An evaluation of the state of spatial point pattern analysis in ecology

Eduardo Velázquez, Isabel Martínez, Stephan Getzin, Kirk A. Moloney and Thorsten Wiegand

E. Velázquez, S. Getzin and T. Wiegand (thorsten.wiegand@ufz.de), Dept of Ecological Modelling, Helmholtz Centre for Environmental Research – UFZ, Permoserstrasse 15, DE-04318 Leipzig, Germany. EV also at: Depto de Biología, Centro Universitario de Coyhaique, Univ. de Magallanes, José Miguel Carrera 485, Coyhaique, Chile. TW also at: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, DE-04103 Leipzig, Germany. – I. Martínez, Doñana Biological Station CSIC, Dept of Conservation Biology, Avda. Americo Vespucio s/n, Isla de la Cartuja, ES-41092 Sevilla, Spain. – K. A. Moloney, Dept of E.E.O.B., 251 Bessey Hall, Iowa State Univ., Ames, IA 50011-1020, USA.

Over the last two decades spatial point pattern analysis (SPPA) has become increasingly popular in ecological research. To direct future work in this area we review studies using SPPA techniques in ecology and related disciplines. We first summarize the key elements of SPPA in ecology (i.e. data types, summary statistics and their estimation, null models, comparison of data and models, and consideration of heterogeneity); second, we review how ecologists have used these key elements; and finally, we identify practical difficulties that are still commonly encountered and point to new methods that allow current key questions in ecology to be effectively addressed.

Our review of 308 articles published over the period 1992–2012 reveals that a standard canon of SPPA techniques in ecology has been largely identified and that most of the earlier technical issues that occupied ecologists, such as edge correction, have been solved. However, the majority of studies underused the methodological potential offered by modern SPPA. More advanced techniques of SPPA offer the potential to address a variety of highly relevant ecological questions. For example, inhomogeneous summary statistics can quantify the impact of heterogeneous environments, mark correlation functions can include trait and phylogenetic information in the analysis of multivariate spatial patterns, and more refined point process models can be used to realistically characterize the structure of a wide range of patterns. Additionally, recent advances in fitting spatially-explicit simulation models of community dynamics to point pattern summary statistics hold the promise for solving the longstanding problem of linking pattern to process. All these newer developments allow ecologists to keep up with the increasing availability of spatial data sets provided by newer technologies, which allow point patterns and environmental variables to be mapped over large spatial extents at increasingly higher image resolutions.

Detailed knowledge of the characteristics of spatial distribution patterns of animal and plant species is fundamental for developing a deep understanding in many branches of ecology. Spatial point pattern analysis (Ripley 1981, Diggle 2003, Illian et al. 2008, Baddeley et al. 2015) provides powerful techniques for the statistical analysis of point pattern data that consist of a complete set of locations of ecological objects within an observation window. These data can be supplemented by additional information characterizing the objects (i.e. marks such as size, or condition such as surviving vs dead) or environmental covariates. Typical examples of point patterns include the distribution patterns of a tree species (Fig. 1A), the spatial association pattern of two life plant stages of a tree species (Fig. 1C), the spatial autocorrelation pattern of dead saplings within the pre-mortality (i.e. surviving and dead) pattern of saplings (Fig. 1D), and the spatial correlation pattern of the sizes of trees (Fig. 1E). Ecologists have increasingly analyzed such data sets to quantify the characteristics of observed spatial patterns with the aims of deriving hypotheses on the underlying

processes or testing hypotheses derived from ecological theory (Wiegand and Moloney 2014).

In ecology, the link between spatial pattern and process was established early on (Watt 1947, Pielou 1977), but did not gain in importance until the most recent two decades, when ecology reached a point where it became necessary to adopt a spatially-explicit perspective to advance the science (Levin 1992). Current ecological theory provides increasing evidence that spatial pattern and process play an important role in the assembly, dynamics, and functioning of plant and animal communities (Hurtt and Pacala 1995, Tilman and Kareiva 1997, Chesson 2000, Brown et al. 2011, Detto and Muller-Landau 2013, May et al. 2015, Velázquez et al. 2015). Thus, an important motivation for studying point patterns is that they may conserve an imprint of the processes that affected the placement of the ecological objects and the values of the marks that characterize the objects. Point patterns are therefore an 'ecological archive' that may contain valuable information on the underlying processes, structure and function of the
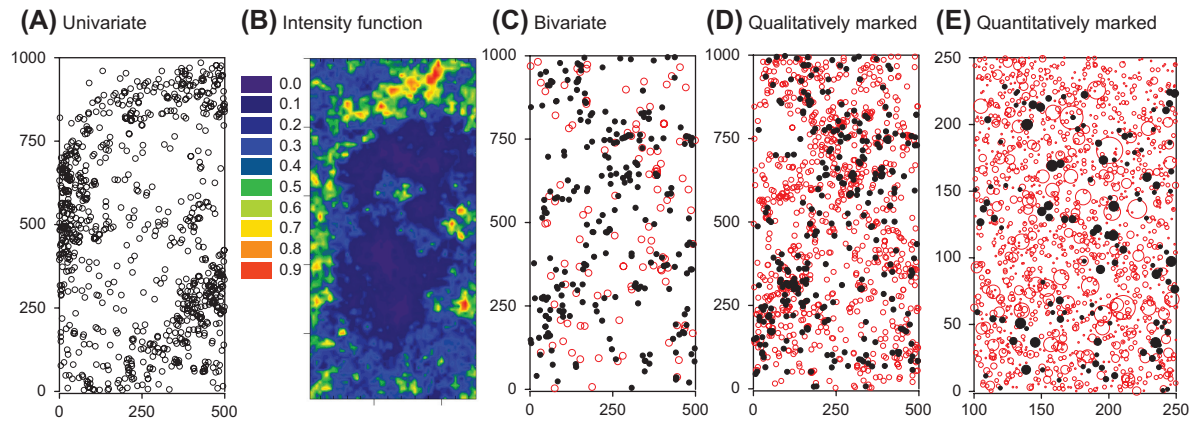
Figure 1. Typical examples for data types that can be analyzed with SPPA. All examples were taken from the 50 ha forest dynamics plot of the tropical forest at Barro Colorado Island (BCI), Panamá (Hubbell et al. 2005). (A) The univariate pattern of saplings (i.e. individuals with diameter at breast height (dbh) smaller than 4 cm) of the canopy tree *Guatteria dumetorum* taken from the 1983 census. (B) Estimate of the intensity function $\hat{\lambda}(x)$ for the pattern shown in (A) based on topographic variables. We show the normalized $\hat{\lambda}(\mathbf{x})/\lambda_{max}$ where λ_{max} is the maximal value of $\hat{\lambda}(\mathbf{x})$. (C) Bivariate pattern of reproductive trees of the midstorey tree *Eugenia galalonensis* (red) in the 1985 census and all newly recruited individuals (black) (i.e. all individuals reaching for the first time dbh ≥ 1 cm). (D) Qualitatively marked pattern of all saplings of *E. galalonensis* from the 1990 census that survived to the 2005 census (red) and that died (black). (E) Quantitatively marked pattern of large trees (dbh > 10 cm) of the mid-story tree *Trichilia pallida* (black) and all other large trees (red) with dbh as quantitative mark indicating tree size. We show only a subplot of the entire data.

system (Wiegand et al. 2003, 2009, McIntire and Fajardo 2009). The main objective of spatial point pattern analysis in ecology is to extract this information (Wiegand and Moloney 2014).

A broader scientific audience was attracted to spatial point pattern analysis in the 1980s through the textbooks of Ripley (1981) and Diggle (1983), and later by the books of Cressie (1993), Stoyan and Stoyan (1994), Diggle (2003) and Illian et al. (2008). Several conceptual articles have presented these techniques specifically to ecologists (Haase 1995, Stoyan and Penttinen 2000, Goreaud and Pélissier 2003, Wiegand and Moloney 2004, Perry et al. 2006, Law et al. 2009, McIntire and Fajardo 2009, Szmyt 2014). However, there is no systematic review on the use of the different elements of SPPA in ecology that could direct future work in this area.

The objectives of our study are to summarize key elements of spatial point pattern analysis (SPPA) in ecology, to review their use, and to discuss future challenges and opportunities. More specifically, we review 308 articles that used SPPA in ecology (and related disciplines) published between 1992 and 2012 (Supplementary material Appendix 3). We first assess how researchers have used five key elements of SPPA (i.e. data types, summary statistics and their estimation, null and point process models, comparison of data with models, and heterogeneity). Based on this assessment, we identify practical difficulties in the use of SPPA in ecology that are still common and we point to newer techniques that allow current key questions in ecology to be more effectively addressed. We illustrate the use of the different elements of SPPA and newer developments using typical real-world examples from the 50-ha tropical forest plot at Barro Colorado Island (BCI), Panama (Fig. 1), where all trees ≥ 1 cm diameter at breast height (dbh) have been mapped, identified to species and repeatedly censused (Hubbell et al. 2005).

Methods

Topic search

We performed an intensive topic search on the ISI Web of Knowledge site using the search mask TS = ((Ripley* OR point-pattern OR 'point pattern' OR 'spatial pattern') AND (Biolo* OR Ecolo* OR Forest*)), which covered ecology and related fields. We only considered scientific articles published in English over the years of 1992–2012, excluding textbooks and conference proceedings. Although we certainly did not detect all articles that used SPPA in ecology and related disciplines, our systematic search based on the above mentioned search mask guaranteed that we obtained a sufficiently representative sample of relevant articles. Our search yielded a total of 360 articles, but we retained 308 for analysis by selecting only those that used techniques of SPPA to address ecological questions or hypotheses or tested new methods with real world data. The analyses to illustrate the use of the different elements of SPPA were conducted with the software 'Programita' (Wiegand and Moloney 2014), which can be accessed at <www.programita.org>.

Evaluation of articles

Supplementary material Appendix 1, Table A1 shows the different categories used to characterize each study. While Supplementary material Appendix 1 presents a detailed (temporal) analysis of the data generated in the literature review, we present here only the most important trends that are relevant for our discussion and recommendation sections.

Key elements of point pattern analysis in ecology
In this section we briefly summarize five key elements of SPPA that appear in typical ecological analyses (Wiegand and Moloney 2014). These elements also structure our

review and they provide the background for the evaluation of the 308 studies analyzed here (Supplementary material Appendix 1, Table A1). However, we have to emphasize that the modern statistical methodology for analyzing spatial point patterns is much wider than that commonly used in ecology. Baddeley et al. (2015) present many of the more recent developments that are not considered in this section. Supplementary material Appendix 4 provides key references and links for SPPA software packages.

Data types

Point patterns comprise the coordinates $\mathbf{x} = (x, y)$ of ecological objects, e.g. trees or shrubs, nests, burrows, 'fairy circles', or termite mounds. These objects are usually represented as points within a given observation window W. The observation window usually corresponds to sampling plots that are rectangular as in Fig. 1. However, the window may also have an irregular shape (Goreaud and Pélissier 1999, Wiegand and Moloney 2004). The data set may be supplemented by environmental covariates (e.g. nutrient contents, slope), and the points may carry additional information (i.e. 'marks') characterizing the objects they represent, for example the number of flowers that set fruits (Fedriani et al. 2015), or surviving vs dead trees (Kenkel 1988).

Depending on the nature of the marks, different data types may arise. In ecological applications we distinguish between 'a priori' and 'a posteriori' properties of the objects (Goreaud and Pélissier 2003, Wiegand and Moloney 2014). The first distinguishes a priori different types of objects such as different tree species in a forest. In contrast, a posteriori properties are created by a marking processes acting upon existing objects (e.g. surviving vs dead trees in a forest, or size of a tree) (Wiegand and Moloney 2014). This differentiation leads to three fundamental classes of objects (Supplementary material Appendix 1, Table A1): 1) unmarked patterns, where the points are characterized only by their locations and their a priori type. These can be univariate, bivariate, or multivariate patterns with one, two or more than two distinct types of objects, respectively (Fig. 1A, C); 2) qualitatively marked patterns, where the points carry an a posteriori generated qualitative mark (e.g. surviving vs dead; Fig. 1D); and 3) quantitatively marked patterns, where the points carry an a posteriori generated quantitative mark (e.g. size of a tree; Fig. 1E).

Summary statistics

Summary statistics are numbers or functions that provide a brief and concise description of point patterns. Because summary statistics condense spatially-explicit information, they inevitably lose information contained in the pattern. Therefore, it is important to use several summary statistics simultaneously in order to obtain as complete an understanding of the multifaceted nature of complex spatial patterns as possible (Wiegand et al. 2013).

Historically, a number of indices were developed to characterize the overall nature of point patterns through a single number (reviewed by Szmyt 2014), many by foresters who developed the earliest techniques for analyzing point patterns. However, these indices are rarely used in modern SPPA, with the notable exception of the intensity metric (i.e. λ – the mean number of points per unit area).

The first-order summary statistics consider the probability that a single point is located within a small area around location $\mathbf{x} = (x, y)$ and are generally presented in the form of the intensity function $\lambda(\mathbf{x})$. If the pattern is homogeneous (also called stationary), it has the same statistical properties over the entire observation window W (i.e. it is invariant under translation). In this case the intensity can be estimated by the scalar constant $\hat{\lambda} = n/A$ where n is the number of points, A is the area of W, and the hat symbol indicates the estimated value. However, if the intensity varies in space the pattern is heterogeneous and it is better characterized by the function $\lambda(\mathbf{x})$. For example, the intensity of the pattern shown in Fig. 1A is significantly affected by environmental variables that vary within W. Figure 1B shows an estimate $\hat{\lambda}(\mathbf{x})$ of the intensity function of that pattern. Estimation of $\lambda(\mathbf{x})$ is the key task in species distribution modeling that aims to explain the occurrence of a species using a set of environmental variables (Elith and Leathwick 2009). Poisson point process models provide important techniques for this (Diggle 2003: section 7.1, Renner et al. 2015).

The second-order summary statistics are the most important summary statistics. They are related to the spatial (co)variance of pairs of points and are calculated based on information from all inter-point distances at or within neighborhoods of radius r. If the pattern is homogeneous we can define the 'typical point' of the pattern and derive summary statistics characterizing the neighborhood of the typical point. For example, the pair correlation function $g(r)$ (Illian et al. 2008: p. 218, Law et al. 2009) is the expected density of points within rings of radius r (and ring width dr) centered on the typical point, divided by the intensity λ of the pattern. Figure 2E shows that the mean neighborhood density of saplings of *Guatteria dumetorum* is at short distances (1–5 m) three times larger than the overall sapling density $\hat{\lambda}$ and still 1.7 times larger at distances of 50 m, suggesting a highly clustered pattern. However, the elevated neighborhood densities at larger distances suggest heterogeneity of the pattern. Even so, because point processes are stochastic, larger values in the empirical pair correlation function may arise purely by chance, and the clustering suggested by Fig. 2E must somehow be verified. This is usually done by confronting the data with Monte Carlo simulations using a suitable stochastic null model (see Null models and point process models).

The widely used K-function is the cumulative version of the pair correlation function, i.e. $K(r) = \int_{r'=0}^{r} g(r') 2\pi r' dr'$ and can be defined as the mean number of points within distance r of the typical point, divided by λ. In ecology the square-root transformation $L(r) = \sqrt{K(r)/\pi} - r$ is mostly used because it stabilizes the variance of the K-function (Besag 1977) and shows departures from complete spatial randomness in a simpler way (Haase 1995). However, statisticians prefer the form $L(r) = \sqrt{K(r)/\pi}$. There are inhomogeneous versions of $g(r)$, $K(r)$ and $L(r)$ (Baddeley et al. 2000) developed for first-order inhomogeneous point processes where $\lambda(\mathbf{x})$ varies by location $\mathbf{x}$ (Fig. 1B, 2H). For this type of pattern, the inhomogeneous functions use an estimate of the intensity function to factor out the first-order structure, thereby leaving behind the residual 'pure'
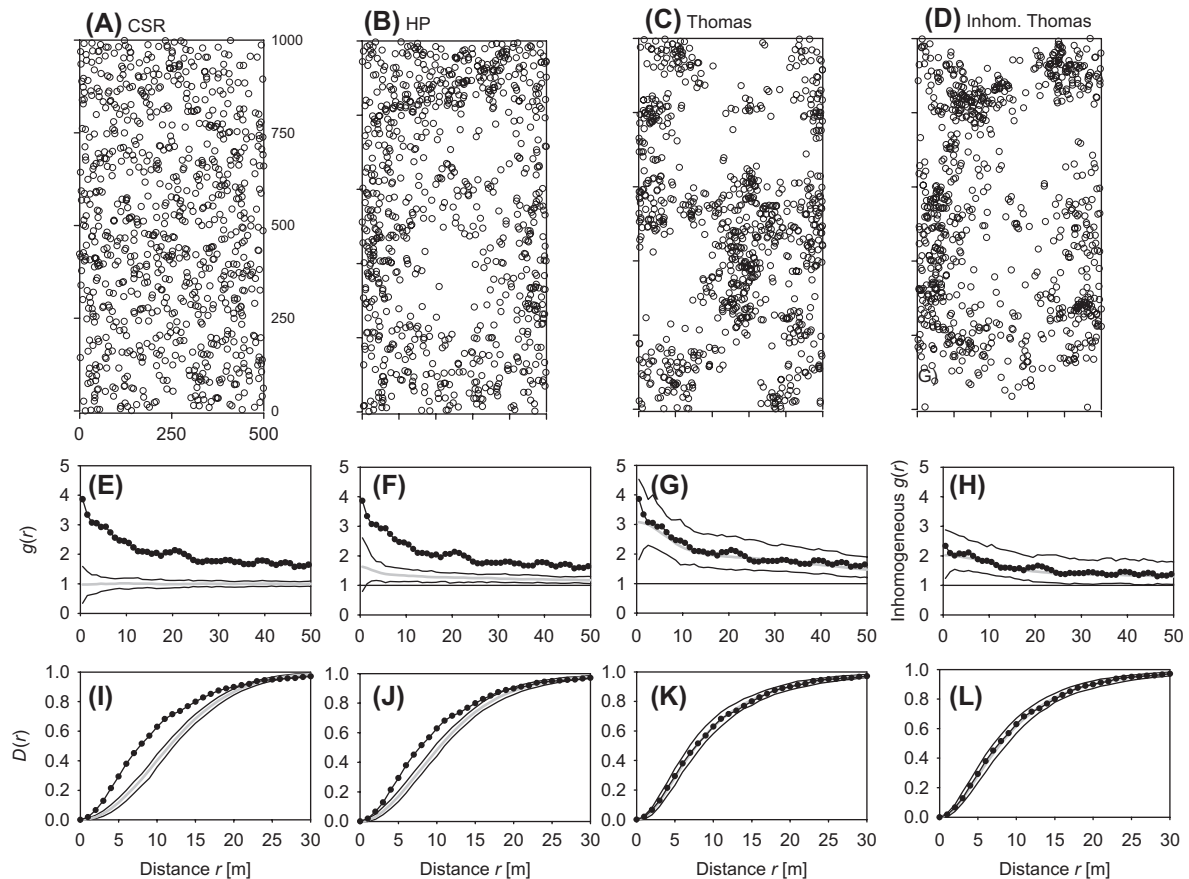
Figure 2. Example of different null and point process models for the univariate patterns of saplings of *G. dumetorum* shown in Fig. 1A. (A) Complete spatial randomness (CSR) where the points of the pattern are randomly and independently distributed within the plot. (B) Heterogeneous Poisson process (HP) where tentative points are randomly and independently placed within the plot, but only accepted with probability $\hat{\lambda}(\mathbf{x})/\lambda_{max}$ (Fig. 1B) (C) A complex (homogeneous) Thomas cluster process (Wiegand and Moloney 2014: their Eq. 4.17) with two critical scales of clustering. Parameter fitting yields small clusters (diameter ≈ 8 m) nested within large clusters (diameter ≈ 60 m), and the distribution of points over the clusters followed a negative Binomial distribution with parameters $\hat{k}_s = 0.1$ and $\hat{k}_l = 0.1$. (D) A complex inhomogeneous Thomas cluster process with two critical scales of clustering based on the intensity $\hat{\lambda}(\mathbf{x})$ shown in Fig. 1B. Small clusters (diameter ≈ 13 m) were nested within large clusters (diameter ≈ 90 m) and the distribution of points over the clusters followed a negative Binomial distribution with $k_s = 0.1$ and $k_l = 0.1$. (E)–(L) Observed summary statistics (black dots), expectation of the point process model (grey bold lines) and simulation envelopes (i.e. 5th lowest and highest values of 199 realizations of the point process model; black lines). The panels are placed below the corresponding example pattern. We used a bandwidth of 1.5 m for estimation of the pair correlation functions.

second-order structure, which is mostly attributed to inter-actions among points (Law et al. 2009). Inhomogeneous functions are very useful in ecology because many real world patterns show heterogeneity (e.g. Fig. 1A, B). However, estimation of $\lambda(\mathbf{x})$ using this approach requires additional information on the environmental variables producing this heterogeneity (Diggle et al. 2007). Second-order inhomogeneity (e.g. both, repulsion and aggregation) can be assessed by comparing pair correlation functions obtained from smaller subareas (Law et al. 2009).

While second-order statistics characterize the pattern with respect to the total number of neighbors within a circle or ring around a typical point, nearest neighbor summary statistics estimate the probability of finding the nearest neighbor (or in a more advanced setting the kth nearest neighbor) within distance r of the typical point [i.e. the nearest neighbor distribution function $D(r)$; Fig. 2I–L] or within distance r of a 'test point' [i.e. the spherical contact distribution or

empty space function $H_s(r)$] (Illian et al. 2008: sections 4.2.5 and 4.2.6). Note that $D(r)$ and $H_s(r)$ are sometimes called $G(y)$ and $F(x)$, respectively (Diggle 2003). Third-order summary statistics based on counting triplets of points exist, but they are rarely used (Illian et al. 2008: their section 4.4.2).

Marked point patterns have their own class of summary statistics. For example, when considering all pairs of points separated by distance r, mark connection functions $p_{lm}(r)$ yield the conditional probability that the first point of the pair is of type l and the second of type m (Illian et al. 2008: p. 331, Wiegand and Moloney 2014: section 2.3.6). Figure 3D shows the mark connection function $p_{22}(r)$ of dead sap-lings (i.e., $l = m = 2$) and Fig. 3F the corresponding pair cor-relation function $g_{22}(r)$. Comparison of both functions shows that the mark connection functions essentially remove the signal of aggregation in the underlying unmarked pattern.

Finally, mark correlation functions are second-order summary statistics adapted to quantitatively marked patterns
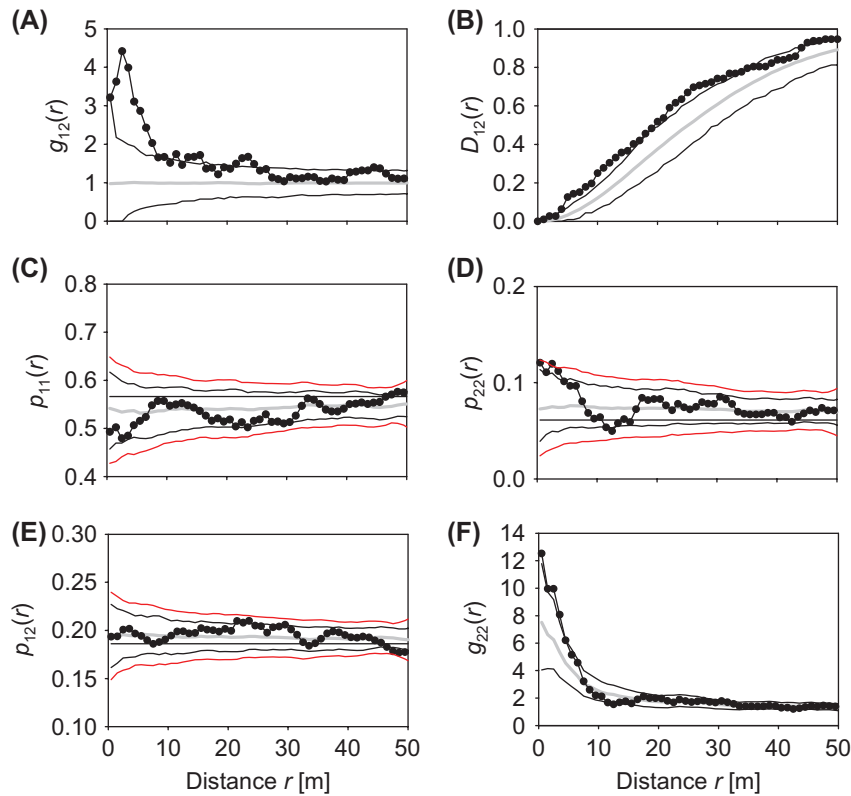
Figure 3. Examples for analyses of bivariate and qualitatively marked patterns. (A) and (B): Bivariate pattern and toroidal shift implementation of the independence null hypothesis to assess possible associations between recruits and reproductive trees shown in Fig. 1C. $g_{12}(r)$: bivariate pair correlation function, $D_{12}(r)$: bivariate nearest neighbor distribution function with reproductive trees (type 1) and recruits (type 2). We used a bandwidth of 2.5 m. (C)–(F) Qualitatively marked patterns (surviving saplings: mark 1, dead saplings: mark 2) and the local random labeling null model (a given mark is not moved more than 100 m) to assess possible spatial correlation in the pattern of dead saplings shown in Fig. 1D). $p_{lm}(r)$: mark connection functions with l, m = 1 or 2 and $g_{22}(r)$: pair correlation function of dead saplings. The black and red lines show the pointwise and global simulation envelopes, respectively. The global envelopes indicate a departure from the null model for distance interval 1–50 m with significance level $\alpha = 0.05$. The black horizontal lines in panels (C–F) show the expectation under local random labeling. We used a bandwidth of 2.5 m and 999 simulations of the null model, all other conventions as in Fig. 2E–L.

(Penttinen et al. 1992, Illian et al. 2008: section 5.3.3, Law et al. 2009, Wiegand and Moloney 2014: section 3.1.7). For example, to analyze marks characterizing the size of trees in a forest plot (Fig. 1E), the mark correlation function $k_{mm}(r)$ visits all pairs i–j of trees separated by distance r, estimates the mean of the product of their sizes m_i and m_j, and divides this by the corresponding quantity taken over all pairs of trees (Illian et al. 2008: p. 346). In our example nearby trees of the species *T. pallida* tend to be smaller than two trees selected at random (i.e. $k_{mm}(r) < 1$; Fig. 4A). This trend, however, is probably caused by heterogeneity (see below). Thus, although mark connection and mark correlation functions are less affected by heterogeneity than K- and pair correlation functions (Illian et al. 2008: p. 281), possible spatial trends in the marks due to heterogeneity should be explored.

An important technical aspect in the estimation of summary statistics is consideration of so-called edge effects, which were widely debated in earlier studies in ecology (Haase 1995, Goreaud and Pélissier 1999). Edge effects can arise if points lying outside the observation window W are not sampled; i.e. only a part of the ring or disk around a point located close to the border of W lies within W. Edge effects lead to underestimation of the neighborhood density and therefore introduce a bias in estimating second-order summary statistics such as $g(r)$, $K(r)$ and $L(r)$. Different strategies of edge correction used in ecology include 1) sampling so that only points with complete neighborhoods in W are used to estimate the summary statistics (minus sampling; Haase 1995); 2) sampling or reconstructing the unknown points outside W (plus sampling), which includes approaches such as toroidal edge correction (where copies of the original pattern are placed outside W), or conditional pattern reconstruction (which can also deal with irregular observation windows; Illian et al. 2008: p. 185); 3) using a weighting factor w_{ij} for each individual point pair i–j that corrects for the unobserved points lying outside the observation window (pairwise weighted edge correction methods; Ripley 1981, Illian et al. 2008: section 4.3.3), and finally 4) global edge correction that uses a weighting factor $w(r)$ that is the same for all point pairs i–j with interpoint distances of r, based on a direct estimate of the bias in the naïve estimators at distance r (e.g. the isotropized set covariance function of W; Ward and Ferrandino 1999, Illian et al. 2008: p. 230, Wiegand and Moloney 2014: p. 148). Edge correction may not be needed when 1) the edges of the observation window are real edges (Lancaster and Downes 2004), 2) the summary statistics are conditional by nature, such as the mark connection and mark correlation
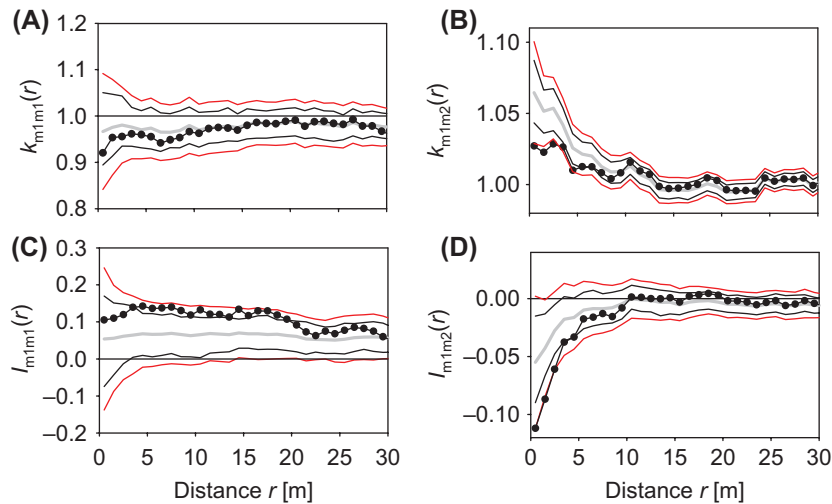
Figure 4. Quantitatively marked patterns and local random marking null model to assess possible spatial correlations in the size (dbh) of large *T. pallida* trees relative to the size of nearby large trees of other species (Fig. 1E). The local random marking null model randomly shuffled the sizes of *T. pallida* trees, but did not move a given mark more than 100 m away. (A) Univariate mark correlation function $k_{mm}(r)$ of the size of large *T. pallida* trees showing no correlations in the mark product. (B) Bivariate mark correlation function $k_{m1m2}(r)$ indicating that the product of the sizes of pairs of conspecific–heterospecific trees are for small distances slightly smaller than expected by the null model. Thus, *T. pallida* trees that have a heterospecific neighbor nearby tend to be smaller than the average *T. pallida* tree. (C) Moran's *I* like correlation function $I_{mm}(r)$ showing that the positive spatial correlation in the sizes of large *T. pallida* trees is driven by the environment. (D) Bivariate Moran's *I* like correlation function $I_{m1m2}(r)$ showing weak negative spatial correlation in the sizes of large *T. pallida* trees and heterospecifics, again indicating that *T. pallida* trees that have a nearby heterospecific neighbor tend to be smaller than the average *T. pallida* tree. We used 199 simulations of the null model, all other conventions as in Fig. 2E–L.

functions (Illian et al. 2008: p. 281), and 3) when nearest neighbor statistics are used, since they are less affected by edge effects than second-order summary statistics (Wiegand and Moloney 2014: section 3.1.3.1).

Null models and point process models

Null models and point process models are the tools of SPPA through which ecological hypotheses are examined. Spatial point process models are mathematical models that provide a stochastic mechanism to generate point patterns. The spatial structure in a point process model is usually governed by a set of parameters (e.g. the degree of clustering), which must be fitted to the observed pattern. Point process models are typically used to describe the data as close as possible and to summarize the statistical properties of the observed point patterns with few parameters (e.g. to investigate if the degree of clustering of tree species is correlated with their dispersal syndrome; Seidler and Plotkin 2006). However, point process models can also be used to represent the expected spatial pattern according to specific ecological hypotheses that are being tested (Shen et al. 2009). Comparison among alternative point process models allows for an assessment of the relative importance of different mechanisms in generating the observed patterns (Shen et al. 2009, Wang et al. 2013, 2015; Fig. 2).

Null models are a subclass of point process models and formalize a particular null hypothesis in ecology. Basically, null models create the spatial patterns that are expected in the absence of a particular ecological mechanism by means of the randomization of ecological data where certain elements of the data are held constant, and others are allowed

to vary stochastically (Gotelli and Graves 1996: p. 3). The null model is therefore used to determine whether there is spatial structure in the data that does not exist in the null model. Although this approach is often not very informative for univariate patterns (e.g. Fig. 2A, E), it can be useful for detecting spatial structure in more complex data types which are often extremely relevant for ecologists (Fig. 3, 4).

The simplest null model for univariate patterns is the homogeneous Poisson process, according to which points are located randomly and independently within the observation window W (i.e. the pattern shows 'complete spatial randomness'; CSR). CSR patterns are realizations of the null hypothesis of the absence of spatial structure in the underlying ecological processes (e.g. there is no spatial trend or associations among points), but these conditions are often not met by real world patterns. For example, saplings of *G. dumetorum* are clearly not distributed randomly, but are aggregated and may be additionally influenced by environmental conditions (Fig. 2A, E, F). This suggests that additional ecological mechanisms, such as dispersal limitation or habitat filtering, are operating.

The hypothesis that a spatial pattern is driven only by the abiotic environment can be represented by the more complex heterogeneous Poisson process (HP). Instead of using a constant intensity λ as in the CSR model, the HP null model is based on a spatially varying intensity function (Fig. 1B), which can be estimated through non-parametric techniques (Wiegand and Moloney 2004, Law et al. 2009) or parametrically using a set of environmental variables (Diggle 2003, Elith and Leathwick 2009, Renner et al. 2015). In our example, the HP null model (Fig. 2B) does not account for all spatial structure in the observed pattern (Fig. 1A), since the observed values of $g(r)$ are substantially greater than their

expectation under HP (closed disks and grey line in Fig. 2F, respectively). Thus, additional clustering mechanisms, independent of the environmental effects, may operate.

The most important point processes that can generate realistic spatial structures for ecological applications are cluster processes (generally called Poisson cluster processes; Diggle 2003). For the most commonly used Thomas cluster processes, there are analytical expressions for $g(r)$ and $K(r)$ (Wiegand et al. 2009, Wiegand and Moloney 2014: section 4.1.4), which allow the parameters of the process to be easily fit from the observed data. These also include more complex types of Thomas processes that can describe two critical scales of clustering, for example small clusters of points located within larger clusters (Fig. 2C). Such a point process is able to generate patterns that closely match several summary statistics [i.e. $g(r)$, $L(r)$, $H_s(r)$, and $D(r)$; Fig. 2G, K]. Cluster processes can also simultaneously account for a spatially varying intensity function (Shen et al. 2009, Waagepetersen and Guan 2009; Fig. 2D, H). Point processes that describe species interactions such as competition, however, require more complex procedures for model fitting (e.g. Gibbs or Markov processes; Diggle 2003: section 5.7, Illian et al. 2008: section 3.6, Genet et al. 2014).

An important null hypothesis for bivariate patterns is that of independence of the two univariate component patterns (Goreaud and Pélissier 2003), which corresponds to the absence of interactions between the two patterns (Getzin et al. 2014). A null model testing for independence must preserve the observed structure of the two univariate patterns, but remove the spatial association between them (Dixon 2002, Wiegand and Moloney 2014). One implementation of the null hypothesis of independence is through the application of a toroidal shift, where one pattern is shifted as a whole against the other, following toroidal geometry (Goreaud and Pélissier 2003). Using this null model we find significant and positive small-scale association between newly recruited *Eugenia galalonensis* individuals and conspecific reproductive trees (Fig. 3A). If the two patterns show a hierarchy where only one pattern is likely to influence the other, as in this example, an antecedent condition null model is appropriate, where the antecedent pattern is fixed and the other pattern is randomized.

The simplest null model for qualitatively and quantitatively marked patterns is random labeling (or independent marking), which conserves the locations of points, but randomly shuffles marks (or the values of the marks) over the points (Kenkel 1988, Goreaud and Pélissier 2003). It corresponds to the null hypothesis that the points of the pattern are independently marked. Random labeling is therefore used to assess whether the marking process acted in a spatially correlated way over the locations of the points. Departures from random labeling may be caused by larger-scale spatial trends in the marks imposed by the environment (first-order effects) or by interactions (second-order effects). To factor out larger-scale trends in the marks we may shuffle the marks only locally (i.e. local random labeling; Wiegand and Moloney 2014: section 4.4.2.2). Random labeling allows important ecological hypotheses to be tested, for example, the random mortality hypothesis which states that mortality of trees or shrubs does not depend on interactions with neighboring individuals. In our example, local ran-

dom labeling cannot reject the random mortality hypothesis (Fig. 3C–F). Comparison of the expected mark connection functions under random labeling (black horizontal lines) with the expectation under local random labeling (grey lines) suggests larger scale heterogeneity in mortality (Fig. 3D). Note that testing for independence or CSR corresponds to different ecological questions than using random labeling (Goreaud and Pélissier 2003), although this approach has been taken by a number of studies, as indicated by the category 'wrong selection of independence' (Supplementary material Appendix 1, Table A1) in our analysis of the literature.

Comparison of data and models

An important step in SPPA is the comparison of the observed pattern with patterns generated by stochastic point process or null models. In ecology, Monte Carlo methods are mostly used for this purpose. First, we generate multiple realizations of the null model or point process (e.g. 199 or 999 replicate patterns), second, we estimate the summary statistics of the observed pattern and of each of the replicated patterns. Third, we compare the summary statistics of the observed pattern to those of the replicated patterns to determine if the observed data fall outside the typical range of the patterns produced by the model (Baddeley et al. 2014). In ecology, 'pointwise' simulation envelopes are mostly used for this purpose. They are for example the 5th lowest and highest values of the pair correlation functions of 199 simulated patterns at distance r (Baddeley et al. 2014), which yield a significance level of $\alpha = 0.05$ for a fixed distance r. If the observed summary statistic lies at some distance r outside the pointwise simulation envelopes it is often taken as evidence of a departure from the null hypothesis. Figures 2–4 show simulation envelopes for various data types and null models. For example, Fig. 3A indicates that recruits of *E. galalonensis* strongly aggregate within distances of 5 m around conspecific reproductive trees because the observed $g_{12}(r)$ is at these distances clearly outside the pointwise simulation envelopes.

However, departures of the observed summary statistic from the pointwise simulation envelopes cannot be used to reject the null model with significance level α because this analysis typically conducts multiple tests, one at each spatial distance r, and is prone to type I error inflation (Loosmore and Ford 2006). More refined simulation envelopes (e.g. global envelopes) or goodness-of-fit tests are required for this purpose (Diggle 2003, Loosmore and Ford 2006, Grabarnik et al. 2011, Baddeley et al. 2014, Myllymäki et al. 2015, 2016). The number of simulations influences the accuracy in the estimate of the simulation envelopes. Therefore, higher numbers of simulations of the null model will be required in a confirmatory context (Loosmore and Ford 2006).

Consideration of heterogeneity

Consideration of heterogeneity is important for biological and technical reasons. First, quantification of the impact of the environment on species distribution patterns is a key task in ecology. In particular, SPPA is used to determine the relative importance of niche vs neutral theories to explain species coexistence (Shen et al. 2009, Wang et al. 2013,

2015). The most elegant solution is to include the information on environmental covariates for estimation of the intensity function $\lambda(\mathbf{x})$ (e.g. Fig. 1B) and apply inhomogeneous second-order summary statistics (Baddeley et al. 2000, Law et al. 2009). Figure 2D shows a realization of an inhomogeneous Thomas cluster process (Waagepetersen and Guan 2009), which considered an estimate $\hat{\lambda}(\mathbf{x})$ of the underlying intensity function in fitting the model. This point process provides a good description of both, the small- and larger scale pattern in the data [i.e. $g(r)$, and $D(r)$; Fig. 2H, L)], yet a heterogeneous Poisson process, which only considers $\hat{\lambda}(\mathbf{x})$ (Fig. 2B), does not describe the full clustering present in the pattern (Fig. 2F, J).

Second, most methods of SPPA were originally developed for homogeneous patterns but real world ecological datasets usually show some level of heterogeneity (Fig. 1A, B). Besides using inhomogeneous summary statistics, several simple methods exist to deal with heterogeneity (Wiegand and Moloney 2014: section 2.6). Failing to consider heterogeneity may result in incorrect inference (Pélissier and Goreaud 2001). For instance, a common problem arises when the L-function is applied to point patterns consisting of large areas void of points. This may for example happen if the observation window includes areas such as rocks or ponds, which cannot be colonized. In this case the diagnosis of 'aggregation at all scales' is frequently made, but may only reflect a first-order effect that obscures possible second-order effects (i.e. virtual aggregation; Wiegand and Moloney 2004).

Results of review

General descriptors

In the 1980s just a few ecological studies applied modern techniques of SPPA (Sterner et al. 1986, Kenkel 1988) but they became more common from 1998 onwards (Fig. 5A). Study sites were spread over most of the globe (Fig. 5B). A majority of the 308 studies focused on plants, mostly trees (65.9%), but included also animal structures or captures (7.8%), or fire events (2.6%) (Fig. 5C). Approximately half of the studies analyzed point patterns with relatively few points (< 100) (Supplementary material Appendix 1, Fig. A1d) and although the analyses were conducted with spatially-explicit data, only 62% of the studies contained at least one map of the point patterns. Most of the articles (55.2%) tested a hypothesis; 29.5% of which addressed specific ecological questions, and 14.9% presented or tested new methods (Supplementary material Appendix 1, Fig. A2a).

Data types

Most of the studies analyzed univariate patterns (82%). In contrast, only 44% considered bivariate patterns, 21% qualitatively marked patterns, and 6% of studies considered quantitatively marked and multivariate patterns (Supplementary material Appendix 1, Fig. A2b). However, a large proportion of the studies analyzed several data types; 39% analyzed both uni- and bivariate patterns, and 16% analyzed univariate and marked patterns.

Summary statistics

Authors have used a considerable variety of summary statistics, and have often adapted the existing ones to better accommodate their specific needs. However, a majority of studies (75%) used K- or L-functions as summary statistics, 53% of them exclusively (Fig. 5D). In contrast, summary statistics of the pair-correlation function family were used in only 27% of the studies (Fig. 5D). This is unfortunate since these are more informative than the K/L-family because they are non-cumulative (i.e. provide better quantification of the effects at specific spatial scales) (Wiegand and Moloney 2004, Perry et al. 2006, Law et al. 2009). Use of multiple summary statistics was not widespread; 10% of the papers combined the K- and g-families of statistics, but only 6% used K- or g-summary statistics together with other summary statistics (but see Sterner et al. 1986, Barot et al. 1999).

In general, the problem of edge correction, which occupied authors of earlier studies, has been mostly resolved. Most of the studies we examined used pairwise-weighted (41%) or global edge correction (21%) (Supplementary material Appendix 1, Fig. A2f).

Null models and point process models

Most of the 254 studies that conducted univariate analysis tested the CSR hypothesis (86%) (Fig. 5E). In contrast, only 15% of them used CSR in combination with another univariate null model or point process model. More than half of all studies used only CSR in combination with the K-function family. The use of null models other than CSR has only recently become more frequent in univariate analyses (Supplementary material Appendix 1, Fig. A3a). The most frequent null model used in the 135 studies conducting bivariate analysis was the toroidal shift (39% of the studies), followed by bivariate CSR (33%). Unfortunately, 26% of all studies that conducted bivariate analysis did not clearly state the null model used (Fig. 5E).

Data comparison

The overwhelming majority of studies (93%) used Monte Carlo simulations and pointwise simulation envelopes, and 12% of all studies also used a goodness-of-fit (GoF) test to assess the overall fit of the null model over a distance interval of interest. The number of simulations of the null model strongly varied but was often low (≤ 100; Fig. 5F).

Heterogeneity

We found that, up to 1998, approximately 80% of the studies examined were conducted for homogeneous patterns, but this proportion dropped to 50% afterwards (black symbols in Supplementary material Appendix 1, Fig. A3e). One quarter of all studies considered heterogeneity explicitly, and
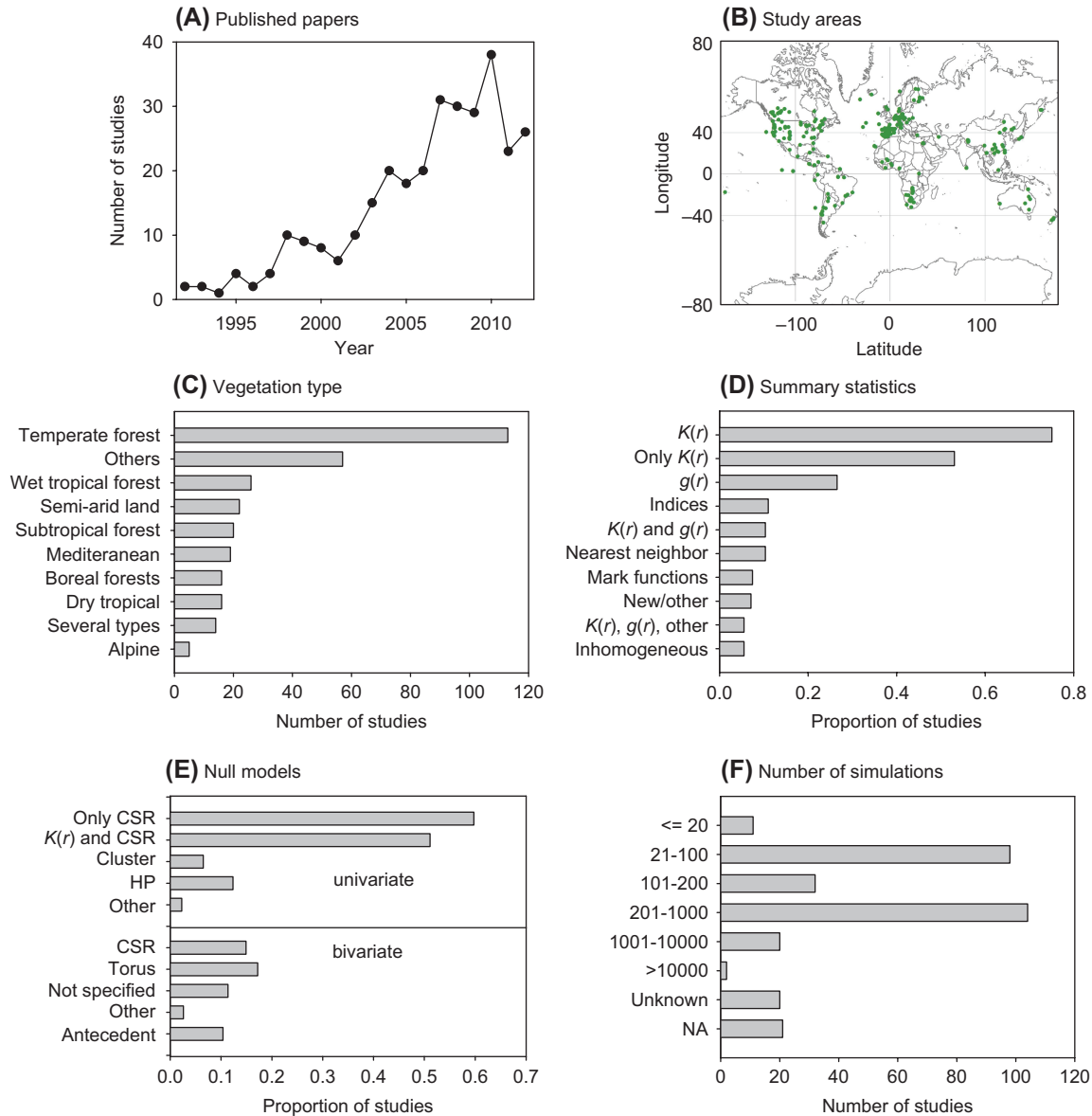
Figure 5. Results of the literature review. (A) Number of studies published per year included in our analysis. (B) Geographical location of the study sites. (C) Number of studies performed in different vegetation types. (D) Proportion of articles that used a given summary statistic or a combination of summary statistics; inhomogeneous refers to inhomogeneous second-order summary statistics, and mark functions to mark correlation or mark connection functions. (E) Proportion of articles using a different null model. The upper part of the panel shows univariate null models and the lower part bivariate null models. (F) Number of articles using a certain number of simulations of the null model.

another quarter of the studies exhibited indications of virtual aggregation. Interestingly, out of the 159 studies that conducted the simplest analysis (i.e. used the *K*-function family together with CSR for univariate patterns), eighty were conducted for homogeneous patterns, but sixty (= 19% of all studies investigated) showed virtual aggregation. Finally, just seventeen studies (11%) used inhomogeneous second-order summary statistics.

Discussion

In this study we reviewed the use of different elements of spatial point pattern analysis (SPPA) in ecology and related disciplines. A major conclusion emerging from our review is that, despite publication of several conceptual papers and books on the topic during the last several decades, the majority of the studies examined here underused the methodological potential offered by modern techniques of SPPA. This is partly understandable since SPPA is not a standard technique learned by ecologists. However, we also detected a creative core of studies that placed SPPA in new contexts and explored a number of exciting opportunities. Below we outline techniques that have great potential in ecological research and provide a list of recommendations for the use of SPPA methods in ecology.

Solved difficulties and persistent challenges

After more than 20 yr of being used in ecology, it appears that a 'standard canon' of techniques of spatial point pattern analysis in ecology has been largely identified and most of the technical issues that occupied users earlier, such as the edge correction, have been solved. The textbook by Illian et al. (2008) provides a comprehensive reference for most of the technical issues that are relevant for the practical use of SPPA in ecology, and more recent techniques are presented in Baddeley et al. (2015). However, our review highlights that many of the most powerful and promising techniques of SPPA have been rarely used in ecology. Indeed, more than half of the reviewed studies were limited to the application of the *K*-function family and the CSR null model for univariate analysis.

An important and persistent challenge in ecology, in general, and in ecological applications of SPPA, in particular, is pattern-process inference; i.e. the problem of establishing the link between spatial patterns and the ecological processes of interest (Watt 1947, Levin 1992, McIntire and Fajardo 2009). This problem partially arises in ecology because SPPA uses static patterns to make inferences on systems where several dynamic processes interact in modifying the spatial patterns. Because of this limitation, we may ultimately not be able to understand the significance of static patterns without implementing a dynamic framework (e.g. individual-based models; Brown et al. 2011, May et al. 2015; see below). However, if spatially-explicit interactions and mechanisms are important for species diversity, community assembly and ecosystem dynamics, spatial patterns observed in these systems should conserve a signature of the underlying processes (Moloney 1993, McIntire and Fajardo 2009).

Beyond the fundamental problem of static patterns vs dynamic processes, we found that difficulties in identifying the pattern-process link are also a consequence of 1) focusing on a single summary statistic, which may fail to detect important features of complex patterns (Wiegand et al. 2013); 2) using null hypotheses such as CSR that are too simplistic to respond to more complex ecological questions; and 3) mistakes in the technical implementation of null models (e.g. heterogeneity not appropriately considered). These three difficulties can be easily overcome by making use of existing techniques. For example, heterogeneity can often be considered in a simple way by heterogeneous Poisson processes with non-parametric kernel estimates (Wiegand and Moloney 2004) or by analyzing internally homogeneous subareas within the observation window (Pélissier and Goreaud 2001).

We also noticed two additional challenges. First, the terminology was quite heterogeneous; many different terms were used for the same summary statistics [e.g. $D(r)$ vs $G(y)$ for the nearest neighbor distribution function], edge correction methods or null models. Second, authors often did not present the data type, the plot size and the number of points in the analyzed patterns. In many cases, graphs showing one or the most typical spatial patterns were neither included, which makes the evaluation of results difficult.

Promising but underused techniques

We start by commenting on general tendencies that emerged through our literature review, before we expand, in more detail, on five recent developments that we find especially promising for ecological applications.

General tendencies

While earlier studies in SPPA were seriously limited by the effort and cost to map point patterns with large sample sizes, this limitation is now less of a concern thanks to the development of new mapping techniques and the increasing availability of remote sensing data sets that can be analyzed with SPPA (Lee and Lucas 2007, Moustakas et al. 2008, Garzon-Lopez et al. 2014). A large number of null models or point processes exist that can be used to test more specific hypotheses or to quantify complex spatial structures. For instance, point processes for characterizing clustering are now quite refined and allow for the detection of two or more critical scales of clustering (Wiegand et al. 2009; Fig. 2C), as are the techniques for the additional consideration of underlying heterogeneity (Waagepetersen and Guan 2009, Wiegand and Moloney 2014; Fig. 2D). The same applies for point processes that consider species interactions (e.g. Gibbs processes; Diggle 2003, Illian et al. 2008, Genet et al. 2014).

However, with exception of a few point process models, where analytical formulas for summary statistics exist (e.g. Thomas processes), fitting of spatial point process models to complex real-world data sets is in general a complicated task. The R package 'spatstat' provides methods to fit a wide variety of point process models as well as diagnostic tools such as residual analysis (Baddeley and Turner 2005, Baddeley et al. 2015). Recent developments include the framework of integrated nested laplace approximation (INLA) that speeds up parameter estimation and can make complex spatial point process models more accessible to scientists of all areas outside of statistics (Illian et al. 2013). New techniques such as wavelet analysis, when applied to point pattern data (Detto and Muller-Landau 2013), also allow for the formulation of biologically motivated point process models and can characterize processes such as dispersal and density-dependent establishment.

Simulation envelopes

Most studies that we reviewed used Monte Carlo simulations and pointwise simulation envelopes to assess departures of the observed point pattern from the null model (e.g. Fig. 2E–L, 3, 4). This is often sufficient for exploratory analysis, but does not allow for rejection of the null model with an a priori defined significance level (e.g. $\alpha = 0.05$ for the 5th largest and smallest values of 199 simulations of the null model; Loosmore and Ford 2006, Baddeley et al. 2014). Myllymäki et al. (2016: their Eq. 17) recently presented a test based on global envelopes that are variable in r and allow for rejection of the null hypothesis with a prescribed significance level α if the observed summary statistic wanders at least at one distance r outside the envelopes (for details see Supplementary material Appendix 2). These global envelopes (red lines in Fig. 3 and 4) are clearly wider than the pointwise simulation

envelopes (black lines) and would reject the null model less often. Because estimation of these global envelopes does not require more simulations than constructing the pointwise simulation envelopes, we encourage their use to avoid spurious rejection of null models. However, all these methods are conservative if parameter fitting is involved (Diggle 2003, Myllymäki et al. 2016).

Sometimes it is important to directly compare the strength of departures from the null model among analyses of different objects, e.g. different species. In this case effect size transformation (also called z-scores or studentized scaling; Myllymäki et al. 2015, Eq. 2 in Supplementary material Appendix 2) of the summary statistics can be used (Getzin et al. 2014, Punchi-Manage et al. 2015). The distribution of the effect sizes for different species at a given distance r provides a better assessment of the nature of departures from the null model than the proportion of species with significant departures.

Quantitatively marked patterns

The low proportion of articles analyzing quantitatively marked patterns is somewhat surprising because these methods exist for a long time (Penttinen et al. 1992) and because most field surveys routinely record properties in addition to the spatial location of ecological objects (e.g. height and diameters of trees). Application of bivariate mark correlation functions allows in our example for a detailed assessment of the relationship between the size of individuals of the focal species *E. galalonensis* and the size of heterospecific trees a distance r away (Fig. 1E). Under interspecific competition we would expect that *E. galalonensis* individuals with nearby heterospecific neighbors would be smaller than expected by a null model that randomly shuffles the sizes of *E. galalonensis* locally (here within 100 m). This null model factors out possible larger-scale heterogeneity in tree sizes. Indeed, we find that tree sizes in the null model simulations show a spatial correlation (grey line in Fig. 4C) which indicates spatial trends in the sizes of *T. pallida*. As a consequence, the assessment of standard random labeling (Supplementary material Appendix 2, Fig. A5a–c) differs from that of local random labeling (Supplementary material Appendix 2, Fig. A5d–f). Figure 4B shows that *T. pallida* trees with a nearby heterospecific neighbor are on average slightly smaller than *T. pallida* trees where heterospecifics are more distant. This result is confirmed by the summary statistic $I_{m1m2}(r)$, the standard Pearson correlation coefficient between the size m_1 of a *T. pallida* tree and the size m_2 of a heterospecific tree a distance r away (Fig. 4D). However, a large part of the negative correlation is caused by the spatial trends in the sizes of *T. pallida* trees (grey line in Fig. 4D).

Multivariate patterns

One of the most difficult challenges of SPPA in ecology is to describe spatial patterns in species, functional and phylogenetic diversity in plant communities through the use of multivariate summary statistics. An increasing number of larger data sets of fully mapped plots from hyper-diverse systems, such as the BCI forests plot in Panama (Condit 1998) or the sclerophyll shrublands of southwestern Australia (Perry et al. 2008), are now available for this purpose. Shimatani (2001) and Shimatani and Kubota (2004)

pioneered the use of spatially-explicit, point pattern extensions of classical diversity indices in multivariate point patterns. For example, they introduced the spatially-explicit Simpson index $\beta(r)$ defined as the conditional probability that two individuals are heterospecific given that their separation distance is r. This summary statistic is related to the distance decay of similarity (Wang et al. 2015). Recently developed multivariate summary statistics include also the individual species–area relationship ISAR (Wiegand et al. 2007, Punchi-Manage et al. 2015), which quantifies the species richness in neighborhoods within radius r of a focal species, and extensions of $\beta(r)$ and ISAR to incorporate pairwise species dissimilarity (Shen et al. 2013, Wiegand and Moloney 2014, Pélissier and Goreaud 2015, Wang et al. 2015, 2016). These new methods allow for detailed quantification of phylogenetic and functional diversity in fully mapped plots and will improve our understanding of the major drivers of biodiversity patterns.

Another interesting and more recent development in multivariate SPPA is the concept of point pattern null communities (Shen et al. 2009, Wang et al. 2013, 2015). Figure 2 illustrates the assembly of null communities: a point process is fitted for each species to its distribution pattern and stochastic realizations for each species are independently superimposed to obtain one null community. Null communities that assume CSR for each species (Fig. 2A) contain no spatial structure and serve as point of reference to evaluate the relative importance of spatial processes (e.g. dispersal limitation) or the environment (i.e. habitat filtering) to produce certain spatial patterns in diversity. In contrast, null communities assembled with the heterogeneous Poisson process (Fig. 2B) are structured only by habitat filtering, whereas null communities assembled with homogeneous cluster processes (Fig. 2C) are structured only by biotic processes, such as dispersal limitation. Finally, null communities based on inhomogeneous Thomas processes (Fig. 2E) or inhomogeneous pattern reconstruction (Wiegand et al. 2013) reproduce all aspects of the general spatial structure of the individual species patterns. Because the null communities assume independent superposition of species patterns, departures from the data can be attributed to the effect of species interactions (Wang et al. 2015).

Linking traits to species patterns

Coupling large multi-species spatial data sets, such as the BCI data, with functional-trait data is a promising approach for linking spatial patterns to ecological processes. In a first step in doing this, key properties of spatial structure, such as the mean cluster size, are quantified for many species by fitting point process models to the data (e.g. Fig. 2C, D). In a second step, these key properties are then correlated to species traits, such as dispersal syndromes, to reveal a link between pattern and process (Seidler and Plotkin 2006). Getzin et al. (2014) and Velázquez et al. (2015) linked point pattern measures of bivariate species co-occurrence to species traits. Getzin et al. (2014) showed that animal dispersed plant species in the BCI forest tended to show independence between recruits and adult conspecifics, whereas species with explosive seed dispersal tended to show positive small scale associations and wind-dispersed segregation. Velázquez et al. (2015) showed that interspecific spatial association of recruits

was in the BCI forest positively related to trait similarity in terms of topographic habitat preferences and dispersal mode, but inversely related in terms of wood specific gravity and shade-tolerance.

Linking SPPA with dynamic models

One of the most fundamental limitations of the current use of SPPA in ecology is that patterns that emerge from the interaction of dynamic processes are studied by analyzing static point patterns (Wiegand and Moloney 2014). This problem can only be overcome by linking SPPA with stochastic, spatially-explicit and individual-based simulation models that incorporate (simplified) representations of the dynamic processes that are hypothesized to generate the patterns (Grimm et al. 2005). Despite some early attempts (Jeltsch et al. 1999), using the full potential of this approach has only become possible with the advent of methods of statistical inference for stochastic simulations models that allow fitting the parameters of dynamic simulation models to point pattern summary statistics (Hartig et al. 2011, Lehmann and Huth 2015). Using this framework, May et al. (2015) showed that multivariate spatial patterns can indeed provide important additional information (compared to e.g. the non-spatial species abundance distribution) that can be used to identify underlying processes.

Recommendations (protocol for methods of SPPA)

We conclude with a brief checklist for authors and reviewers on the use and documentation of common key elements of SPPA in ecology. Such a list can help to avoid the most common pitfalls. To reduce confusion in the use of terms and mathematical symbols, we recommend using those of the reference textbook of Illian et al. (2008).

Data types

The data type, plot size and number of points of the analyzed point patterns should always be presented. A figure showing one or more typical spatial patterns should also be included (at least in an appendix), to allow better evaluation of the results.

Summary statistics

Non-cumulative, second-order summary statistics are the preferable tool because they allow for an intuitive assessment of scale dependent effects. However, they should be complemented by additional summary statistics (e.g. cumulative and nearest neighbor based ones) to depict different aspects of the spatial structure present in the data. The edge correction method, and the software used should be reported. When fitting parametric point processes to the data, the best possible estimator should be selected because the detailed shape of the summary statistic matters.

Null models and point process models

Null models and point process models translate ecological questions and hypotheses into the language of point pattern statistics. Therefore, the research questions or hypotheses should be clearly stated and the null model should be properly justified. The first step of an analysis is usually to confirm that the data contain non-random structures caused by heterogeneity or species interactions (see below 'Heterogeneity'). However, the next step of deriving or testing hypotheses on the underlying ecological processes often requires more specific point process models. If the task is to test predictions, point process models should represent a priori hypotheses based on ecological theory and knowledge.

Model data comparison

If the objective of the study is exploratory and the main interest of the analysis is to find out if the null model can be clearly accepted or rejected, it is sufficient to use pointwise simulation envelopes with an intermediate number of simulations (e.g. 199). However, if the objective is confirmatory and/or requires a better resolution of the 'blurry' zone where data are close to the null model, substantially more simulations may be required. This is especially true for patterns with a smaller numbers of points. To avoid problems of simultaneous inference, goodness-of-fit tests (Loosmore and Ford 2006) or global envelopes (Myllymäki et al. 2016; Supplementary material Appendix 2) can be used. Finally, figures showing observed vs. expected summary statistics and the simulation envelopes should be included if possible.

Heterogeneity

The data should be checked for signals of heterogeneity that may compromise the conclusions of the analysis. This can be done, for example, by investigating for heterogeneity of the intensity function or trends in the values of the marks, or by use of CSR, toroidal shift or random labeling null models, Getzin et al. (2008). To remove the effects of heterogeneity researchers can now choose among several relatively simple methods, but more refined approaches based on parametric estimation of the intensity function and inhomogeneous summary statistics are also available.

Conclusions

After 20 yr of use, the basic techniques of spatial point pattern analysis have now largely been incorporated into ecological studies. They provide a powerful battery of methods to extract information about the underlying processes from the spatial locations of ecological objects such as plants or animal structures and captures. The results of our literature review indicate that some challenges, such as developing multivariate summary statistics or appropriately establishing the links between the spatial patterns and the processes of interest, still remain. Given the rapid advance in remote sensing and digital mapping technologies, which allow easy collection of data sets unthinkable a few years ago, exciting new possibilities emerge for applying SPPA. However, our results also highlight that many of the most powerful and promising techniques, some of them available for one or two decades and relatively easy to apply (e.g. methods to analyze marked point patterns), are still unknown to a broader audience of ecologists. We can firmly state after our review that a majority of studies substantially underused the potential offered by modern SPPA. We argue that point pattern analysis is more than the *K*-function and random (CSR) null models, which are frequently associated with the use of

SPPA by ecologists. Instead, they would greatly benefit from adopting the wide range of available techniques to decode the cryptic but valuable information comprised by spatial point patterns in nature.

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Supplementary material

Appendix 1-3

Appendix 1. Detailed results of literature review

Appendix 2. Additional results of global envelopes

Appendix 3. List of papers analyzed

Appendix 4. Key references and links for software packages appearing in Figure 4F.

Appendix 1. Detailed results of literature review

Evaluation of articles

Table A1 shows the different categories we used to describe each study. We first recorded a number of basic descriptors such as the year of publication, the journal, the ecological object (e.g., trees or fire events), the vegetation type, and how SPPA was used (e.g., if specific hypotheses were tested or if the study presented mainly a new method). Next we recorded details on the basic elements of SPPA described above (i.e., data types, summary statistics, null models, data comparison, and heterogeneity). Finally, we also recorded the software used for the point pattern analysis.

In some cases we simply report the relative proportion of studies that fall into the different categories shown in Table A1; however, in other cases we were interested in the temporal development of the use of different elements of SPPA. In these cases we used an index $C(t, c)$ that gives the proportion of all studies published up to year t that fall within a given category c. We estimate this "proportion of cumulative studies" as $C(t, c) = P(t, c)/a(t)$ where $P(t, c)$ is the number of cases where category c applied up to year t and $a(t)$ is the number of articles in our sample published up to year t. Some of the categories were non-exclusive so that the index $C(t, c)$ may add up to a value larger than one. Because only 11 studies in our sample were published before 1997 (Fig. 1A), we estimated $C(t, c)$ for years 1997 to 2012.

Results

General descriptors

In the 1980s just a few studies applied modern techniques of SPPA to ecological questions (e.g., Galliano 1982, Sterner et al. 1986, Getis and Franklin 1987, Kenkel 1988). By the 1990s such studies appeared more regularly, becoming increasingly common from 1998 onwards (Fig. A1a). Study sites were spread over most of the globe with some local clusters in central

Europe (Fig. A1b). The 308 Studies on SPPA analyzed here were published in 92 different journals, but the distribution of studies over the journals was highly skewed; nine journals accounted for half of the studies, with *Journal of Vegetation Science* (39 studies), *Forest Ecology and Management* (38), and *Plant Ecology* (21) being the journals where most of the studies were published. When looking at categories of journals publishing more than 5 studies, we found that 71 studies were published in journals focusing on plant ecology, 62 studies were published in forestry journals, and 54 in general ecology journals (e.g., *Ecography*, *Ecology*, or *Acta Oecologica*). The ecological objects studied closely mirrored the subject matter of the respective journals, with an overwhelming number of studies conducted on trees (203), followed by shrubs (26), animal structures or captures (24), herbs (21) and fire events (8). Most of the studies of vegetation were conducted in forests (175), primarily in temperate latitudes (113). A small number of studies were also conducted in areas of semi-arid vegetation (22) and Mediterranean climate (19) (Fig. A1c). Approximately half of the studies analyzed point patterns with relatively few points (< 100), but the other half considered 100 to 800 points (Fig. A1d). Although the analyses were conducted with spatially explicit data, only 62% of the studies contained at least one map of the point patterns.

When looking at the way SPPA was used in the 308 articles, we found that most articles (170) tested a hypothesis, 91 articles addressed specific ecological questions, and 46 articles predominantly presented new methods or tested new methods. The proportion of articles that tested methods decreased after 1998 (blue symbols in Fig. A2a) and those presenting new methods increased after 2000 (green symbols in Fig. A2a).

Data types

Most of the studies examined presented analysis of univariate patterns (82%). In contrast, 44% considered bivariate patterns, 21% qualitatively marked patterns, and only 6% of studies considered quantitatively marked and multivariate patterns (Fig. A2b). The relative

proportions of the different types of analyses also did not change much over time (Fig. A2b). A large proportion of the studies analyzed several data types. Thirty-nine percent of the papers analyzed both uni- and bivariate patterns, and 16% analyzed univariate and marked patterns.

Summary statistics

Authors have used a considerable variety of summary statistics, and have often adapted existing ones to better accommodate their specific needs. However, a majority of studies (75%) used K- or L-functions as summary statistics, 53% of them exclusively (Fig. A2c). In contrast, summary statistics of the pair-correlation function family, which are often more informative, were used in only 27% of all studies. Indices were used in 11% of the studies and nearest neighbor distribution functions in 10% (Fig. A2c). Use of multiple summary statistics was not widespread; 10% of the papers examined combined the K- and g-families of statistics, but only 6% used K- or g summary statistics together with other summary statistics (Fig. A2c). Early exceptions are the studies by Sterner et al. (1986) and Barot et al. (1999).

Figures A2d and e show how the use of the different summary statistics changed over time. During the last ten years, the proportion of articles using $K(r)$ or $L(r)$ functions has decreased while the number of those using $g(r)$ functions or functions adapted for quantitatively marked or inhomogeneous patterns has increased (Fig. A2d). Regarding the different types of summary statistics, indices and nearest neighbor summary statistics were frequently used before 2000, but their use has strongly declined since then (Fig. A2e).

Edge correction

Roughly one quarter of all studies did not clearly state the edge correction method used (Fig. A2f) and often referred to papers that presented several edge correction methods. In 8% of the studies the authors did not use edge correction, whereas 8% and 4% of studies (mostly old

ones) used minus- or plus sampling edge correction, respectively (Fig. A2f). In most of the studies, various pairwise-weighted edge correction (41%) and global edge correction (21%) methods were used. After 2003, the proportion of studies using pairwise-weighted edge correction methods declined somewhat at the expense of global edge correction methods (Fig. A2f), especially within the context of the use of the software *Programita*.

In general, the problem of edge correction, which occupied authors of earlier studies, has been mostly resolved. Recent textbooks (Illian et al. 2008, Wiegand and Moloney 2014) now provide a detailed treatment of the different options for uni- and bivariate patterns. Pairwise-weighted and global edge-correction methods provide generally similar results in the estimation of second-order summary statistics.

Null models

Most of the 254 studies that conducted univariate analysis used CSR as the null model (86%) (Fig. A3a). In contrast, only 15% of all univariate studies used CSR in combination with another univariate null model or point process model. More than half of all studies exclusively used the CSR null model in combination with the *K*-function family of pattern analysis (Fig. A3a). Surprisingly, the use of null models other than CSR has only recently become more frequent in univariate analyses (Fig. A3a). The heterogeneous Poisson process (HP) was used in 15% of all univariate studies, and cluster processes in 8%, while only 5% of the studies analyzing univariate patterns did not clearly state the null model used.

The most frequent null model used in the 135 studies conducting bivariate analysis was the toroidal shift (39% of the studies), followed by bivariate CSR (33%). Both null models were frequently used over the entire period examined by this review (Fig. A3b). One quarter of all bivariate analyses considered structural constraints, such as an antecedent condition, but the bivariate, heterogeneous Poisson process model was rarely used (9.6% of the studies). It is also interesting that 14% of all bivariate studies modified widely used null

models to better respond to their specific questions and hypotheses. However, 26% of all studies that conducted bivariate analysis did not clearly state the null model used (Fig. A3b). Sixty-four studies used random labeling correctly for qualitatively marked patterns, but eleven studies confused the null models for independence and random labeling.

Data comparison

The overwhelming majority of studies (93%) used Monte Carlo simulations, and 12% of all studies also used a goodness-of-fit test (GoF) to assess the overall fit of the null model over a distance interval of interest. Several studies mentioned the GoF test, but did not use it because of the exploratory character of the study. Interestingly, the proportion of cumulative studies using GoF test dropped to 6% in 2003 but since 2004, it has constantly increased up to 12% (Fig A3c). Because the Monte Carlo simulations are stochastic, there is some uncertainty in the assessment of the simulation envelopes, especially if less than 100 simulations are used. The number of simulations used by the authors in the null model strongly varied. In most cases it was between 200 and 1000 (34 % of published articles) or between 20 and 100 (32%). However, 6% of all studies did not provide the number of simulations (Fig. A3d).

Heterogeneity

We found that, up to 1998, approximately 80% of studies were conducted for homogeneous patterns, but this proportion dropped to 50% afterwards (black symbols in Fig. A3e). The proportion of studies that overlooked heterogeneity (blue symbols in Fig. A3e) and studies that recognized it but used homogeneous techniques (yellow symbols in Fig. A3e) accounted for 14% and 13% of all cases, respectively. In contrast, studies considering heterogeneity in the point pattern methods increased after 2005, making up one quarter of all cases (green symbols in Fig. A3e). Finally, studies that exhibited indications of virtual aggregation made up one quarter of all studies. This reached a peak of 33% in 2000, but then declined due to the

increasing consideration of techniques accounting for various aspects of heterogeneity (Fig. A3e). Interestingly, out of the 159 studies that conducted the simplest analysis (i.e., used the *K*-function family together with CSR for univariate patterns), 50% were conducted for homogeneous patterns, but 38% of these studies showed virtual aggregation.

Software

Appendix 4 in Supplementary material shows the references and links for the most frequently used software programs. The most used software was *Programita* (56) (Wiegand and Moloney 2004, 2014) and spatstat (46) (Baddeley and Turner 2005), which appeared after 2005. All other packages were used in less than 8% of all studies (Fig. A3f). However, 23% of all studies (71) did not specify the software used.

Additional references

Galliano, E.F. 1982. Pattern detection in plant populations through the analysis of plant-to-all-plants distances. - Vegetatio 49:39–43.

Getis, A. and Franklin, J. 1987. Second-order neighborhood analysis of mapped point patterns. - Ecology 68: 474–477.

Table A1. Descriptors and categories used to characterize how the reviewed studies used the five key elements of spatial point pattern analysis in ecology (bold, numbers 1 to 5). The different categories under each key element are given in italics and normal fonts.

Basic descriptors of papers	3) Null models and point process models
year of publication	*Univariate*
journal	homogeneous Poisson (CSR)
number of points	cluster processes
map of pattern included (yes, no)	heterogeneous Poisson (HP)
location of study area	others
*ecological object**	not specified
vegetation type †	*bivariate*
Use of SPPA	antecedent condition
hypothesis testing	toroidal shift
answer specific question	homogeneous Poisson (CSR)
method presentation	heterogeneous Poisson (HP)
method test	other
	not specified
1) Data types	*qualitatively marked patterns*
unmarked	random labeling
univariate	not specified
bivariate	wrong selection of independence
multivariate	
qualitatively marked	**4) Data comparison**
quantitatively marked	*Monte Carlo methods* (yes, no)
	Number of simulations
	Goodness-of-fit test (yes, no)
2) Summary statistics	
indices	**5) Heterogeneity**
second-order summary statistics	homogeneous
$K(r)$ or $L(r)$	heterogeneous, but not recognized
$g(r)$ or $O(r)$	heterogeneity recognized, no specific method
inhomogeneous versions	Heterogeneity recognized, specific methods
nearest neighbor summary statistics	*virtual aggregation* (yes, no)
mark connection or mark correlation functions	
others	**Software**
Edge correction	not specified
minus sampling	*Programita* (Wiegand and Moloney 2014)
plus sampling	Spatstat (Baddeley and Turner 2005)
pairwise weighted edge correction	SPPA (Haase 2001)
global edge correction	ADE (Thioulouse et al. 1997)
no edge correction	other
not specified	

* trees, shrubs, herbs, animal captures or structures, fire events, others

† alpine, boreal forests, dry tropical, Mediterranean, semi-arid land, subtropical forest, temperate forest, wet tropical forest**,** others, several types.
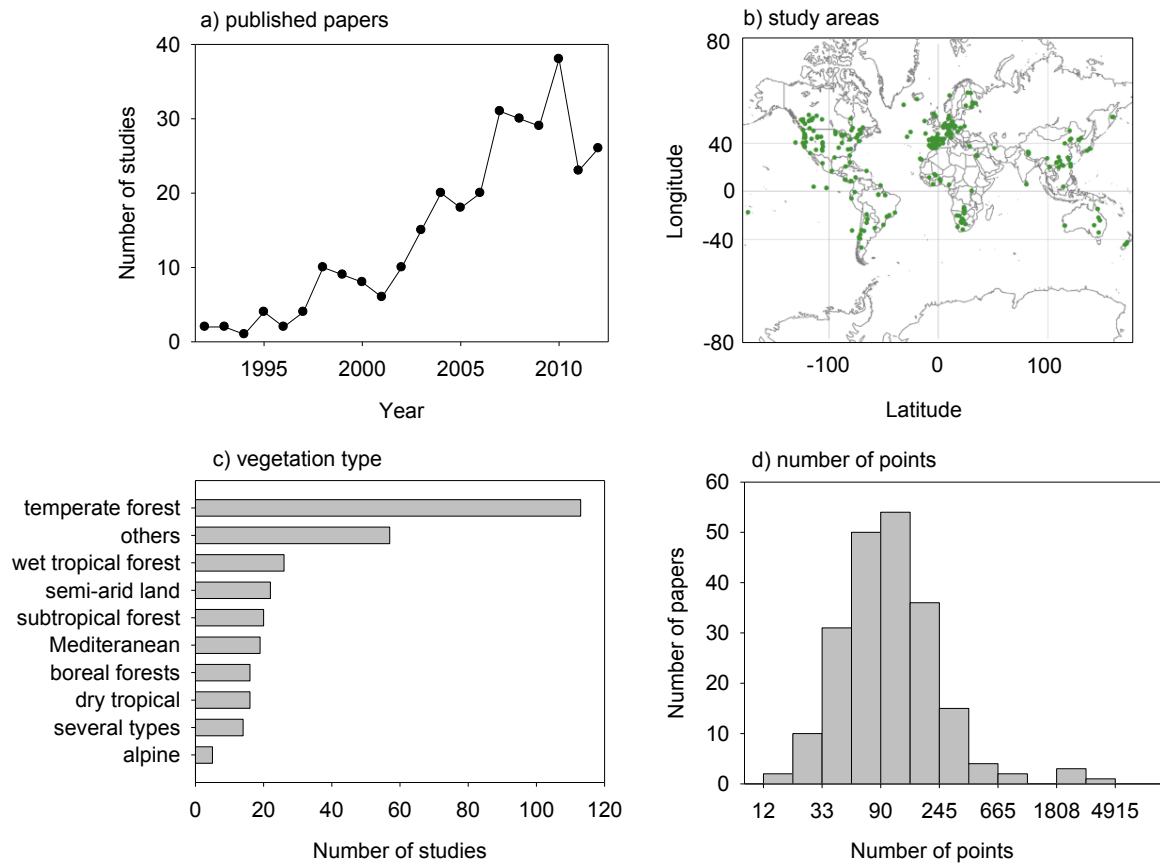
Figure A1. Basic descriptors of the 308 articles using point pattern analysis in ecology and related disciplines over the 1992-2012 study period. (a) Number of studies published per year included in our analysis. (b) Geographical location of the 308 articles using point pattern analysis in ecology and related disciplines. (c) Number of studies performed in different vegetation types. (d) Frequency distribution of the number of points in the patterns.
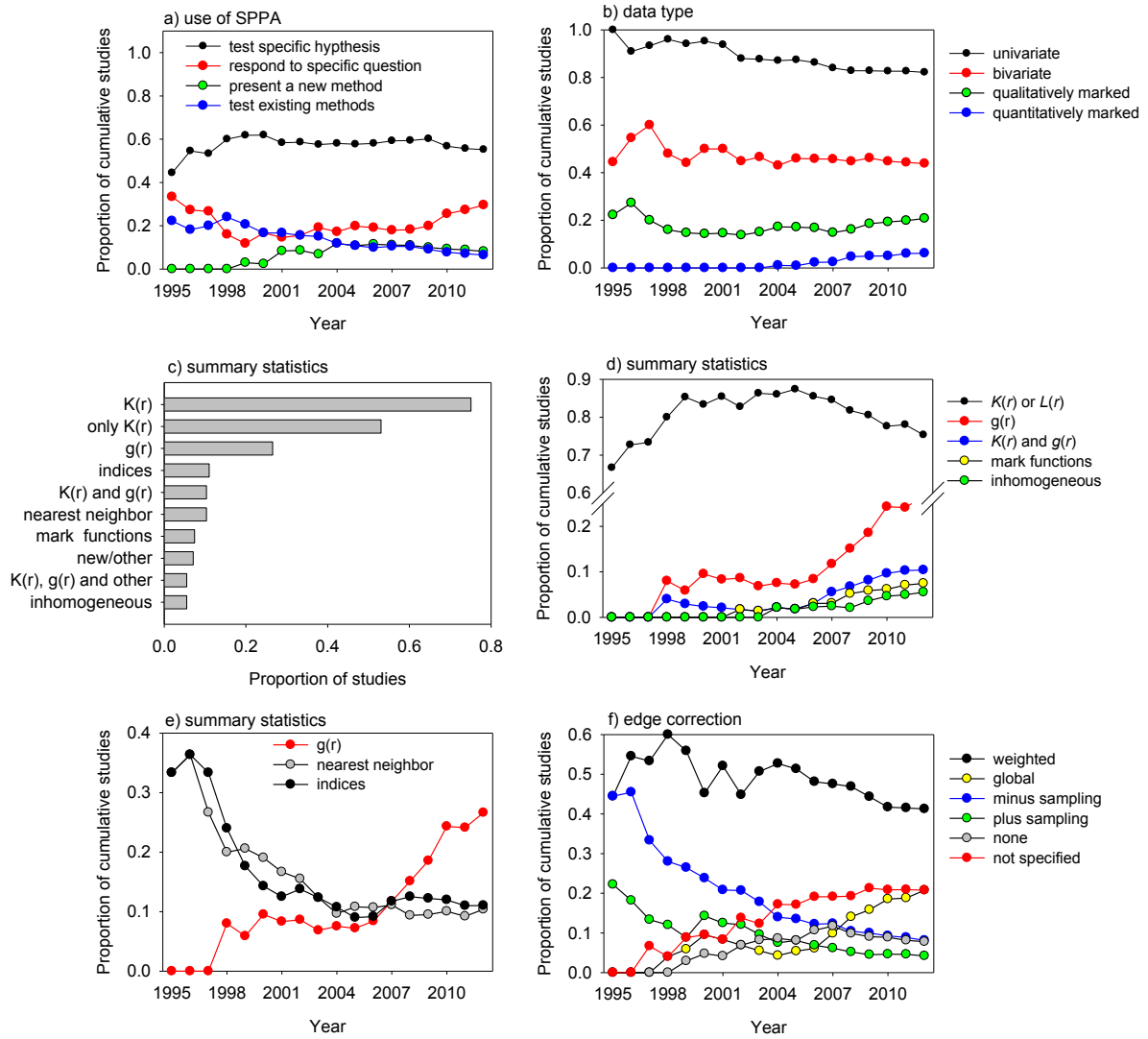
Figure A2. Use of spatial point pattern analysis, data types, summary statistics, and edge correction methods in the 308 studies analyzed. Temporal change in the proportion of articles; (a) that tested hypotheses, answered specific questions, or presented/tested new methods, (b) that analyzed different data types. (c) Proportion of articles that used a given summary statistic or a combination of summary statistics; *inhomogeneous* refers to inhomogeneous second-order summary statistics, and *mark functions* to mark correlation and mark connection functions. (d) Temporal change in the proportion of articles using different types of summary statistics. (e) Same as d), but for indices, nearest neighbor statistics and the pair correlation function. (f) Temporal change in the proportion of articles using different edge correction methods; *weighted* and *global* indicate pairwise weighted edge correction and global edge correction, respectively.

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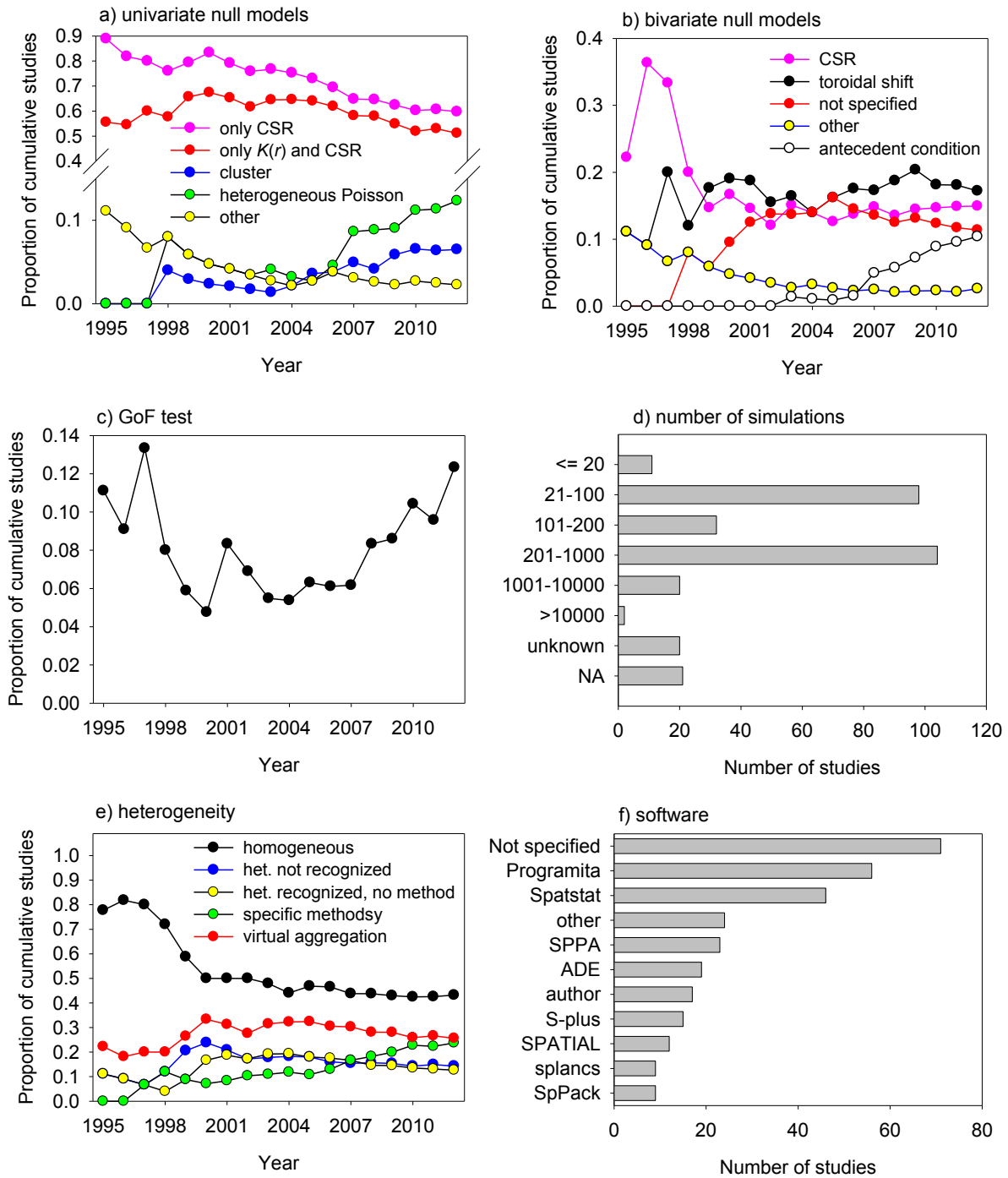
Figure A3. Null models, data comparison, heterogeneity, and software as used in the 308 articles analyzed. Temporal change in the proportion of articles using; (a) different univariate and (b) bivariate null models, (c) a goodness-of-fit test, (d) a certain number of simulations of the null model, (e) different methods to deal with heterogeneity. (f) Number of articles using different software packages. References for software are given in Appendix 4 in Supplementary material.

Appendix 2. Additional results of global envelopes

Global envelopes $S^+(r)$ and $S^-(r)$ that are variable in r were proposed by Myllymäki et al. (2015b) in their section 5 as "global scaled maximum absolute difference (MAD) envelopes". They have the desired property that the null model can be rejected over a given distance interval with significance level α if the observed summary statistic $S(r)$ wanders at one or more distances r outside the simulation envelopes. Note that the pointwise envelopes do not have this property because of the problem of multiple inference (Loosmore et al. 2006).

The global envelopes $S^+(r)$ and $S^-(r)$ are constructed in three steps. First, the summary statistics $S_i(r)$ are estimated from the observed data ($i = 0$) and from the s realizations of the null model ($i = 1,.. s$), and the mean $\bar{S}(r)$ and the standard deviation $\hat{\sigma}_S(r)$ of the $S_i(r)$ are estimated for $i = 1,.. s$. Then, the original summary statistics $S_i(r)$ are student transformed:

$$ S_i^{ses}(r) = \frac{S_i(r) - \bar{S}(r)}{\hat{\sigma}_S(r)}, \tag{1} $$

In ecology this transformation is called standardized effect sizes. Notably, the pointwise simulation envelopes $G_p^-(r)$ and $G_p^+(r)$ of the student transformed summary statistic (e.g., for $\alpha = 0.05$ the 5th lowest and highest values of $S_i^{ses}(r)$ taken from $i = 1, .., 199$) approximate for all distances r the critical value $G_p^-(r) = -z_\alpha$ and $G_p^+(r) = z_\alpha$ with $z_\alpha = 1.96$ for $\alpha = 0.05$. Thus, we have constant pointwise simulation envelopes. This works if the distribution of the $S_i(r)$ for $i = 1, …s$ approximates for fixed values of r a normal distribution. This assumption can be tested by comparing the $G_p^-(r)$ and $G_p^+(r)$ with the critical values z_α and $-z_\alpha$. If the distribution is not symmetric for some values of r one can either use upper and lower quantiles proposed by Myllymäki et al. (2015a,b) or exclude these distances from the distance interval where the global envelope test is applied.

Second, the standard "maximal absolute difference" (MAD) test introduced by Diggle (1979) and Ripley (1979) is applied for the studentised summary statistics $S_i^{ses}(r)$. This test makes sense because the variance of $S_i^{ses}(r)$ under the null model is the same for all distances

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r. The functional summary statistic $S_i^{ses}(r)$ of the ith simulation of the null model is reduced to its minimum and maximum value S_i^{min} and S_i^{max}, respectively, taken over the distance interval $r = r_{min}, .., r_{max}$ of interest. The kth largest value of the S_i^{max} is the upper global envelope G^+, and the kth smallest value of the S_i^{min} is the lower global envelope G^-. Note that this test conducts only one test for the entire interval. For this reason, the problem of multiple inference (Loosmore et al. 2006) does not occur and we can reject the null model with significance level α if $S_0^{ses}(r) > G^+$ or $S_0^{ses}(r) < G^-$ for one or more distances r ($r \geq r_{min}$ and $r \leq r_{max}$).

Third, to obtain the desired global simulation envelopes $S^+(r)$ and $S^-(r)$ that are variable in r we apply the inverse transformation of (1) to G^+ and G^- (see eq. 19 in Myllymäki et al. 2015b):

$$S^+(r) = \bar{S}(r) + \hat{\sigma}_S(r)G^+$$
$$S^-(r) = \bar{S}(r) - \hat{\sigma}_S(r)G^-$$

(2)

The global envelopes $S^+(r)$ and $S^-(r)$ are implemented in the software *Programita*, which can be accessed at www.programita.org

Additional references

Ripley, B.D. 1979. Tests of randomness for spatial point patterns. - Journal of the Royal Statistical Society B 41:368-374.

Diggle, P.J. 1979. On parameter estimation and goodness-of-fit testing for spatial point patterns. - Biometrics 35:87-101.
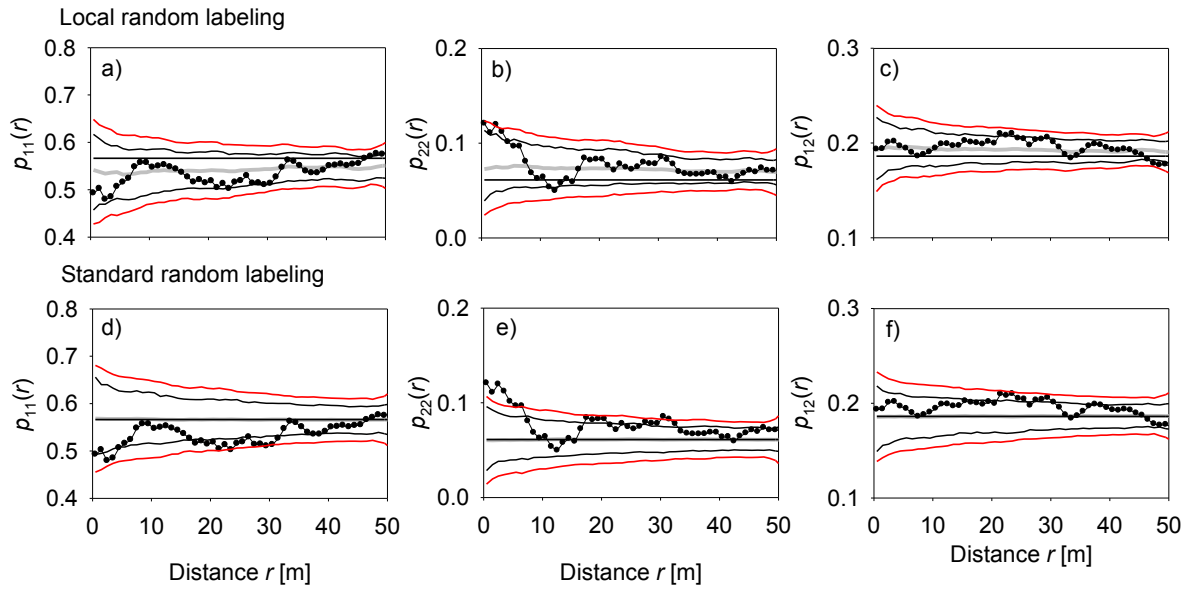
Figure A4. Comparison of the results of standard random labeling and local random labeling for the data of surviving and dead saplings of *E. galalonensis* shown in figure 1D. a) - c) Results for local random labeling (where a given mark is not moved more than 100m), they are the same as in figures 3C - E. The horizontal black line shows the expectation of standard random labeling. Comparison with the expectation of local random labeling (grey bold line) shows that mortality of *E. galalonensis* shows spatial trends. d) -f) Same as a) - c), but for standard random labeling where the marks are randomly shuffled among all saplings.
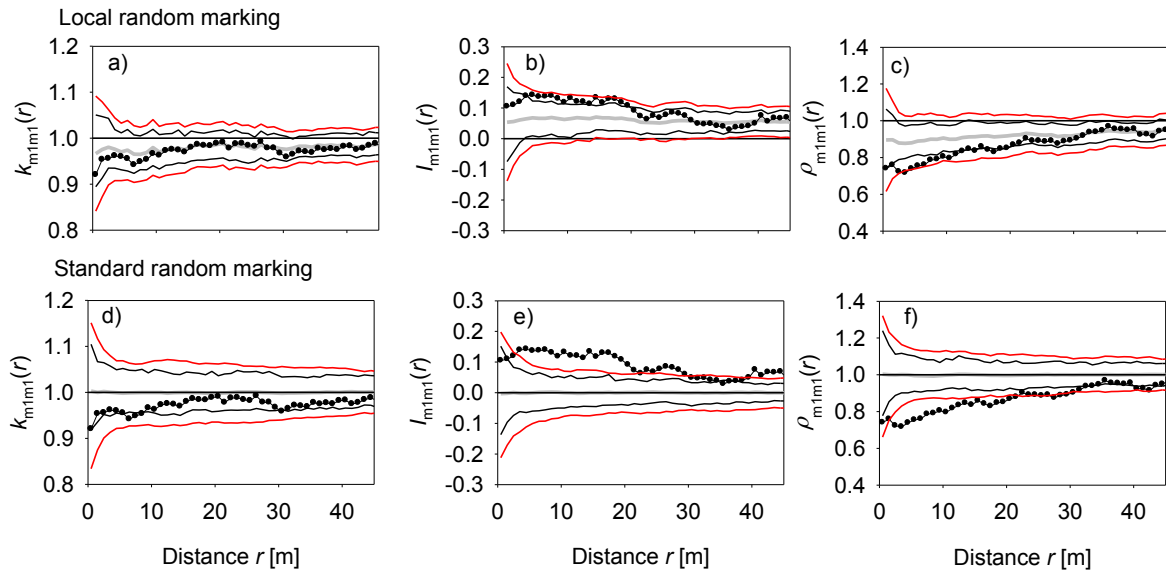
Figure A5. Comparison of the results of standard random marking and local random marking for the quantitatively marked pattern of large trees (dbh > 10cm) of the mid-story tree *Trichilia pallida* shown in figure 1E. a) - c) Results for local random marking (where a given mark is not moved more than 100m). a) is the same as Fig. 5A and b) the same as Fig. 5C, and in c) we show additionally the mark variogram. Comparison with the expectation of local random marking (grey bold line) shows that sizes of *T. pallida* shows spatial trends. d) -f) Same as a) - c), but for standard random marking null model where the marks are randomly shuffled among all large trees.

Appendix 3. List of papers analyzed

Aakala et al. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates and temporal variation. Canadian Journal of Forest Research 37: 50-61.

Aakala et al. 2012. Spatially random mortality in old-growth red pine forests of northern Minnesota. Canadian Journal of Forest Research 42: 899-907

Akhavan et al. 2012. Spatial patterns in different forest development stages of an intact old-growth Oriental beech forest in the Caspian region of Iran. European Journal of Forest Research 131: 1355-1366.

Aldrich et al. 2003. Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession. Forest Ecology and Management 180: 475-491.

Ali et al. 2009. Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. Global Change Biology 15: 1230-1241.

Andersen 1992. Spatial analysis of two-species interactions. Oecologia 91: 134-140.

Arévalo and Fernández-Palacios 2003. Spatial patterns of trees and juveniles in a laurel forest of Tenerife, Canary Islands. Plant Ecology 165: 1-10.

Arévalo et al. 2005. Regeneration in a mixed stand of native *Pinus canariensis* and introduced *Pinus pinea species*. Acta Oecologica-International Journal of Ecology 28: 87-94.

Atkinson et al. 2007. Investigating spatial structure in specific tree species in ancient semi-natural woodland using remote sensing and marked point pattern analysis. Ecography 30: 88-104.

Awada et al. 2004. *Picea glauca* dynamics and spatial pattern of seelings regeneration along a chronosequence in the mixedwood section of the boreal forest. Annals of Forest Science 61: 789-794.

Barbeito et al. 2009. Response of pine natural regeneration to small-scale spatial variation in a managed Mediterranean mountain forest. Applied Vegetation Science 12: 488-503.

Barot et al. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. Ecology 80(6): 1987-2005.

Batista and Maguire 1998. Modelling the spatial structure of tropical forests. Forest Ecology and Management 110: 293-314.

Batllori et al. 2010. Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime. Journal of Biogeography 37: 1938-1950.

Bayard and Elphick 2010. Using spatial point pattern assessment to understand the social and environmental mechanisms that drive avian habitat selection. The Auk 127(3): 485-494.

Beghin et al. 2010. *Pinus sylvestris* forest regeneration under different post-fire restoration practices in the northwestern Italian Alps. Ecological Engineering 36: 1365-1372.

Béland et al. 2003. Structure, spatial distribution and competition in mixed jack pine (*Pinus banksiana*) stands on clay soils of eastern Canada. Annals of Forest Science 60: 609-617.

Belinchón et al. 2011. Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean region. Fungal Biology 115:1270-1278

Berg and Hamrick 1994. Spatial and genetic structure of two sandhills oaks: *Quercus laevis* and *Quercus margaretta* (Fagaceae). American Journal of Botany 81(1): 7-14.

Beverly et al. 2008. Assessing spatial attributes of forest landscape values: an internet-based participatory mapping approach. Canadian Journal of Forest Research 38: 289-303.

Biganzoli et al. 2009. Fire-mediated interactions between shrubs in a South American temperate savannah. Oikos 118: 1383-1395.

Bilek et al. 2011. Managed vs. unmanaged. Structure of beech forest stands (*Fagus sylvatica* L.) after 50 years of development, Central Bohemia. Forest Systems 20: 122-138.

Birkhofer et al. 2010. Assessing spatiotemporal predator-prey patterns in heterogeneous habitats. Basic and Applied Ecology 11: 486-494.

Boudreau et al. 2010. Population dynamics of *Empetrum hermaphroditum* (Ericaceae) on a subarctic sand dune: Evidence of rapid colonization through efficient sexual reproduction. American Journal of Botany 97:770-781

Bourgignon et al. 2011. Are the spatio-temporal dynamics of soil-feeding termite colonies shaped by intra-specific competition? Ecological Entomology 36: 776-785.

Boyden et al. 2005. Spatial and temporal patterns in structure, regeneration, and mortality of an old-growth ponderosa pine forest in the Colorado Front Range. Forest Ecology and Management 219: 43-55.

Burke et al 1998. Effect of density on predation rate for turtle nests in a complex landscape. Oikos 83: 3-11.

Camarero et al. 2000. Spatial pattern of subalpine forest-alpine grassland ecotines in the Spanish Central Pyrenees. Forest Ecology and Management 134: 1-16.

Camarero et al. 2005. Spatial patterns of tree recruitment in a relict population of *pinus uncinata*: forest expansion through stratified diffusion. Journal of Biogeography 32: 1979-1992.

Carcaillet et al. 2009. Spatial variability of fire history in subalpine forests. Ecoscience 16: 1-12.

Castagneri et al. 2010. Diachronic analysis of individual-tree mortality in a Norway spruce stand in the eastern Italian Alps. Annals of Forest Science 67: 304.

Castilla et al. 2012. Disturbance-dependent spatial distribution of sexes in a gynodioecious understory shrub. Basic and Applied Ecology 13: 405-413.

Castillo-Núñez et al. 2011. Delineation of secondary succession mechanisms for tropical dry forests using LiDAR. Remote Sensing of Environment 115: 2217-2231.

Caylor et al. 2003. Tree spacing along the Kalahari transect in southern Africa. Journal of Arid Environments 54: 281-296.

Chen and Bradshaw 1999. Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. Forest Ecology and Management 120: 219-233.

Christopher and Goodburn 2008. The effects of spatial patterns on the accuracy of forest vegetation simulator (FVS) estimates of forest canopy cover. Western Journal of Applied Forestry 23: 5-11.

Chung et al. 2006. Fine-scale genetic structure among genetic individuals of the clone-forming monotypic genus *Echinospora koreensis* (Fabaceae). Annals of Botany 98: 165-173.

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Appendix 4. Key references and links for software packages appearing in Figure 4F.

Software	Key reference	Link
ADE	Thioulouse, J., D. Chessel, S. Dolédec, and J. M. Olivier. 1997. ADE-4: a multivariate analysis and graphical display software. Statistics and Computing 7:75-83.	http://pbil.univ-lyon1.fr/ADE-4/
SPATIAL	Duncan, R. P. 1990. SPATIAL analysis program. Department of Plant Science, Lincoln University, New Zealand.	
Programita	Wiegand, T., and K.A. Moloney. 2014. *Handbook of spatial point pattern analysis in ecology.* Chapman and Hall/CRC press, Boca Raton, FL.	www.Programita.org
Spatstat	Baddeley, A., and R. Turner. 2005. Spastat: An R package for analyzing spatial point patterns. Journal of Statistical Software 12: 1-42	http://spatstat.github.io/
splancs	Rowlingson, B. and Diggle, P. 1993 Splancs: spatial point pattern analysis code in S-Plus. Computers and Geosciences 19: 627-655	www.maths.lancs.ac.uk/ ~rowlings/Splancs/
S-plus	INSIGHTFUL CORPORATION. 2005. S-Plus 7 for Windows user' guide. Insightful Corporation, Seattle, WA.	
SPPA	Haase 2001. Can isotrpy vs anisotropy in the spatial association of plant species reveal physical vs biotic facilitation? Journal of Vegetation Science 12: 127-136.	
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