Measurement & maintenance of local diversity

Key concepts

- Relative abundance
- Species abundance distribution
- α-, β-, and γ-diversity
- Species richness
- Simpson's index
- Shannon's index
- Intermediate disturbance hypothesis
- Janzen-Connell effects
- Keystone species

Tropical forest diversity

One of the key questions of community ecology is why an ecosystem displays the specific diversity of life forms that it does. Why are coral reefs so rich in color, shape, and species while prairies are comparatively poorer? Why are tropical streams so rich in fish while streams in the tundra are home to at most a few species? Why this much diversity and not more or less? What explains the presence of these species and not others? These questions concern *community composition.*

From the principle of competitive exclusion and theory of limiting resources, the extraordinary diversity exhibited by such hyperdiverse ecosystems as coral reefs and tropical forests would seem particularly difficult to explain. What processes allow so many species to coexist simultaneously? Tropical forests are justly famous for their diversity. Nowhere on Earth has tropical forest diversity been studied more intensively than on Barro Colorado Island. Lake Gatun was created in 1913 by the damming of Chagres River in Panama. As the waters

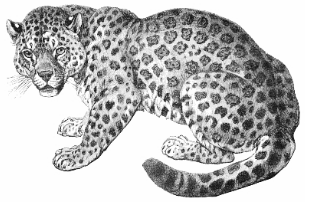

Figure 1: The jaguar (*Felis onca*) is hypothesized to be a keystone species, maintaining tree species diversity in tropical forests.

rose to cover the surrounding rain forest an area of 15.6 km^2 of high ground remained above the lake surface forming Barro Colorado Island. Barro Colorado Island was set aside as a nature reserve in 1923 and has been the site of a biological field station ever since. Now it is home to the Smithsonian Tropical Research Institute.

Diversity of Barro Colorado Island is truly extraordinary. According to a recent survey, a single 1 ha plot (100m × 100m) may contain 89 tree species and 166 species of plants. A total of 465 species of vertebrate animals are known to live on the island and invertebrates include 400 and species, 1,000 species of bedbugs, 100 cockroach species, >500 butterflies and >1,500 species of moths.

Diversity and space

Importantly, the mechanisms maintaining diversity may not be the same at all *spatial scales*. That is, there may be differences between tropical and temperate forests in the typical number of species found within areas of 10 m^2, 100 m^2, 1000 m^2 and larger areas and the determinants of diversity in each case may be different. Diversity may therefore be measured along a continuum of spatial scales. The two extremes of this continuum are referred to as α-diversity (diversity of a site) and γ-diversity (diversity of a large ecologically defined region). A third form of diversity, β-diversity, refers to the *turnover* in community composition along a transect. An area that has a low α-diversity may nonetheless exhibit a high γ-diversity if the turnover in species composition along a transect across the region is high. By contrast, if β-diversity is low (the same community is encountered continuously across a region) then the total set of species encountered in a large region (γ-diversity) may be no greater than the set encountered at one site within that region (α-diversity).

Quantification of diversity

Biological surveys aim to quantify the contribution of each species to the composition of the ecological community at a site. Depending on the life form of interest (trees, herbs, birds, *etc.*) and the aim of the study, species abundance may be reported in units of biomass, coverage, or the number of individuals encountered (Figure 2). Regardless of the units chosen, the contribution of each species to the total is typically reported in terms of relative abundance,

$$\pi_i = x_i / \sum_i x_i, \tag{1}$$

where x_i is the abundance of species i. On Barro Colorado Island,

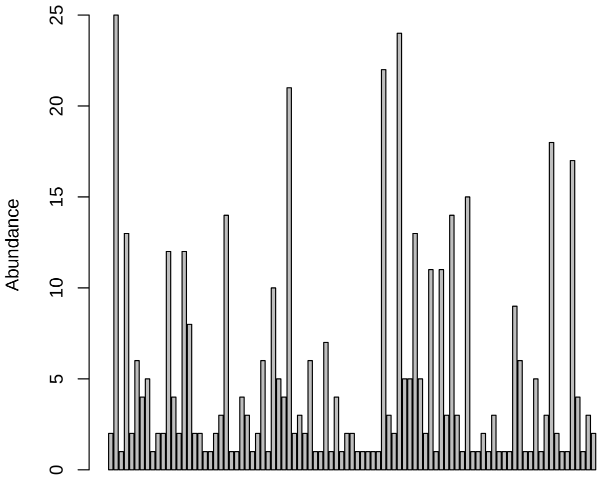

Figure 2: Abundance of 93 tree species >10 cm dbh in a plot at Barro Colorado Island.

fifty 1 ha plots have been selected for monitoring. Figure 3 shows the relative abundance of species at one of these plots. As this plot shows, relative abundance consists of the same information (the graphs are the same). It has merely been rescaled so that each shows the proportional contribution to the total.

If we order the relative abundances π_i from the most abundant to the least abundant we produce the *species abundance distribution* (Figure 4). Communities in different ecosystems may exhibit different patterns, reflecting both the origin of species present, their life histories and ecological requirements, and their interactions with other species. When used to compare different communities, species abundance distributions are often plotted on a logarithmic scale (Figure 5). A key problem for community ecology is to determine what maintains a community in its summary characteristics (*e.g.* diversity) and composition (*i.e.* the particular species it consists of).

Three measures of α-diversity

The remainder of this chapter concerns the measurement and maintenance of α-diversity at Barro Colorado Island. Large scale diversity (β- and γ-diversity) will be picked up again in a later chapter.

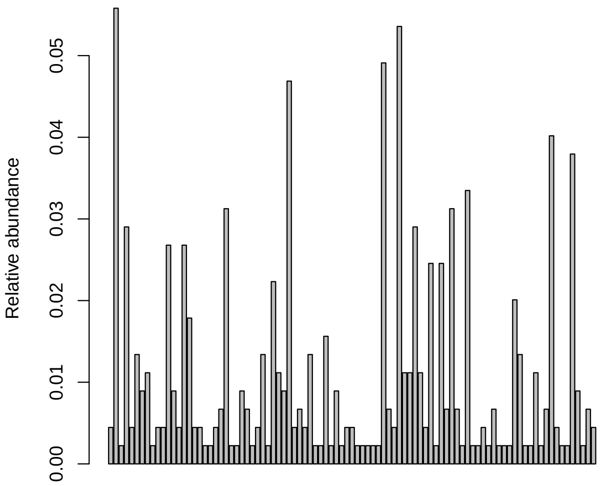

Figure 3: Relative abundance of 93 tree species >10 cm dbh in a plot at Barro Colorado Island.

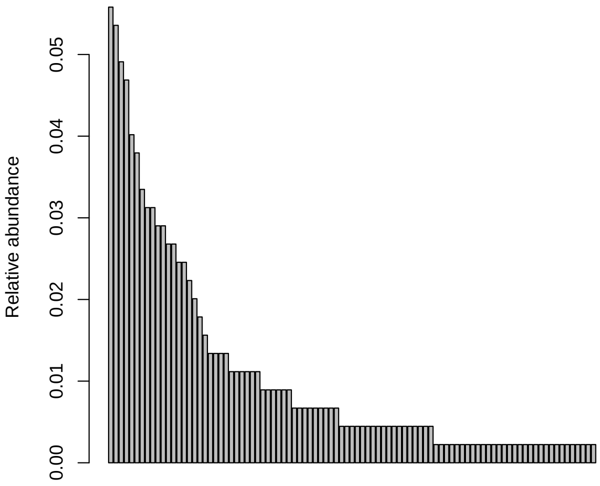

Figure 4: Species abundance distribution for 93 tree species >10 cm dbh in a plot at Barro Colorado Island.

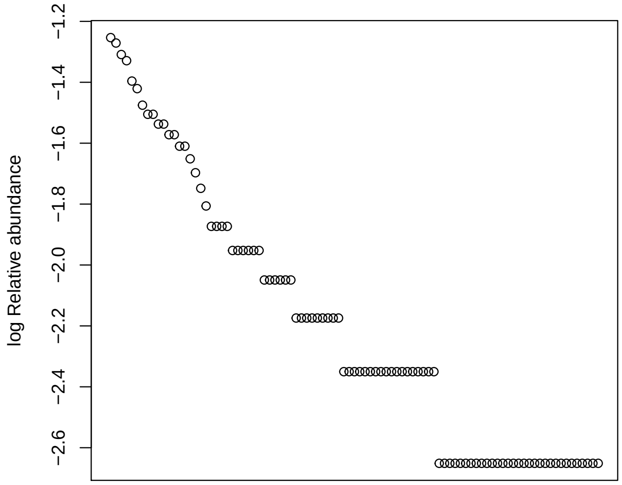

Figure 5: Species abundance distribution on a logarithmic scale for 93 tree species >10 cm dbh in a plot at Barro Colorado Island.

Diversity as a concept

To better formulate our question "What maintains α-diversity?" we require both a clear answer to the question "What is diversity?" and a way to quantify it. Intuitively, the concept of diversity concerns differences in a collection of items. Although community ecology is primarily concerned with species diversity, one might also consider other dimensions of diversity such as genetic diversity and functional diversity. One way to quantify diversity is therefore to tabulate the number of different species represented in a community: a community comprised of fifty species is thus more diverse than a community comprised of fifteen species. This aspect of diversity concerned with the enumeration of species is called *species richness*, which is denoted S.

Additionally, however, one also intuitively understands that diversity should concern the distribution of different individuals among species in the community. Thus, for two communities each comprised of ten species, that community in which the relative abundances of each species are most similar is most diverse. This aspect of diversity concerned with the distribution of species among individuals is called *species evenness*.

If both species richness and species evenness are aspects of diversity, what is diversity itself? Patil & Taillie[1] have suggested that it is the property of *average rarity*. This is appealing. By stating that diversity is the average of something, then it is a summary of the community in terms of a quantity that may be measured for each species. Further,

[1] G P Patil and C Taillie. Diversity as a concept and its measurement. *Journal of the American Statistical Association*, 77(379): 548–561, 1982. ISSN 01621459. DOI: 10.2307/2287709. URL `http://www.jstor.org/stable/2287709`

rarity is a property of species in communities that ecologists have long considered of special interest. But, what is rarity? Roughly speaking, it is the relative improbability of being encountered.

Species richness

Our first index of diversity supposes that rarity of species i is the average time to encountering an individual of species i. Suppose we take all the individuals of all species in a community and shuffle them so that they are encountered independently. Equivalently, we sample individuals in proportion to their representation in the species abundance distribution. We ask the question, "How many individuals of other species will I encounter before encountering the first individual of species i?" and call this our measure of rarity, R. The answer is, on average, $R_i = (1 - \pi_i)/\pi_i$. If diversity is the property of average rarity, we simply calculate the weighted average of this formula

$$\sum_S \pi_i R_i = S - 1 \tag{2}$$

Thus, one measure of diversity (average rarity) is simply the species richness less one.

Simpson's Index

Another index of α-diversity is Simpson's index. An intuitive derivation of Simpson's index is as follows. Randomly select an individual from the population. By the definition of relative abundance, it will be an individual of species i with probability π_i. Now select a second individual. If the community is large (so that removing the first individual doesn't noticeably affect the relative abundance of individuals remaining), then the probability that it is *not* species i is $R_i = 1 - \pi_i$. The quantity R_i is another natural measure of rarity of the individuals of species i. Summing over all species, the average rarity is

$$\sum_i \pi_i(1 - \pi_i) = 1 - \sum_i \pi_i^2. \tag{3}$$

This formula was first proposed by Simpson[2] as a measure of diversity. Note that Simson's index is equal to zero when $\pi_i = 1$, that is when the community consists of a single species (monoculture).

Shannon's Index

A final index of α-diversity is Shannon's index. Shannon's index supposes that rarity should be measured by $R_i = -\ln \pi_i$ rather than $1 - \pi_i$. Some reasons for this choice are given in Patil & Taillie[3]. Now,

[2] E.H. Simpson. Measurement of diversity. *Nature*, 163:688, 1949

[3] G P Patil and C Taillie. Diversity as a concept and its measurement. *Journal of the American Statistical Association*, 77(379): 548–561, 1982. ISSN 01621459. DOI: 10.2307/2287709. URL `http://www.jstor.org/stable/2287709`

average rarity is

$$\sum_i \pi_i(-\ln \pi_i) = -\sum_i \pi_i \ln \pi_i. \tag{4}$$

This formula was first proposed in classified work by Claude Shannon during World War II to measure the information content of an encoded message. Note that Shannon's index is also equal to zero when $\pi_i = 1$.

The maintenance of α-diversity

Now that we have a way to measure α-diversity, we proceed to ask how this level of diversity is maintained in particular ecosystems.

Intermediate disturbance hypothesis

One candidate process for the maintenance of diversity is disturbance. Scour in stream ecosystems, light gaps in forests, and wave action on rocky intertidal pools all represent considerable, but predictable forms of disturbance that physically remove individuals from the community. When competitively dominant individuals are removed they create space – and access to resources – that might allow competitively inferior species to persist (at least for a time and if they can get there first). The *intermediate disturbance hypothesis* holds that species diversity should be greatest at intermediate levels of disturbance. The intermediate disturbance hypothesis is a manifestation of the goldilocks principle: if disturbance is too infrequent or not sufficiently severe, then one or a few species that are particularly successful at resource extraction are expected to dominate, extirpating other species; in contrast, if disturbance is too frequent or too severe then few species will arrive in time to colonize before the next disturbance and those that do will be unable to physically withstand the physical force of the disturbance.

Hubbell et al.[4] tested the intermediate disturbance hypothesis using data on woody plants $\geq$ 1 cm dbh on a 50 ha plot at Barro Colorado Island. The primary form of disturbance in this ecosystem is tree fall creating light gaps which may then be colonized by species that would otherwise be excluded due to light competition. As expected, light gaps were rapidly colonized and showed a higher density of stems compared with interior control plots. Additionally, light gaps contained more species on average than comparable plots in mature forest. However, this increase in the number of species present was due to the larger number of individuals growing up in light gaps. The relative abundance of species was the same in light gaps as in non-gap forest.

[4] S. P. Hubbell. Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science*, 283(5401):554–557, January 1999. ISSN 00368075. DOI: 10.1126/science.283.5401.554. URL `http://www.sciencemag.org/content/283/5401/554.short`

Although the intermediate disturbance hypothesis was not found to influence diversity at Barro Colorado Island, it has been shown to be an important process for maintaining diversity in other ecosystems, particularly rocky intertidal communitiesand even other tropical forest ecosystems.

Janzen-Connell effect

A second hypothesis concerning the maintenance of tropical forest diversity was independently developed by Daniel Janzen and Joseph Connell and is commonly referred to as the *Janzen-Connell effect*. Unlike the intermediate disturbance hypothesis, which has been proposed as a mechanism for the maintenance of diversity in many ecosystem types, the Janzen-Connell effect is species to tropical forests. The key assumption of the Janzen-Connell effect is that the recruitment of trees is primarily limited by specialist predators (such as herbivorous insects) or pathogens (such as fungi). The hypothesized mechanism is that such specialist predators and pathogens will be more highly concentrated in the vicinity of a host individual, so that seeds falling near to a parent plant will face significant mortality compared both with seeds falling at a larger distance from the parent plant and recruits of other species. The net effect is that parent trees facilitate the recruitment of other species more than their own, increasing local diversity.

Numerous studies have investigated Janzen-Connell effects, though such evidence has typically been indirect. Due to logistical obstacles to performing experiments on numerous species simultaneously, the majority of studies have only established that the underlying assumptions of a Janzen-Connell effect are valid. Particularly, many studies have found that per capita recruitment increases with distance from a parent plant, but are not able to establish either that this is a general phenomenon (that it occurs in multiple species) or that it is the primary cause of high α-diversity in tropical forests.

A study by Mangan et al.[5] at Barro Colorado Island did investigate the prevalence of Janzen-Connell effects in multiple species. Their experiment comprised six different species ranging in abundance at Barro Colorado Island. The selection of species that range in abundance was important to determine that Janzen-Connell effects may occur in any species, not just those that are dominant or those that are rare. Mangan *et al* planted replicate seedlings of each species in pots of sterilized soil. To these pots, they then added a soil inoculum that (depending on treatment) was (i) either live or sterilized, and (ii) either collected from under a conspecific parent tree or from under a heterospecific parent tree. By crossing these treatments, they were

[5] Scott A Mangan, Stefan A Schnitzer, Edward A Herre, Keenan M L Mack, Mariana C Valencia, Evelyn I Sanchez, and James D Bever. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466(7307): 752–5, August 2010. ISSN 1476-4687. DOI: 10.1038/nature09273

able to determine (from treatment ii) whether the hypothesized effects of distance to parent actually occurred, and (from treatment i) whether those effects were due to abiotic features of the soil, or biotic features (namely, microorganisms).

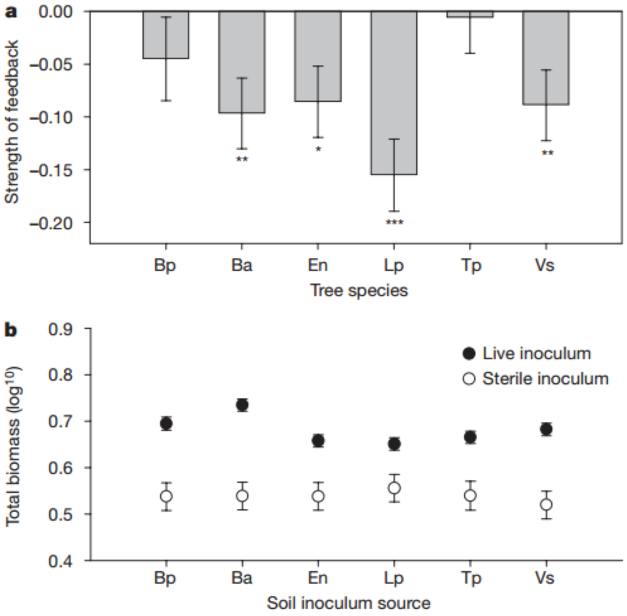

Figure 6: Results of a soil inoculation experiment using six tropical tree species from Barro Colorado Island. (Figure reproduced from Mangan *et al.* (2010).)

The results of this experiment supported the hypothesis that Janzen-Connell effects act across tree species at Barro Colorado Island. Figure 2 shows some of these results. In the top panel, the strength of conspecific negative feedbacks are plotted. In four out of the six species tested, inoculum with soil from a different species promotes growth and recruitment more than inoculum with soil from a conspecific tree. The bottom panel shows that this effect is due to the microorganisms in the soil, since the growth of each species was greater with a biologically active inoculum than with a sterilized inoculum. Further, the effects of the active inoculum differed from species to species, indicating a difference in the importance of the soil microorganism community to each species. These results imply that soil microorganisms mediate the negative interactions between parent plants and offspringand are consistent with the idea that Janzen-Connell effects are a key component of tropical forest species diversity.

Keystone species

A *keystone species* maintains community diversity through a *trophic cascade*. In the case of tropical forests, the theory is that large predators, particularly cats such as puma (*Felis concolor*), jaguar (*Felis onca*), and ocelot (*Felis pardalis*) exert a top-down control on productivity by consuming mid-sized herbivorous mammals, releasing regenerating tree species from herbivory. This trophic cascade is analogous to the way in which the presence of starfish regulates diversity of invertebrates in some coastal marine ecosystems.

Barro Colorado Island allows the possibility of investigating this hypothesis through comparison with other tropical locations because puma and jaguar are not found on the island. Particularly, Wright *et al.*[6] compared Barro Colorado Island with Cocha Cashu, Peru, where puma and jaguar are both present. (The role of ocelots is controlled for by the fact that this species is found at both sites in similar abundance.) There are a number of specific conditions that each must be met for the keystone species mechanism to work. First, top predators must indeed limit their prey – that is the ecosystem must be governed by "top-down regulation". Wright et al. confirmed this in the case of Barro Colorado Island from the historical records, which showed that when the island was created and puma and jaguar extirpated from the ecosystem the abundance of mid-sized mammals increased dramatically. Second, the accompanying release from predation must affect forest diversity, particularly regeneration. Studies of the complete removal of browsing species at a site in Mexico showed strong effects on forest regeneration. Thus, there is a precedent that plant release from herbivory in tropical forests would act to increase diversity. Further, mammal exclosures or comparison with nearby sites where mammals were hunted showed that completely excluding mammals yielded higher seed survivorship and recruitment at Barro Colorado Island. These results suggest that the necessary conditions for keystone predatory cats to control tropical forest tree diversity do exist.

Colonization-extinction balance

A final possible explanation for the maintenance of high species diversity is a shift in the balance of colonization and extinction. Since colonization and extinction at a site change the number of species in opposite ways (colonization results in an increase in the number of species and extinction results in a decrease), the net change in the number of species is the balance between them. The theory of island biogeography – to be discussed later – takes this a step further and posits that species number of at equilibrium. Whether species number is at equilibrium or not, it is intuitively appealing to think that conditions promoting colonization or reducing extinction would result in increased diversity and plausible that this might be a mechanism for the maintenance of diversity in tropical forests. However, since this hypothesis really reflects the interaction of diversity at a site with that of the larger surrounding region (the source of colonizing species), we

[6] S.J. Wright, M.E. Gompper, and B. DeLeon. Are Large Predators Keystone Species in Neotropical Forests? The Evidence from Barro Colorado Island. *Oikos*, 71:279–294, 1994

will defer further discussion to a later chapter.

Test yourself

1. What is diversity?
2. Why does spatial scale matter to diversity?
3. What are three measures of α-diversity? How are they calculated?
4. What are the leading hypotheses to explain tropical forest diversity?

Homework

1. Work out the steps to show what the equality in equation 2 is true.
2. The following table reports birds encountered in the 2011 Christmas Bird Count in Athens, Georgia. To assess the diversity of the bird community at this site, perform the following analyses.
    - Calculate the relative abundance of each species
    - Sketch the species-abundance distribution
    - Compute species richness, Simpson's index, and Shannon's index

Species	Count	Relative abundance
Canada Goose	431	
Wood Duck	25	
Mallard	82	
Redhead	1	
Ring-necked Duck	3	
Hooded Merganser	77	
Ruddy Duck	34	
duck sp.	2	
Wild Turkey	8	
Pied-billed Grebe	10	
Great Blue Heron (Blue form)	23	
Black Vulture	160	
Turkey Vulture	413	
Northern Harrier	1	
Sharp-shinned Hawk	4	
Cooper's Hawk	9	
Accipiter sp.	1	
Red-shouldered Hawk	20	
Red-tailed Hawk	32	
American Kestrel	8	
American Coot	1	
Killdeer	143	
Wilson's Snipe	1	
American Woodcock	14	
Rock Pigeon	321	
Eurasian Collared-Dove	8	
Mourning Dove	352	
Great Horned Owl	1	
Barred Owl	2	
Belted Kingfisher	16	
Red-headed Woodpecker	17	
Red-bellied Woodpecker	174	
Yellow-bellied Sapsucker	54	
Downy Woodpecker	84	
Hairy Woodpecker	21	
Northern Flicker	47	
Pileated Woodpecker	8	
Eastern Phoebe	86	
Loggerhead Shrike	3	
Blue-headed Vireo	2	
Blue Jay	153	
American Crow	652	
Fish Crow	34	
Horned Lark	4	
Carolina Chickadee	394	
Tufted Titmouse	329	
White-breasted Nuthatch	13	
Brown-headed Nuthatch	72	
Brown Creeper	15	

Species	Count	Relative abundance
Carolina Wren	255	
House Wren	1	
Winter Wren	15	
Golden-crowned Kinglet	98	
Ruby-crowned Kinglet	177	
Eastern Bluebird	335	
Hermit Thrush	43	
American Robin	485	
Gray Catbird	2	
Northern Mockingbird	175	
Brown Thrasher	40	
European Starling	1,725	
American Pipit	115	
Cedar Waxwing	595	
Orange-crowned Warbler	7	
Yellow-rumped Warbler	255	
Pine Warbler	30	
Palm Warbler	10	
Black-and-white Warbler	1	
Eastern Towhee	143	
Chipping Sparrow	780	
Field Sparrow	43	
Savannah Sparrow	88	
Fox Sparrow	8	
Song Sparrow	197	
Swamp Sparrow	40	
White-throated Sparrow	488	
White-crowned Sparrow	6	
Dark-eyed Junco	92	
Northern Cardinal	359	
Red-winged Blackbird	450	
Eastern Meadowlark	123	
Rusty Blackbird	45	
Common Grackle	1,898	
Brown-headed Cowbird	27	
blackbird sp.	1,305	
Purple Finch	1	
House Finch	221	
American Goldfinch	127	
House Sparrow	20	
Total	15,190	

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[1] S. P. Hubbell. Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science*, 283 (5401):554–557, January 1999. ISSN 00368075. DOI: 10.1126/science.283.5401.554. URL `http://www.sciencemag.org/content/283/5401/554.short`.

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