The memory of spatial patterns
Spatial aggregation can be used as a marker for ecosystem change

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Motivation - From pattern to process
The early detection of changes in ecological communities is important for their conservation in a changing climate. Judging the stability of ecosystems is particularly challenging for diverse ecosystems with long-lived individuals such as tropical forests. Directly observing ecological processes can be difficult or even impossible. However, observing the patterns that are the result of those processes is much more feasible. The spatial pattern of trees in a forest, for example, contains information about the underlying factors that helped to shape that particular pattern.

Hypothesis - Spatial aggregation in rainforest trees
Due to restricted dispersal of seeds, tree species generally show an aggregated spatial pattern, i.e. individuals from one species are not randomly distributed throughout the forest but clumped together. Interestingly, rare species are found to be more aggregated than more abundant species. We therefore propose that an increase or decrease in the local abundance of a tree species should in the long-term affect the spatial aggregation of that species. Because change in the aggregation will take time to occur, the current aggregation is likely to hold information on past changes in species abundance.

Simulation results
- Computer simulations show that differences in aggregation between rare and common species can result from local seed dispersal, even if species only differ in their abundance and not in any other ecological trait or process.
- Changes in the abundance of a species will lead to a long-term change in its aggregation. However, in the short-term, a population with growing abundance is expected to be more aggregated than a population with shrinking abundance.

Conclusion
- Computer simulations imply that changes in species abundances leave their mark on the spatial aggregation of species.
- Statistical analysis of data from canopy species at Barro Colorado Island (BCI) support the hypothesis that spatial aggregation might be used to detect changes in the abundance of species.
- The non-significance of the expected pattern in understory species might be due to the lack of statistical power, because of the smaller number of those species, or due to differences in their ecology. More work on confounding factors will need to be done in the future.

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Rainforests - hugely complex ecosystems
Rainforests are immensely diverse and complex ecosystems. In the rainforest plot at Barro Colorado Island (BCI), on which our analyses were based, there are more than 200,000 individual trees on an area of 1000 times 500 metres – among them trees from about 300 different species.

Results from field data
- Change of abundance can explain part of the between species variation in aggregation for canopy species at Barro Colorado Island (BCI) both over a 20-year interval ($R^2=0.28$ for the full model using both the current abundance as well as change of abundance as explanatory variables, compared to $R^2=0.13$ for a model using only the current abundance; adding change of abundance to the model significantly improves model fit with $p=0.014$) as well as a 5-year interval (full model: $R^2=0.33; p=0.002$).
- For understory tree and shrub species the contribution of past changes in abundance to aggregation is not significant.

Statistical analysis of field data
Fitting a linear regression model we used relative abundance change over 20 years and current abundance to explain the variation in within species aggregation between the 94 most abundant canopy tree species at BCI.

Fig. 1: Left: Difference in mean aggregation of a population that has a constant abundance and a population with growing (blue), or shrinking (red), abundance. After 10 generations the abundance was kept constant for both populations and the difference in aggregation diminishes over time. Right: Map of a shrinking (top) or growing (bottom) simulated population of 1000 individual trees.

Fig. 2: Barro Colorado Island (BCI) in Panama is one of the best studied tropical rainforests in the world.

Fig. 3: Depicted is the linear fit of the change in abundance to the aggregation of species corrected for the aggregation explained by the current abundance.