Community assemblage and succession on decomposing logs

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Abstract: Although successional models have been well studied in plant communities, little is known about the successional patterns and community structure of decomposer communities. We tested whether the communities of fungi and insects that occupy decaying logs follow either of two alternative models that have been developed for plant communities. The deterministic model posits that succession follows a predictable sequence through time, while the alternative trajectory model posits that succession can follow any one of several trajectories depending upon initial conditions. We surveyed 100 decaying logs in tropical primary forest for decay level and fungal and insect community composition. Our findings tend to support the deterministic model over the trajectory model. Using a Bray-Curtis ordination analysis, we found that ordination axis 1 was correlated with decay level, indicating that fungal community composition was changing in a predictable way over time. Presence of several fungal morphotypes was related to level of decay, and variance in the fungal community tended to decrease over time. Because fungal communities are critical for ecosystem processes, their successional patterns over time could impact decomposition rates, gap regeneration and plant and animal diversity.

Key Words: alternative trajectory model, coarse woody debris, decay, decomposition, deterministic model, fungi, mites, plant community theory, termites

Introduction

Decomposition is a critical process within all ecosystems, including tropical forests. One of the striking features of lowland tropical forests is the scarcity of soil organic matter. Although treefalls and litterfall occur continuously, decomposers quickly break down this organic matter, releasing carbon to the atmosphere and other nutrients to the soil. Despite the importance of decomposers, their community assemblage and successional patterns have not been extensively studied. Models describing successional patterns have been well developed for autotrophic plant communities, but it is not known whether they apply to heterotrophic fungal communities and their associated insects, such as termites. We tested how well two alternative models of plant succession apply to tropical forest decomposer communities.

The deterministic model of plant succession posits that species colonize and dominate in a deterministic sequence through time. Under this model, we expect species presence to be correlated with time since disturbance and all communities to converge over time towards a single climax community. Alternatively, communities might tend to develop along one of several trajectories that depend strongly on initial conditions and can lead to very different end points. We refer to this as the alternative trajectory model. Alternative trajectories would be more likely in communities that involve facilitation, a process in which one species, by altering biotic or abiotic conditions, promotes subsequent colonization by another species. Thus, the alternative trajectory model would predict that positive and negative associations among species would be common, i.e. some species will tend to occur together while others will co-occur only infrequently. The alternative trajectory model also predicts that the variance in community structure will increase over time, as trajectories diverge further. We evaluated patterns of fungal succession by examining the structure of fungal communities occupying logs at different stages of decay.

Methods

Our study was conducted on 2 - 4 February 2002 at Sirena Biological Station, Corcovado National Park, Costa Rica. We surveyed 100 decaying logs along the Pavo and Espevales Trails with visible Basidiomycota fruiting bodies. Log size ranged from 30 – 300 cm long. We recorded all visible basidiocarp morphotypes and their abundances, measured by either number of individuals or area covered by the fungus (in cases where individual fruiting bodies were too difficult to count). We also noted presence or evidence of termites and visually scanned the log for mites for 20 s. We measured photosynthetically active radiation (PAR) with a quantum light sensor three times above each log and recorded the mean value.

Degree of log decay was measured in two ways: first, we drove a trowel into each log in three random places and calculated the mean depth of penetration; second, we estimated the percent of the original log volume that was no longer visible due to decay. Trowel depth was assigned an ordinal score as follows: 0 = 0 cm, 1 = 1 - 2 cm, 2 = 3 - 4 cm, 3 = ≥5 cm. Percent of log volume lost was also assigned an ordinal score: 1 = ≤5%, 2 = 6 - 15%, 3 = 16 - 30%, and 4 = ≥31 %. These two scores were averaged to give an index of decay for each log.

We tested for nonrandom associations between pairs of our five most abundant fungal morphotypes, termites and mites using a chi-square statistic. We tested for relationships between index of decay and presence for these same groups using logistic regression models. The relationship between species richness per log and index of decay was analyzed using a linear regression.

To compare community similarity across logs, we performed a Bray-Curtis ordination (using PC-ORD Version 4.10, MjM Software, Glenedon Beach, Oregon). This analysis is a version of principal components analysis in that it reduces multiple variables (i.e., presence of each species) to one or a few composite axes. We used correlation and regression analyses to test for relations among logs in: decay depth, percent decay, index of decay, PAR and the Bray-Curtis ordination values on axis 1 and axis 2.

Results

We found 32 Basidiomycota morphotypes (see Table 1 for five most common), including six that we identified to species: *Polyporus tricholoma, Cookeina speciosa, Hymenochaete luteo-badia, Auricularia polytricha, Hexagonia papyracea* and *Coprinus disseminatus.* Most species were rare (Fig. 1). Mean species richness per log was slightly less than two. The species richness curve rose steeply and did not saturate over the course of our 100 log

TABLE 1. Five most common fungal morphotypes found on decomposing logs at Corcovado National Park, Costa Rica.

Morphotype ID	Occurrence (number of logs)	Description	Probable species ID
A	15	Porous shelf fungus, brown and tan rings, yellow underside	NA
B	13	Porous shelf fungus, gray and tan rings, white underside	NA
C	21	Mushroom-shaped, white, porous underside	*Polyporus tricholoma*
D	9	Shelf-like, smooth, brown, rubbery, no visible pores or gills	NA
E	9	Porous shelf fungus, dark brown	NA

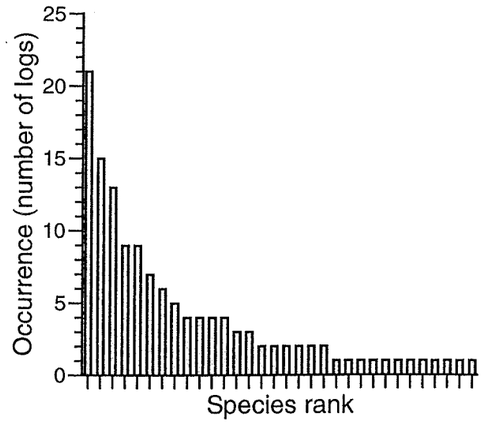

FIG.1. Rank-abundance curve for fungal morphotypes on decaying logs.

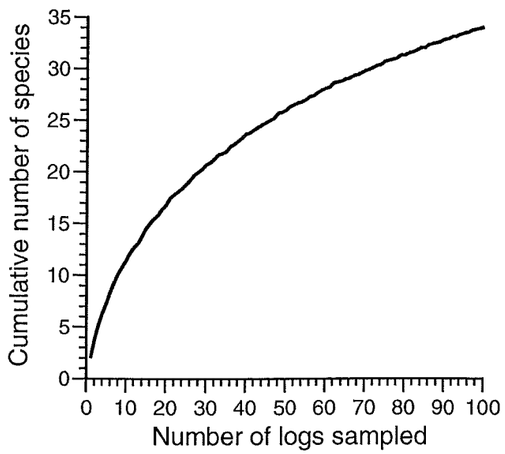

FIG. 2. Species-area curve for decomposer species (primarily fungal) on logs in a tropical lowland forest. Function indicates average number of species for random sets of 1 - 100 logs.

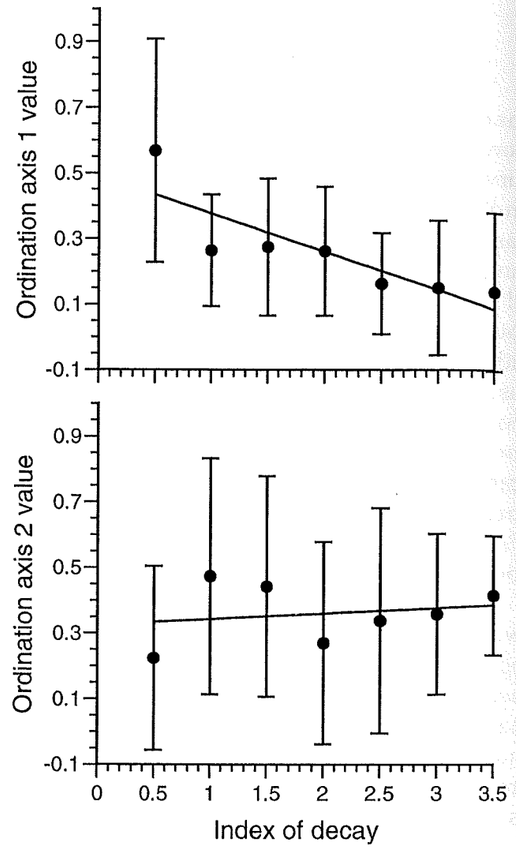

FIG. 3. Mean Bray-Curtis ordination values (axes 1 and 2) versus decay index. Error bars represent standard deviation.

sample (Fig. 2). Four pairs of morphotypes were negatively associated with each other (Table 2). Fungal morphotype C, *Polyporus tricholoma*, was positively associated with termites. Abundance of fungal morphotype E was positively correlated with decay index (Table 2). Abundances of termites and fungal morphotype C, *Polyporus tricholoma*, were negatively correlated with decay index (Table 2). Species richness per log increased slightly with index of decay ($r = 0.17$, $df = 99$, $P = 0.09$) and with surface area of the log ($r = 0.24$, $df = 99$, $P = 0.02$).

Bray-Curtis ordination axis 1 explained 17% of the variance in species presence among plots. Axis 2 explained another 26% of the variance, for a total of 43%. Across logs, there was a negative correlation between decay index and values along Bray-Curtis axis 1; communities differed along a gradient of decay ($r = -0.40$, $df = 99$, $P << 0.001$; Fig. 3). Variance in axis 1 and axis 2 values tended to decrease with decay index, but this trend was not significant in either case ($P = 0.34$ and 0.14, for correlations between decay index and variance in axes 1 and 2, respectively; $n = 7$). PAR was not correlated with log characteristics or community composition (Table 3).

TABLE 2. Results of chi-square tests for associations among pairs of morphotypes and (bottom row) of logistic regression test for relationship between index of decay and morphotype presence. NS = not significant.

Morphotype	A	B	C	D	E	Termites	Mites
A		NS	NS	$X^2 = 3.08$, $P = 0.08^a$	$X^2 = 3.08$, $P = 0.08^a$	NS	NS
B			NS	NS	NS	NS	NS
C				$X^2 = 4.47$, $P = 0.03^a$	$X^2 = 4.47$, $P = 0.03^a$	$X^2 = 2.85$, $P = 0.09^b$	NS
D					NS	NS	NS
E						NS	NS
Termites							NS
Mites							
Decay index	NS	NS	$P < 0.001^a$	NS	$P = 0.009^b$	$P = 0.003^a$	NS

[a]Negative association
[b]Positive association

TABLE 3. Correlation matrix among log characteristics, number of fungal species per log and values for Bray-Curtis ordination axes 1 and 2.

Variable	Depth of decay	Percent decay	Index of decay	PAR*	Number of species	Axis 1 value	Axis 2 value
Depth of decay	1.00	0.54	0.82	-0.09	0.24	-0.40	0.04
Percent decay		1.00	0.81	-0.07	-0.02	-0.20	-0.09
Index of decay			1.00	-0.13	0.17	-0.40	0.01
PAR*				1.00	-0.10	0.24	-0.12
Number of species					1.00	-0.52	-0.13
Axis 1 value						1.00	0.21
Axis 2 value							1.00

*Photosynthetically active radiation

Discussion

Overall, our results appear to support the deterministic model of succession over the trajectory model. The Bray-Curtis ordination analysis indicates that there are predictable changes in community composition associated with degree of decay, and that communities tend to become more similar over time (Fig. 3). This is as expected if patterns of initial colonization are somewhat stochastic but the community tends to converge over time on a deterministic end point.

The deterministic model also predicts that species presence is associated with decay time, while the alternative trajectory model predicts numerous associations among species that are not necessarily related to decay time. Our results do not unequivocally support either one of these predictions. We found three species whose presence was related to decay level. In addition, we found five nonrandom species associations. However, most species were rare, and small sample sizes pre-

cluded statistical tests for most species. By sampling more logs or by sampling during the wet season when fruiting bodies are more abundant, we could determine whether species tended to be more strongly associated with decay level or with other species on the same successional trajectory.

It could be that neither the deterministic nor the alternative trajectory model is adequate for understanding community assemblage and succession on decaying logs. An alternative hypothesis is that fungi and other decomposers are dispersal limited, and community composition is simply a function of which species make it to the log. From this hypothesis, we would predict clumped dispersions of species in the landscape. Another alternative is that fungal communities depend upon the tree species of the decaying log. A third possibility is that communities are not structured with respect to space, time or other species (random assemblages). These alternatives warrant further consideration. However, our results suggest non-random species associations and temporal patterns in species distributions. We recommend sampling during the wet season, when fruiting bodies are more abundant. In addition, spores and mycelial fungal cells could be cultured to more completely describe the fungal community composition.

There could be important ecosystem implications depending on which model of succession applies to decomposer communities inhabiting coarse woody debris. If communities follow the alternative trajectory model of succession, we would expect increased variance among these communities over time. This could affect nutrient recycling rates, potentially creating a more heterogeneous soil environment, which could contribute to increased plant and animal diversity (Bembenek et al. 1996). This model also predicts that strong associations among species are more common than in the deterministic model of succession. This implies that keystone species would be more frequent in communities that match the alternative trajectory model, and that ecosystem processes such as nutrient cycling will be more sensitive to the addition or deletion of particular species.

Literature Cited

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