Equilibrium theories of maintenance of diversity: niche and neutrality

Constancy of community occupancy and of species abundance suggests existence of assembly rules and is consistent with niche differentiated communities – examples?

Density-dependent process can arise from ______, and are most important at ______ stages. Often call negative DD.

Initial ideas on how density dependence maintain diversity focused on seeds and seedlings (granivores and herbivores), ignored _________

Increasing evidence that species are rare because _________
What about groups of organisms other than plants??

Classical theory (Hutchinson 1957, 1959) argues that fine partitioning of feeding niches can support the diversity of herbivores.

Increasing body size of organisms at higher trophic levels limits population density and may limit how finely feeding niches are divided - constraining diversity?

Very few tests of theories of diversity maintenance for insects - a hyperdiverse group of primary consumers…

What would you need to do to test equilibrium vs non-equilibrium models for the maintenance of insect diversity??
Novotny et al. (2002) Host specificity of herbivorous insects in New Guinea

Analyzed host preferences of 900 insects on 51 plant species

-Most species feed on several (congeneric) host species. *Tight specificity (one insect, one host plant) was surprisingly rare*

-Even phylogenetically distant hosts shared a third of herbivores (*remember phylogenetic signal?*)

An average tree New Guinean tree hosted:
- 33 Coleoptera
- 26 Lepidoptera
- 20 orthopterids
$F_T = \text{total number insect species associated with } T \text{ host species}$

Mean number of insect spp/host * $T$ hosts

Butterflies

Other lepidoptera

Coleoptera

Orthopterids
Novotny et al. (2002) results challenged paradigm of strong host specialization (niche partitioning) of insect communities

Suggest that non-equilibrium explanations needed to account for insect diversity

Also need to re-evaluate estimates of insect diversity which are based on host specialization.

Maybe ‘only’ 4-6 million insects, not 31 million insects?
Summary:

Long term studies of communities have shown similarity in species composition over long time scales that cannot be accounted for by random sampling from a regional species pool.

BUT… Fine-scale niche partitioning is probably not sufficient to account for hyper-diverse communities. Non-equilibrial processes must be important? Or… density-dependent process most important in regulating maximal abundance?

*How can we build a model to explain diversity maintenance?*

Either start with all the niche differences we can find? Which of these are truly important?

Or start with nothing (null model) add only the necessary biology
The Neutral Theory of Biodiversity and Biogeography

Hubbell (1979) Community drift model

Disturbance kills $D$ out of $K$ trees at random with respect to their species identity

Under assumption of ecological equivalence of species

Let $D$ new trees replace the vacancies, with the proportion of replacement trees contributed by each species given by the proportional abundance of the species in the community after the disturbance

When species are unable to immigrate into the community what is the consequence for species relative abundance?
Simulated forest stand K=20

Each model iteration: one tree dies. Probability of replacement is proportional to its relative abundance in the community

Probability of replacement by green is 8/20, red is 7/20...
Species abundances will take a “random walk” (random drift).

Over the long term, with *no immigration or recolonization* of the local site, all but one species will be lost by extinction.

Over the short term the model leads to *lognormal relative abundances*, and over the mid-term to a geometric distribution (assuming no immigration or recolonization)
Species abundance distribution (SAD)
Species abundance distribution (SAD)

Does SAD represent a balance between species loss by extinction and gain by speciation?

Can mathematically describe the shape of the SAD using Fisher’s alpha.
Premise of Hubbell’s model...

*Island biography theory doesn’t predict species abundances*
*Relative abundance theory doesn’t predict species richness*

If we incorporate *speciation* into an island biogeography model can we predict species richness and abundance?

Based on (1979) random drift model because:

Model appropriate for communities of *trophically similar, competing species* e.g., forest trees, coral reefs, ???
**Similarities with Island Biogeography**

Concerns *local communities* (= sampled areas of habitat), whose communities are linked to ‘mainland’ *metacommunity* by migration.

Individuals die on the ‘island’ (local community) and are replaced by an individual drawn at random.

But… can be an individual drawn at random from the local community *or at random from the ‘mainland’* (metacommunity) - an ‘immigrant’

Metacommunity is fixed in size (*n*) and includes all species that could potentially colonize a local community
Dynamics of the metacommunity

Number of individuals in the metacommunity, $J_M$ is constant

At each time step one random individual dies and is either
replaced by an individual of a new species (ie speciation
occurs) with a very small probability of $\nu$ (‘nu’ the speciation rate)
or, the dead individual can be replaced by an offspring of one of
the remaining surviving individuals with probability $1-\nu$

Math of the model is analagous to drift in population genetics

asks: “What is the probability that the $i$th species will be at any
abundance from 0 (≡extinct) to $J$ (≡monodominant)?
Find that the species abundance distribution (SAD) is determined by the compound parameter $\theta = 2 J_M \nu$

When $\theta$ is small (small metacommunity size and/or low speciation rate) then rank abundance curve is steep and geometric-like. When $\theta$ is high, curve becomes more S-shaped

$\theta$ has been called the ‘fundamental biodiversity number’

_Found that $\theta$ is exactly the same as Fisher’s $\alpha$_
\( \theta \) is exactly the same as Fisher’s \( \alpha \)

**Log series:** (aka Fisher’s alpha - from lecture 16…)

Log series takes the form: \( \alpha x, \alpha x^2/2, \alpha x^3/3, \ldots \alpha x^n/n \)

Where \( \alpha x \) is the number of species predicted to have one individual, \( \alpha x^2 \) to have two individuals etc…

Estimate \( x \) from the iterative solution of:
\[
\frac{S}{N} = \frac{1-x}{x(-\ln(1-x))}
\]
where \( S = \) number of spp, \( N = \) total individuals

Once you know \( x \), calculate \( \alpha \) the diversity index
\[
\alpha = \frac{N(1-x)}{x}
\]
Derivation of $\alpha$ explains why it’s a good diversity index (product of two stable numbers $J_M$ and $\nu$)

Also explains what $x$ is (previously just a fit parameter)

$x$ of Fisher’s alpha log series is ratio of the average per capita birth rate to death rate ($b/d$)

$x$ must be slightly $<1$ or metapopulation size is infinite

Over entire metacommunity $b/d$ will be very nearly at unity. (small difference is made up for by speciation).

Now, can use the neutral model to fit relative abundances of species in communities
Fig. 4. Expected metacommunity dominance-diversity distributions for a random sample of 64 individuals from the metacommunity, for various values of the fundamental biodiversity number $\theta$. 
Hang on though, don’t species relative abundances fit the Preston log-normal better than the log series???

Logseries: Singleton is always the most frequent size class

When sampling of communities is more complete then leads to an interior modal size class
The log normal distribution is a *bell-shaped curve*. If data come from a finite sample *the left hand portion of the curve* (representing rare and unsampled spp) *may be missing*. Preston termed this truncation point the ‘veil line’. For small samples the log series may fit data as well as log normal.
Hubbell’s insight was that Preston’s log-normal distribution would arise if the dynamics of a local community was uncoupled from that of the metacommunity.

Metacommunity model ignores spatial structure and dispersal.

Local communities are ‘semi-isolated’ from the surrounding metacommunity; individuals will disperse between local communities with probability $m$ per birth.

To fit the local species abundance distribution (SAD) need $\theta$, $J$ (local community pop size) and $m$, migration rate. As $m$ smaller SAD becomes more skewed as rare species become rarer (with low immigration it takes longer for rare species to re-immigrate back into a local community).
Actual relative abundance

Expected relative abundance $m=0.1$

Expected relative abundance $m=1.0$

$N = 20,541$ trees $> 10$ cm dbh of 235 species in 50 ha
How does Hubbell’s model prediction compare with the Preston log-normal?
If Hubbell interpretation of SADs is correct then should be able to show that SAD of the metacommunity is log series

Don’t know SAD of metacommunity, but can estimate it by sampling across it at different spatial locations. This should reduce effect of localized dispersal

Amazonia: RAINFOR plot network has sampled tree species across Peru, Bolivia, Brazil, Colombia, Ecuador, Guianan Shield (ter Steege et al. 2006)

>280,000 trees

Species ids not completed, but generic ids should show similar patterns to species under neutrality (just take longer to originate and go to extinction)
Relative abundance distribution of tree genera in the Amazon (Hubbell et al. 2008)

Fisher’s alpha = 71. Inset shows Preston style histogram of genera binned into doubling classes of abundance
Neutral model summary:

1. Random drift in the metacommunity generates a predictable species abundance distribution (SAD) based on community size and speciation rate $= \theta$

2. $\theta$ turns out to be the same as Fisher’s $\alpha$

3. Drift dynamics of local populations depend on how tightly they are coupled to the metapopulation by migration $= m$

4. It is possible to generate very good fits of observed local abundance distribution patterns using two free parameters, $\theta$, and $m$.

5. Values of $m$ seem reasonable, $\theta$ more difficult to assess.
Recent additions to the neutral theory

Neutrality means that *per capita birth and death rates are equivalent across species* - no functional differences among spp.

Several new components added to the model since the 2001 monograph

Volkov et al. (2005) Addition of density-dependence to the neutral neutral (‘symmetric neutral theory’)

(density dependence does not violate neutrality so long as applied ‘symmetrically’ *i.e.*, every species experiences equivalent density dependence when at the *same abundance*)
Fitting density dependence has equivalent effect to fitting $m$ for dispersal limitation from the metacommunity.

SADs for 6 large forest plots. $x$ axis is doubling abundance classes.

Both density-dependence and dispersal limitation operate in tree communities.

Figure 1 | Fits of density-dependent symmetric model (red line) and dispersal-limitation model (blue circles) to the tree species abundance data from the BCI, Yasuni, Pasoh, Lambir, Korup and Sinharaja plots, for trees $\geq 10$ cm in stem diameter at breast height (see Table 1). The frequency distributions are plotted using Preston’s binning method as described in ref. 3. The numbers on the $x$ axis represent Preston’s octave classes.
Is the assumption of symmetric density dependence valid?

Hubbell argues that density dependent effects do not regulate populations because they dissipate within a few meters.
Ricklefs (2003) Neutral model assumptions about speciation and species lifetimes

Hubbell offers two potential modes of speciation

‘Point mutation’ - a new species arises as a *single new individual*

‘Fission speciation’ - randomly bisect the population of a species in two. Akin to speciation by vicariance (eg separation of populations by a mountain, large river etc…)

Point mutation model:

Difficult to recognize ‘new’ species formed by mutation - some population growth and differentiation may be needed.
Many new species, whose population size is initially 1, will go immediately extinct.

Remember the random drift model rate of species loss? What is the converse of this??????

Random fission model (not included in original neutral model):

Populations of species split with frequency of $\nu$. Average life span of species under this model is **much longer**
Under the fission model, reasonable estimates for the metapopulation size, and speciation rate yield too many species

Hubbell’s (2003) response:

“The issue is easily resolved if one considers point mutation speciation and random fission speciation as the theoretical extremes of a speciation continuum”

Proposes a third mechanism of species “Peripheral isolate speciation” - will yield species with intermediate initial population sizes and therefore intermediate mean lifespans.
Conclusion

Neutral theory provides a parsimonious explanation for community properties, and has refocused attention on how evolutionary processes at large spatial scales are coupled to local community dynamics. It is controversial in as much as it is considered more than a ‘null model’ for community organization.

“One of the main goals in producing the neutral theory was to stir the scientific pot vigorously, which in my opinion has been overdue in community ecology for a long time. I am please to say that positive results from this stirring seem to be happening”