Analysing spatial and temporal variability in diversity

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Diversity in diversity...

**How Standards Proliferate:**

(See: A/C chargers, character encodings, instant messaging, etc)

**Situation:** There are 14 competing standards.

14?! Ridiculous! We need to develop one universal standard that covers everyone’s use cases. Yeah!

**Soon:**

**Situation:** There are 15 competing standards.
Overview

• Partitioning Diversity
  – Alpha, Beta and Gamma diversity
• Barro Colorado Island
  – Spatial Partitioning
  – Temporal Partitioning
Different kinds of diversity

• Diversity, even biodiversity, can mean lots of different things to different people
• Individual diversity measures can reflect many different aspects of this
• As a result measures can often disagree with one another about what is diverse
• This is often correct, but we need to understand what each measure is telling us and which measure (if any) answers the question we are interested in
• What do we mean when we talk about partitioning diversity?
Partitioning Diversity

• Imagine we have divided up our ecosystem into N sub-communities

• We want to know:
  – How many distinct parts are there?
  – Which are the interesting ones?
  – Which should we conserve?
Partitioning Diversity

• How do we divide up the “total” diversity into the diversity “within” the sub-communities, and the diversity “between” the sub-communities?
  – This is usually described as partitioning the \textit{gamma} (global) diversity into \textit{alpha} (average) and \textit{beta} (between) components
Partitioning Diversity

\[ \bar{p}_i = \left( \sum_{j=1}^{n} p_{ij} \right)^{\frac{1}{n-1}} \]

mean proportional species abundance; the weighted generalised mean with exponent \( q - 1 \) of the \( p_i \) values

\[ \bar{q}_r = \sum_{i=1}^{n} \frac{p_{ij}}{p_i} \]

basic sum of order \( q \) in relation to the ylabel classification; the sum of \( p_{ij} \) values over all species \( i \), or mean proportional species abundance raised to the power \( q - 1 \)

\[ D = 1 / \bar{p} \]

true diversity of order \( q \); the inverse of mean proportional abundances of the types of interest, or the numbers equivalent of \( \bar{q} \)

\[ \gamma' \]

Shannon entropy; the logarithm of true diversity of order 1, or the logarithm of the inverse of the geometric mean of the proportional abundances of the types of interest

\[ \alpha' \]

the raw value of a species diversity index as calculated using the entire dataset, e.g. \( \gamma' \) or \( H' \)

\[ \gamma' \]

the alpha component obtained when partitioning \( \gamma' \)

\[ \beta' \]

the beta component obtained when partitioning \( \gamma' \)

\[ D_{ij} = \gamma = 1 / \bar{p}_j \]

classification of total effective number of species in the dataset (measurement unit: effective species or \( sp_{ij} \))

\[ \bar{p}_{ij} = \left( \sum_{j=1}^{n} p_{ij} \right)^{\frac{1}{n-1}} \]

mean proportional species abundance within sampling unit \( j \); the weighted generalised mean with exponent \( q - 1 \) of the \( p_{ij} \) values corresponding to sampling unit \( j \)

\[ D_{ij} = 1 / \bar{p}_{ij} \]

gamma diversity (= effective number of species) within sampling unit \( j \) (measurement unit: \( sp_{ij} \))

\[ \bar{p}_{ij} = \left( \sum_{j=1}^{n} p_{ij} \right)^{\frac{1}{n-1}} \]

mean proportional species abundance in the dataset; the weighted generalised mean with exponent \( q - 1 \) of all \( p_{ij} \) values

\[ \alpha = D_{ij} = \bar{p}_j \]

mean species diversity within sampling units: weighted generalised mean with exponent \( 1 - q \) of the \( D_{ij} \) values with \( w_j \) used as weights (measurement unit: \( sp_{ij} \))

\[ \alpha = \frac{D_{ij}}{\alpha} \]

ture alpha diversity; effective number of species per virtual sampling unit of mean species diversity, or per compositional unit (measurement unit: \( sp_{ij}/CU \))

\[ \bar{q}_{ij} = \sum_{j=1}^{n} \frac{p_{ij}}{p_j} \]

effective number of species abundance values per effective sampling unit (measurement unit: \( sp_{ij}/CU \))

\[ \beta_{ij} = D_{ij}/D_{ij} \]

ture beta diversity; number of compositional units in the dataset (measurement unit: \( CU \))

\[ \gamma = \frac{\gamma_{ij}}{\gamma_{ij}} \]

tional-to-local diversity ratio (measurement unit: \( sp_{ij}/sp_i \))

\[ \beta_{ij} = D_{ij}/D_{ij} \]

two-way diversity ratio (measurement unit: \( sp_{ij}/sp_{ij} \))

\[ \beta = D_{ij} - D_{ij} \]

tional diversity excess; absolute effective species turnover (measurement unit: \( sp_{ij} \))

\[ \beta_{ij} = \frac{\gamma_{ij}}{\gamma_{ij}} \]

Whittaker’s species turnover; effective species turnover expressed in multiples of the species diversity in a single compositional unit (measurement unit: \( sp_{ij}/sp_i \))

\[ \beta_{ij} = \gamma_{ij} \]

proportional species turnover; effective species turnover expressed as a proportion of total species diversity (measurement unit: \( sp_{ij}/sp_i \))

\[ H_{ij} = -\sum_{i=1}^{n} p_{ij} \log(p_{ij}) \]

beta Shannon entropy (measurement unit: depends on the base of the logarithm)

\[ H_{ij} = -\sum_{i=1}^{n} p_{ij} \log(p_{ij}) \]

regional Shannon entropy excess (measurement unit: depends on the base of the logarithm)

\[ \gamma'_{ij} = \gamma - \alpha_{ij} \gamma_{ij} \]

regional variance excess (measurement unit: \( sp_{ij}/sp_i \))
• What do we mean when we talk about beta diversity?
  – Very broadly there are two definitions...
Partitioning Diversity

• What do we mean when we talk about beta diversity?
  1. Effective number of unique communities
Unique communities

**Alpha Diversity:** 100

**Gamma Diversity:** 600
Unique communities

**Alpha Diversity:** 100

**Gamma Diversity:** 400
Unique communities

**Alpha Diversity:** 100

**Gamma Diversity:** 200
Unique communities

**Alpha Diversity: 100**

**Gamma Diversity: 100**
Unique communities

Beta diversity:
- 6
- 4
- 2
- 1
Partitioning Diversity

• What do we mean when we talk about beta diversity?
  1. Effective number of unique communities
  2. Turnover between communities
<p>| | | | | | |</p>
<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td><strong>TURNOVER:</strong></td>
<td><strong>100%</strong></td>
<td></td>
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</tbody>
</table>
Partitioning Diversity

TURNOVER: 80%
Partitioning Diversity

**TURNOVER: 60%**
TURNOVER: 40%
Partitioning Diversity

**TURNOVER: 20%**
Partitioning Diversity

• What do we mean when we talk about beta diversity?
  1. Effective number of unique communities
  2. Turnover between communities

• These turn out to be the same thing...
The effective number of species:
- the number of species when all species are present at equal frequency
- the more uneven the distribution, the fewer species are “effectively” present
Diversity Profiles

SR: Species richness
SE: Shannon entropy
SD: Simpson diversity
BP: Berger–Parker
Diversity Profiles

- SR: Species richness
- SE: Shannon entropy
- SD: Simpson diversity
- BP: Berger–Parker

Species richness vs. Effective # alleles for different q values (q=0, q=1, q=2, q=∞).
The effective number of species:

- the number of species when all species are present at equal frequency
- the more uneven the distribution, the fewer species are “effectively” present
- the more similar species are, the less “effectively present” each species is
### Diversity Profiles with Similarity

<table>
<thead>
<tr>
<th>Name</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Power mean of order $r$ of $x$ weighted by $w$</td>
<td>$M_r(w, x) = \begin{cases} \left[\sum_{i=1}^{S} w_i x_i^r \right]^{1/r} &amp; r \neq 0 \ \prod_{i=1}^{S} x_i^{w_i} &amp; r = 0 \end{cases}$</td>
</tr>
<tr>
<td>Hill numbers</td>
<td>$qD(p) = M_{q-1}(p, p)^{-1}$</td>
</tr>
<tr>
<td>Similarity-sensitive diversity</td>
<td>$qD^Z(p) = M_{q-1}(p, Zp)^{-1}$</td>
</tr>
<tr>
<td></td>
<td>$[qD(p) = qD^I(p)]$</td>
</tr>
</tbody>
</table>
Partitioning Diversity

• What’s different?
  – We think in terms of individual sub-communities as much as the whole ecosystem

• Coming from that perspective allows us to answer specific questions:
  – Which sub-communities are the most diverse?
  – Which sub-communities are the most distinct?
  – Which sub-communities contribute the most to overall diversity?

**Alpha Diversity**

**Beta Diversity**

**Gamma Diversity**
### Partitioning Diversity

<table>
<thead>
<tr>
<th>Diversity measure</th>
<th>Sub-community diversity (d)</th>
<th>Ecosystem diversity (D)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alpha diversity</strong></td>
<td>( q\alpha^Z_j(\bar{P}<em>j) = M</em>{q-1}((\bar{P}_j, ZP_j)^{-1} )</td>
<td>( q\alpha^D(Z(P) = M_{1-q}((w, q\alpha^Z_j(\bar{P}_j)</td>
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<td>( q\hat{\alpha}_j^Z(\bar{P}_j) = qD^Z(\bar{P}_j)^* = w_j \times q\hat{d}_j^Z(\bar{P}_j))</td>
<td>( q\hat{\alpha}^D(Z(P) = M_{1-q}((w, q\hat{\alpha}^Z_j(\bar{P}_j)</td>
</tr>
<tr>
<td><strong>Beta diversity</strong></td>
<td>( q\beta^Z_j(\bar{P}<em>j, p) = M</em>{q-1}((\bar{P}_j, \frac{ZP_j}{Zp}))</td>
<td>( q\beta^D(Z(P) = M_{1-q}((w, q\beta^Z_j(\bar{P}_j, p)</td>
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<tr>
<td></td>
<td>( q\hat{\beta}_j^Z(\bar{P}<em>j, p) = M</em>{q-1}((\bar{P}_j, \frac{Z\hat{P}_j}{Zp}) = \frac{q\beta_j^Z(\bar{P}_j, p)}{w_j})</td>
<td>( q\hat{\beta}^D(Z(P) = M_{1-q}((w, q\hat{\beta}^Z_j(\bar{P}_j, p)</td>
</tr>
<tr>
<td><strong>Gamma diversity</strong></td>
<td>( q\gamma_j^Z(\bar{P}<em>j, p) = M</em>{q-1}(\bar{P}_j, Zp)^{-1} )</td>
<td>( q\gamma^D(Z(P) = M_{1-q}((w, q\gamma^Z_j(\bar{P}_j, p)</td>
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<tr>
<td></td>
<td>([q\gamma_j^D(Z(P) = q\gamma^D(Z(P) = qD^Z(p)^*)</td>
<td></td>
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</tbody>
</table>
Sub-community diversity

\[ q \alpha_i^Z \] 
Patch diversity

\[ q \beta_i^Z \] 
Distinctiveness from others

\[ q \gamma_i^Z \] 
Contribution to total diversity
Real World Example
Barro Colorado Island
Barro Colorado Island

• 50 ha plot in Panama
  – Every individual tree and sapling recorded
  – Species, Size, Location
  – Work done by Center for Tropical Forest Science and many others, funded by multiple sources
What can we tell from total beta diversity?
What can we tell from total beta diversity?

Beta diversity vs communities

- **x-axis**: Number of communities
- **y-axis**: Beta diversity

The graph shows a linear relationship between the number of communities and beta diversity, indicating an increase in diversity as the number of communities increases.
What can we tell from total beta diversity?

• Not much!
  – and total alpha and gamma diversity are similar...
How about individual alpha diversity?
What can we assess?

\[ q \alpha_i^Z \] Value in terms of patch diversity

\[ q \beta_i^Z \] Value in terms of distinctiveness

\[ q \gamma_i^Z \] Value in term of contribution to total diversity
Value in terms of patch diversity
Value in terms of patch diversity

• We are beginning to see patterns here...
  – Picking out area with a lot of trees of high diversity
  – But not necessarily distinct from other areas, so selecting these, we may repeat ourselves with some species and miss others
What are these areas?
What are these areas?
What are these areas?
What are these areas?
What does Beta Diversity mean though?
What does Beta Diversity mean though?
What does Beta Diversity mean though?

- Areas of high “distinctiveness”, but no regard for diversity or number of trees
- It identifies two areas, but one of them is largely devoid of trees...
What can we assess?

Value in terms of patch diversity

\[ q \alpha_i^Z \]

Value in terms of distinctiveness

\[ q \beta_i^Z \]

Value in term of contribution to total diversity

\[ q \gamma_i^Z \]
Value in terms of distinctiveness
Value in terms of distinctiveness

• It identifies areas that contribute a lot to total beta diversity
• Specifically finds one area, the area with high individual beta diversity but which also has trees in it!
But is this what we want?
What can we assess?

- \( q \alpha_i \) Value in terms of patch diversity
- \( q \beta_i \) Value in terms of distinctiveness
- \( q \gamma_i \) Value in terms of contribution to total diversity
Value in terms of contribution to total diversity
Value in terms of contribution to total diversity

- It identifies areas that contribute a lot to the total gamma diversity of the whole plot
- Which areas this encompasses varies depending on your meaning of diversity!
Temporal Beta Diversity

- Comparing a community at one timepoint to the “ecosystem” of that community measured at all timepoints
Temporal beta diversity

- One area has particularly high temporal beta diversity
  - and we’ve seen it before...
What’s happening in this patch – 1981

Tree density

Lat

Long
What’s happening in this patch – 1985

Tree density

Long

Lat
What’s happening in this patch – 1990

Tree density

Lat

0 100 200 300 400 500

Long

0 200 400 600 800 1000
What’s happening in this patch – 1995

Tree density

Long

Lat

0 100 200 300 400 500

0 200 400 600 800 1000
What’s happening in this patch – 2000

Tree density

Lat

0 100 200 300 400 500

Long

0 200 400 600 800 1000
What’s happening in this patch – 2005

Tree density

Lat

Long
What’s happening in this patch?

• The trees are filling in...
Revisiting Beta Diversity – 1985

Beta diversity

![Beta diversity graph](image-url)
Revisiting Beta Diversity – 1995

Beta diversity
Revisiting Beta Diversity – 2005

Beta diversity

0 100 200 300 400 500

0 200 400 600 800 1000
Temporal beta diversity

• Correctly identifies an interesting area where there were few, but distinct, trees in the 1980s, but now the area has filled in with lots of more normal trees...
Conclusions

• We have a generalisation of existing measures of beta diversity that incorporates similarity

• We have a new concept of individual alpha, beta and gamma diversity, which tell us
  – which specific communities are most distinct
  – which contribute most to overall diversity
  – which are changing most over time

• We can use these to identify areas of interest and well as measuring overall diversity, turnover and beta diversity...
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