

Stress Increases Holeyness of Trait-Space Occupation in Plant Communities

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Introduction

Functional diversity is an aspect of biodiversity that captures trait-based differences in communities and it is important for understanding how communities are assembled from regional species pools.

Functional diversity is often measured as the convex hull hypervolume or area occupied by a community in multidimensional trait space. While hypervolumes offer valuable insights into the degree of variation within a community, it has been suggested the “solid” nature of calculated hypervolumes could be deceptively simplistic (Blonder et al. 2014).

Blonder (2016) has proposed that the observed “presence or absence of features within hypervolumes”, or “holes” can be quantitatively determined and observed. With the establishment of absences of trait combinations within hypervolumes, new insights can be made into the evolution of species pools and community assembly. We aim to apply Blonder’s method of detecting holes within hypervolumes to data collected among a variety of unique plant communities with several questions in mind:

- Are holes commonly found in plant communities?
- Does the degree of holeyness vary in any systematic way across the landscape?
- What does variation in holeyness tell us about biodiversity?

Results & Discussion

Figure 2. Holes in individual plant communities ranging from dry to wet for forest and prairie/grassland environments, axes follow Fig. 1. The small dark red dots are the observed data. Multicolor dots show holey areas that represent missing species combinations. There appears to be more holes in both the dry and wet sites.

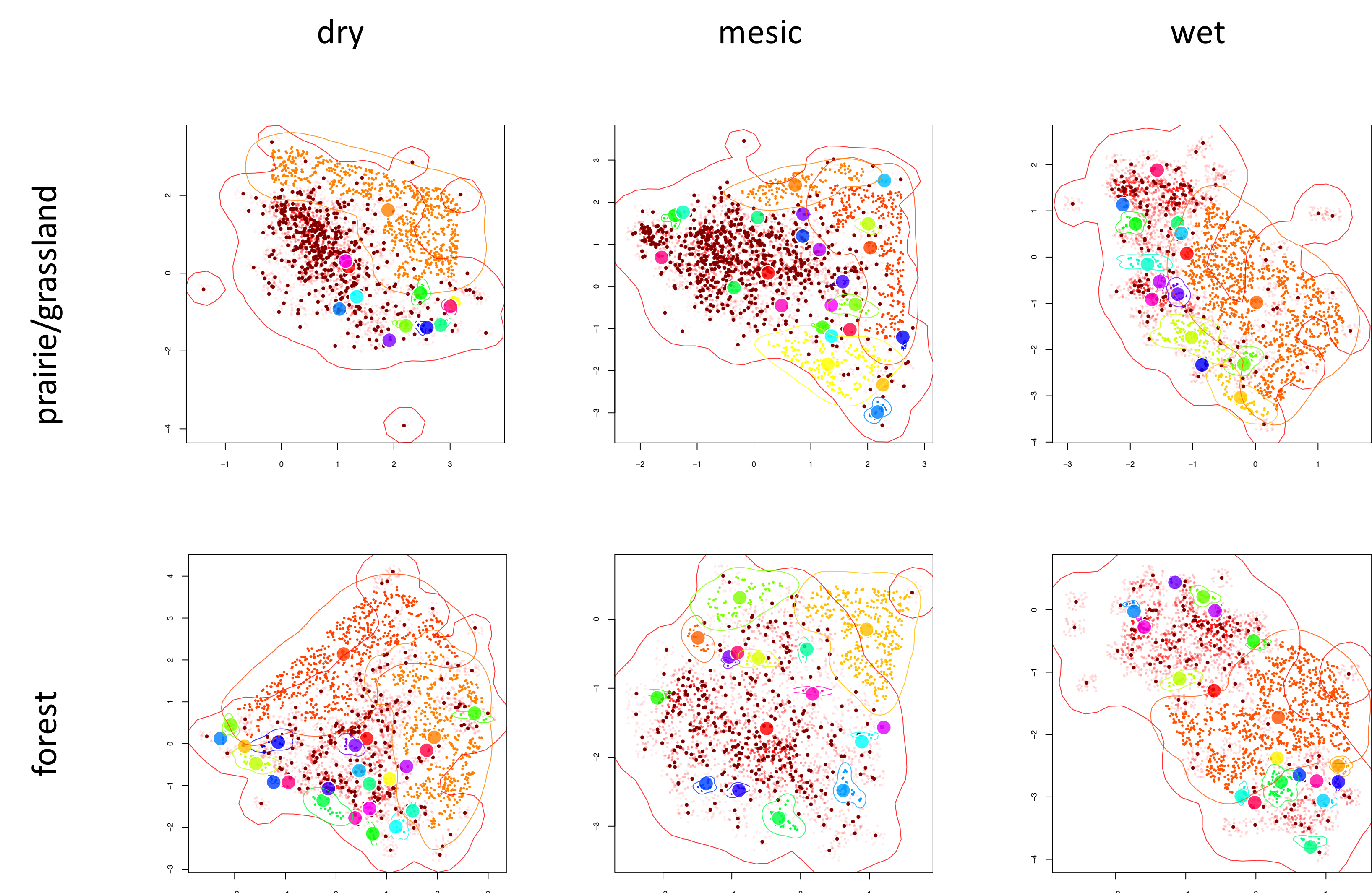
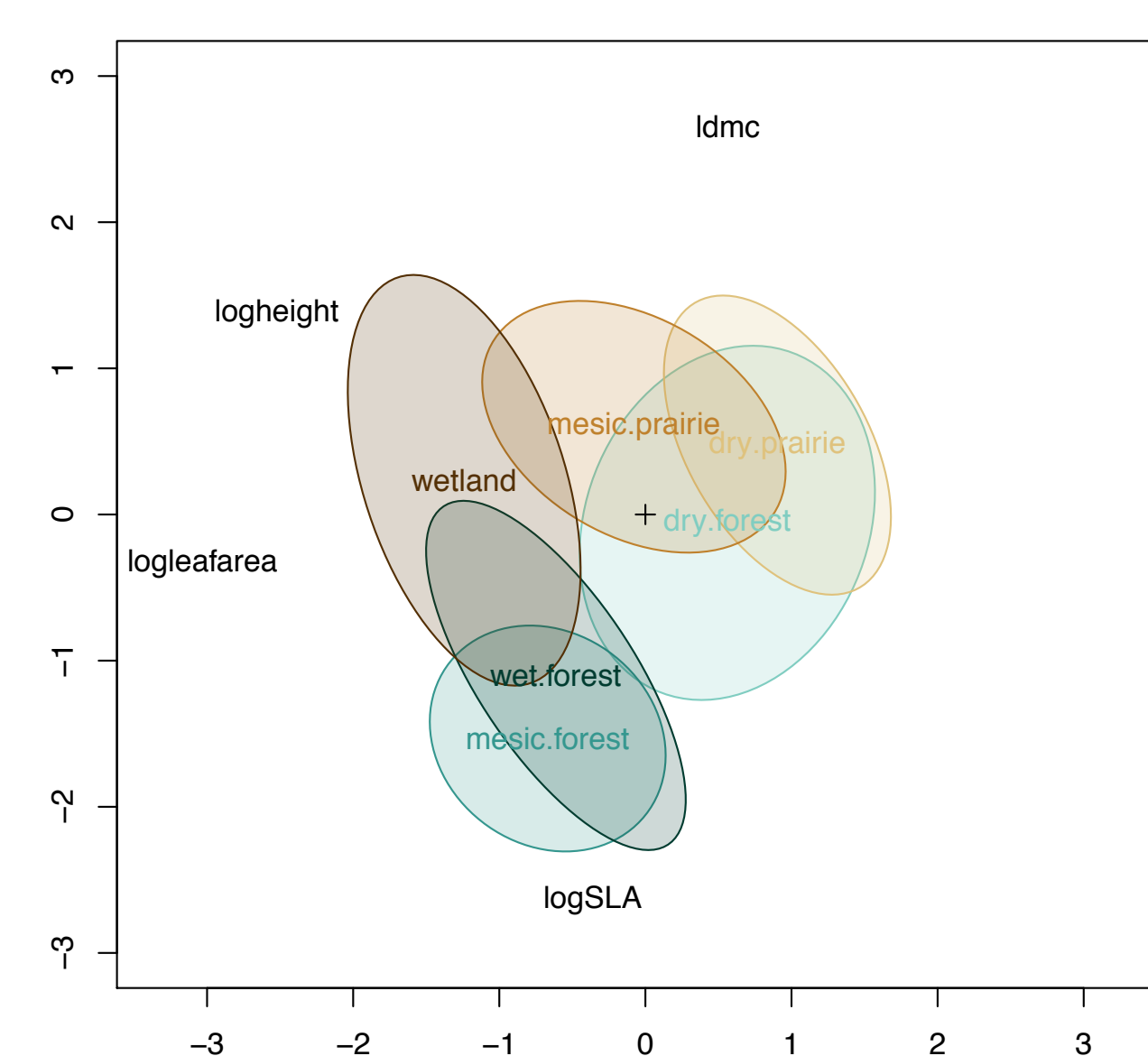


Figure 1. Principal component analysis of species traits in the six vegetation types.

The first component was associated with leaf economics (here shown as the y-axis to align with Fig. 2), with prairies having tougher leaves and mesic and wet forests having shade-adapted leaves with larger areas per unit mass.

The second component was associated with size (here shown as the x-axis), with wetter sites having larger plants.

Ellipses are one standard deviation around the mean because this was the most informative choice.



Methods

Study Sites:

- We sampled dry, mesic (medium), and wet forests and open grasslands/wetlands (6 sites). The grasslands/wetlands and wet forest sites were in Tiffany Wildlife Management Area (Buffalo County, WI). The mesic forest site was in Schmidt Maple Forest State Natural Area (Clark County, WI). The dry forest site was in Coon Fork Barrens State Natural Area (Eau Claire County, WI).

Plot Setup:

- Plots were created using a nested design with a starting plot area of 0.0225 m² (15 cm by 15 cm) and continued until a 64 m² area was achieved (see figure at right, note that plot 10 is 1 by 1 m in size).

Data Collection:

- For each species of plant per plot we measured plant height and took a leaf sample from the uppermost fully developed leaf. Leaves were weighed, scanned, and oven dried to obtain leaf area (cm²), specific leaf area (SLA, area per g dry mass, cm² g⁻¹), and leaf dry matter content (LDMC, percent dry matter of fresh leaves).

Data Analysis:

- Trait data were simplified using principle component analysis in R. The first two components captured 73% of the variation in the four traits and were used in the analyses. Component one was associated with leaf economic traits (SLA, LDMC), while component two was associated with size (height, leaf area).
- For each 64 m² plot, hypervolume size was measured using the hypervolume package in R, the total convex hull volume (Villéger et al. 2008) was measured using the convhulln function in the geometry package in R, and we calculated holeyness as (convex hull volume – hypervolume)/convex hull volume.

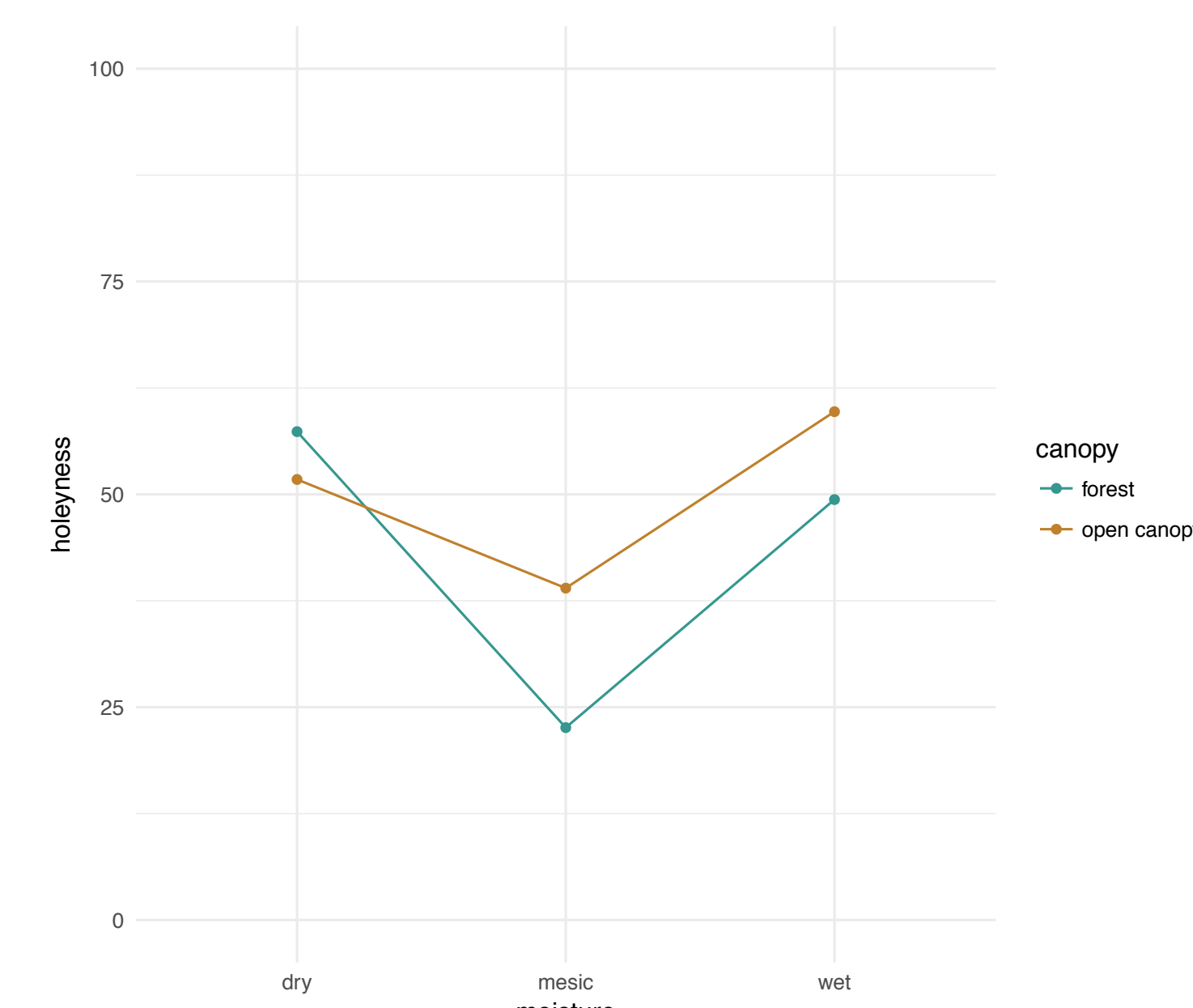
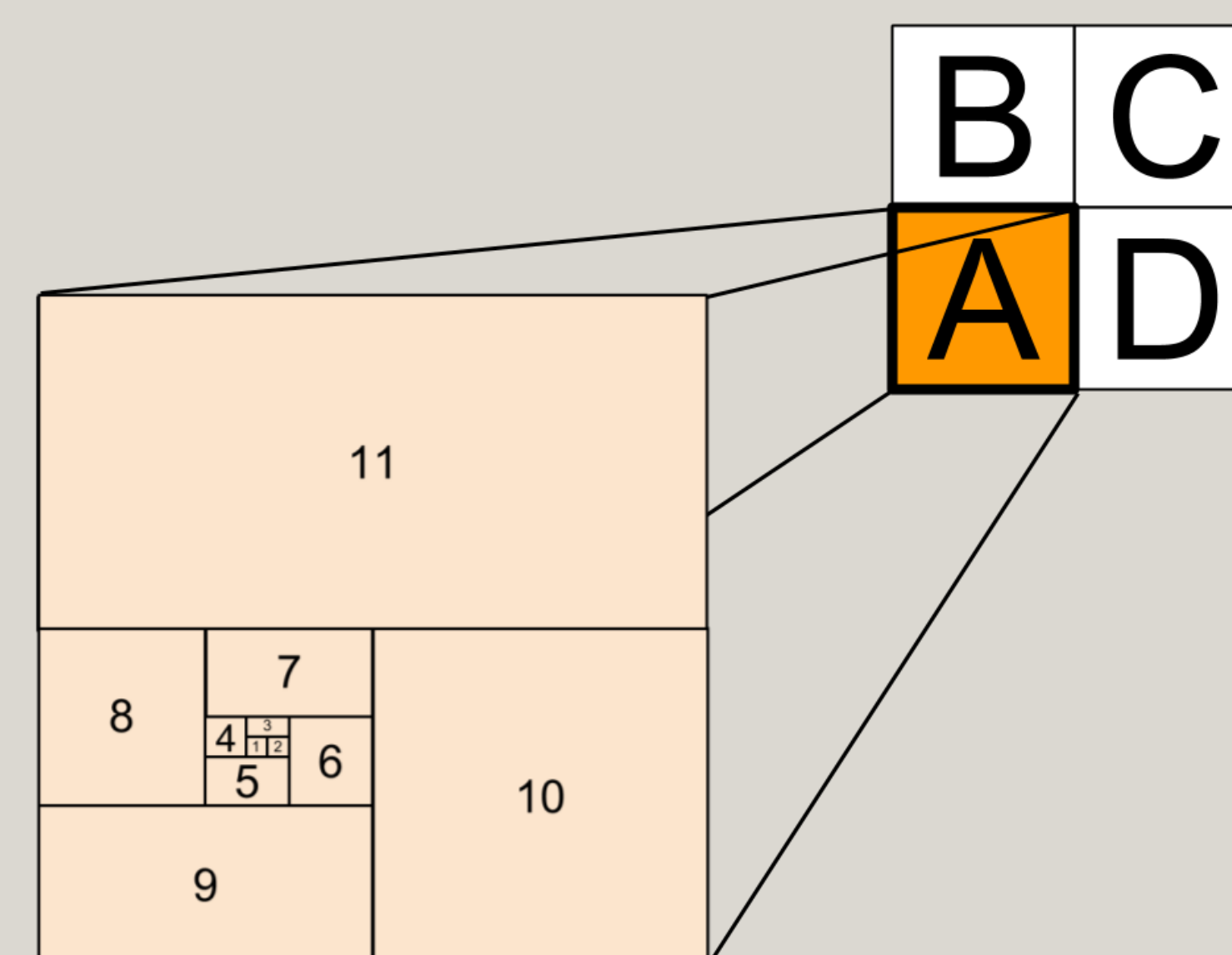


Figure 3. Holeyness (measured as the percent of total convex hull trait space that is unoccupied) was greater in both the dry and wet sites regardless of tree canopy cover.

Stressful sites had missing trait combinations. Therefore functional diversity may be over estimated and biased in some locations.

Why are some missing more trait combinations? There may be a requirement for more specialized trait combinations in stressful sites. Filtering by latent, unmeasured traits may also reduce the filling of trait space.

Important follow-up questions:

- (1) Is holeyness confounded with species richness?
- (2) Can we devise a null model (shuffling scheme) to compare these results to random assembly?

References

Blonder, B. 2016. Do hypervolumes have holes? *The American Naturalist* 187: E93-E105.

Blonder, B., C. Lamanna, C. Violle, and B.J. Enquist. 2014. The n-dimensional hypervolume. *Global Ecology and Biogeography* 23: 595-609.

Acknowledgements

Funding Sources:

Blugold Commitment Differential Tuition grant to D. Lonzarich and E. Weiher.