Relative importance of environmental and biotic factors shaping community assembly of arboreal ants in rubber plantations and rainforests

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Key Processes of Community Assembly and Biodiversity

- Regional species pool -> Species in a landscape (e.g. rainforest trees)
- Coexistence of rare species in a given landscape: may be explained by neutral processes, multiple niche dimensions, stochastic processes and historic contingency
- These mechanisms and local habitat heterogeneity maintain high local β diversity

Mori et al. 2018 TREE
Community Assembly and Biodiversity—Ecosystem Functioning with an “additional” filter

- An “additional” filter (anthropogenic disturbances) removes available species at a given landscape (e.g., rubber plantations)

- Reduction of both common and rare species results in weakened neutrality and decreased niche dimensions

- Altered mechanisms and homogenised local habitats result in low local $\beta$ diversity

Decreased niche dimensions = more competition?
Rubber plantations in Xishuangbanna

- **Rubber plantation: most dominant landscape in Xishuangbanna** (Hammond et al. 2015, ICRAF Working Paper)

- **In Menglun (XTBG), 324% increase in rubber plantation from 1988 to 2003** (Liu et al. 2006 Mountain Research and Development)

- **Subsequent loss of biodiversity** (Ahrends et al. 2015 Global Environmental Change)
Arboreal ant diversity in rainforests and rubber plantations

- Spatial structure of arboreal ant assemblages: thought to be driven by competitive interactions (Bluthgen and Stork 2007 Austral Eco, Fayle et al. 2013 Ecography)
- "Ant mosaics": competitive interaction explains spatial structure of arboreal ant assemblages (Bluthgen & Stork 2007 Austral Eco)
- Classical studies about ant mosaics primarily came from plantations
- Ant mosaics may or may not work in complex primary forests (Fayle et al. 2013 Ecography)
- We know little about how strength of interactions change across habitats
Arboreal ant baiting in Xishuangbanna

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Tree species</th>
<th>Sampling seasons</th>
<th>Number of locations</th>
<th>Number of plots per location</th>
<th>Number of trees per plot</th>
<th>Number of traps per tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rubber plantation</td>
<td><em>Hevea brasiliensis</em></td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>Rain forest</td>
<td>Mix tree species</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>10</td>
<td>3</td>
</tr>
</tbody>
</table>

Total number of samples: 2160
Arboreal ant diversity in rainforests and rubber plantations

- **Lower $\gamma$ diversity** in rubber plantations:
  - Dry season rainforest = 48 species
  - Wet season rainforest = 52 species
  - Dry season rubber = 22 species
  - Wet season rubber = 30 species

- **Lower $\beta$ diversity** in rubber plantations:
  - $F=19.3$ $df=3$ $p<0.001$ (from `betadisper`)

- Significant **differences in ant species composition** between rainforests and rubber but **no seasonal differences**

- Reduced common and rare species = **weaker neutrality in rubber plantations**

  *Oecophylla smaragdina* is always the most dominant!

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Dry rainforest  | Wet rainforest  | Dry rubber  | Wet rubber  |
Challenges in measuring species interactions (incl. competition)

1. Environmental conditions may confound species interactions (i.e. species that have no interactions appear to have interactions due to their habitat requirements)

2. Indirect vs direct species interactions

3. Interaction between two species diminish when more species are associated
\[ P(X_a) = P(X_a | X_b)P(X_b) + P(X_a | X_c)P(X_c) + \ldots \]

4. Conventionally, probability of species co-occurrence is understood by presence/absence
\( X = \text{Bernouilli dist'n} \)
Gaussian copula graphical model (GCGM)
(Popovic et al. 2019 MEE)

• This model fits generalized linear models for multivariate abundance data (manyglm, Wang et al. 2012)
  ➢ Can **accommodate wide variety of data types** (binomial, Poisson, negative binomial, multinomial, Tweedie)
  ➢ Covariance matrices can be obtained **after controlling for environmental variables** (e.g., elevation)

• Indirect vs direct interactions can be teased apart by calculating conditional dependence relationships between species by **examining residual precision matrices** of the focal and other species

• The best model (presence and strength of interactions between species) is modelled iteratively until convergence is achieved

• The R package, ecoCopula, is available on github (beware – the original R package fails with errors when associations are weak)
  ➢ Bug fix available from github written by Buchi
    ("mattocci27/ecoCopula@fix")
Strength of positive (blue) and negative (pink) associations can be visually assessed
Unsolved problem in GCGMs

- Interaction between two species diminish when more species are associated

$$P(X_a) = P(X_a | X_b) P(X_b) + P(X_a | X_c) P(X_c) + \ldots$$

It is unclear whether the interactions do not exist OR interactions were masked by inclusion of many species

This is the problem when comparing the strength of interactions between two habitats (e.g., primary vs disturbed forests) with different number of species
Unsolved problem in GCGMs – our solution (so far)

Compare the strength of association given a number of species in GCGMs
Strength of species interactions between rainforests and rubber plantations

- GCGM models
  1. Select common ant species (n>5 samples)
  2. Use multivariate model averaging (mgImn, Katabuchi and Nakamura 2015) to select a set of environmental variables that best explains the ant species compositional variation
  3. PCA to summarise the environmental variables (PC1 and PC2)
  4. Fit GLM (PC1 and PC2 as environmental variables) for multivariate abundance data (mvabund, Wang et al. 2012)
  5. Fit Gaussian copula graphical lasso (ecoCopula, Popovic 2019)
  6. Calculate the mean values of positive and negative associations between ant species
  7. Repeat the above processes using different number of species (our solution for the unsolved problem in GCGM)

Dry rainforest

Number of species included

Negative = -0.11 ; Positive = 0
Strength of species interactions between rainforests and rubber plantations

- Stronger negative interactions (competition) during dry season in rainforest
- Competition became stronger in rubber plantation in both dry and wet seasons
- Little positive interactions among all data
Summary

• We demonstrated not only the reduction in $\gamma$ and $\beta$ diversities (also $\alpha$)

• Community assembly of ants is likely driven by competition in rubber plantations (same as Fayle et al 2013 Ecography from oil palm plantation)

At local scales (i.e., after the anthropogenic filter)...

Environment drives assembly mechanisms in rainforests

Competition drives assembly mechanisms in rubber plantation
Thank you! 谢谢大家！

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