

RESEARCH ARTICLE

Percolation threshold analyses can detect community assembly processes in simulated and natural tree communities

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Abstract

1. Studies of spatial point patterns (SPPs) are often used to examine the role that density-dependence (DD) and environmental filtering (EF) play in community assembly and species coexistence in forest communities. However, SPP analyses often struggle to distinguish the opposing effects that DD and EF may have on the distribution of tree species.
2. We tested percolation threshold analysis on simulated tree communities as a method to distinguish the importance of thinning from DD EF on SPPs. We then compared the performance of percolation threshold analysis results and a Gibbs point process model in detecting environmental associations as well as clustering patterns or overdispersion. Finally, we applied percolation threshold analysis and the Gibbs point process model to observed SPPs of 12 dominant tree species in a Puerto Rican forest to detect evidence of DD and EF.
3. Percolation threshold analysis using simulated SPPs detected a decrease in clustering due to DD and an increase in clustering from EF. In contrast, the Gibbs point process model clearly detected the effects of EF but only identified DD thinning in two of the four types of simulated SPPs. Percolation threshold analysis on the 12 observed tree species' SPPs found that the SPPs for two species were consistent with thinning from DD processes only, four species had SPPs consistent with EF only and SPP for five reflected a combination of both processes. Gibbs models of observed SPPs of living trees detected significant environmental associations for 11 species and clustering consistent with DD processes for seven species.
4. Percolation threshold analysis is a robust method for detecting community assembly processes in simulated SPPs. By applying percolation threshold analysis to natural communities, we found that tree SPPs were consistent with thinning from both DD and EF. Percolation threshold analysis was better suited to detect DD thinning than Gibbs models for clustered simulated communities. Percolation threshold analysis improves our understanding of forest community assembly processes by quantifying the relative importance of DD and EF in forest communities.

KEYWORDS

community assembly, density-dependence, environmental filtering, spatial pattern analysis

1 | INTRODUCTION

Spatial point pattern (SPP) analysis (Baddeley et al., 2015; Wiegand & Moloney, 2014) has become an established method for examining the ecological processes driving plant species coexistence and community assembly (Condit, 2000; McIntire & Fajardo, 2009; Sterner et al., 1986; Velázquez et al., 2016). Specifically, SPP analyses have been used to quantify the role that density-dependence (DD; e.g. Janzen–Connell effects and competition) and environmental filtering (EF) play in shaping community assembly in natural forest communities (McIntire & Fajardo, 2009; Velázquez, Martínez, et al., 2016).

Generally, negative DD decreases spatial clustering of trees (Connell, 1971; Janzen, 1970; Moeur, 1997; Velázquez et al., 2016) by decreasing the survival of individuals due to increased herbivory or resource competition with nearby individuals (i.e. crowding). In contrast, EF increases clustering of trees (Bagchi et al., 2011; Getzin et al., 2008; Shen et al., 2013) by decreasing the survival of individuals in marginal or poor habitats. While EF typically refers to abiotic conditions that prevent the establishment and presence of species across sites (Kraft et al., 2015), we are defining EF to be the process by which small spatial-scale abiotic heterogeneity prevents the within-site establishment and survival of species (e.g. abiotic heterogeneity within forest plots related to topography (Tateno & Takeda, 2003) and soil nutrients (Uriarte et al., 2015)).

The majority of SPP analyses have focused on detecting one clustering process at a time because DD and EF generate different clustering patterns (but see Bagchi et al., 2011; Shen et al., 2013), or on separating the effects of DD or EF from other clustering mechanisms, such as dispersal limitation (Russo et al., 2006; Seidler & Plotkin, 2006). However, the spatial distribution of species is likely to reflect the combined effects of both DD and EF, highlighting the need for an approach that will simultaneously account for both processes, or at the very least, identify which process predominate.

One approach to distinguish between DD and EF relies on examining the SPPs of individuals of the same tree species based on size classes or status (i.e. living/dead). Typically, these analyses compare differences in spatial clustering or spatial association with environmental covariates (Bagchi et al., 2011; Condit, 2000; Getzin et al., 2008; Moeur, 1997; Sterner et al., 1986; Velázquez, Martínez, et al., 2016). Density-dependence can also affect the growth and survival of trees (Comita et al., 2009; Coomes & Grubb, 1998; Lewis & Tanner, 2000; Uriarte et al., 2009) and reduce the cluster density of living and large trees compared to dead or small trees (Bagchi et al., 2011; Getzin et al., 2008; Moeur, 1997; Murrell, 2009; Velázquez, Kazmierczak, et al., 2016). In contrast, EF can increase clustering of living and large trees compared to dead or small trees (Bagchi et al., 2011; Getzin et al., 2008; Shen et al., 2013; Wiegand et al., 2009) by increasing the survival and growth of trees in suitable environments (Clark et al., 1998; Comita & Engelbrecht, 2014). Although differences in tree clustering by size or status can detect DD or EF in specific circumstances, conclusions from these studies

are often limited by insufficient sample sizes or by the difficulty of capturing relevant environmental heterogeneity using spatial covariates (Baddeley et al., 2015; Bagchi et al., 2011). Another challenge in identifying EF is that unlike DD, which is strongest at small scales, EF within sites may act at several spatial scales depending on the specific filter.

Percolation threshold theory is a method to examine point clustering at various spatial scales and provides an estimated probability that individual points occupy the same cluster (Hall, 1987; Plotkin et al., 2002). In percolation theory, clusters are defined by connecting points closer than a specified distance, such that there is a percolation threshold distance d_c above which all points amalgamate into one cluster (Plotkin et al., 2002). According to percolation threshold theory, we can quantify differences in clustering strength using the rationale that sparse, or weak, clusters must have a larger d_c than dense clusters. By comparing the d_c of remaining points after the removal of points from either DD or EF thinning processes to the d_c of removed points (e.g. comparing d_c of living vs. dead trees), we can link clustering strength to the predicted effects of thinning by DD and EF processes on tree SPPs. Thus, percolation threshold analysis provides a powerful tool to quantify and test the predictions of DD and EF thinning on SPPs.

The expected importance of DD and EF on observed SPPs differs among species according to life-history theory (Grime, 1979; Lohbeck et al., 2013). For example, early successional species adapted to high-light environments and showing rapid growth—a growth habit often linked to low wood density, low leaf mass per area (LMA) and shade intolerance—are more susceptible to thinning from DD compared to shade-tolerant species (Coley, 1980; Comita & Hubbell, 2009; Comita et al., 2009; Lohbeck et al., 2013; Poorter et al., 2009). Additionally, these species often increase in abundance in treefall gaps or after large-scale disturbance events (e.g. hurricanes: Comita et al., 2009; Uriarte et al., 2004). In contrast, slow-growing species—a growth habit linked to high wood density, high LMA and shade tolerance—are often less susceptible to DD and may respond more strongly to EF compared to shade-intolerant species (Comita & Hubbell, 2009; Comita et al., 2009; Uriarte, Canham, et al., 2004). These slow-growing species are more likely to exhibit clustering of adult trees (Murrell, 2009). Species' functional traits and shade tolerance offer a framework for categorizing species' SPPs and the expected importance of DD and EF in mediating species distributions.

To test the efficacy of percolation threshold analysis to detect SPP dynamics resulting from DD and EF processes, we first applied percolation threshold analysis to randomly generated SPPs that were thinned (had points removed) to stimulate stochastic (random), DD and EF thinning processes. We then analysed these simulated SPPs using Gibbs point process models to evaluate clustering and associations with simulated environmental heterogeneity. Finally, we applied percolation threshold analyses and Gibbs point process models to observed SPPs for mapped trees (by size and status) in the Luquillo Forest Dynamics Plot (LFDP) in Puerto Rico to detect DD and EF processes in a natural community, as well as test for

environmental associations and clustering within the observed SPPs. Specifically, we:

1. Generated random point patterns representing tree SPPs and thinned each pattern randomly, by density or by a simulated environmental gradient. We then tested if percolation threshold analysis could disentangle the effects of thinning from random, DD and EF processes. We predicted that SPPs thinned randomly would show no difference in clustering between remaining and removed points ($d_{c\text{-remaining}} - d_{c\text{-removed}} \approx 0$), SPPs thinned by DD would have weaker clustering (larger d_c) of remaining points than removed points ($d_{c\text{-remaining}} - d_{c\text{-removed}} > 0$) and SPPs thinned by EF would have stronger clustering of remaining points than removed points ($d_{c\text{-remaining}} - d_{c\text{-removed}} < 0$) (Figure 1).
2. Fitted Gibbs point process models to the simulated SPPs to test for environmental associations with the simulated environmental gradient used to thin the SPPs and for interactions (η) between points (i.e. clustering or overdispersion). We predicted that SPPs thinned by EF would have stronger associations with the simulated environmental gradient compared to SPPs thinned randomly or by DD. We also predicted that SPPs thinned by DD would have weaker clustering for remaining points than removed ones ($\eta_{\text{remaining}} < \eta_{\text{removed}}$) compared to patterns thinned randomly or by EF.
3. Applied our findings from the simulated percolation threshold analysis to examine the role of DD and EF on the observed spatial distributions of tree species. We compared living versus dead (i.e. remaining vs. removed) and large versus small individuals of 12 focal tree species. Living and large trees represent the individuals remaining after the cumulative historical effects of thinning processes, therefore we predicted that DD would weaken the clustering of living and large trees (remaining) compared to dead and small (removed) (i.e. $\eta_{\text{remaining}} < \eta_{\text{removed}}$).
4. Fitted Gibbs point process models to the observed SPPs to test for interactions between points and for spatial associations with

topography, a well-known driver of species' distributions at the LFDP (Johnston, 1992). We predicted that observed SPPs for species affected by EF, as derived from percolation threshold analyses, would have stronger associations with topography and land use for living and large trees (remaining points) compared to dead and small trees (removed points). We also predicted that species thinned by DD would have smaller interaction coefficients (η) for living and large trees compared to dead and small trees.

5. Evaluated whether percolation threshold results are congruent with results obtained using Gibbs point process models for both simulated and observed SPPs.

2 | MATERIALS AND METHODS

2.1 | Generation of simulated SPPs

To investigate the effect of percolation threshold analyses on simulated point patterns, we first randomly generated four types of SPPs: (a) a homogeneous Poisson process, (b) an inhomogeneous Poisson process, (c) a homogeneous Thomas cluster process and (d) an inhomogeneous Thomas cluster process. These four pattern types represent SPPs commonly used to test for spatial clustering and environmental associations of observed tree SPPs (Velázquez, Martínez, et al., 2016). Each SPP was generated within a 400 m × 400 m window using an average intensity (λ) of 0.00625 points per m² (average of 1,000 points). Inhomogeneous patterns were created by allowing λ to vary proportionally across the window given by $\lambda(x, y) = (x + y)^2$. Thomas cluster patterns were generated by allowing cluster centres to follow either a homogeneous or inhomogeneous Poisson process across space (Wiegand & Moloney, 2014). The number of points within Thomas clusters were generated from a Poisson distribution with a mean of 10 points and with locations determined from a Gaussian distribution with a standard deviation of 8 m (Wiegand & Moloney, 2014).

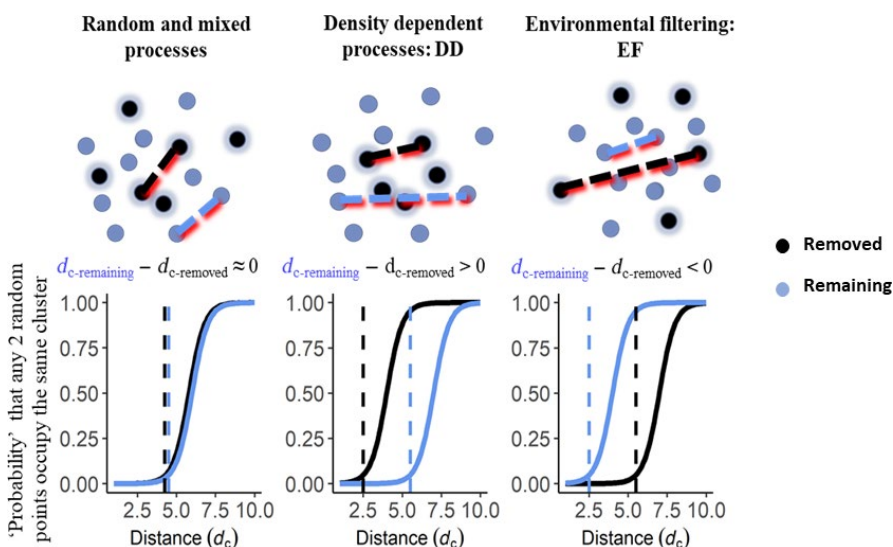


FIGURE 1 Predictions for effects of thinning from stochastic/mixed processes, density-dependence (DD) and environmental filtering. Expectations for clustering differences following thinning processes for 'remaining points' (i.e. living or large trees) and 'removed points' (i.e. dead or small trees). Environmental filtering decreases d_c of remaining points (i.e. living or large trees) compared to removed points (i.e. dead or small trees). In contrast, DD increase d_c of remaining points compared to removed points

2.2 | Percolation threshold analysis: Simulated SPPs

To test whether percolation threshold analysis can capture the thinning effects of random, DD and EF thinning processes, we simulated three scenarios of point removal for each of the four simulated SPP types: (a) random thinning; (b) DD thinning and (c) EF (Supplementary Methods for R code). To simulate random thinning, we applied a thinning algorithm in which each point in the pattern had a constant probability of removal $p = 0.5$. For DD thinning, we allowed p to vary as a function of point density such that points with more neighbours had a higher probability of removal. Environmental filtering was simulated by allowing p to vary with a simulated patchy environmental map; points in 'suitable' areas had a lower probability of removal than points in 'poor' areas.

To estimate the uncertainty around the effects of pattern generation and thinning on percolation curves, we randomly generated and thinned 1,000 SPPs for each SPP type and thinning scenario. For each simulation scenario, percolation curves were calculated according to the study by Plotkin et al. (2002) with a periodic edge correction (Wiegand et al., 2004). All statistical analyses were completed using the 'SPATSTAT' package in R (Baddeley et al., 2015; R Core Team, 2017).

For the percolation threshold analyses, we fit piecewise linear regressions ('MCP' in R: Lindeløv, 2020) to each percolation curve to identify the percolation threshold distance d_c . Briefly, these regressions estimated the slope and intercept for a specified number of linear segments (n) with segment-breakpoints ($n - 1$) fit to each percolation curve. For this analysis, we limited model segments to $n = 3$ and required that segments be continuous (i.e. segment _{$n+1$} starts at the last x and y values of segment _{n}). Practically, this formulation identified breakpoints for significant changes to slope between segments. We defined d_c as the first segment-breakpoint for each percolation curve; the first breakpoint represents the distance at which points begin to amalgamate into a single cluster. Because we limited our analysis to a single d_c for each percolation curve, this analysis precludes the detection of multiscale clustering, an alternative use of percolation analyses (Plotkin et al., 2002). To compare d_c values between different SPPs, we standardized the d_c by the number of points in each pattern (Plotkin et al., 2002). The MCP packages uses Bayesian inference to estimate segment-breakpoints; breakpoints were estimated using Markov chain Monte Carlo (MCMC) methods with uninformed random initial values across three chains. The first 5,000 iterations were discarded, and each chain ran for 10,000 iterations.

We then compared the median d_c estimates of remaining points and the removed points for each simulation (i.e. $d_{c\text{-remaining}} - d_{c\text{-removed}}$) to determine the relative effects of random, DD and EF thinning processes for each pattern. Because DD and EF have opposing effects on clustering, we expected the percolation threshold for a pattern influenced by both DD and EF to be most similar to whichever process is stronger or indistinguishable from zero when the processes are equal in strength.

2.3 | Gibbs point process model analysis: Simulated SPPs

Gibbs point process models are a common tool to analyse SPPs (Baddeley et al., 2015) and allow us to test the relationship between the intensity function $\lambda(u)$, which represents the expected number of points per unit area at a spatial location (u), and spatial covariates $B(u)$ related to environmental heterogeneity. Gibbs point process models also incorporate interactions between points (i.e. clustering or overdispersion), by modelling the conditional intensity $\lambda(u|\rho)$ of each point at location u given all points ρ , as a function of $B(u)$ and $l(u, r, \rho)$, such that:

$$\lambda(u|\rho) = e^{B(u) + l(u, r, \rho)}. \quad (1)$$

We used the *ArealInter* function (Baddeley et al., 2015) for the inter-point interaction $l(u, r, \rho)$ because it allows for both clustering and overdispersion.

$$l(u, r, \rho) \sim \eta^{\gamma_r(u, \rho)} \quad (2)$$

In this formulation, the conditional probability $\gamma_r(u, \rho)$ at location u given points ρ is proportional to the fraction of circle area with radius r centred at u that intersects with nearby points ρ . Significant values of η ($\eta \neq 1$) indicate biotic interactions between points ranging from overdispersion ($\eta < 1$) to clustering ($\eta > 1$). Overall, DD is expected to weaken the clustering of remaining points relative to thinned or removed ones ($\eta_{\text{remaining}} < \eta_{\text{removed}}$).

We fit the Gibbs point process models (Baddeley et al., 2015) to each of the 1,000 randomly generated SPPs for the four SPP types and three thinning scenarios. For these simulated SPPs, $B(u)$ was the simulated environmental gradient used for thinning. The value of r for Equation 2 was calculated for each point pattern as the value of r between 0.5 and 15 m that maximized the likelihood of a model with only inter-point interactions. We then compared the median η estimates of remaining and removed points for each simulation to determine the relative effects of random, DD and EF thinning processes for each simulated pattern. Coefficients for $B(u)$ that do not overlap zero represent significant spatial associations between points and environmental covariates and should match percolation threshold results for EF thinning processes.

2.4 | Observed tree SPPs: Study site and tree data

The LFDP is 16-ha (320 m $\times$ 500 m) permanent, mapped forest plot in north-eastern Puerto Rico. The forest is classified as a subtropical wet forest in the Holdridge life-zone system (Ewel & Whitmore, 1973) and is characteristic of other Caribbean forests with community dynamics strongly influenced by periodic hurricanes (Boose et al., 2004; Brokaw et al., 2012). Since 1990, all stems in the LFDP with a diameter ≥ 1 cm at 1.30 m height above the ground (DBH) have been mapped, identified to species and

measured following standard protocols (Thompson et al., 2002). Approximately every 5 years, stems are remeasured and their status as living or dead is assessed. New stems are added as they are found at each census. The 12 focal species examined in this study represent a range of life-history strategies and accounted for >60% of all trees in the LFDP as of 2016 (Table 1). We used the 2016 census for analyses of living trees and collated all dead trees recorded in the 2005, 2011 and 2016 censuses for mortality analyses; including dead trees from these censuses ensured sample sizes of dead trees could support robust analyses and allowed us to capture the long-term effects of filtering on tree mortality. We did not include trees killed directly by hurricanes, as the last major hurricane to affect the forest prior to the 2016 census was Hurricane Georges in 1998 (Canham et al., 2010). For size analyses, we categorized living trees

as 'large' or 'small' based on a diameter above or below the species' median DBH using the 2016 census.

The LFDP covers a range of land-use histories and has highly variable topography (Thompson et al., 2002); we used both historical land use and topography as environmental covariates in the Gibbs point process models. We considered areas with lesser than 80% forest cover in 1936 to be 'high historical land use' and areas with greater than 80% forest cover to be 'low historical land use' (Figure S1; Thompson et al., 2002). Additionally, to capture small-scale topographic variation in the LFDP, a continuous measure of concavity (values <0 are ridges and >0 are valleys) was calculated from a digital elevation model (DEM) by fitting a six-term polynomial over a moving window with a radius of 33 m to the DEM (Hurst et al., 2012; Wolf et al., 2016).

TABLE 1 Median DBH of living individuals for each species calculated from the 2016 census. For percolation threshold analysis, a smaller d_c for living versus dead or large versus small indicates dominance of environmental filtering (EF). The opposite scenario, a larger d_c for living versus dead or large versus small, indicates dominance of density-dependence (DD). Statistically equivalent clustering strengths for either comparison indicates equal strengths of EF and DD. For Gibbs models, DD denotes significant differences in interaction coefficients consistent with DD thinning ($\eta_{\text{living}} < \eta_{\text{dead}}$ or $\eta_{\text{large}} < \eta_{\text{small}}$). EF for Gibbs models denotes significant associations with measured covariates (topography or land use) for large/small and living dead trees. n.s. = not significant. * indicates that coefficients are significantly greater for large and living trees relative to small and dead ones

Species (species code)	Median DBH	Number of trees in SPPs by size and status classification	Percolation threshold comparison of d_c		Gibbs process model results (η)	
			Living/dead	Small/large ($\leq$ vs. > median DBH)	Living/dead	Small/large ($\leq$ vs. > median DBH)
<i>Alchornea latifolia</i> (ALCLAT)	21.25	$n_{\text{large}} = 79; n_{\text{small}} = 79$ $n_{\text{living}} = 158; n_{\text{dead}} = 546$	Equal	DD	DD EF/EF	EF/n.s.
<i>Buchenavia tetraphylla</i> (BUCTET)	42.25	$n_{\text{large}} = 90; n_{\text{small}} = 90$ $n_{\text{living}} = 180; n_{\text{dead}} = 133$	EF	DD	DD EF/n.s.*	DD EF/EF
<i>Casearia arborea</i> (CASARB)	4.09	$n_{\text{large}} = 1,383; n_{\text{small}} = 1,385$ $n_{\text{living}} = 2,768; n_{\text{dead}} = 2,703$	Equal	Equal	EF/EF	DD EF/EF*
<i>Cecropia schreberiana</i> (CECSCH)	20.9	$n_{\text{large}} = 395; n_{\text{small}} = 401$ $n_{\text{living}} = 796; n_{\text{dead}} = 2,284$	Equal	EF	n.s./EF	
<i>Dacryodes excelsa</i> (DACEXC)	22.9	$n_{\text{large}} = 696; n_{\text{small}} = 703$ $n_{\text{living}} = 1,399; n_{\text{dead}} = 148$	DD	Equal	EF/EF	EF/EF
<i>Guarea guidonia</i> (GUAGUI)	20.9	$n_{\text{large}} = 179; n_{\text{small}} = 179$ $n_{\text{living}} = 358; n_{\text{dead}} = 338$	EF	DD		DD
<i>Inga laurina</i> (INGLAU)	6.9	$n_{\text{large}} = 409; n_{\text{small}} = 415$ $n_{\text{living}} = 824; n_{\text{dead}} = 628$	EF	Equal	EF/EF	DD EF/EF
<i>Manilkara bidentata</i> (MANBID)	7.3	$n_{\text{large}} = 846; n_{\text{small}} = 859$ $n_{\text{living}} = 1705; n_{\text{dead}} = 323$	EF	EF	EF/n.s.	EF/EF
<i>Prestoea acuminata</i> (PREMON)	14.05	$n_{\text{large}} = 4,614; n_{\text{small}} = 4,614$ $n_{\text{living}} = 9,228; n_{\text{dead}} = 1544$	EF	EF	DD EF/n.s.*	EF/EF*
<i>Schefflera morototoni</i> (SCHMOR)	12.5	$n_{\text{large}} = 338; n_{\text{small}} = 351$ $n_{\text{living}} = 689; n_{\text{dead}} = 2,338$	DD	EF	EF/EF	EF/EF
<i>Sloanea berteriana</i> (SLOBER)	3.44	$n_{\text{large}} = 1,298; n_{\text{small}} = 1,304$ $n_{\text{living}} = 2,602; n_{\text{dead}} = 1,223$	DD	EF	DD EF/EF	DD EF/EF*
<i>Tabebuia heterophylla</i> (TABHET)	9.35	$n_{\text{large}} = 143; n_{\text{small}} = 143$ $n_{\text{living}} = 286; n_{\text{dead}} = 486$	EF	DD	n.s./EF	

2.5 | Percolation threshold analysis: Observed SPPs

To examine the contribution of DD and EF thinning processes to observed LFDP tree species' SPPs, we first calculated the percolation curves for living, dead, large and small tree SPPs for each species. The percolation threshold d_c for each SPP was then estimated as the first breakpoint from a piecewise linear regression, as described above. Uncertainties around d_c values were calculated as the 95% credible intervals around breakpoint estimates. We then compared the d_c of SPPs based on living versus dead and large versus small for each species. Percolation threshold d_c differences (i.e. $d_{c\text{-living}} - d_{c\text{-dead}}$ and $d_{c\text{-large}} - d_{c\text{-small}}$) are significant if the 95% credible intervals do not overlap zero.

To examine how the strength of DD and EF varies by species' traits, we fit simple linear models to trait data and the median d_c estimates for each species; each model included only one trait. We used trait data on dry seed mass, wood density and LMA (Swenson & Umana, 2015) and species' shade tolerance derived from sapling mortality from shading (Uriarte, Canham, et al., 2004).

2.6 | Gibbs point process model analysis: Observed SPPs

We applied the Gibbs point process models to living, dead, large and small tree SPPs for each species. To model the conditional probability, we used two environmental covariates for $B(x)$: historical land use and concavity (Figure S1), which are known to influence the distribution of tree species in the LFDP (Thompson et al., 2002). To accommodate for spatial clustering or overdispersion that may occur independently of environmental covariates, we also included inter-point interactions. Significant differences in interaction

coefficients (η) for living versus dead ($\eta_{\text{living}} < \eta_{\text{dead}}$) or large versus small ($\eta_{\text{large}} < \eta_{\text{small}}$) are consistent with DD thinning. The optimal interaction r for each species was determined as the value of r between 0.5 and 15 m that maximized the likelihood of a model with only inter-point interactions. Coefficients for land use and concavity that do not overlap zero represent significant spatial associations between points and these covariates.

3 | RESULTS

3.1 | Simulated SPPs

3.1.1 | Percolation threshold results

We first tested whether percolation threshold analysis could detect thinning from random, DD and EF processes in simulated SPPs. Using the percolation threshold distance, d_c , as a measure of clustering, we found that random, DD and EF thinning processes created different clustering patterns (Figure 2). Random thinning of homogeneous and inhomogeneous Poisson and Thomas cluster SPPs showed no clustering differences between the remaining and removed points ($d_{c\text{-remaining}} - d_{c\text{-removed}} \approx 0$). In contrast, DD thinning produced weaker clustering (larger d_c) of remaining compared to removed points ($d_{c\text{-remaining}} - d_{c\text{-removed}} > 0$) for the inhomogeneous Poisson SPPs and for the homogeneous and inhomogeneous Thomas SPPs. However, the trends for the homogeneous Poisson patterns were not strong enough to be significant. Patterns thinned using EF showed stronger clustering of remaining compared to the removed points ($d_{c\text{-remaining}} - d_{c\text{-removed}} < 0$) for all four simulated SPP types. Overall, these results indicate that differences in d_c may be reliable measures of the thinning effects of DD and EF.

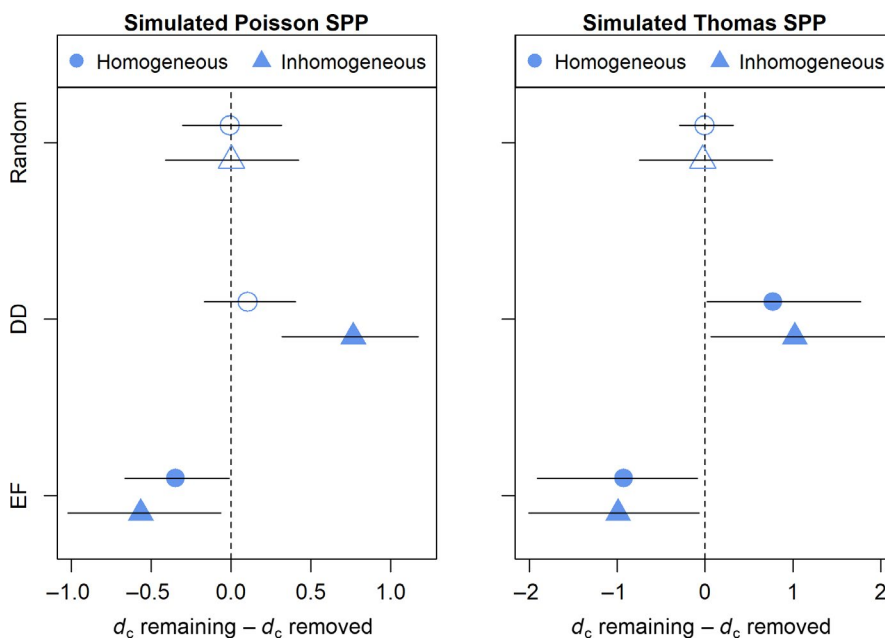


FIGURE 2 Percolation threshold (d_c) comparison from percolation analysis of simulated point patterns. Percolation threshold analysis of simulated data with point removal by random thinning, by density-dependence (DD) or by environmental filtering (EF). Points right of zero (dashed line) match predictions for patterns with thinning influenced by DD while points left of zero represent patterns with clustering influenced by environmental filtering (EF). Symbols show the median estimate and black lines show the 95% confidence intervals

3.1.2 | Gibbs point process model results

We modelled SPP intensity using Gibbs point process models to detect the effects of thinning from random, DD and EF processes. We found no significant spatial associations using the simulated environmental gradient for points thinned randomly or from DD for any of the four randomly generated SPP types (Figure 3; Table S1). In contrast, simulated thinning from EF produced significant positive associations with the simulated environmental gradient for the remaining points and negative associations for the removed points for all four randomly generated SPP types.

Interaction coefficients (η) for the Poisson homogeneous and inhomogeneous SPPs only detected significant point interactions for patterns with DD thinning. For these DD thinned patterns, we found significant clustering ($\eta > 1$) for removed points and overdispersion ($\eta < 1$) for the remaining points, consistent with the simulated DD (Figure 4; Table S1). In contrast, we found $\eta > 1$ (clustering) for all Thomas homogeneous and inhomogeneous SPPs and across the three thinning scenarios. In general, patterns thinned by DD had higher $\eta_{\text{remaining}}$ compared to η_{removed} ; however, the difference in $\eta_{\text{remaining}}$ and η_{removed} was only significant for simulated Poisson SPPs. These results indicate that Gibbs point process models can detect clustering, but may not be proficient at differentiating between the effects of simulated thinning from EF and DD for clustered SPPs.

3.2 | Observed tree SPPs

3.2.1 | Percolation threshold results

Living and dead trees

We predicted that DD would result in stronger clustering of dead trees compared to living trees ($d_{\text{c-living}} - d_{\text{c-dead}} > 0$) while EF would result in stronger clustering of living trees ($d_{\text{c-living}} - d_{\text{c-dead}} < 0$). Using percolation threshold analyses, we found that three species had SPPs consistent with DD thinning for living versus dead trees. We also identified six species with SPPs consistent with EF (Table 1; Figure 5). Three species showed no clustering differences between living and dead tree SPPs.

Large and small trees

We predicted that DD would result in stronger clustering of small trees compared to large trees ($d_{\text{c-large}} - d_{\text{c-small}} > 0$) and that EF would result in stronger clustering of large trees ($d_{\text{c-large}} - d_{\text{c-small}} < 0$). Comparison of d_{c} values for each species based on large versus small tree size identified four species with SPPs consistent with DD thinning (i.e. stronger clustering of small trees), five species with SPPs consistent with EF and three species with no difference in clustering between large and small trees (Table 1; Figure 5). The results for living versus dead stems and large versus small trees were only consistent for three species.

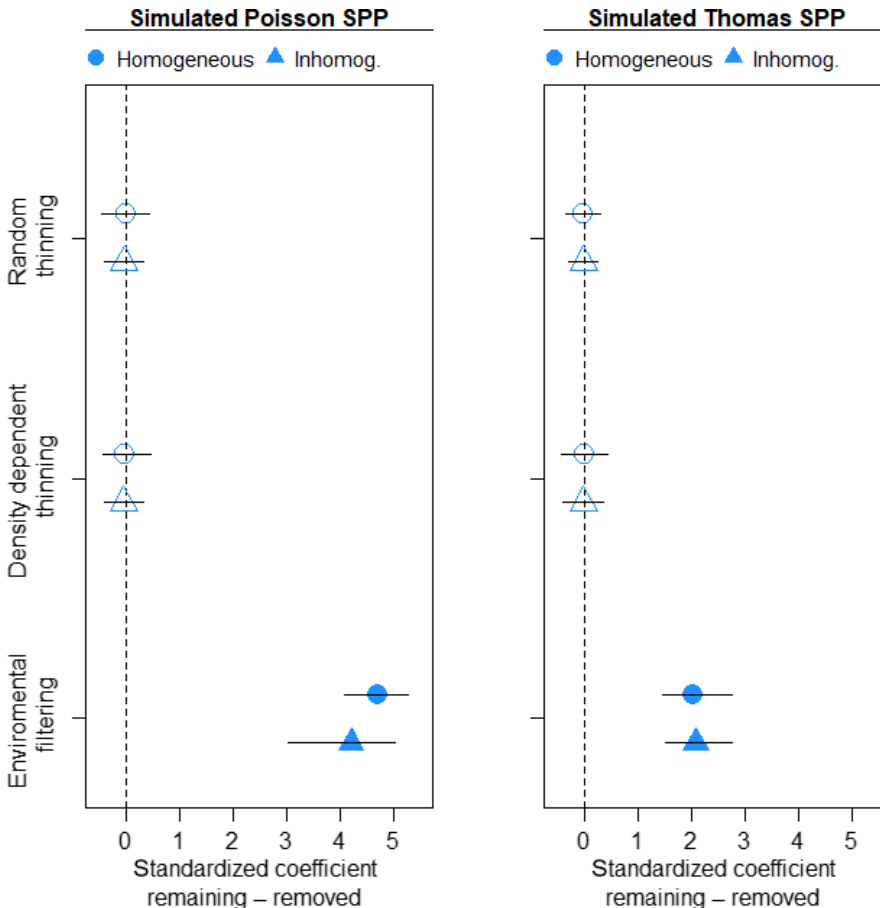


FIGURE 3 Environmental associations of Gibbs process model from simulated point patterns. Differences in standardized model coefficients of simulated data with point removal by random thinning, by density-dependence (DD) or by environmental filtering (EF). Points show differences in median parameter values and black lines show 95% confidence intervals. Filled symbols are significantly non-zero at $p \leq 0.05$

FIGURE 4 Differences in interaction coefficients (η ; i.e. Gibbs process models for simulated remaining and removed point patterns). Points show differences in log(median) parameter values and black lines show 95% confidence intervals. Filled symbols are significantly non-zero at $p \leq 0.05$

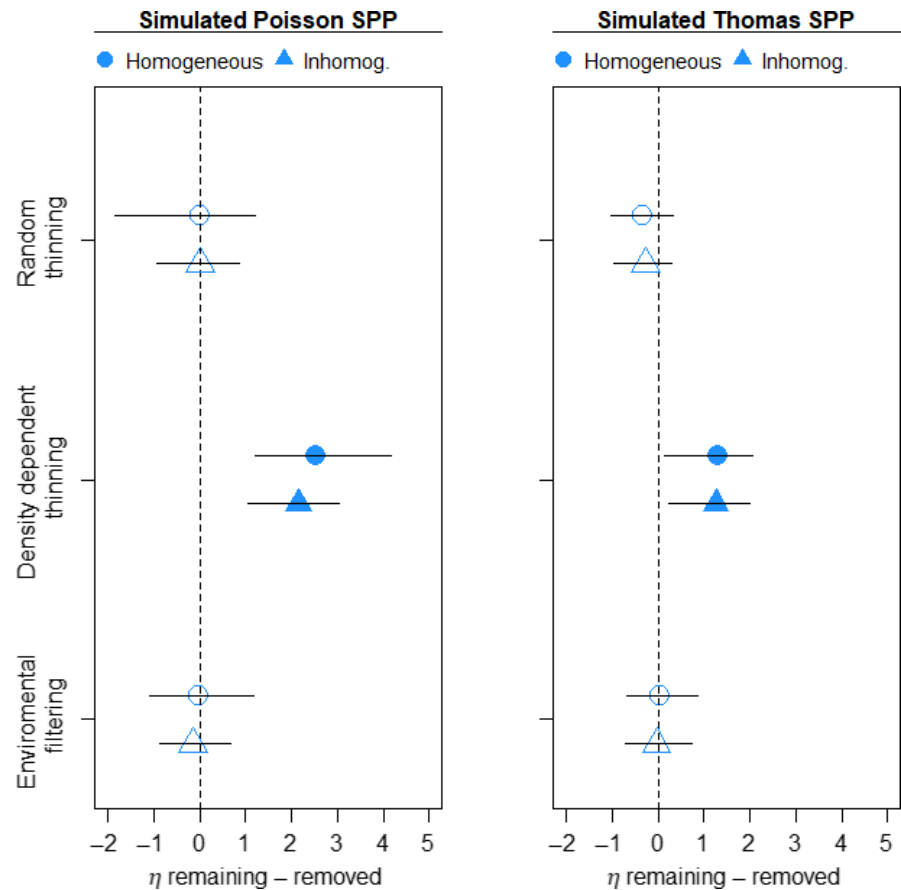
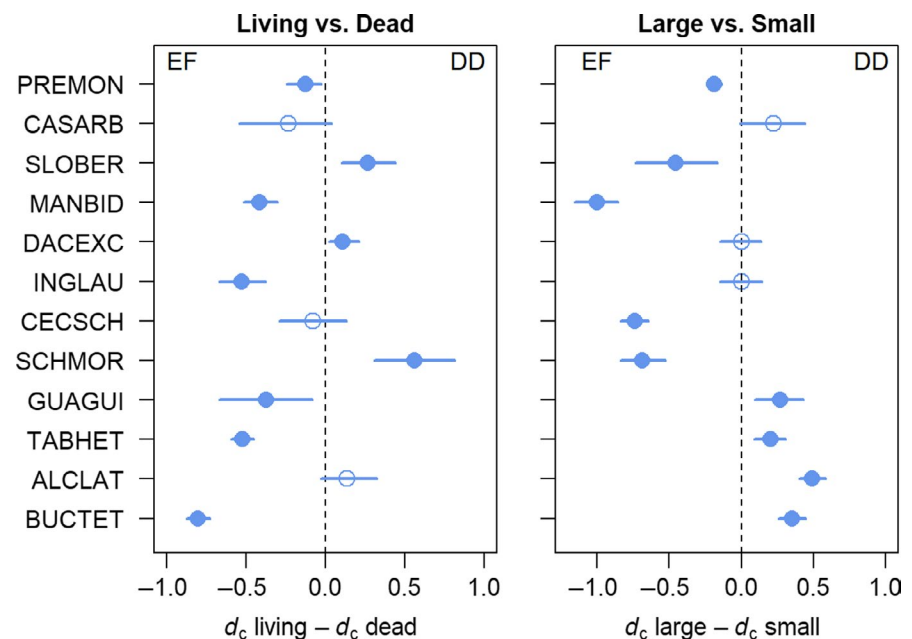


FIGURE 5 Clustering strength (d_c) from percolation analysis of observed point patterns. Positive x coordinates indicate species with clustering of living or large stems influenced by density-dependence (DD) while negative values represent species with clustering influenced by environmental filtering (EF). Circles show the median estimate and dotted lines show 95% confidence intervals. Significant results are filled symbols



3.2.2 | Gibbs point process model results

When applied to observed tree data, Gibbs point process models revealed significant associations with concavity for both living and dead trees for three species, only living trees for four species and only dead trees for two species (Table 1; Figure 6a). No species had

significantly stronger associations for living relative to dead trees. We also found associations with concavity for large and small trees for four species, only large trees for two species and only small trees for two species (Table 1; Figure 6b). All associations with concavity indicated that species were more common on ridges. Spatial distributions for eight of the 12 species also differed significantly

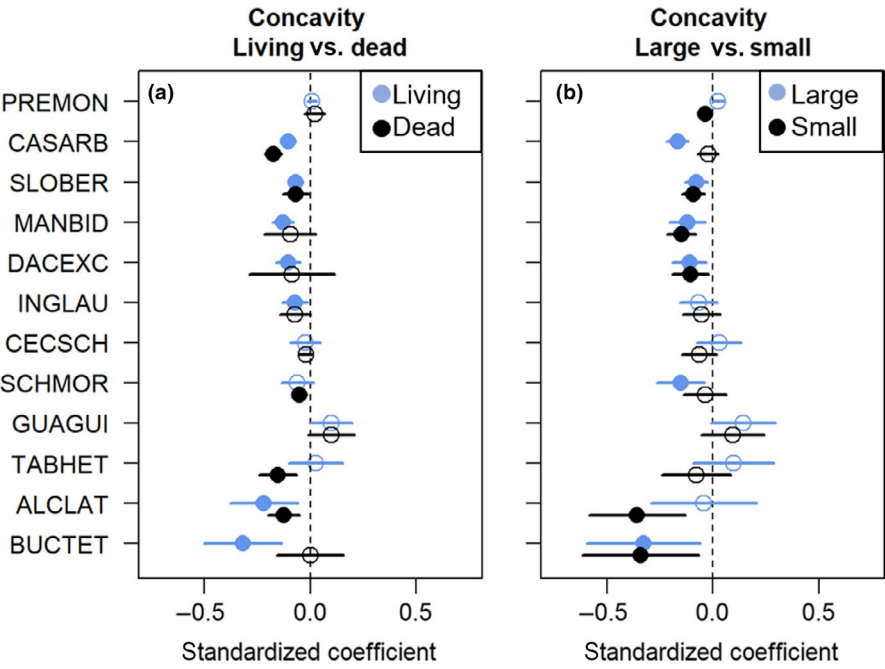


FIGURE 6 Associations between concavity and SPPs of living versus dead stems (a) and large versus small stems (b). Values to the left of zero (dashed line) indicate associations with ridges while those to the right of zero indicate associations with valleys. Species listed from most to least abundant (top to bottom). Filled symbols are significantly non-zero at $p \leq 0.05$. Lines show 95% confidence intervals

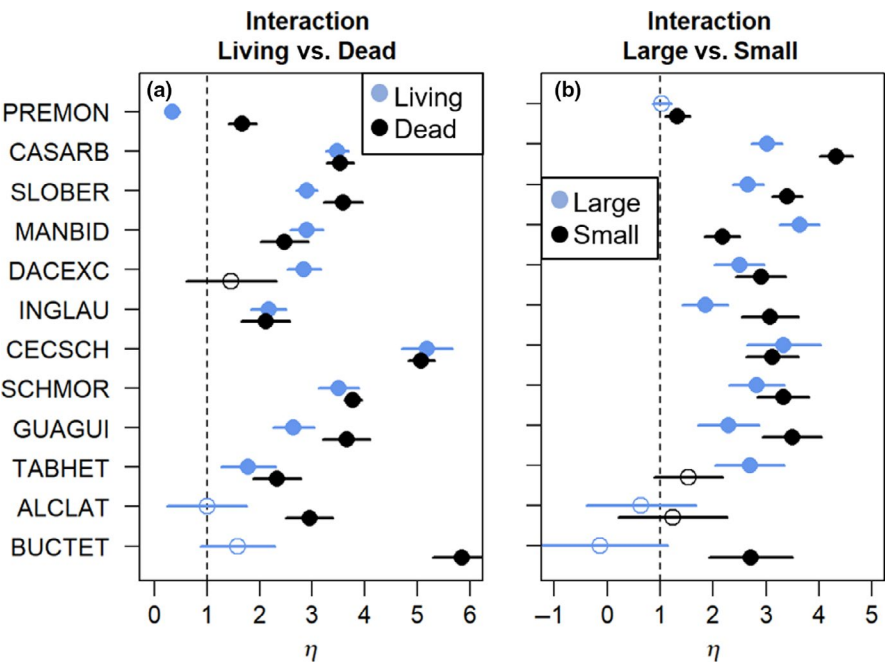


FIGURE 7 Interaction coefficients (η) of Gibbs process models for observed point patterns. Interaction estimates for SPPs of living versus dead stems (a) and large versus small stems (b). Values to the left of 1 (dashed line) indicate overdispersion between points while values to the right of 1 indicate clustering between points. Filled symbols are significantly non-zero at $p \leq 0.05$. Lines show 95% confidence intervals

across historical land use, justifying our inclusion of this covariate in the model (Table S2; Figure S2). Five species were more abundant on areas of high historical land use and three on low historical land use. Associations with land use differed between large and small and between living and dead trees but these differences were only significant for two species, *P. acuminata* and *S. berteriana*, in a manner consistent with stronger EF for large and living stems (Table S2).

Clustering independent of concavity and historical land use was ubiquitous across living, dead, large and small tree SPPs ($\eta > 1$). Living tree SPPs for nine of the 12 species showed evidence of clustering,

one species had evidence of overdispersion ($\eta < 1$) and two species had no clustering (Table 1; Figure 7a; Table S3). In contrast, 11 species had significant clustering of dead stems. Large tree SPPs for nine species showed clustering, while three species had no significant clustering (Figure 7b). Similarly, 10 species had significant clustering of small tree SPPs. Gibbs process models of living versus dead trees estimated interaction coefficients consistent with DD thinning for five species ($\eta_{\text{living}} < \eta_{\text{dead}}$; Table 1; Figure 7a). Models of large versus small trees also detected DD for five species ($\eta_{\text{large}} < \eta_{\text{small}}$; Figure 7b); two of these species were the same for both comparisons (*Buchenavia tetraphylla* and *Sloanea berteriana*).

3.3 | Comparing percolation threshold analysis to Gibbs point process model results

Overall, the detection of DD or EF processes according to the percolation threshold analysis was not always congruent with results from the Gibbs point process models. Percolation threshold results showed that six species had living and dead tree SPPs consistent with EF; in contrast, Gibbs point process models determined that nine species had SPPs of living trees with significant environmental associations (Table 1). Only four of the species had living SPPs consistent with EF according to both percolation threshold analysis and Gibbs process models (*Buchenavia tetraphylla*, *Inga laurina*, *Manilkara bidentata* and *Prestoea acuminata*). Similarly, percolation threshold analysis identified five species with large and small tree SPPs consistent with EF compared to the nine species with significant environmental associations for large trees as determined by Gibbs point process models. Only four species overlapped between percolation threshold analysis and Gibbs point process models for the effects of EF on both large versus small trees (*Manilkara bidentata*, *Prestoea acuminata*, *Schefflera morototoni* and *Sloanea berteriana*). Although we predicted that the species with SPPs consistent with EF according to the percolation threshold analyses would exhibit stronger topographic associations in the Gibbs models for living and large trees compared to dead and small trees, we actually found that the majority of species had associations with topography or land use independent of status or size (Table 1; Table S3; Figure 6).

Congruence in detection of DD for percolation threshold analysis and Gibbs process models were generally weaker than for EF detection. Only four species were identified as having SPPs consistent with DD by both percolation threshold analysis and Gibbs process models (Table 1). For living versus dead trees, only one species with SPPs consistent with DD according to the percolation threshold analysis also had interaction coefficients from the Gibbs process model consistent with DD (*Sloanea berteriana*). Similarly, only two species had patterns consistent with DD for both the percolation threshold analysis and Gibbs process models for large versus small trees (*Buchenavia tetraphylla* and *Guarea guidonia*).

3.4 | Percolation threshold analyses and species functional traits

The relationship between species' traits and the influence of DD versus EF did not fully reflect our predictions. We had expected that species with early successional life-history characteristics (shade intolerant with low LMA and wood density) would show stronger patterns from DD processes. The only significant relationship between percolation threshold analysis and species traits was for LMA. Specifically, species tended to shift from DD to EF as LMA increased ($p = 0.037$, $R^2 = 0.366$; Table S4).

4 | DISCUSSION

The spatial distributions of tree species reflect the cumulative result of individual tree recruitment, growth and survival that are in turn determined by initial seed dispersal, environmental conditions and biotic interactions. Environmental and biotic interactions result in thinning processes such as negative DD (Janzen, 1970; Uriarte et al., 2004) and EF (Webb & Peart, 2000; Wiegand et al., 2009). However, it has been difficult to detect and quantify the relative importance of these thinning processes on tree SPPs in natural forests.

This study examined the efficacy of percolation threshold analysis (Plotkin et al., 2002) in detecting simulated DD and EF thinning processes and then examined forest census data to detect evidence of DD and EF thinning in observed SPPs. Results from percolation threshold analysis were then compared to Gibbs point process models (Baddeley et al., 2015) to better understand the performance and congruence of these two methods. Percolation threshold analysis was able to successfully distinguish between DD and EF thinning in simulated tree SPPs and performed better than Gibbs point process models in detecting DD processes for clustered patterns (e.g. Thomas processes). Nevertheless, both percolation threshold analysis and Gibbs models detected SPPs that are consistent with DD thinning processes in a natural forest community. Both methods also captured widespread EF in the natural community. Nevertheless, there was limited overlap in results for individual species relative to differences between small/large and living/dead individuals. Taken together, these results suggest that percolation threshold analysis offers a useful framework for investigating how community assembly processes shape natural communities, particularly when coupled with approaches that can identify associations with known environmental covariates (e.g. Gibbs models).

By applying random-, DD- and EF-based thinning to simulated SPPs, we verified that percolation threshold analyses could detect the expected results of these processes on the clustering of trees. We found that simulated thinning as a function of point density (DD) resulted in weaker clustering of remaining points ($d_{c\text{-remaining}} - d_{c\text{-removed}} > 0$), while thinning along a simulated environmental gradient (EF) yielded stronger clustering of remaining points ($d_{c\text{-remaining}} - d_{c\text{-removed}} < 0$). These simulated results are consistent with findings from studies that examined tree clustering patterns in natural forest communities, namely that DD decreased the clustering (Bagchi et al., 2011; Janzen, 1970; Uriarte, Condit, et al., 2004) and EF increased the clustering of living trees (Shen et al., 2013; Webb & Peart, 2000; Wiegand et al., 2009). Although the Gibbs point process models also detected the effects of simulated EF, these models were only able to detect evidence of DD thinning in patterns without clustering (i.e. Poisson processes).

After applying percolation threshold analysis to observed tree SPPs, we identified species with SPPs consistent with thinning from DD and EF for living versus dead and for large versus small trees. Percolation threshold analysis detected seven species consistent

with DD, nine species consistent with EF and five species with SPPs consistent with both DD and EF thinning processes when looking across both living versus dead and large versus small tree results. Only two species had SPPs consistent with EF for both living versus dead and large versus small tree results and two species had SPPs consistent with DD and no evidence of EF, although both of these species had a non-significant d_c comparison for either living versus dead or large versus small tree results. In contrast, the Gibbs process models detected environmental associations for nearly all species. The ubiquitous detection of SPPs consistent with EF in both the percolation threshold analysis and Gibbs process models suggests that environmental variation is an important driver of species distributions at this site.

Density-dependence responses are often strongest for seedlings and saplings (Comita et al., 2014). Although the tree census data used in this study restricted our analysis to trees with a DBH ≥ 1 cm, using a comparison of living versus dead and large versus small tree clustering strength allowed us to identify several species with SPPs consistent with DD thinning. While DD in our study captures mortality from both conspecific competition and herbivory, differences in tree species' susceptibility to herbivory from generalists or specialists may also influence our ability to detect DD thinning. Our finding that species with low LMA had stronger evidence of DD compared to species with high LMA supports results from other studies that examined how DD mortality varies among species' successional traits—specifically, trade-offs between acquisitive and competitive traits (Grime, 1979; Lohbeck et al., 2013).

The efficacy of percolation threshold analyses was comparable to Gibbs process models applied to observed SPPs. The positive association with ridges (i.e. negative concavity) for most of the species tested is consistent with findings for this forest that these tree species grow and survive better on ridges. In this site, valleys are often wetter than ridges (Daws et al., 2002; Silver et al., 1999; Tromp-van Meerveld & McDonnell, 2006) and trees in valleys have lower growth and survival (Uriarte et al., 2018). Nevertheless, the Gibbs point process models failed to detect significant topographic associations for four species that percolation threshold analysis identified as SPPs with distributions consistent with EF thinning. This difference may be due to environmental covariates not captured by topography (e.g. light availability), which are difficult to incorporate in point process models. This suggests that Gibbs point process models are useful for identifying environmental filters but should be complemented by percolation threshold analysis to capture potential effects of unknown environmental covariates.

The interaction coefficients from the Gibbs point process models indicated that eight species had significant clustering of both living and dead stems and eight species had significant clustering of both large and small stems independent of environmental covariates. However, only four species had evidence that DD was sufficiently strong to remove clustering of living compared to dead trees (*Alchornea latifolia*, *Buchenavia tetraphylla*, *Prestoea acuminata* and *Sloanea berteriana*) and five species showed evidence of DD for

large relative to small trees. Although our simulations did not reveal Gibbs point process patterns to be proficient at detecting DD thinning in clustered patterns, the weaker clustering for living and large compared to dead and small trees for several species suggests that DD thinning is sufficiently strong in this forest to influence SPPs. However, it is also possible that this model detected clustering due to unmeasured environmental variation independent of our measure of topography.

Percolation threshold analysis relies on thinning processes that affect the clustering patterns of species, and several factors may obscure clear differences in thinning from DD or EF processes. Although many species experience thinning from both DD and EF processes, this thinning often occurs at different spatial scales (Plotkin et al., 2002; Wiegand et al., 2007), and percolation threshold analysis should detect the predominant thinning process. Another issue typically experienced by many SPP analyses is accounting for differences in the abundance of species (i.e. the number of points in an SPPs; Chacón-Labelle et al., 2017; Murrell, 2009; Rajala et al., 2019; Wiegand et al., 2012). One advantage of percolation threshold analysis is that the critical distance d_c is standardized by the number of points before comparison across SPPs. Additionally, this method does not rely on assumptions about the probability of point co-occurrence with other point-types or environmental features (Chacón-Labelle et al., 2017; Rajala et al., 2019; Wiegand et al., 2012). Nonetheless, differences in point abundance is a critical issue with any SPP analysis. For percolation threshold specifically, theoretical models show that the percolation transition occurs at the same d_c for a range of abundances, but that the transition becomes more gradual as sample size increases ($n = 100$ – $12,500$; Plotkin et al., 2002). In this analysis, a more gradual percolation transition due to small sample sizes would be detected as a smaller d_c . However, examination of species' SPPs with large abundance differences between living versus dead or large versus small does not reveal any consistent bias. For example, $n_{\text{living}} \gg n_{\text{dead}}$ for both *Dacryodes excelsa* and *Manilkara bidentata*, but percolation thresholds determined that SPPs for these species were consistent with DD and EF respectively.

We propose percolation analysis is a useful tool for understanding the simultaneous effects of DD and EF on SPPs with some advantages and disadvantages over traditional spatial analyses (e.g. Gibbs point process models and spatial summary statistics). The percolation threshold analysis of clustered patterns successfully distinguished thinning of simulated point patterns by random, DD and EF processes. Although Gibbs point process models detected thinning from EF, these models could only detect DD effects on Poisson SPPs. Thus, we recommend percolation threshold analysis be limited to SPPs with significant clustering as determined from second-order summary statistics (Baddeley et al., 2015). One advantage of Gibbs point process models is their ability to associate patterns with specific environmental covariates; they also allow separation of EF components into measured and unmeasured covariates, since the latter should increase clustering (η). However, when accurate maps of covariates are unavailable, percolation

threshold analysis offers a useful and complementary approach for detecting EF. Regardless of the method chosen to examine the spatial patterns of tree species, the big technical challenge of teasing apart the importance of DD and EF in natural communities is that both processes occur simultaneously and may be impossible to detect without a clear separation of spatial scales, replication or known environmental covariates.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

A.Q. and M.U. conceived the study; J.T., M.U. and J.K.Z. collected data; A.Q. analysed data with input from R.D. and M.U.; A.Q. and M.U. wrote first draft of the manuscript and all authors contributed to the final version of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13676>.

DATA AVAILABILITY STATEMENT

Tree data are available at <https://luq.lter.network/research/luquillo-forest-dynamics-plot-lfdp>. Code is available at https://github.com/mu2126/MEE_21-03-211 and in the study by Quebbeman et al. (2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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