

# Niche differentiation and neutral theory: an integrated perspective on shrub assemblages in a parkland savanna

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**Abstract.** Investigations of structure in ecological communities need to move beyond the dichotomy between niche and neutral theory to broader conceptual frameworks that accommodate both neutral stochastic and biological structuring processes in organizing species assemblages. We propose and test a framework that integrates niche and neutral-assembly perspectives and determines their relative contributions in structuring diverse shrub species assemblages in a parkland savanna. Our approach proposes that stochastic dispersal processes initially govern the assemblage of species in discrete shrub clusters developing in grassland, but that community structure subsequently develops through the progressive action of first positive, then negative interactions among species. A comparison of observed patterns of occurrence and niche models for 12 shrub cluster species against neutral predictions revealed that neutral stochastic, island biogeographic processes accounted for most patterns of species occurrence. One species showed strong evidence of successional differentiation, whereas evidence of slight recruitment biases for five others was equivocal. Our results demonstrate the usefulness of an approach that accommodates contributions of both neutral and niche assembly rather than assuming either process alone is sufficient to account for community structure. Further development and testing of robust and falsifiable neutral theory will allow ecologists to critically evaluate the relative roles of niche differentiation and neutral, stochastic processes in structuring communities.

**Key words:** *Akaike information criterion (AIC); assembly rules; model selection; Prosopis glandulosa; species assemblage; succession; Texas AgriLife La Copita Research Area, Texas, USA.*

## INTRODUCTION

Ecologists have long used patterns in ecological communities as a touchstone for evaluating the influence of causal ecological processes. It has often been assumed that structure and pattern in species assemblages originate from niche differentiation, functional differences in the way species partition limiting resources and respond to gradients in environmental and microclimatic conditions. This view has been challenged by “neutral theory,” which posits that trophically similar species are functionally equivalent and that patterns in community organization can be accounted for by stochastic processes (Hubbell 2001, 2006). While there has been contentious debate over the merits of these contrasting viewpoints, sufficient evidence has emerged in support of both perspectives; and it is apparent that neither theory alone is sufficiently broad to account for the full range of observed patterns in natural communities (McGill 2003, Turnbull et al. 2005, Volkov et al. 2007).

There is a growing consensus for the need to move beyond this dichotomy to a broader theory of community structure that can simultaneously accommodate neutral stochastic and biological structuring processes (Gravel et al. 2006, Leibold and McPeck 2006, Chu et al. 2007).

In this paper we demonstrate the usefulness of an approach that combines neutral and niche theory to interpret community structure. First, we briefly summarize key aspects of each theory and develop an integrated framework (Fig. 1) based on a case study of shrub aggregates in a southern Great Plains, USA, savanna parkland. We then apply this approach to field observations to determine the relative contributions of neutral stochastic processes and successional differentiation in accounting for observed patterns in species assemblages.

## Competing paradigms

One of the main strengths of neutral theory is that it has stimulated critical debate over long-held assumptions about the functional role of differences between species in structuring communities (Alonso et al. 2006). In particular, it has exposed the theoretical weakness in approaches to community ecology that start with the uncritical assumption that structure in communities arises from functional differentiation among species (Hubbell 2006). When neutral theory has been tested against real-world observations it has been found to be

Manuscript received 11 June 2008; revised 11 May 2009; accepted 29 June 2009; final version received 6 August 2009. Corresponding Editor: J. A. Jones.

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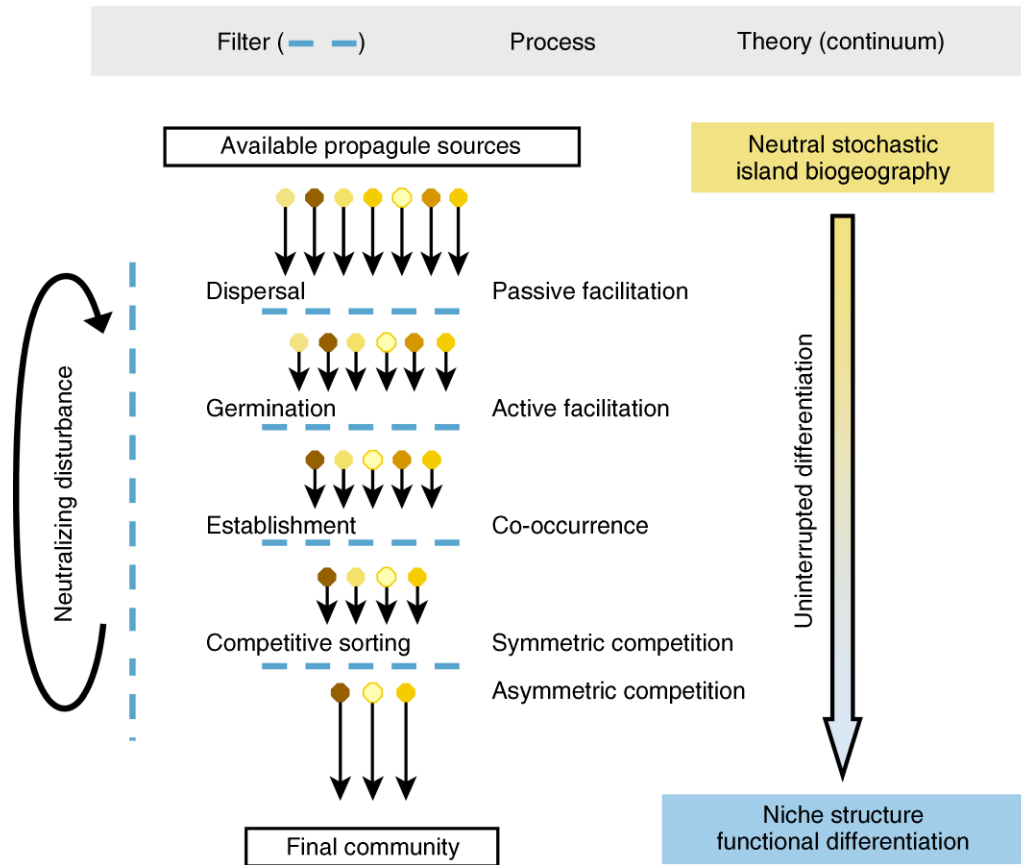


FIG. 1. Proposed adaptations of the “filter paradigm” to accommodate contributions from both neutral stochastic and biological structuring (niche) processes to patterns in plants species assemblages during community development. Stochastic processes associated with seed dispersal initially dominate. Successive “filtering” of available species, accompanied by changes in soils and microclimate, leads to progressive changes in the role of biotic interactions in structuring communities (after Harper [1977], Keddy [1992], and Archer [1995]).

consistent with species abundance distributions (SADs) in a diverse range of assemblages (Hubbell 2001, Volkov et al. 2007). However, since contrasting ecological processes can give rise to identical or similar SADs, it has long been recognized that there is limited value in efforts to infer community processes from SADs alone (Cohen 1968). Clearly there is a need to extend neutral theory beyond SADs to a broader set of readily falsifiable predictions based on the null assumption of functional equivalence among species (Leigh 2007).

The “filter paradigm” (Fig. 1) has been widely employed to conceptualize the action of biological structuring processes in organizing the mix of species in plant communities (Harper 1977, Keddy 1992). In this paradigm, communities can be viewed as being assembled by the combined “filtering” action of a set of biotic interactions, each of which favors some organisms while eliminating others from a larger potential pool of species. Positive plant interactions often involve facilitated recruitment and growth under the ameliorated microsite conditions provided by previously established nurse plants. The nature of the interaction among plants in these aggregates is likely to change over time,

becoming progressively more negative (e.g., Archer 1995, Greenlee and Callaway 1996). Competition within plant aggregates often becomes increasingly asymmetrical and can lead to a successional sequence of species replacements as pioneer plants become outcompeted (Fig. 1). Early-successional communities are likely to be the most disordered and “individualistic” (Gleason 1926), while later stages of succession tend to produce species assemblages structured by greater functional differentiation among species (Richardson 1980). Empirical evidence supports the approach of recognizing both stochastic dispersal and niche differentiation in structuring communities. For example, a study of communities in experimental ponds showed that stochastic colonization initially produced highly variable species assemblages, but that subsequent effects of drought forced convergence toward more similar (stress-tolerant) species assemblages (Chase 2007).

*Shrub islands in a grassland sea: an integrated approach*

Shrub clusters developing in grasslands in southern Texas, USA (Appendix B: Fig. B1), provide a good case study for testing an integrated approach to understand-

ing plant assemblages, because there is a good basis to expect that both stochastic dispersal processes and successional niche differentiation could contribute to patterns of species occurrence. Facilitation among shrub species has led to strongly aggregated patterns among encroaching shrubs as these former grasslands have undergone a recent physiognomic transformation to parkland savannas (Archer 1995). Once a pioneering individual shrub, usually *Prosopis glandulosa* Torr. (honey mesquite), establishes in open grassland, it facilitates the progressive establishment of a diverse suite of understory shrubs forming a discrete “shrub cluster” that expands over time (Archer et al. 1988, Archer 1989). Tree ring analyses that allow aging of the founding mesquite (Stoker and Archer 1996) have confirmed that larger clusters are older, the largest being over 90 years of age (Boutton et al. 1998). Soils and microclimate change as clusters develop and expand (Archer 1995, Hibbard et al. 2001), and shrub species within clusters differ with respect to leaf longevity (Nelson et al. 2002), daily and seasonal patterns of photosynthesis and water relations (Barnes and Archer 1999), functional rooting depths (Midwood et al. 1998, Zou et al. 2005), and nitrogen responses (Zitzer et al. 1996, Boutton et al. 1999), suggesting a potential successional basis for differentiation among cluster species. This has been supported by space-for-time observations of a sequential pattern of appearance by shrub species during cluster development, where those species with high frequencies of occurrence in nascent clusters have been considered early successional (Archer et al. 1988) (Appendix C: Fig. C1). However, interpretation of these patterns is confounded by differences in abundance among shrub species. For example, species that are the most abundant and produce the most recruits have a high probability of being present in small (pioneer) clusters by random chance alone (e.g., Chesson and Warner 1981). Observed patterns of species occurrence therefore need to be compared against appropriate null models describing the baseline patterns that would be expected from neutral stochastic recruitment processes.

Evidence for facilitation in shrub clusters suggests that this process is mainly passive, whereby shrubs in the grassy matrix provide perching structures that enhance seed dissemination by birds (Archer 1995), a highly stochastic process. Island biogeographic processes (MacArthur and Wilson 1967), involving stochastic gains and losses of species, would therefore also be expected to play an important role in determining species assemblages in clusters. In attempting to explain the observed patterns of species occurrences in shrub clusters in this savanna parkland, we therefore propose that the “filter paradigm” of community assemblage be extended to include stochastic influences associated with island biogeographic theory (Fig. 1). In this integrated framework, an initial dispersal filter stochastically distributes propagules to vegetation patches as they

establish and expand. Subsequent filters reflect how the dominant processes shaping community structure change as clusters develop and mature (Archer 1995). As a test of this integrated framework, we used field data on species occurrence and turnover to determine the relative contribution of neutral stochastic processes and successional differentiation in accounting for observed patterns in shrub species assemblages.

## METHODS

### *Study site*

The Texas AgriLife La Copita Research Area (27°40' N, 98°12' W) near Alice, Texas, USA, is situated in the Rio Grande Plains of the Tamaulipan Biotic Province. Mean annual precipitation of 680 mm is bimodally distributed (spring and autumn), and the mean annual temperature is 22.4°C. Vegetation on convex uplands of sandstone-derived sandy loam soils consists of discrete clusters of woody plants embedded within an herbaceous matrix (Appendix B: Fig. B1). See Archer (1995) for additional details on climate, soils, and vegetation.

### *Patterns of species occurrence and establishment*

We consider four perspectives on patterns of species occurrence in developing shrub clusters: (1) within whole shrub clusters (for competing neutral and niche models); (2) within sample units of equivalent area; (3) spatial dependence of species occurrences in paired sample units within shrub clusters; and (4) turnover of species over a 10-year period. For each of these perspectives we generate null model predictions of the patterns of species occurrences that would be expected from purely neutral, stochastic processes. We then compare field observations against our null models to test for deviations that would indicate the expression of niche differentiation in structuring shrub assemblages.

### *Whole-shrub clusters: changing species patterns during cluster development*

First, we investigated patterns of species establishment in whole-shrub clusters by considering competing neutral and niche models that describe the probability,  $P(a)$ , of a given species occurring in a particular cluster as a function of the area (and stage of development) of the cluster. To generate neutral occurrence-area curves, consider the random variable  $A_1$ , which represents the area of a developing cluster when the first individual of a particular species establishes in it. For neutrality, assume the Markov property,

$$\text{Prob}(A_1 > a_1 | a_2 \times A_1 > a_1) = \text{Prob}(A_1 > a_2)$$

i.e., assume that the probability of the species being added to a cluster in any growth increment of area  $a_2$  is independent of its previous size ( $a_1$ ) or any other interactions with preexisting attributes of the cluster (see Boswell et al. [1979] for background theory):

$A_1$  has Markov property

$$\begin{aligned} &\Leftrightarrow A_1 \sim \exp(d) \text{ (exponential distribution)} \\ &\Leftrightarrow P(a) = 1 - e^{-da} \text{ (cumulative density function for } A_1). \end{aligned} \tag{1}$$

This is the required neutral model giving the expected probability of a species occurring in a cluster,  $P(a)$ , as a function of cluster size,  $a$ , and a fitted constant representing the abundance of the species,  $d$ . As required by the neutral property of per capita equivalence, this assumes that a species that is twice as abundant will produce twice as many recruits and will therefore be twice as likely to be represented each time a new recruit is added to the cluster.

To illustrate the link between this statistical theory and the underlying biology, consider the following coin-tossing (50:50 chance) analogy. Let us say that a shrub cluster expands in discrete growth increments and that a species has a probability of 0.5 of being added to a cluster in any growth increment. The probability of the species being in a cluster after the first growth increment would be 0.5, after the second it would be 0.75, and generally, after  $n$  growth increments the expected probability of the species occurring in the clusters,  $P(n)$ , would be

$$P(n) = 1 - (1 - 0.5)^n. \tag{2}$$

The exponential distribution used in the null model above (Eq. 1) can be thought of simply as the continuous form of the geometric distribution (used in Eq. 2).

Our null model, based on the assumption of neutrality, represents how species would be expected to occur in clusters if the chance of a species being added to a cluster in each growth increment remained constant (in proportion to its abundance) through each stage of cluster development (and unaffected by changing microenvironment and species interactions as clusters mature). If there is successional niche differentiation among species, then rates of species recruitment and survival in clusters would be expected to vary along a temporal (successional) gradient of cluster development,  $a$ , which would be expressed as deviations from baseline neutral expectations (curves of constant accumulation; Fig. 2).

For formal comparison with the neutral model, we propose three niche models that allow species-specific influences of cluster succession on recruitment and mortality. We represent these by replacing the constant rate of recruitment for each species ( $d$ ) in Eq. 1 with a function  $D(a)$  [such that  $P(a)$  becomes  $1 - e^{-D(a)a}$ ], where  $D(a)$  is the net cumulative rate of recruitment in clusters of size  $a$ . In the first niche model [niche 1,  $D_1(a)$ ; Fig. 2a],  $D_1(a)$  is a Gaussian (“bell curve”) function of the stage of cluster development:

$$D_1(a) = G(a) = ue^{-[(a-v)^2/2w^2]} \tag{3}$$

where  $G$  is the Gauss function,  $a$  is cluster area (describing the potential successional gradient),  $u$  ( $>0$ ) is the maximum value at the peak of the function (an abundance scaling parameter),  $v$  is the value of  $a$  at the

peak of the function (the center of the niche along the gradient), and  $w$  ( $>0$ ) is a parameter determining the spread of the bell curve (describing niche width). Unlike the neutral model, this model accommodates both the accumulation of species in clusters and net losses, by allowing the occurrence of some species (e.g., early-successional species) to decline as clusters mature. Where there is support for the niche models the Gaussian parameters provide the required objective measures of the successional ranking of species (the niche center parameter,  $v$ ) and degree of specialization ( $w$ ).

For the second niche model (niche 2:  $D_2(a)$ ; Fig. 2b), we considered that species might only be added to shrub clusters (as with the neutral model) with minimal net loss, but that the instantaneous rate of recruitment is a Gaussian function of the stage of cluster development. To derive the net cumulative rate of recruitment in a cluster of size  $a$  [the required function for  $D_2(a)$ ], we need to calculate the average by integrating the instantaneous rate between 0 and  $a$  and dividing by  $a$ :

$$\begin{aligned} D_2(a) &= \frac{\int_0^a G(t)dt}{a} \\ &= \frac{uw\sqrt{\frac{\pi}{2}}}{a} \left[ \text{Erf}\left(\frac{v}{w\sqrt{2}}\right) - \text{Erf}\left(\frac{v-a}{w\sqrt{2}}\right) \right] \end{aligned} \tag{4}$$

where  $\text{Erf}(x)$ , the error function, is defined as

$$\text{Erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-t^2} dt \tag{5}$$

and other parameters ( $a$ ,  $u$ ,  $v$ ,  $w$ ) are as described for Eq. 3. (The Gauss function was integrated algebraically using Mathematica [*available online*].)<sup>3</sup>

In the niche 1 and niche 2 models, it is possible for niche width ( $w$ ) to be made so broad that  $P(a)$  mimics the neutral model. (As  $w \rightarrow \infty$ ,  $G(a)$ ,  $D_1(a)$ , and  $D_2(a) \rightarrow u = d$  [a constant, unaffected by  $a$ ], and  $P(a) = 1 - e^{-D(a)a}$  becomes Eq. 1, the neutral model.) The third niche model (based on niche 1; Fig. 2a) therefore imposes a constraint on niche width such that  $w$  cannot exceed 20, enforcing moderate niche specialization; this constraint ensured that approximately two-thirds of the area under the fitted Gaussian curve (the underpinning “niche component” of the model, Eq. 3) was concentrated within half of the potential successional gradient (observed cluster size,  $a$ , range of 0–60  $m^2$ ). By restricting the most generalized model (niche 1) to the subset of cases in which some niche differentiation is enforced (and neutral behavior is excluded), the niche 3 model allows us to explicitly test for evidence of niche differentiation in field observations. In addition, for all niche models,  $v$  was constrained in the range –20 to 80 to maintain the fitted center of the niche within the proximity ( $\pm 33\%$ ) of the observed range of cluster sizes and prevent

<sup>3</sup> (<http://integrals.wolfram.com>)

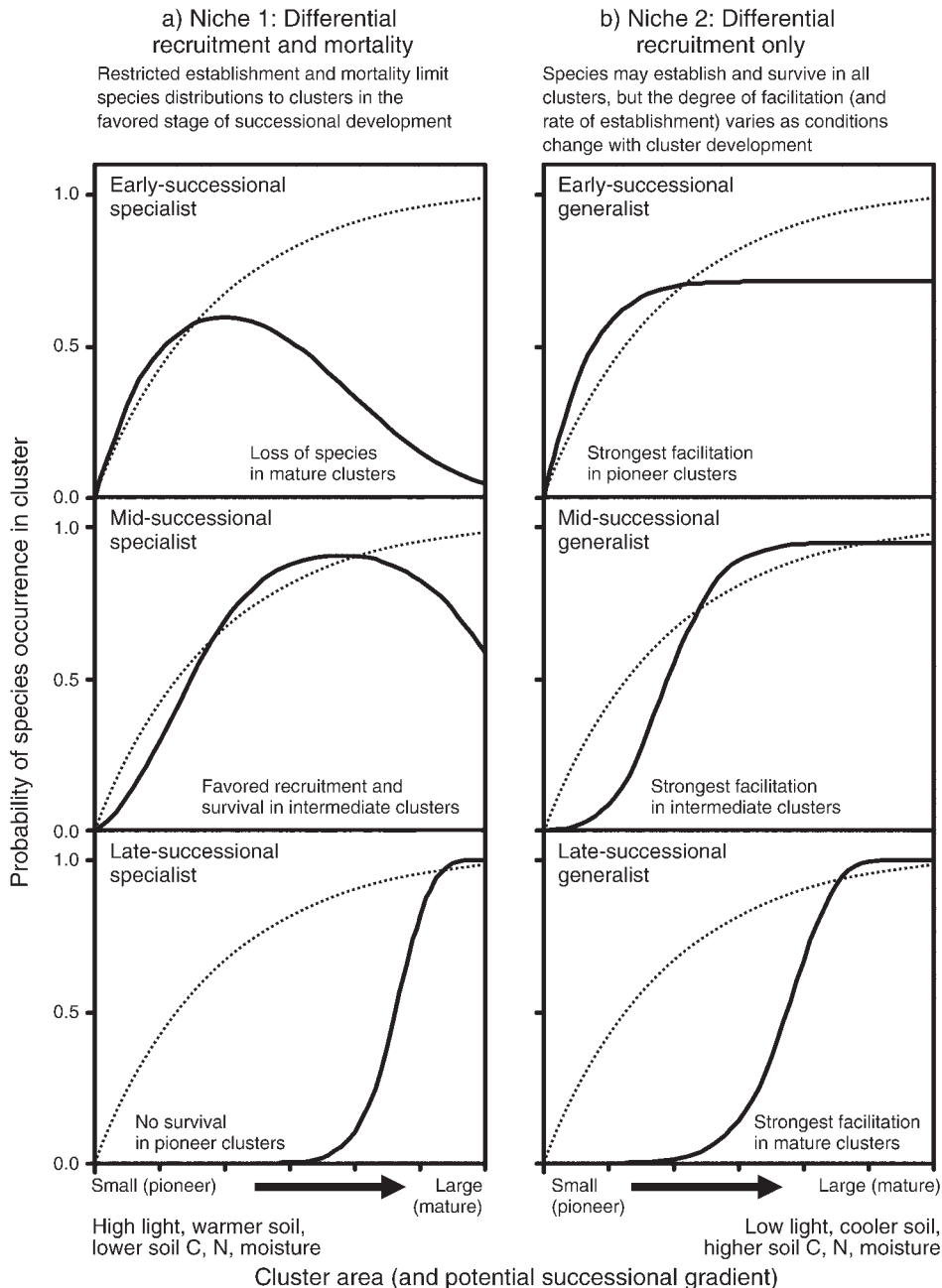


FIG. 2. Possible patterns of species occurrence in developing clusters. The neutral model (dotted curves) assumes that recruitment of each species occurs at a constant (abundance-dependent) rate along a potential successional gradient of cluster expansion and development. Niche theory (solid lines) would predict that recruitment and survival rates (niche 1 model) or recruitment rates alone (niche 2 model) would change along the successional gradient, causing deviations from the neutral model. The niche 1 and niche 2 models are illustrated for cases in which niche specialization occurs but are generalizable enough to duplicate the neutral model. The niche 3 model imposes differential recruitment and survival on the niche 1 model (as illustrated), preventing neutral behavior (see *Methods*).

the parameter optimization from “zooming in” on the extreme tails of the Gauss curve.

Ninety-two shrub clusters were sampled to test field observations against the neutral and niche models. We measured the canopy area of each cluster and invento-

ried the shrub species beneath the canopy of the central, founding *Prosopis* plant. Twelve understory shrub species occurred in the surveys (Table 2). An initial goodness-of-fit test was conducted to determine (1) whether there were deviations from the neutral model

that would indicate successional niche differentiation (Fig. 2) and (2) whether the most generalized of the competing models (niche 1) could provide an adequate fit to observed data. To quantify how patterns of occurrence for each of these species changed during cluster development, we categorized clusters into seven size classes (based on equal quantile divisions). For each cluster size class we counted the observed number of clusters in which each species was present or absent and compared these counts against fitted model predictions (Eq. 1) using a  $G$  test (Sokal 2005).

We complemented this initial test with information-theoretic model selection to identify which of the proposed neutral and niche models was most strongly supported by the field observations (Burnham and Anderson 1998). Using the individual presence/absence observations for each species and model predictions of the probability of occurrence, we constructed a negative-log-likelihood (NLL) function based on a binomial distribution. The parameters for each model were then fitted using the NLM optimization routine (R version 2.8.1 statistical software; R Foundation for Statistical Computing, Vienna, Austria) to minimize NLL. The minimized NLL was used to calculate the corrected Akaike's information criterion ( $AIC_c$ ) to compare the support for each model (Burnham and Anderson 1998). An aggregate  $AIC_c$  was derived for the ability of each model to describe the patterns of species occurrence for the full assemblage of species by combining the NLLs (and parameter estimates) across all 12 species.

#### *Fixed-area sampling units*

The implication of the neutral model (Eq. 1) is that the most abundant species would be more likely to occur in small clusters by random chance alone. Therefore, to further explore patterns of species organization, we developed a sampling design to control for the confounding effects of cluster maturity on the sample unit area (which increase together as clusters expand). We subsampled the same 92 clusters using nested wedge-shaped sample units (SUs) of fixed area (2.5, 5, and 10 m<sup>2</sup>) (Appendix D: Fig. D1). Clusters too small for this complete set of sampling units (11 clusters < 5 m<sup>2</sup> and 31 clusters < 10 m<sup>2</sup>) were excluded from some of the subsequent analyses.

Clusters were categorized as either large (greater than median area) or small for analysis. Under the assumption of neutrality, patterns of species occurrence in equally sized SUs from clusters in different stages of development should be the same. For each species (and each SU size), counts of occurrences and absences in fixed-area SUs were tested (Pearson's  $\chi^2$ ) for biases toward smaller (younger) or larger (older) clusters that would indicate successional niche differentiation. To counteract the biasing effects of small expected frequencies, Yates' chi-square corrections were applied for any test involving an expected frequency of less than five (Sokal 2005).

#### *Spatial dependence of species occurrence*

Neutral models for patterns of species occurrence (Eq. 1) tested only whether the establishment of the first individual of each species in a cluster was random. However, niche differentiation could also be expressed by spatial dependence in shrub recruitment, whereby the establishment of the first recruit in a cluster could indicate favorable local site conditions that would favor subsequent recruitment of that species. If subsequent additions of the same species within a cluster are positively related, then that species should occur in both SUs of a pair more often than expected by chance (the binomial expectation). We used the paired, adjacent 2.5-m<sup>2</sup> SUs (Appendix D: Fig. D1) to test ( $\chi^2$ ) for spatial dependence in the occurrences of each species within clusters. We repeated the tests for the paired, opposite 5-m<sup>2</sup> SUs.

#### *Species turnover*

To directly assess whether changing conditions in maturing clusters influenced species additions and losses, we used repeated sampling of 99 clusters over a 10-year interval. Cluster size (area), species composition, and the total density of woody plants (for all species combined) were measured in 1988 and species were re-inventoried in 1998. There was insufficient species turnover to analyze each species separately, so we summarized the changes for each cluster as the total number of new species added to each cluster and the number of previously occurring species that were lost. To account for the fact that larger clusters in 1988 tended to start with more species, we also calculated for each cluster the percentage of species loss (the number of species lost relative to the number of species initially in the cluster) and the percentage of gain (the number of species gained relative to the potential pool of species not yet in the initial cluster). If plant interactions play a predominant role in structuring shrub assemblages (indicating progression down the continuum in Fig. 1), it might be expected that these influences would be strongest (1) in larger, more mature clusters and (2) in clusters with higher shrub densities, where new species recruitment might be relatively low and where the loss of existing species might be relatively high. Conversely, if island biogeographic processes predominate (the top of the continuum in Fig. 1), then (1) larger clusters might be expected to provide larger "islands" that enhance shrub species recruitment and (2) clusters with higher shrub densities would provide greater buffering against local stochastic species loss. We used Spearman's rank correlations to test whether cluster size and shrub density influenced patterns of species gains and losses.

## RESULTS

Goodness-of-fit  $G$  tests showed that patterns of occurrence for the 12 species of understory shrubs were closely approximated by the neutral model predictions (Appendix E: Fig. E1). Only one species, *Colubrina*,

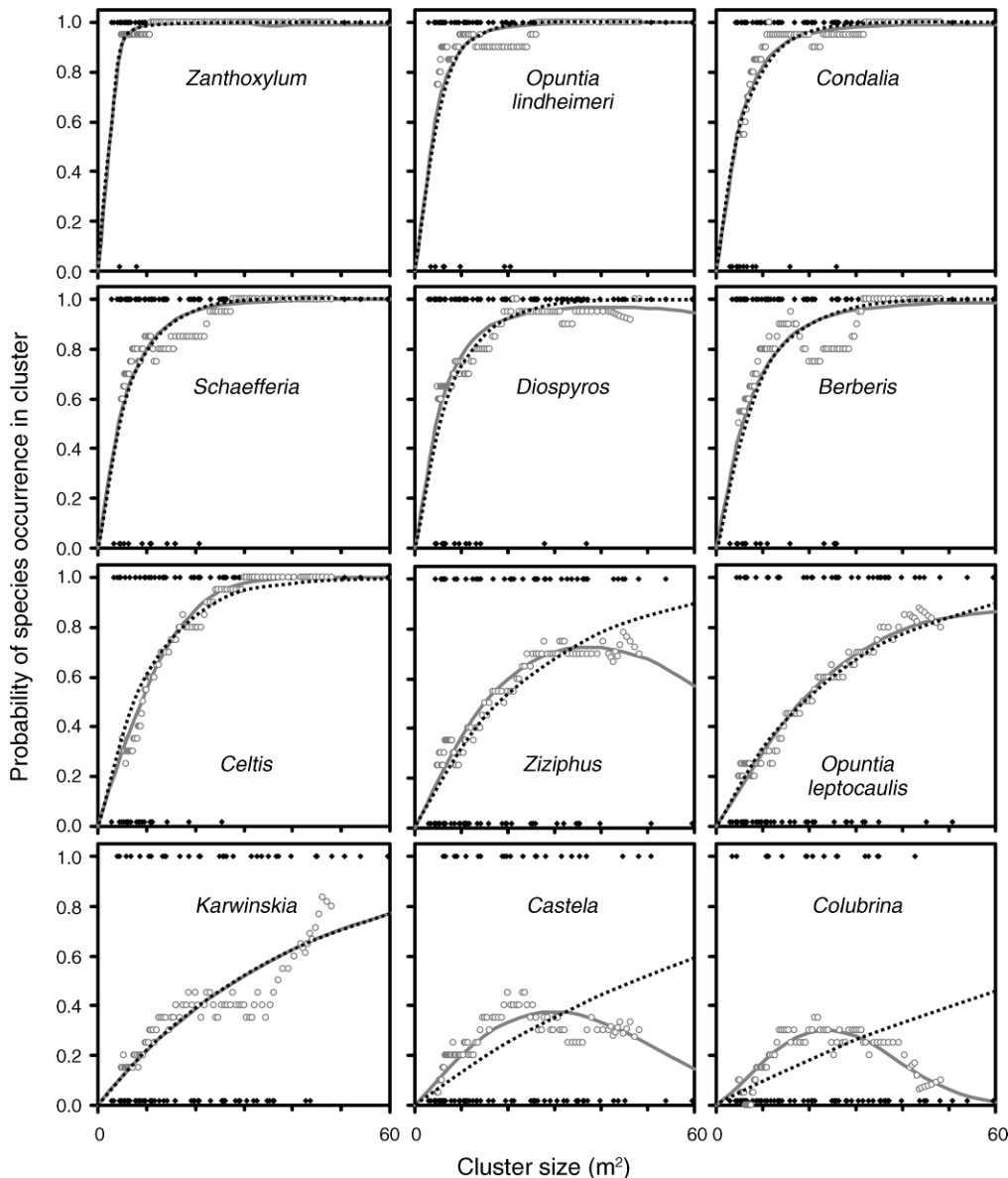


FIG. 3. Comparison of fitted models of patterns of species occurrence in shrub clusters based on neutral (dotted line) and niche processes (solid line). The niche 1 model (shown) was the best of three alternatives tested. Solid symbols indicate observed species presence (1) and absence (0) data. Moving averages (of 10 adjacent points) provide a rough visualization of patterns of species occurrence in the field (open circles). Increases in cluster size represent development along a potential successional gradient (see Fig. 2). See Table 1 for formal model comparisons. The study was conducted in the Texas AgriLife La Copita Research Area near Alice, Texas, USA.

showed significant deviation, with a bias toward clusters in the early stages of development. In this instance the niche 1 model provided an adequate fit, confirming that the candidate set of models was sufficient for subsequent model selection (Appendix E: Fig. E1). Model selection based on  $AIC_c$  showed that on aggregate, and for most species individually, the neutral model had the most support from observed patterns of species assemblage (Fig. 3, Table 1). The most generalized niche model (niche 1) had less support, except for the case of *Colubrina* (where it had the most support) and it had

similar support to the neutral model for four other species (*Celtis*, *Diosperis*, *Ziziphus*, and *Castela*). With the exception of *Colubrina*, the niche 2 model (based on differential recruitment alone, without net species losses) had as much support as niche 1, indicating little evidence of differential species mortality during cluster succession (Table 1). However, the fitted curves for the niche 1 and niche 2 models tended to approximate the neutral model by employing generalist niches (large values of the niche width parameter  $w$ ) that maintained relatively constant rates of recruitment ( $D(a) \approx u \approx d$ ) during cluster

TABLE 1. Maximum-likelihood parameter estimation and comparison of a neutral model against three alternate niche models for patterns of species occurrence in shrub clusters based on corrected Akaike information criterion (AIC<sub>c</sub>).

Model	Zan	Op1	Con	Sha	Dio	Ber	Cel	Ziz	Op2	Kar	Cas	Col	AGG
Neutral (net cumulative rate of recruitment, $D(a)$ , proportional to species abundance, $d$ )													
$d$	0.48	0.22	0.16	0.16	0.13	0.11	0.093	0.038	0.037	0.025	0.015	0.010	{<<<<}
AIC <sub>c</sub>	18.4	53.4	58.0	66.5	83.0	85.0	77.7	116.4	106.0	110.7	103.2	94.2	970.7
Niche 1 (Gaussian net cumulative rate of recruitment, gains and losses of species, $D(a) = \text{Eq. 3}$ )													
$u$ (max)	0.50	0.24	0.20	0.17	0.18	0.13	0.20	0.046	0.04	0.025	0.022	0.019	{<<<<}
$v$ (center)	-20.0	-20.0	-20.0	-20.0	-20.0	-20.0	80.0	15.4	32.5	80.0	9.4	13.1	{<<<<}
$w$ (width)	94.1	69.3	58.3	89.9	49.8	72.3	51.3	28.9	46.5	665.4	24.6	15.9	{<<<<}
AIC <sub>c</sub>	22.6	56.5	61.9	70.6	84.0	88.2	80.1	117.8	110.1	114.9	103.1	90.1	1015.0
Niche 2 (Gaussian instantaneous rate of recruitment, species can only accumulate, $D(a) = \text{Eq. 4}$ )													
$u$ (max)	0.49	0.23	0.18	0.165	0.14	0.12	0.47	0.047	0.043	0.025	0.019	0.013	{<<<<}
$v$ (center)	-20.0	-20.0	-20.0	-20.0	-20.0	-20.0	80.0	-20.0	21.3	-20.0	-20.0	-20.0	{<<<<}
$w$ (width)	88.0	76.5	67.9	82.4	66.4	73.4	39.6	48.2	26.1	148.3	50.1	49.7	{<<<<}
AIC <sub>c</sub>	22.6	57.2	62	70.6	86.2	88.7	80.1	119.0	110.1	114.9	105.8	96.4	1028.8
Niche 3 (niche 1 with niche width constrained ( $w \leq 20$ ) to enforce moderate specialization, $D(a) = \text{Eq. 3}$ )													
$u$ (max)	0.72	0.24	0.20	0.23	0.09	0.14	0.14	0.05	0.047	0.015	0.022	0.019	{<<<<}
$v$ (center)	24.9	14.2	19.8	24.9	24.9	17.6	31.2	21.6	29.0	25.0	14.9	13.1	{<<<<}
$w$ (width)	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	{<<<<}
AIC <sub>c</sub>	23.5	60.6	63.8	76.1	104.8	94.6	81.3	118.6	111.8	134	103.2	90.1	1077.6
$\Delta_i$ (difference in AIC <sub>c</sub> , for model comparison)													
Neutral	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0.2</b>	4.1	<b>0</b>
Niche 1	4.2	3.1	3.9	4.1	<b>1.0</b>	3.1	2.4	<b>1.4</b>	4.1	4.2	<b>0</b>	<b>0</b>	44.3
Niche 2	4.2	3.8	4.0	4.1	3.2	3.7	2.3	2.6	4.1	4.3	2.7	6.3	58.1
Niche 3	5.1	7.2	5.8	9.6	21.8	9.6	3.6	2.2	5.8	23.3	<b>0.1</b>	<b>0</b>	106.9

Notes: Column headings are abbreviated species' names, listed in full in the same order as in Table 2. For niche models,  $u$ ,  $v$ , and  $w$  are parameters for the Gauss function "niche component" of species gain/loss functions (Eqs. 3 and 4). The abbreviation "AGG" refers to an aggregated comparison of the combined community of 12 species for each model. For model comparisons, a  $\Delta_i$  of "0" indicates the model(s) with the lowest AIC<sub>c</sub> (in boldface),  $\Delta_i < 2$  indicates similar support for models (in boldface),  $\Delta_i > 4$  indicates weak support relative to the "leading" model, and  $\Delta_i > 10$  indicates virtually no support (Burnham and Anderson 1998). The study was conducted in the Texas AgriLife La Copita Research Area near Alice, Texas, USA.

development (Table 1). The niche 3 model (which imposed moderate niche specialization) generally had little to no support, except for *Colubrina*, *Castella*, and *Ziziphus* (where fitted models were identical or similar to niche 1; Table 1).

Similarly, the  $\chi^2$  tests of fixed-area sampling units showed that, with only two exceptions, species occurrences were not significantly biased toward smaller or larger shrub clusters (Table 2). *Condalia* occurred 33% ( $\chi^2 = 5.7$ ,  $P < 0.05$ ) more often than expected in 2.5-m<sup>2</sup> SUs of small clusters. This species showed a similar bias (42%,  $\chi^2 = 10.4$ ,  $P < 0.05$ ) in 5-m<sup>2</sup> SUs, but no bias in 10-m<sup>2</sup> SUs. *Celtis* showed an opposite bias, occurring 46% ( $\chi^2 = 7.3$ ,  $P < 0.05$ ) more often than expected in 5-m<sup>2</sup> SUs of large clusters, but exhibited no detectable biases in 2.5-m<sup>2</sup> and 10-m<sup>2</sup> SUs. Tests among paired SUs within clusters only showed limited evidence of spatial dependence in shrub recruitment (Appendix A: Table A1), with possible positive spatial dependence of recruitment within clusters for two of the least abundant species (*Colubrina* and *Karwinskia*).

On average, shrub clusters gained 1.1 new species (19% of the potential number of species that could have been gained) and lost 0.6 species (11% of the initial species present) over the 10-year period between repeat sampling. Larger clusters gained more species ( $r = 0.30$ ,  $P < 0.01$ ,  $n = 99$ ), despite the fact that they contained

more species to start with ( $r = 0.61$ ,  $P < 0.01$ ). In contrast, rates of species loss decreased with increasing cluster size ( $r = -0.37$ ,  $P < 0.01$ ). There was no evidence that shrub density affected either percentage of gain ( $r = 0.07$ ,  $P > 0.05$ ) or percentage of loss of species ( $r = -0.21$ ,  $P > 0.05$ ; Appendix F: Fig. F1).

TABLE 2. Values of  $\chi^2$  for tests of biases in species distributions toward large (+) or small shrub (-) clusters.

Species	Size of fixed-area sample unit (m <sup>2</sup> )		
	2.5 ( $N = 92$ )	5 ( $N = 81$ )	10 ( $N = 61$ )
<i>Zanthoxylum fagara</i>	0.96	[0.10]	[-]
<i>Opuntia lindheimeri</i>	0.00	0.73	[0.04]
<i>Condalia hookeri</i>	5.72* -	10.4* -	[0.11]
<i>Schaefferia cuneifolia</i>	0.70	1.15	[0.17]
<i>Diospyros texana</i>	0.42	1.22	[1.34]
<i>Berberis trifoliata</i>	0.75	1.06	[1.67]
<i>Celtis pallida</i>	1.22	7.27* +	[0.56]
<i>Ziziphus obtusifolia</i>	0.93	0.03	0.14
<i>Opuntia leptocaulis</i>	0.65	1.85	3.48
<i>Karwinskia humboltiana</i>	1.53	0.41	0.13
<i>Castela texana</i>	[1.60]	[0.08]	[0.00]
<i>Colubrina texensis</i>	[1.23]	[0.98]	[0.17]

Notes: Significant biases are indicated by an asterisk ( $\chi^2_{1,0.95} = 3.84$ ). If any expected frequency was less than 5, Yates' corrections were applied (bracketed values; see *Methods* for details). Species are ranked in order of decreasing abundance.  $N$  indicates the number of shrub clusters sampled in each case.

\*  $P < 0.05$ .



## DISCUSSION

Observed patterns of species occurrences across a sequence of cluster development (where increases in cluster area represent the passage of time) conformed very closely to neutral predictions (Fig. 3, Table 1; Appendix E: Fig. E1). This was despite the fact that the neutral predictions were based on the simplistic, readily falsifiable assumption that species accumulate at a constant rate, (1) without the net rate ever being affected by changing conditions in the cluster, (2) without there ever being a net loss of species, and (3) without species ever being excluded by physical conditions or biological interactions at any stage of cluster development (Fig. 2). Differences in abundance of species (with stochastic per capita equivalence among recruitments) were therefore capable of accounting for a large proportion of the observed patterns of species occurrence. These results highlight the danger of uncritically assuming that apparent structure in species assemblages reflects the expression of functional differences among species.

There was, however, strong evidence for niche differentiation in one species, wherein the distribution of *Colubrina* was biased toward early-to-mid stages of cluster development and declined in older clusters. Niche models had similar support to the neutral model for four other species (*Celtis*, *Diosperis*, *Ziziphus*, and *Castela*) (Table 1). Fixed-area sampling units provided some additional evidence of slight differences in the rates at which *Condalia* (early successional) and *Celtis* (late successional) accumulated in clusters at different stages of maturity (Table 2). Furthermore, the central *Prosopis* has a distinctive role in facilitating the establishment of the understory shrubs beneath it. Thus, while neutral processes accounted for most of the observed patterns of species assemblage in shrub clusters, there was also evidence of successional differentiation among species.

Neutral models for patterns of species occurrence dealt only with the first addition of any species to a cluster. But subsequent additions of a species to the same cluster would be expected to be autocorrelated if (1) recruitment within clusters occurs in batches (e.g., delivery of a batch of bird-dispersed seeds), (2) local microsite conditions that favored the first recruit continue to favor recruits of the same species, or (3) the first recruit of a species propagates itself within the cluster. There was some evidence of positive spatial correlation for two species of low abundance, but generally these processes were not strongly expressed. This suggests local propagation of shrubs within clusters is limited and that seeds for establishment are mainly coming from external sources in independent recruitment events.

Surveys repeated over a 10-year interval confirmed that species accumulation was the dominant process in cluster maturation. Moreover, species loss rates declined and recruitment rates increased in larger, more developed clusters. These results, and the increase in the number of species with cluster size, are consistent with

interpreting clusters as biogeographic “islands” of different sizes (MacArthur and Wilson 1967). Furthermore, there was no evidence that patterns of species turnover were negatively affected by the stage of cluster development or the density of shrubs in clusters (indicators of the potential strength of competitive interactions).

Using an integrated framework that accommodated both niche and neutral assembly (Fig. 1), we set out to determine the relative roles of niche differentiation and neutral stochastic processes in structuring shrub cluster assemblages in savanna parklands of southern Texas. Patterns of species occurrences in shrub clusters indicated that most species were successional generalists (Fig. 3), but there was also evidence of limited successional differentiation. In terms of our original framework (Fig. 1), our case study therefore fits toward the top end of the continuum, where shrub species co-occur in largely neutral stochastic assemblages with relatively weak expression of biological structuring processes. Passive facilitation of seed dispersal from sources outside the cluster appears to account for most of the observed patterns of species organization in clusters. It may be that the physiognomic conversion of this landscape from grasslands to savanna parklands has been too recent (mostly over the past 60–70 years; Archer 1995) for community structure to be fully expressed. Since these shrubs are long-lived, current vegetation patterns may still strongly reflect initial recruitment processes rather than equilibrium conditions (i.e., demographic inertia). Functional differentiation among species may become more pronounced with the passage of time as available resources in clusters become fully exploited, as interactions among maturing plants become stronger, and as the initial colonizing plants start to die and be replaced (Fig. 1).

We have not intended to provide “proof-by-example” for either niche or neutral theory. Rather, we have demonstrated the value of an integrated framework that accommodates both processes without making a priori assumptions and allows observations to reveal the relative contributions of each. This approach allowed us to detect the influence of both types of processes, although in this example, one was much stronger than the other. Neither theory alone was sufficient to explain the assemblages of species in the shrub clusters we studied. The comparison of niche and neutral models further emphasized the continuum between neutral and niche processes in demonstrating that the neutral model was a special case of the more generalized niche model. In this context, neutral assemblages can be thought of as communities in which all species have very broad/similar niches, and as the interactions of individual organisms become more strongly dependent on characteristics associated with species identity, niches become more defined and niche differentiation becomes more important in structuring species organization. It is thus a matter of degree, rather than a binary distinction

between niche and neutral organization. In addition, although the framework for our particular case study (Fig. 1) implies that the sequential action of “filtering” processes leads to progressive niche differentiation, this need not necessarily be the case. Any disturbance or process (filters) that affects individuals of different species equivalently will have a neutral effect in randomizing species assemblages, while conditions and processes that allow the uninterrupted expression of functional differences among species will tend to generate niche differentiation.

Caution should be exercised in extrapolating inferences about neutral species assemblage derived from community-level investigations to evolutionary and biogeographic scales. Just because differences between species play little role in shaping the species assemblage at a specific location and point or short span in time does not necessarily mean that a species’ distinguishing characteristics will not be important in other contexts (i.e., mixes of species and physical environments) that may occur at other locations and instances over broader spatial and/or temporal scales. More generally, the relative importance of niche differentiation and neutral processes in species assemblage will only become clear through further development of integrated frameworks (such as the one proposed here) and by then applying these approaches to a wide, unbiased set of cases. It is only by scrutinizing assumptions underlying sacred cornerstones of ecological theory and subjecting them to rigorous testing that positive evidence for their role in the natural world can be established. Further development of a rigorous and more comprehensive neutral theory with a broad set of readily falsifiable predictions would provide a powerful tool to (1) reveal patterns of community structure that have uncritically been ascribed to niche differentiation, (2) serve as a baseline theory providing an idealized, widely generalizable first approximation of expected community behaviors and characteristics in the absence of functional differentiation among species, and (3) provide objective evidence for the action of biological structuring processes where observations deviate from neutral predictions.

#### ACKNOWLEDGMENTS

This research was funded in part by the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas, NSF Ecosystems grant DEB 9981723, and a Small Grant from The Nature Conservancy of Texas. Brian Northup kindly provided survey data from previously sampled shrub clusters. We thank Alex Kutt, Katie Predick, and two anonymous reviewers for helpful comments and suggestions on an earlier draft of the manuscript.

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#### APPENDIX A

Results of  $\chi^2$  tests for spatial dependence in species distributions within clusters (*Ecological Archives* E091-082-A1).

#### APPENDIX B

A photograph of shrub clusters at study site (*Ecological Archives* E091-082-A2).

#### APPENDIX C

Contrasting explanations for the sequential appearance of species in expanding shrub clusters (*Ecological Archives* E091-082-A3).

#### APPENDIX D

Sample design for partitioning shrub clusters into nested, fixed-area sampling units to measure species occurrence (*Ecological Archives* E091-082-A4).

#### APPENDIX E

Goodness-of-fit  $G$  tests for the neutral and niche 1 models against observed patterns of species occurrence (*Ecological Archives* E091-082-A5).

#### APPENDIX F

Species turnover in shrub clusters over a 10-year period in relation to the initial area and initial shrub density of clusters (*Ecological Archives* E091-082-A6).