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COMMENTARY

Statistical challenges of evaluating diversity patterns across environmental gradients in mega-diverse communities

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Abstract

Ibanez et al. (*Journal of Vegetation Science*, this issue) applied sample size- and coverage-based rarefaction to analyse the elevational richness pattern in New Caledonian tree communities. We comment on the statistical assumptions behind rarefaction/extrapolation and suggest pooling small plot data to effectively assess/detect the diversity pattern. Broadening the analysis to include abundance-sensitive diversity measures and phylogenetic information can provide important additional insights.

Vegetation scientists commonly have to compare diversities of equal-area samples that differ in numbers of individuals. Among diversity measures, species richness is notoriously sensitive to sample size, and direct comparisons of observed sample richnesses can be highly misleading, especially in mega-diverse communities. The standard way to deal with this is to rarefy and/or extrapolate samples to a common sample size, and then compare richnesses of the standardized sample size. However, this still does not equalize sample completeness, which depends on community structure as well as sample size, and it will generally underestimate the relative richness differences among the assemblages. We recently proposed an alternative method (Chao & Jost 2012) that compares samples of equal completeness, as measured by sample coverage. In this issue, Ibanez et al. (2016) evaluate the importance of correcting observed species richnesses by using both these standardization methods, in order to better detect species richness patterns across environmental gradients.

Ibanez and colleagues collected tree species data (DBH $\geq$ 5 cm) from 201 plots (each 20 $\times$ 20 m) along an elevational gradient in the mega-diverse tropical rain forest of New Caledonia. They examined the change in sample richness with increasing elevation (5–1292 m). They locate the elevation of peak richness by fitting a parametric curve to the uncorrected data and the data corrected by the two forms of rarefaction/extrapolation. The elevation of peak richness depended strongly on whether the sample richnesses were used directly or were corrected for differences in size or coverage.

Rarefaction/extrapolation (R/E) of species richness

Curve-fitting results depend on the parametric model used. R/E can provide a direct non-parametric approach which does not assume a specified parametric function to model diversity patterns. However, long-range and asymptotic extrapolation of richness is statistically difficult in mega-diverse assemblages, especially for small plots. R/E methods assume the data are representative of the assemblage, so that the richness/diversity pattern obtained from data can be used to infer that of entire assemblages. The sample size must also be large enough so that reliable estimates for sample completeness and richnesses/diversities of rarefied/extrapolated samples can be obtained and interpreted (Chao & Jost 2012).

For species richness, the extrapolation range can be extended only up to double the observed sample size and the corresponding sample completeness (Chao et al. 2014). Since the sample size in the New Caledonia plots ranged from 55 to 325, we can only compare species richnesses across plots up to a size of 110 (twice the minimum sample size), which sets the minimum sample coverage to 76%. Such a narrowly restricted range of sample sizes and coverage values does not always effectively reveal richness patterns. Moreover, for mega-diverse communities, long-range extrapolated richness estimates are subject to large uncertainties due to small sample sizes, leading to wide and overlapped confidence intervals with neighbouring categories. Thus significant difference in richness across plots may not be statistically detected via R/E sampling curves, and data may be inconclusive.

Diversity (Hill numbers) pattern

By contrast, abundance-sensitive diversity measures can be extrapolated to their asymptotes if data are sufficient. Hill numbers (effective number of species) are increasingly used for this purpose. They are parameterized by a diversity order q, which determines the measures' sensitivity to species relative abundances. Hill numbers include the

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three widely used species diversity measures as special cases: Species richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$); see Appendix S1 for a brief review. Chao et al. (2014) extended R/E methods for species richness to Hill numbers and developed the software iNEXT for implementation. For diversity order $q \geq 1$, rare species have less impact on these diversities, and we generally can extrapolate these diversities to their asymptotes. A more general diversity (including richness) pattern based on Hill numbers (especially for $q = 0$, 1 and 2) is thus more informative and more reliable.

Pooling data

We suggest dividing 201 plots into several elevation groups to assess diversity patterns non-parametrically. Within each group, we can form two types of data: (1) abundance data: species abundances are pooled over plots in a group, and (2) incidence data: we can treat each plot as a sampling unit, and only species presence/absence in a plot is recorded. Depending on the question of interest, the number of groups used in this analysis is flexible. Here we use five elevation groups for illustration: 0–200, 200–400, 400–600, 600–800 and 800–1300 m, as these groups have approximately the same sample coverages (Other groupings yield similar results). The corresponding observed richnesses and sample sizes (in parentheses) are respectively 296 (3309), 429 (8241), 448 (6249), 331 (3538) and 285 (3931).

Within each elevation group, the sample size is now large enough to provide an accurate estimate of diversity with a narrow confidence interval so that significant differences in diversity can be detected. For both incidence and abundance data, it is now more likely that we have 'representative' data of assemblages of specified elevation ranges, and we can compare diversity estimates at greater sample sizes/coverages. The diversity curves can now even be extrapolated to their asymptotes for $q \geq 1$ measures. We can also now assess not only α-diversity, but also β-diversity between elevation groups. Pooling data also relieves problems with spatially clustered species. Incidence data are more robust to clustering, so that patterns revealed by the incidence-based analysis may be more reliable than those based on abundances. All analysis details are provided in Appendix S1, where the coverage-based R/E curves based on the two types of data all reveal that the diversity in 400–600 m is significantly higher in magnitude than any of other groups, and that the 95% confidence interval for this diversity does not overlap with those of its neighbours, confirming the authors' conclusions.

Extension to phylogenetic diversity

Hill numbers, and their corresponding R/E methods, were recently generalized to incorporate evolutionary history among species. The program iNEXT has also been generalized to iNEXT-pd to compute this phylogenetic diversity; see Appendix S1 for an introduction. Patterns of phylogenetic diversity in New Caledonia might reveal interesting differences between elevations and might provide important guidance for setting conservation priorities.

Additional thoughts/suggestions

In addition to elevation, Ibanez et al. (2016) also recorded other environmental variables for each plot. We can build a statistical model to find the relationship between the diversity estimates and all environmental variables, and detect which variables significantly affect the diversity estimates. The New Caledonian data also stimulates statisticians to address a challenging statistical issue: how to develop R/E methods for β-diversity and similarity/dissimilarity measures when there are undetected species.

Conclusion

When investigating richness/diversity patterns, it is always necessary to standardize samples using rarefaction and extrapolation. Our analysis (Appendix S1) shows that standardization by sample completeness rather than sample size produces clearer and more informative patterns, as Ibanez et al. (2016) also observed.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Statistical analysis with brief reviews.

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