved for relatively high association strengths of ca. $0.7 < \alpha < 0.8$ (removing 70–80% of all individuals from the corresponding habitat). Even if no

individuals were present in the corresponding habitat ($\alpha = 1.0$), the detection rate of negative associations did not reach 100% for any of the four methods.

For incorrect detections (opposite association, no significant association, or correct association to a wrong habitat) the overall trend was similar to correct detections (Appendix S5). First, patterns simulated using a Poisson point process model had lower incorrect detection rates than initial patterns based on a Thomas process. Second, positive habitat associations had a lower incorrect detection rate than negative associations. Thus, the lowest incorrect detection rates were present for positive associations and (initial) CSR patterns, whereas the highest incorrect detection rates were present for negative associations and (initial) clustered patterns.

Correct detection rates were generally slightly higher on average in less-fragmented landscapes (correct$_{average} = 68.7\%$) than in highly fragmented ones (correct$_{average} = 66.2\%$). Mean correct detection rates were higher on average with 99 simulated null model randomizations (correct$_{average} = 68.4\%$) than with 499 simulated null model randomizations (correct$_{average} = 66.5\%$). Incorrect detection rates were also lower in less-fragmented landscapes than in highly fragmented ones (low fragmentation incorrect$_{average} = 32.2\%$; high fragmentation incorrect$_{average} = 34.3\%$). They were also lower when we simulated few null model randomizations than when we simulated many (99 simulated null model randomizations incorrect$_{average} = 32.2\%$; 499 simulated null model randomizations incorrect$_{average} = 34.3\%$). However, none of these differences were statistically significant using t-tests. Finally, we emphasize that we do not consider a correct detection rate of 50% as sufficient to confidently detect species–habitat associations. We highlight this value only to assist comparisons among the four methods we analyzed in our study.

4 | DISCUSSION

We conducted a comprehensive simulation study of methods commonly used to analyze species–habitat associations. This included the gamma test (Plotkin et al., 2000), pattern reconstruction (Tscheschel & Stoyan, 2006), the torus-translation test (Harms et al., 2001), and the randomized-habitats procedure (Harms et al., 2001). Although the methods are mainly applied to fully mapped forest dynamics plots (e.g., see the ForestGEO network; Davies et al., 2021), they can be applied to all study plots of fully mapped plants or other immobile species. Interestingly, the four methods performed equally well. Correct and incorrect detection rates were mostly influenced by the initial spatial distribution of the point patterns (the point process model used to simulate the initial pattern), and to a lesser degree by the fragmentation of the landscape, as well as by the number of simulated null model randomizations. These findings thus match the consistent species–habitat associations for the most dominant tree species obtained by a previous study applying the four methods to a dataset from a European temperate forest (Hesselbarth, 2020). Thus, differences between species–habitat associations in

previously published results (Plotkin et al., 2000; Harms et al., 2001; Yamada et al., 2006; Lan et al., 2012; Garzon-Lopez et al., 2014; Guo et al., 2016; Yang et al., 2016; Du et al., 2017; Furniss et al., 2017) seem to be connected to species characteristics or local environmental conditions rather than to which methods were used.

However, each of the four methods have advantages and disadvantages. Advantages of the gamma test are that it is conceptually straightforward and applicable to irregular study plots. Its disadvantage, however, is that it requires a suitable point process model to simulate the point pattern, which is difficult for complex patterns (Wiegand et al., 2007, 2009). Pattern reconstruction is possible for irregular study plots and is able to simulate complex point patterns. Its disadvantage, however, is that it is costly to compute (Tscheschel & Stoyan, 2006). However, these computational demands are probably of minor importance given the small differences of $g(r)$ between 99 and 499 simulated null models (Appendix S6). Nevertheless, pattern reconstruction is the best of the four methods for preserving the spatial structure of both the environmental data and the point pattern data. The torus-translation test preserves well the internal spatial structure of the original data (Wiegand & Moloney, 2014). However, it can only be applied to rectangular study plots. In addition, if strong gradients are present within the study area, these will not be preserved (Wiegand & Moloney, 2014). Yet, using landscapes with strong environmental gradients still resulted in comparable performances for all methods. Even though correct detection rates decreased slightly, especially for initially clustered patterns with negative habitat associations, the torus-translation test did not result in considerably lower correct detection rates (Appendix S7). By contrast, the randomized-habitat procedure is applicable to irregular study plots, but the spatial structure of the data is poorly preserved. In particular, habitat gradients are not taken into account and null model data might be rather artificial.

For data from a tropical forest dynamics plot (Barro Colorado Island, Panama), the randomized-habitats procedure showed 38% fewer significant habitat associations than the torus-translation test (Harms et al., 2001). This is not in agreement with our simulation study. We observed no differences between the four methods in terms of correct and incorrect detections of habitat associations. It is possible that this lack of difference arose because the spatial structure of the simulated neutral landscapes was sufficiently preserved by the procedure, whereas real-world landscape structure might be harder to preserve. In addition, our modification of the procedure allowing the procedure to jump to a non-neighboring cell might have increased its ability to preserve the landscape structure. The original method often results in a few very large patches, which may not resemble the observed landscape. Our small rates of incorrect detections, especially for positive associations, are in accordance with similar studies. Using random labeling, Comita et al. (2007) showed that for an approximated significance level of $p \approx 0.05$ there were only very few false-positive detections (1–4% for most of their five habitats).

With increasing positive association strength (i.e., more individuals within the habitat), point patterns become increasingly clustered (Yamada et al., 2006; Shen et al., 2013). This effect was surprisingly weak even though the initial CSR patterns became more clustered with increasing positive association strength (Appendix S8). Thus, for the gamma test, even a Poisson process point model resulted in a high correct detection rate for positive associations. This indicates that if the spatial structure of the point pattern resembles CSR, even for strong associations, the results should be similar to the generally less conservative χ^2 test (Plotkin et al., 2000; Harms et al., 2001). Furthermore, initially clustered patterns remained clustered after adding or thinning points. However, the clustering decreased with increasing positive association strength, whereas the clustering increased with increasing negative association strength (Appendix S8). This was because not all of the initial cluster centers were necessarily located in the associated habitat.

For highly clustered point patterns, all methods performed less well (Appendix S9). However, the performance depended on the level of landscape fragmentation. In less-fragmented landscapes, positive and negative species–habitat associations were detected at least partly correct. However, in highly fragmented landscapes, none of the methods was able to detect species–habitat associations to a satisfying level. Overall, the randomized-habitat procedure had the lowest performance in detecting species–habitat associations for the case of highly clustered point patterns, whereas the other methods performed better and similarly to each other.

The performance of the four methods was worse for negative habitat associations than for positive associations. This was possibly because of the simulation study design. With increasing habitat association strength, the probability of removing an individual from the habitat increased. In consequence, the overall number of individuals decreased. Thus, for stronger negative habitat associations it is possible that the number of remaining individuals was too small for successful analysis (Wiegand & Moloney, 2014).

Correct detection rates were lower at the high fragmentation level than at the low level for all four methods. In addition, simultaneously, incorrect detection rates were higher. This is not surprising given that correct and incorrect detection rates are not exactly contrary, but highly related to each other. The smaller average habitat patch size in landscapes with high fragmentation makes preservation of the spatial structure during randomization increasingly unlikely. This is an important finding given the increasing fragmentation of natural landscapes (Haddad et al., 2015; Bryan-Brown et al., 2020). In our study, we simulated all neutral landscapes with the same algorithm and parameters and landscapes were only visually validated to be realistic. Thus, future research should look further into the influence of landscape composition and configuration, as well as that of spatial extent and grain on the performance of methods used to detect species–habitat associations. For such research, landscape metrics could be a suitable tool to quantify the spatial characteristics of the landscapes themselves (Uuemaa et al., 2013).

Although our simulation study is an important analysis of the power of the methods, further research should explore additional potential factors affecting results. Such factors include the spatial resolution and extent of environmental data, the number or composition

of discrete habitat classes, the absolute number of mapped individuals, and the scale and strength of association (but see Garzon-Lopez et al., 2014 for an analysis of sampling scale). In addition, new developments in spatial point pattern analysis, such as multivariate pattern reconstruction (Wudel et al., 2023), provide the possibility of analyzing species–habitat associations on a community level and not just on the level of single species. Further research is needed on comparisons of the four methods of investigating species–habitat associations based on the simplifying assumptions of discrete habitat patches to methods exploring continuous environmental data.

5 | CONCLUSIONS

Our simulation study showed that the four methods suggested by the literature for analyzing species–habitat associations were able to detect positive and negative associations in a satisfactory and similar way. We revealed that positive associations were detected more reliably than negative associations. Similar associations in patterns with initially randomly distributed individuals were detected more reliably than in initially clustered patterns. Thus, our recommendation is to choose the method that best suits the available data. If strong environmental gradients are present, we advise randomizing the point pattern rather than the habitat classes. In addition, when an appropriate point process model is available, we suggest using the gamma test because it is computationally less costly than the other methods. Otherwise, we suggest using pattern reconstruction. Where there are no strong environmental gradients, randomizing the habitat classes is also a viable option. For rectangular study plots, we suggest using the torus-translation test. For irregular study plots, however, we recommend using the randomized-habitats procedure. To facilitate their use, we implemented the four methods in the open-source and freely available R package *shar* (Hesselbarth, 2021).

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SUPPORTING INFORMATION

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

Appendix S1. Mean parameters of the fitted Thomas cluster processes.

Appendix S2. Pair-correlation functions of a simulated point pattern using the *gamma*-test and pattern reconstruction.

Appendix S3. Relative area of habitat classes.

Appendix S4. Characteristics of simulated point patterns.

Appendix S5. Incorrect detection rates of the simulation study.

Appendix S6. Pair-correlation functions of simulated point patterns using different numbers of simulated null model randomizations.

Appendix S7. Correct detection rates of the simulation study for landscapes with strong environmental gradients.

Appendix S8. Pair-correlation functions of the initially simulated point patterns.

Appendix S9. Correct detection rates of the simulation study for highly clustered point patterns.