
Contributed Paper

Metacommunity Dynamics Over 16 Years in a Pyrogenic Shrubland

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Abstract: *Metacommunity theory allows predictions about the dynamics of potentially interacting species' assemblages that are linked by dispersal, but strong empirical tests of the theory are rare. We analyzed the metacommunity dynamics of Florida rosemary scrub, a patchily distributed pyrogenic community, to test predictions about turnover rates, community nestedness, and responses to patch size, arrangement, and quality. We collected occurrence data for 45 plant species from 88 rosemary scrub patches in 1989 and 2005 and used growth form, mechanism of regeneration after fire, and degree of habitat specialization to categorize species by life history. We tested whether patch size, fire history, and structural connectivity (a measure of proximity and size of surrounding patches) could be used to predict apparent extinctions and colonizations. In addition, we tested the accuracy of incidence-function models built with the patch survey data from 1989. After fire local extinction rates were higher for herbs than woody plants, higher for species that regenerated only from seed than species able to resprout, and higher for generalist than specialist species. Fewer rosemary specialists and a higher proportion of habitat generalists were extirpated on recently burned patches than on patches not burned between 1989 and 2005. Nestedness was highest for specialists among all life-history groups. Estimated model parameters from 1989 predicted the observed (1989–2005) extinction rates and the number of patches with persistent populations of individual species. These results indicate that species with different life-history strategies within the same metacommunity can have substantially different responses to patch configuration and quality. Real metacommunities may not conform to certain assumptions of simple models, but incidence-function models that consider only patch size, configuration, and quality can have significant predictive accuracy.*

Keywords: Florida rosemary scrub, nestedness, patch connectivity, patch-incidence model, patch quality, shrubland

Dinámica de la Metacomunidad Durante 16 Años en un Matorral Pirogénico

Resumen: *La teoría de metacomunidades permite predicciones de la dinámica de ensambles de especies potencialmente interactuantes que están conectadas mediante la dispersión, pero son raras pruebas empíricas robustas de la teoría. Analizamos la dinámica de la metacomunidad de matorral de romero de Florida, una comunidad pirogénica distribuida heterogéneamente, para probar predicciones sobre tasas de recambio, anidamiento de la comunidad y respuestas al tamaño, arreglo y calidad del parche. Recolectamos datos de ocurrencia de 45 especies de plantas en 88 parches de matorral de romero en 1989 y 2005 y utilizamos la forma de crecimiento, el mecanismo de regeneración después de fuego y el nivel de especialización de hábitat para clasificar a las especies por historia natural. Probamos si el tamaño del parche, la historia de incendios*

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3 y la conectividad estructural (una medida de proximidad y tamaño de parches circundantes) se podrían
 4 utilizar para predecir las extinciones y colonizaciones aparentes. Adicionalmente, probamos la precisión de
 5 los modelos de función de incidencia que desarrollamos con los datos del muestreo de parches en 1989. Después
 6 de un incendio, las tasas de extinción local fueron mayores para hierbas que para plantas leñosas, mayores
 7 para especies que regeneraban solo de semillas que para especies capaces de rebrotar y mayores para especies
 8 generalistas que especialistas. Pocas especialistas y una mayor proporción de generalistas fueron extirpadas
 9 de parches recién quemados que de parches no quemados entre 1989 y 2005. El anidamiento fue mayor
 10 para especialistas en comparación con los demás grupos de historia de vida. Los parámetros estimados por el
 11 modelo con datos de 1989 predijeron las tasas de extinción observadas (1989–2005) y el número de parches
 12 con poblaciones persistentes. Estos resultados indican que especies con diferentes estrategias de historia de vida
 13 dentro de la misma metacomunidad pueden tener respuestas sustancialmente diferentes a la configuración
 14 y calidad de los parches. Puede que las metacomunidades reales no cumplan con ciertas suposiciones de
 15 modelos simples, pero los modelos de función de incidencia que solo consideran el tamaño, la configuración
 16 y calidad del parche pueden tener una precisión predictiva significativa.

17 **Palabras Clave:** anidamiento, calidad del parche, conectividad de parches, matorral, matorral de romero de
 18 Florida, modelo de incidencia de parche

20 Introduction

21
 22 As the loss and fragmentation of natural communi-
 23 ties continues, interacting species increasingly occur in
 24 metacommunities—assemblages of species occurring on
 25 discrete patches of habitat linked by dispersal. Under-
 26 standing the spatial and temporal dynamics of metacom-
 27 munities is critical to informing decisions that preserve
 28 the long-term stability of ecosystem function and species
 29 diversity of landscapes (Holt et al. 2005). It would be
 30 ideal to be able to base predictions about future meta-
 31 community structure on a minimum of data. A conven-
 32 ient method of modeling metacommunity dynamics is
 33 to assume individual species will respond equivalently
 34 to a landscape (Chave 2004). However, this approach is
 35 too simplistic to provide predictive accuracy (Cottenie
 36 2005). Each species in a metacommunity may have a
 37 unique extinction rate and colonization rate within a
 38 landscape due to its particular life-history strategy (Yu
 39 & Wilson 2001). Individual species may differ in their
 40 response to patch size and quality. If dispersal among
 41 patches is high, the patch environment may act as a filter
 42 and, thus, sort the species composition of a patch (Chase
 43 & Leibold 2003; Leibold et al. 2004). In addition, ex-
 44 tinctions and colonizations may be influenced by patch
 45 connectivity, a measure of the distance to and number
 46 and size of surrounding patches (Amarasekare & Nisbet
 47 2001; Mouquet & Loreau 2003). An incidence-function
 48 model of metacommunity dynamics incorporates infor-
 49 mation about patch size, quality, and connectivity with
 50 presence-absence data of individual species to make pre-
 51 dictions about future dynamics (Hanski 1994).

52 Recent metacommunity modeling and empirical in-
 53 vestigation has revealed metacommunity dynamics are
 54 more complex than assumed in incidence-function mod-
 55 els (e.g., Driscoll & Lindenmayer 2009; Hodgson et al.
 56 2009; Matter & Roland 2010). For example, common
 57 assumptions, such as an equilibrium between extinc-
 58 tion and colonization and independence among predictor

variables, are often not met in real metacommunities. One
 difficulty particular to modeling plant metacommunities
 is the presence of seed banks. Species present in the seed
 bank, but absent aboveground, will not be detected in
 most surveys. Seed banks may alter the spatial dynamics
 that are assumed in metacommunity models (Freckleton
 & Watkinson 2002). Although it is desirable to account
 for these complications, the cost and time of obtaining
 large amounts of detailed information for all species in a
 metacommunity may be prohibitive. If presence-absence
 data can be used to make accurate predictions even in sit-
 uations in which some model assumptions are violated,
 then they can inform land management. Empirical tests
 of the accuracy of these incidence-function models re-
 quire information on patch size and connectivity, habitat
 quality within a patch (hereafter patch quality), and ex-
 tinctions and recolonizations within patches of all species
 in the metacommunity. However, empirical studies that
 meet these requirements are rare (Holyoak et al. 2005).

One potentially fruitful way to understand metacom-
 munity dynamics in real systems is to divide species into
 groups on the basis of life-history strategies and to com-
 pare the strength of responses to patch-level variables
 among groups. An emerging conclusion from this ap-
 proach is that ruderal species respond more strongly
 to patch quality than to patch configuration or connec-
 tivity (Van de Meutter et al. 2007; Collins et al. 2009;
 Minor et al. 2009). Responses may also differ between
 habitat specialists and generalists, with species that oc-
 cur only in patches being more responsive to patch
 connectivity than species that occur in patches and in
 the matrix between patches (Dupre & Ehrlen 2002;
 Murphy & Lovett-Doust 2004). Life-history groups, such
 as specialists, that are more sensitive to changes in patch
 quality may have higher rates of extinctions and coloniza-
 tions, if patch quality fluctuates over time. Alternatively,
 if patch variables do not change substantially across space
 and time, specialists may experience lower extinction
 rates. Patches may represent marginal habitat for some

1
2
3 generalists; thus, generalists may occur in low densities
4 and experience higher turnover rates than specialists.

5 Nestedness is another spatial property of metacommu-
6 nity structure that may differ among life-history groups.
7 In nested systems, patches with lower species richness
8 have a predictable subset of the species that occur in
9 patches with higher richness (Atmar & Patterson 1993;
10 Almeida-Neto & Ulrich 2010). In a highly nested meta-
11 community, the presence of a locally uncommon species
12 is associated with a high probability of presence of more
13 common species. If species within a particular life-history
14 group have strong and similar associations with patch
15 variables including patch quality, then the group may be
16 more strongly nested than the overall community (Wang
17 et al. 2010). Individual species may also exhibit nested-
18 ness if they occur only on patches with a particular set of
19 more common species. Species most responsive to patch
20 variables may have the highest relative nestedness within
21 their life-history group (Hecnar & McLoskey 1997).

22 We used presence-absence survey data, patch char-
23 acteristics, and life-history categories of species of a
24 well-studied metacommunity in Florida (U.S.A.), rose-
25 mary scrub, to investigate whether life-history traits affect
26 the association of a species with spatial (patch size and
27 structural connectivity) and environmental (patch qual-
28 ity) variables, and to examine whether current patterns
29 of species distribution can be used to accurately predict
30 future metacommunity structure.

31 We predicted herbs and species that regenerate af-
32 ter fire through seeds (hereafter seeders) would expe-
33 rience higher turnover rates than the longer lived woody
34 plants and species that regenerate after fire by resprout-
35 ing (resprouters), but did not form a hypothesis about
36 the relative turnover rates of habitat generalists and spe-
37 cialists. We predicted extinction rates would be lower
38 and colonization rates higher on large patches than on
39 small patches and that patch connectivity would show
40 a stronger positive relation with turnover of specialists
41 than generalists. We also hypothesized that species rich-
42 ness of specialists would decrease as time since fire in-
43 creased because fire creates open space and reduces com-
44 petition (Menges & Hawkes 1998; Boughton et al. 2006).
45 We predicted that if specialists are more strongly associ-
46 ated with patch variables than other life-history groups,
47 then they will show the highest level of nestedness.

48 Methods

49 Study System

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51
52 The study was conducted in the western section of Arch-
53 bold Biological Station, an independently operated bi-
54 ological station in central Florida. Archbold is on the
55 Lake Wales Ridge, a paleo-dune system that supports
56 the xeric, nutrient-poor, fire-prone shrubland known as
57 Florida scrub (Abrahamson et al. 1984; Menges 1999).
58 One of the most xeric types of Florida scrub, rosemary

scrub, covers 38.9 ha (4%) of the western section of Arch-
bold (Abrahamson et al. 1984). It is discretely distributed
on locations with the most well-drained soils (Menges
1999). Rosemary scrub is dominated by Florida rosemary
(*Ceratiola ericoides*), dwarf oaks (*Quercus* spp.), and
other shrubs (nomenclature follows Wunderlin [1998]).
Rosemary-scrub patches are commonly surrounded by
the more extensive and denser scrubby-flatwoods plant
association (Menges 1999). Some plant species that oc-
cur in scrubby flatwoods are present in patches of rose-
mary scrub, but they are less abundant (Boughton et al.
2006). Despite overlap in species composition, rosemary
scrub is easily delineated from the surrounding matrix by
the presence of Florida rosemary and the prevalence of
shrubless patches of open sand, which can cover 10–40%
of the area (vs. <10% of scrubby flatwoods; Menges &
Hawkes 1998; Menges et al. 2008). Perhaps due to lower
soil moisture content (Weekley et al. 2007), fire-return
intervals of the larger gaps in rosemary scrub are longer
than in scrubby flatwoods (Menges 1999). Because com-
petition for water and other nutrients is lower in gaps
than near large shrubs, gaps represent a favorable micro-
habitat for many small-statured species, including several
species endemic to rosemary scrub. Fire increases gap
size and number and benefits vital rates of specialists
(Menges & Hawkes 1998; Quintana-Ascencio et al. 2003;
Menges et al. 2008).

Plant Surveys

We surveyed all 88 patches of rosemary scrub within the
study area 4 times between June 1988 and August 1989.
We recorded all species of vascular plants and ground
lichens found on each patch. Presences were combined
across surveys to create the 1989 data set (Quintana-
Ascencio & Menges 1996). We resurveyed patches from
November 2004 through March 2005 to create the 2005
data set. Two nearby patches from 1989 had become con-
tinuous by 2005 and were combined, creating 88 total
patches. We defined *colonization* as a species' above-
ground absence in a patch in 1989 and presence in that
patch in 2005 and *extinction* conversely. These defini-
tions do not account for species present only in the seed
bank. Therefore, our analyses refer to apparent extinc-
tions and colonizations; true extinctions may be underes-
timated and true colonizations overestimated (Freckleton
& Watkinson 2002; Alexander et al. 2009). Because all life-
history groups included species with seed banks, com-
parisons among groups should not be greatly affected
(Menges & Kohfeldt 1995).

We classified species according to life history in 3
ways—habitat requirements (specialists vs. generalists),
growth form (herbs vs. woody plants), and regenera-
tion mechanism after fire (seeds vs. resprouting). Cate-
gorization largely followed Menges and Kohfeldt (1995)
(Supporting Information). We categorized species as

rosemary scrub specialists if they occurred exclusively or primarily in rosemary scrub and as generalists if they also occurred commonly in the matrix between patches. Woody plants included all shrubs and subshrubs regardless of height. We categorized other species as herbs, with the exception of ground lichens, which were not included in this classification. We categorized plants killed by fire that must recruit after fire from seed as seeders. We compared seeders with plants that survive fire by regrowing from belowground organs (i.e., resprouters; Menges & Kohfeldt 1995). Species with unknown regeneration mechanisms and ground lichens were not included in this classification. Assignment to categories was independent (χ^2 tests, $p > 0.25$ for all pairwise comparisons).

Patch Variables

We calculated the area, connectivity, and, as a measure of patch quality, time since the most recent fire for each rosemary patch. These 3 variables are thought to affect species distributions in metacommunities. To calculate patch area, we used the limits defined by 1:4800 resolution vegetation maps that delineated plant communities on the basis of soil drainage and dominant vegetation type (Abrahamson et al. 1984). Area was log transformed for all analyses. Our observations indicated no substantial changes in patch size between survey years.

We considered patch connectivity a landscape property that depends only on the arrangement of patches and not on species identity or attributes of the matrix. Following the methods of Hanski (1998), we calculated the connectivity of each patch (S_i) in MATLAB (version 7.6; 2008) as $S_i = \sum_{j \neq i} A_j \exp(-\alpha d_{ij})$, where A is area of a patch j , and d is distance in kilometers from the center of patch j to the focal patch i . Alpha, a measure of dispersal ability, is difficult to parameterize (Quintana-Ascencio & Menges 1996); therefore, we calculated the logistic coefficient of the patch occupancy data for all individual species across a range of potential alpha values (0.75–2). Coefficients generally increased as alpha increased, indicating the strongest effect of distance on occupancy occurred when distances among patches were relatively short. Therefore, we set alpha to 2 for an average between-patch dispersal distance of 500 m. The relative differences in coefficient values among species remained constant across the range of alphas, indicating the value of alpha will not strongly alter results.

To determine time since fire as of 2005 to the nearest year, we used detailed fire history records available for Archbold. We considered a patch burned if we observed evidence of fire over >50% of the total patch area as determined from ground and aerial surveys.

Extinctions and Colonizations

We used SPSS (version 11.5; IBM Corporation, Armonk, NY, U.S.A.) unless otherwise noted. We tested whether

the study area represented a stable metacommunity, defined as occurring when the majority of species had an approximately equal number of patch extinctions and colonizations. Following Dupre and Ehrlén (2002), we analyzed only species that occurred on between 10% and 90% of the patches in both years; thus, we removed correlations between extinction or colonization rates and percent occupancy. We used Mann-Whitney U tests to compare extinction rates (extinctions per patches occupied in 1989) and colonization rates (colonizations per patches unoccupied in 1989) of target species between specialists and generalists, herbs and woody plants, and seeders and resprouters. For each life-history group, we used stepwise linear-regression models to test whether patch size, connectivity, time since fire, or their interactions were correlated with the number of extinctions or colonizations in a patch. We further investigated the relation between fire and extinctions and colonizations on a subset of patches. To do so, we used Mann-Whitney U tests to compare extinction and colonization rates of populations on patches that did not burn between 1989 and 2005 (unburned) with those on patches that burned between 1989 and 2005 and had a time since last fire in 1989 that was 12 or more years greater than in 2005 (recently burned). We corrected significance values for multiple tests with a sequential Bonferroni procedure.

Metacommunity Nestedness

Degree of nestedness is difficult to compare among life-history groups because commonly used nestedness metrics are sensitive to the size and structure of the species-by-sites matrix and are subject to type I errors (Cook & Quinn 1998; Wright et al. 1998; Almeida-Neto et al. 2008). Therefore, to quantify the relative degree of nestedness, we calculated r nestedness ratios for the 6 life-history groups in both survey years. For each species pair, r nestedness is number of patches on which both species occur divided by the total number of patches occupied by the species with fewer occurrences (Sizling et al. 2009). If both species occupied the same proportion of patches but were randomly distributed on the patches, then one would expect r nestedness to equal the proportion of patches on which the more common species occurs. To test whether species were more nested than by chance, we divided the actual r nestedness by the expected r nestedness—a value we call the r -nestedness ratio. We calculated r -nestedness ratios for all species pairs in both years. When r -nestedness ratios were <1, species co-occurred less often than by chance. Ratios >1 indicated nestedness. We calculated an r -nestedness ratio for each life-history group by averaging all pairwise ratios of the group. Because r -nestedness ratio values had near-normal distributions, we used t tests to determine whether differences in the degree of nestedness between life-history groups were statistically significant.

Metapopulation Model

We tested the ability of an incidence-function model developed by Hanski (1994) and modified by 2 of us on the basis of the 1989 data (Quintana-Ascencio & Menges 1996) to predict both relative extinction rates and the association of patch area with species persistence. We assumed colonization probability increases as patch connectivity increases, extinction probability decreases as patch area increases, and the number of extinctions and colonizations of a given species are equal and lead to a constant proportion of occupied patches. We published maximum-likelihood estimates of 2 model variables, e' and x , for 25 species, including species in all 6 life-history categories (Quintana-Ascencio & Menges 1996).

In the model, e' is a composite variable representing turnover rate (extinction probability \times colonization ability; Quintana-Ascencio & Menges 1996). The value of x describes the sensitivity of extinction probability to changes in patch size. At a given e' , high values of x represent higher probability of extinction on small patches. We estimated values of e' and x with the formula $J_i = 1 / \{1 + [e' / (S^2_i A^x_i)]\}$, where for patch i , J_i is the occupancy state (species present or absent), S is the patch connectivity, and A is the patch area.

Because estimates of colonization ability require data on changes in occupancy over time, we could not estimate colonization ability from the 1989 data. However, because we assumed an extinction-colonization equilibrium, e' is predicted to be greater for species with higher extinction probabilities in a given landscape. Therefore, we determined whether e' values were positively correlated with the observed extinction rates over the 2 survey years. We also examined the relation between x , average size of occupied patches in 1989, and the number of patches on which the target species was present in both survey years. We expected a strong negative relation between patch size in 1989 and number of patches occupied in both years because rare species tended to occur on larger patches and common species occurred on both small and large patches. However, some of the variation in this relation may be explained by differences in the sensitivity of the individual species' persistence to patch size. Therefore, we used stepwise linear regression to test whether the inclusion of the estimated patch-size sensitivity parameter, x , would significantly improve the accuracy of predicted patterns of persistence.

Results

Extinctions and Colonizations

The data included 7806 patch occurrence records, 332 extinctions, and 1040 colonizations. Eighty-six species were recorded in at least 1 patch in both the 1989 and 2005 surveys. Forty-five species occurred on 10–90% of

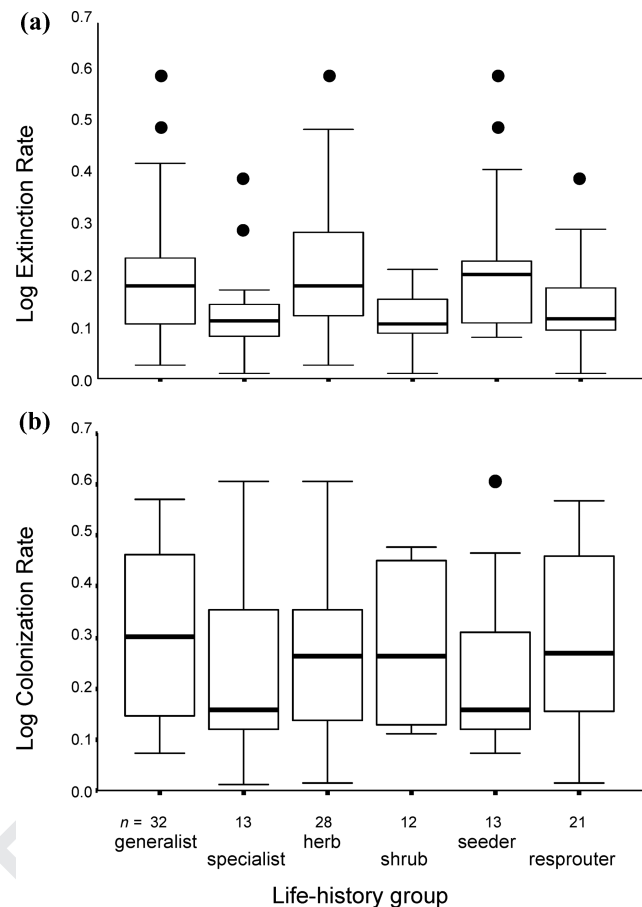


Figure 1. Comparison of extinction rate (extinctions/patches occupied in 1989) and colonization rate (colonizations/patches unoccupied in 1989) among plant life-history groups (vertical lines, range of values; box length, interquartile range; horizontal bar, median value; dots, outliers beyond 1.5 box lengths from edge of box).

the patches (8–80 patches) in both years and were considered target species (Supporting Information). Between 1989 and 2005, these species accounted for 684 colonizations (29% of unoccupied patches) and 278 extinctions (17% of occupied patches). The number of extinctions and colonizations of individual species were not correlated (Pearson correlation = -0.11 , $p = 0.47$, $n = 45$; Supporting Information).

Extinction rates varied as a function of the life history of the plant species (Fig. 1). After a sequential Bonferroni adjustment, herbs ($n = 28$) had higher extinction rates than woody plants ($n = 12$, one-tailed Mann-Whitney $U = 93$, $p = 0.01$), and seeders ($n = 13$) showed higher extinction rates than resprouters ($n = 21$, $U = 79$, $p = 0.02$). The difference in extinction rate between generalists ($n = 32$) and specialists was not statistically significant, although generalists had slightly higher rates of extinction ($n = 13$, two-tailed $U = 131$, $p = 0.06$).

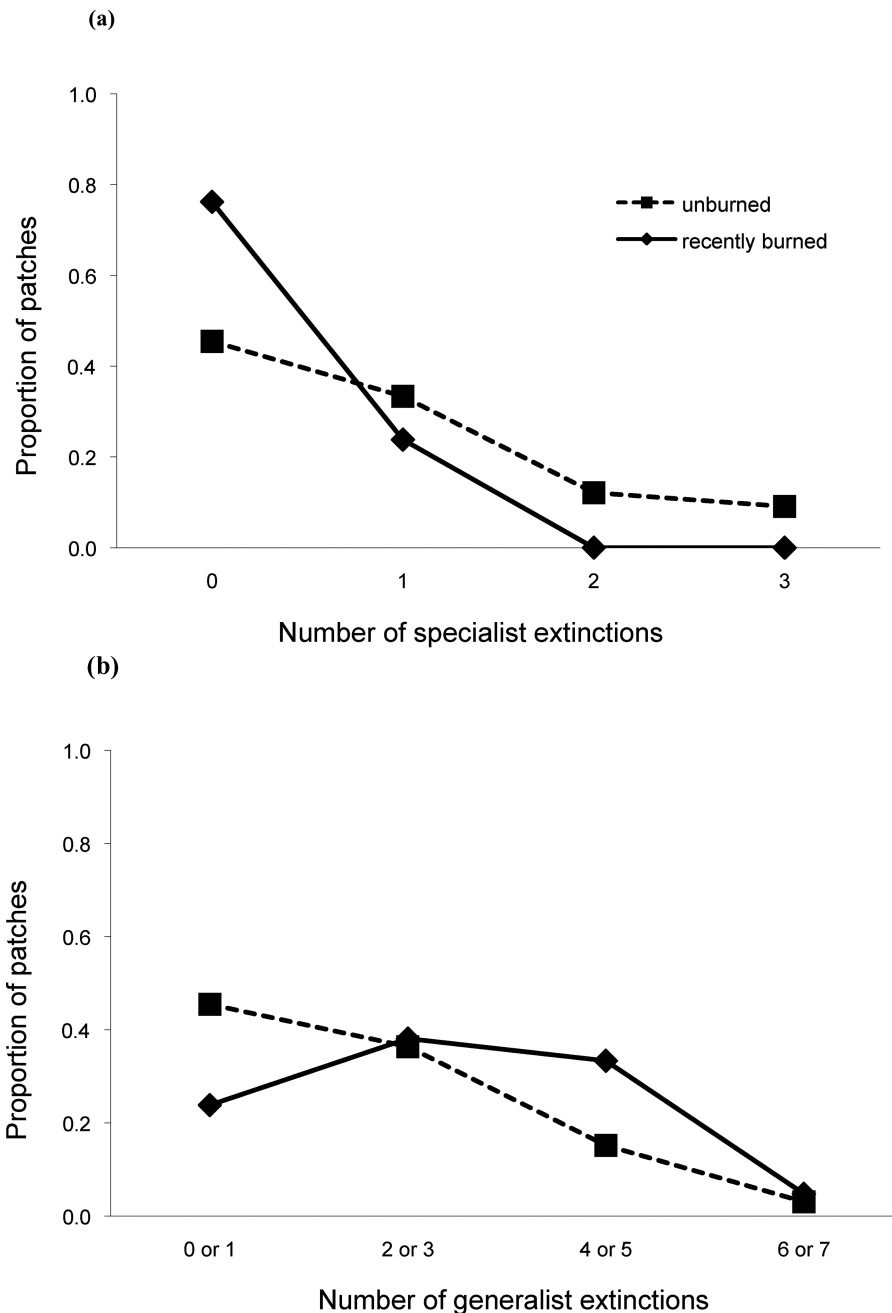


Figure 2. Proportion of patches that had particular numbers of extinctions of (a) specialist and (b) generalist plant species on patches unburned between survey years (unburned, 31 patches) and patches burned between 1989 and 2005 and had a time since last fire in 1989 that was 12 or more years greater than in 2005 (recently burned, 21 patches).

Standard deviations of extinction rates were also much higher for herbs, seeders, and generalists than for woody plants, resprouters, and specialists. Life-history traits were not significantly correlated with colonization rates (Fig. 1). Average turnover rate (number of extinctions + number of colonizations/average number of patches occupied in both years) was significantly greater for generalists than specialists ($U = 88.5$, $p < 0.01$).

Stepwise linear-regression models showed extinctions and colonizations per patch were not significantly associated with area or connectivity. The number of extinctions of generalists and seeders decreased slightly as time since fire increased, but after a sequential Bonfer-

roni adjustment, only the relation between time since fire and generalist extinctions was significant ($df = 87$, $\text{adj. } r^2 = 0.07$, $\text{mean squares} = 22.8$, $F = 7.69$, $p < 0.01$). Twenty-one patches were classified as recently burned and 33 as unburned. Recently burned patches averaged fewer extinctions of specialists than unburned patches (means of 0.24 and 0.85, respectively; one-tailed $U = 222.5$, $p < 0.01$; Fig. 2a). More extinctions of generalists occurred on recently burned patches than unburned patches, but the trend was not significant (means of 2.90 and 2.12, two-tailed $U = 258.5$, $p = 0.11$; Fig. 2b). Extinction rates for seeders, resprouters, herbs, and woody were not significantly different between fire-history

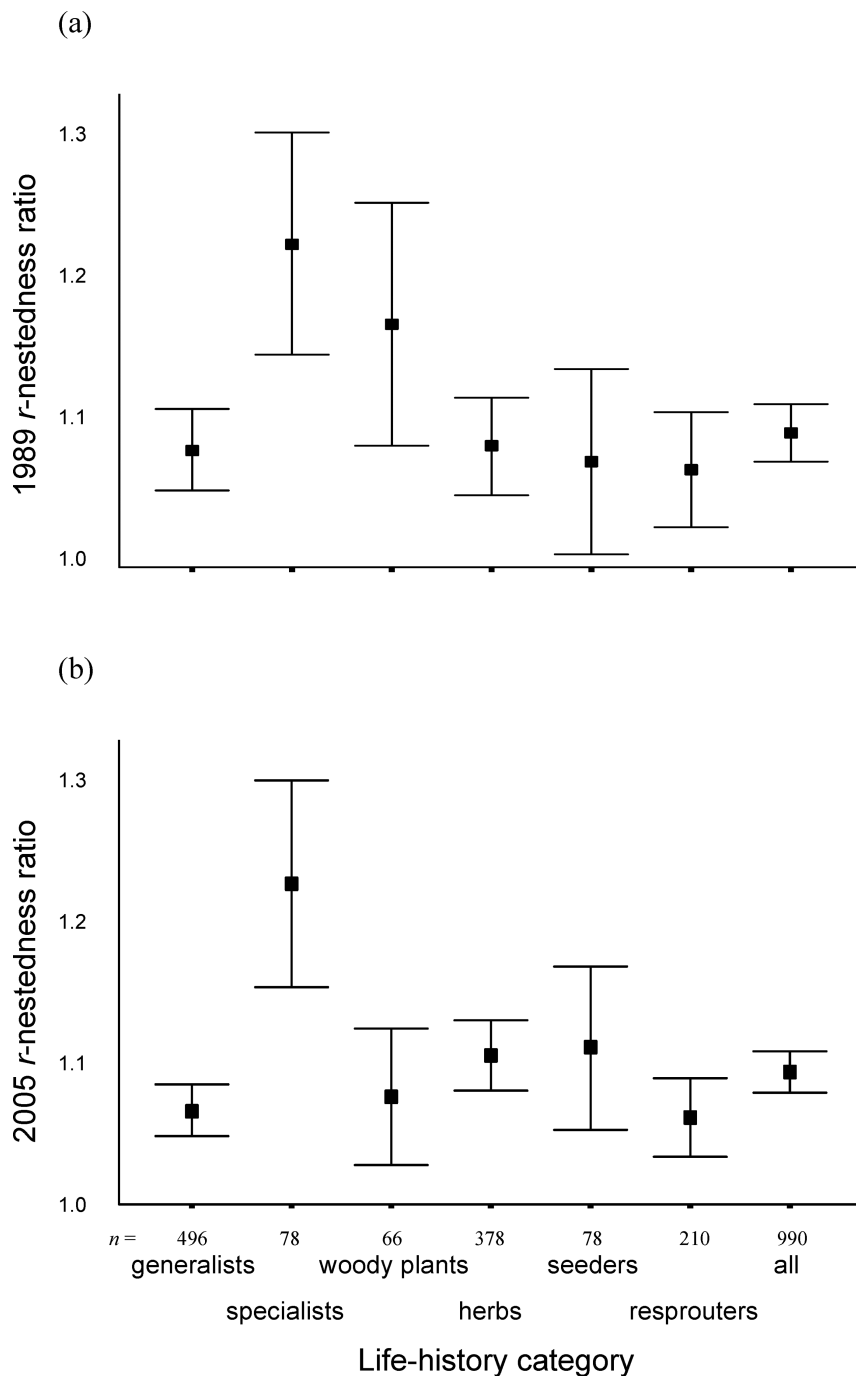


Figure 3. The r -nestedness ratios of Florida rosemary scrub plants classified in 6 life-history groups for (a) 1989 and (b) 2005. Values >1 indicate a pattern of nestedness across habitat patches (dots, mean; bars, 95% CIs).

categories or between colonization rates for any life-history group.

Metacommunity Nestedness

All 6 life-history groups had r -nestedness ratios >1 , indicating nestedness ($p < 0.02$ for all comparisons; Fig. 3). As predicted, specialists had higher r -nestedness ratios than generalists in both years (1989 $t = 3.69$, 2005 $t = 4.24$, $p < 0.001$ for both). The r -nestedness ratios were not significantly different within life-history groups between years. Woody plants were more nested in 1989

than 2005, but the difference was not statistically significant after sequential Bonferroni adjustment ($t = 1.97$, $p = 0.05$). There were no significant differences in r -nestedness ratios between herbs and woody plants or between seeders and resprouters.

Metapopulation Model

The metapopulation model fit with the 1989 occurrence data was a strong predictor of future metacommunity dynamics. The estimated values of e' (turnover rate) were positively associated with observed extinction rates of

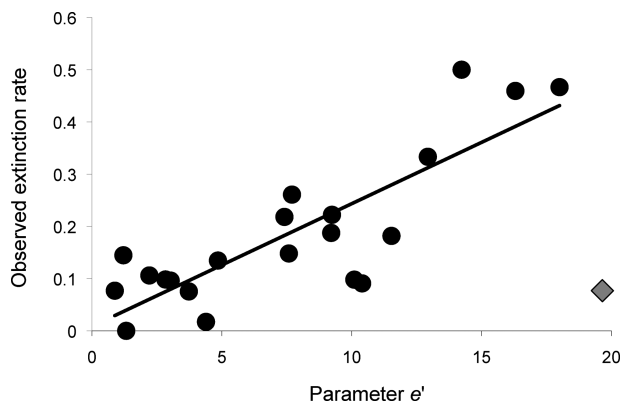


Figure 4. Correlation between e' , a composite variable expected to predict turnover rate calculated from a patch-occupancy model (Quintana-Ascencio & Menges 1996), and observed extinction rate of 25 Florida rosemary scrub species (regression line: $y = 0.0166x + 0.0464$, $r^2 = 0.43$). When the outlier *Polygonella robusta* (gray diamond) is removed, r^2 increases to 0.64.

the 25 tested species ($r^2 = 0.41$, $F = 17.45$, $p < 0.001$; Fig. 4). Largeflower jointweed (*Polygonella robusta*), was an outlier, with a residual of -2.7 and high statistical leverage. When this species was removed, e' showed substantially stronger predictive accuracy ($r^2 = 0.64$, $F = 39.14$, $p < 0.001$). Average patch area in 1989 and x (sensitivity to patch size) predicted the relative number of permanently occupied patches with high accuracy in a stepwise linear-regression model and did so with higher significance than average patch area alone (patch area: adjusted $r^2 = 0.68$, $F = 46.99$, $p < 0.001$; patch area and x : adjusted $r^2 = 0.84$, $F = 58.66$, $p < 0.001$; Fig. 5).

Discussion

Our results indicate metacommunity dynamics can differ among life-history groups. When species were categorized by growth form or regeneration mechanism, extinction rates were higher for herbs than shrubs and for seeders than resprouters. These differences are likely due to longer generation times for shrubs and resprouters. Long generation times are thought to decrease the effects of changes in patch quality on abundance and thus, increase probabilities of species persistence (Mouquet & Loreau 2003; Van de Meutter et al. 2007). Species grouped by habitat requirements differed in metacommunity dynamics more than species grouped by growth form or regeneration mechanism. Specialists had lower extinction rates and were more nested than generalists. Specialists also experienced fewer extinctions on recently burned patches, whereas generalists were more likely to persist on unburned patches.

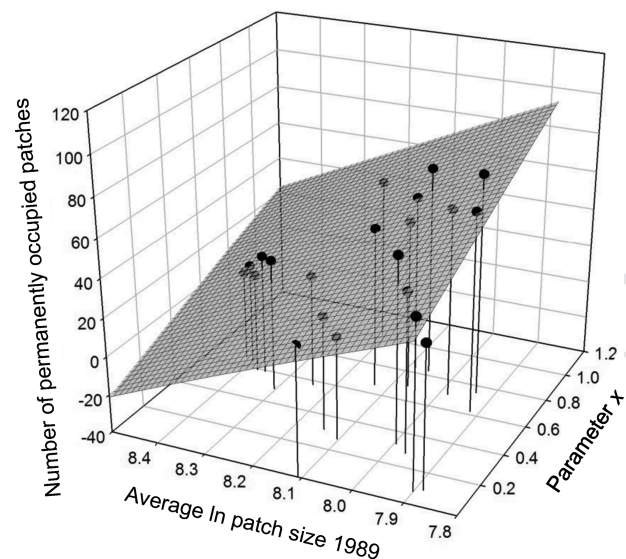


Figure 5. Relation between parameter x , a variable expected to predict a species' sensitivity of extinction rate to changes in patch size, average patch size in 1989 (in ha), and the actual number of occupied patches in 2005 for 25 Florida rosemary scrub species (adjusted $r^2 = 0.84$, $F = 58.66$, $p < 0.01$).

Our finding of higher extinction rates for generalists than specialists, contrasts with previous work in this system that showed more variable growth rates and survival in 2 specialist species relative to their generalist congeners (Maliakal-Witt et al. 2005). All else being equal, these more variable vital rates of specialists should lead to a lower probability of persistence when patch quality is low. However, differences in spatial distribution and abundance between groups may explain our results. Many generalist species may mainly occur at low abundances on the patch periphery, where the environment is most similar to the surrounding scrubby flatwoods. Lower overall abundances are expected to increase extinction rates in generalists, despite the possibility that changes in patch quality may have less of an effect on vital rates. This relation between vital rates, patch-level abundance, and species turnover is not fully understood. For example, models show that temporal variability in vital rates combined with even moderate dispersal can dramatically improve probabilities of patch-level persistence of specialists (Roy et al. 2005).

We expected the lack of relation between generalist extinctions and colonizations and patch connectivity because generalists occur in the matrix between patches. In fact, it has been argued that habitat generalists should not be included in traditional metacommunity models (Freckleton & Watkinson 2002; Murphy & Lovett-Doust 2004). Dispersal distances of specialists, which grow poorly in the scrubby flatwoods matrix and often are gravity-dispersed (69% of specialists vs. 53% of

generalists; Supporting Information), are likely to be smaller than those of generalists (Menges & Kohfeldt 1995; Menges & Hawkes 1998). The lack of a strong relation between specialists and patch area or connectivity may reflect the influence of persistent seed banks (Menges & Kohfeldt 1995; Slapcinsky et al. 2010; Navarra et al. 2011). However, if larger, more-connected patches have larger aboveground populations, they likely have larger seed banks. Therefore, these populations would persist longer or appear to be recolonized more often than those on smaller, less-connected patches. Seed banks may lower the true extinction and colonization rate of a species, but likely do not eliminate the effect of spatial variables on predictions of where extinctions and colonizations occur. This conclusion is consistent with the predictive accuracy of the incidence-function models that included spatial variables and with the correlation between larger and more-aggregated patches and higher overall species richness in both survey years (Quintana-Ascencio & Menges 1996).

In contrast to spatial variables, time since fire was associated with extinction rates. This result is consistent with Dupre and Ehrlen's finding (2009) that occurrence is more often associated with patch quality than patch configuration. The results indicate determinants of patch quality may differ between generalists and specialists. Specialists often recruit from seed banks shortly after fire (Quintana-Ascencio et al. 2003; Menges & Quintana-Ascencio 2004). Generalists are stronger competitors, and they persist longer as the rosemary patch becomes more similar to the surrounding scrubby flatwoods in the absence of fire (Boughton et al. 2006).

High specialist nestedness in both years is consistent with our hypothesis that specialists respond strongly and in a similar fashion to patch variables. Among specialists, species with the lowest occupancies also tended to show the highest r -nestedness ratios. Thus, the patches most likely to be occupied by a locally rare specialist are those with a large number of other specialist species. A few species with low patch occupancy are also globally rare. For instance, wedge-leaf eryngo (*Eryngium cuneifolium*; listed as endangered under the U.S. Endangered Species Act) had the lowest occupancy and the highest r -nestedness ratio of any specialist in both years. High specialist richness may indicate patches where wedge-leaf eryngo is absent aboveground, but could colonize from another patch or from the seed bank. These patches may also be candidates for human introduction of wedge-leaf eryngo. The idea of targeted monitoring or reintroduction of rare species on basis of the presence of more common species with similar life history may be applicable to other metacommunities.

The model developed in Quintana-Ascencio and Menges (1996) accurately predicted both relative extinction rates and population persistence of individual species. This is somewhat surprising because the assump-

tion of an extinction-colonization equilibrium was not met (Hanski 1994). The high number of colonizations relative to extinctions may relate to the positive correlation between connectivity and time since fire in 2005 (Pearson correlation = 0.58, $r^2 = 0.33$, $p < 0.001$). The southern part of the study area had the highest density of rosemary patches and contained large unburned areas. This clustering may have allowed continued colonization or persistence of specialists through rescue effects from populations on neighboring patches, reducing apparent extinctions despite lower patch quality (Mouquet & Loreau 2003). Because unburned patches represent high patch quality for generalists, the correlation would have further increased the colonization rates of generalists. Correlations between spatial and environmental variables are common in real metacommunities because factors that influence patch environment often act at extents larger than an individual patch (Harrison & Quinn 1989).

Our work here involves a relatively simple metacommunity model that does not account for spatial autocorrelation, abundances of each species, seed-bank dynamics, species interactions, and other variables that may predict future metacommunity dynamics. Consistent differences among life-history groups, predictable and repeatable nestedness patterns, and the strong predictive accuracy of the patch-incidence model suggest that meaningful information about long-term metacommunity dynamics can be accurately inferred from a single thorough survey. Because long-term monitoring takes time and resources, it is extremely valuable to be able to infer metacommunity dynamics from one survey.

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Supporting Information

Information on the life-history classification and extinction and colonization rates of the individual species used (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Queries

- Q1** Author: A running head short title was not supplied; please check if this one is suitable and, if not, please supply a short title that can be used instead.
- Q2** Author: Please provide author initials for author “Leibold” in reference Leibold et al. [2004].
- Q3** Author: Please provide year of publication for reference “Roy et al.”