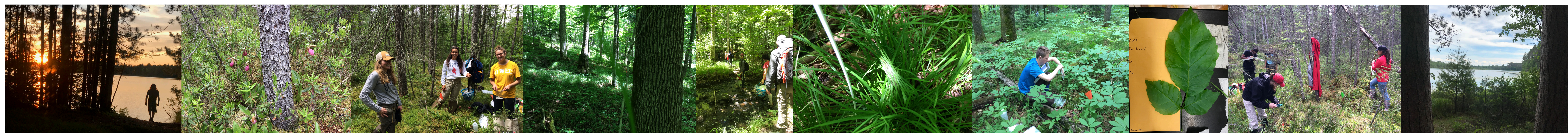


Functional Community Assembly is Increasingly Deterministic at Larger Spatial Grain Sizes

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Introduction

Community assembly is the result of ecological selection processes, dispersal processes, and random drift processes (Vellend 2010). Selection processes can cause coexisting species to be more similar or more different in traits, depending on the strength of environmental filtering or the strength of competition.

Scale in terms of the spatial extent can influence how trait similarity differs from random drift. For example, a grassland could have higher than expected trait diversity by having tall, medium and short species in most samples. But if the scale is expanded to include forests with tall trees, then the grassland plants may have lower than expected trait diversity (Weiher and Keddy 1995).

Scale also includes the sample scale or grain size. We sampled forest vegetation Northern Wisconsin at three grain sizes (0.1 m², 1 m², and 10 m²) to investigate how grain size and spatial extent influence our conclusions about community assembly.

Methods

Field sites were chosen based on habitat type including: wet, mesic (medium), and dry forests across Northern Wisconsin. Sites were in the Coon Fork Barrens State Natural Area (Eau Claire County), Chequamegon-Nicolet National Forest (Taylor County), Putnam Park (Eau Claire County), Schmidt Maple Forest State Natural Area (Clark County), Frog Lake State Natural Area (Iron County), Toy Lake Swamp State Natural Area (Vilas County), and Twin Lakes Bog State Natural Area (Taylor County).

Sample locations were chosen haphazardly in areas of relative homogeneous vegetation. Around each of three points per location, we sampled all vascular plant species at three grain sizes: 0.1 m², 1 m², and 10 m² with 10 m between plots. For each plant, we measured four functional plant traits that are associated with the two main global trends in plant variation. Two traits are associated with plant size: height (to the highest mature leaf, cm) and leaf area (surface area of the entire leaf including the petiole, cm²). Two traits are associated with leaf economics (slow vs. fast growth): specific leaf area (SLA, leaf area per gram dry mass, m² kg⁻¹) and leaf dry matter content (LDMC, dry mass ÷ fresh mass). Height, leaf area, and SLA were log_e transformed because they have a lognormal distribution.

At each scale, we used a Monte Carlo simulation in R to determine if the coexisting plants were more similar or more different than what would be expected if the trait values were assigned randomly. We determined three measures of functional diversity (FD): trait range, variance, and mean pairwise distance in trait values. The regional null model shuffled traits across all sample points 1000 times while the local null model shuffled traits across the three sample points within each location. The overall mean FD and standard deviation of the random mean FD were calculated. The standardized effect size (SES) was calculated as (observed mean FD – overall random mean FD)/(standard deviation of the random mean FD). SES < -2 indicates significant trait similarity and ecological filtering, while SES > 2 indicates significant trait differences and competitive exclusion (Gotelli and McCabe 2002).

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Results

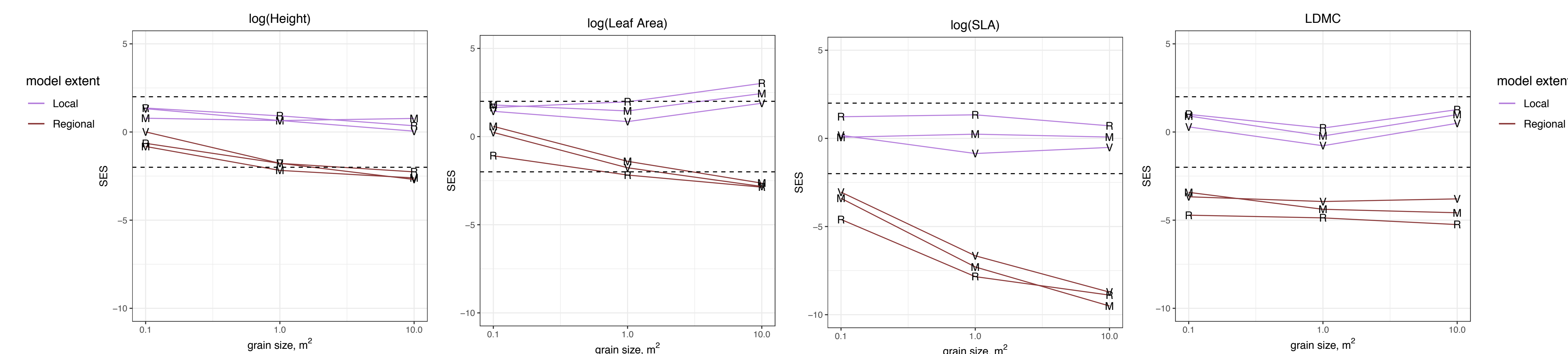


Figure 1. Standardized Effect Size (SES) of four functional traits measured at three grain sizes using both a large spatial extent (regional) null model and a small spatial extent (local) null model for three measures of functional diversity (R = Range, V = Variance, M = Mean pair-wise distance). SES more extreme than ± 2 are considered statistically significant (dashed lines).

- (1) Regional null models led to lower than expected SES of Functional Diversity for all traits in at least the largest grain size. Therefore, ecological selection from the regional species pool produces communities with similar trait values. This is consistent with environmental filtering.
- (2) Local null models led to SES of Functional Diversity that was within random expectation (except in one case). Therefore, community assembly from the local species pool is largely random.
- (3) Larger grain sizes often showed stronger effects (i.e., away from zero) with regional null models, but this was usually not true with local null models. Grain size had no effect for one trait (LDMC) and it had noticeable effects with both null models for one trait (Leaf Area). The interaction of grain size and null model was inconsistent across the traits.
- (4) There was evidence for greater than expected SES in one case (Leaf Area with local null model at the largest grain size). This overdispersion of traits is consistent with resource partitioning associated with competitive sorting of species.

Discussion

The relative strength of ecological selection processes and random drift processes are dependent on the size of the sample and the spatial extent of the null model. Ecological selection processes (i.e., filtering) has a stronger effect at the larger sample size while random drift processes are stronger at the smaller sample sizes and smaller species pools.

Similar effects of scale have been observed in other plant communities (Weiher et al. 2011) and in neotropical bird assemblages for size traits (Trisos et al. 2014). However, in bumble bee assemblages, there were similar effects of scale only for phylogenetic diversity but not trait diversity (Harmon-Threatt and Ackerly 2013).

The results support the idea that community composition may be understood best at larger spatial scales (e.g., at the regional scale Ricklefs 2008), but even so, our samples still represent very small samples. Therefore, the results do not fully support Ricklefs (2008), but do call into question the use of very small samples for assessing ecological filtering processes.

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