

REPLY TO WILLIS:

Powerful predictions of biodiversity from ecological models and scaling laws

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Knowing the number of species (S) in an ecological system (i.e., species richness) is of primary importance to understanding biodiversity. Willis (1) states that the only “statistically admissible” way to estimate S is by modeling the number of species with $n = 1, 2, 3, \dots$ individuals, which is known as the frequency ratio method (2). Once this is accomplished, Willis (1) states that S can then be estimated via extrapolation through probabilistic models. However, extrapolations of richness estimates across orders of magnitude can be unsound (1, 3) and the data required by statistical estimators, such as frequency ratios, do not exist for large systems. For example, despite major sequencing efforts over the last decade, we only have minuscule fractions for even the most frequently sampled microbiomes (e.g., human gut).

Recently, we predicted S of large microbiomes using the lognormal model of biodiversity and published estimates of total abundance (N) and the abundance of the most abundant species (N_{max}) (3). The model also used the abundance of the rarest species (N_{min}), which we assumed to be 1 according to ref. 4. Because we used values of N and N_{max} that matched the scale of our predictions, our approach did not rely on extrapolation. Rather, the predictions are derived from an extension of one of ecology’s most successful models, the dynamics of which underpin a unifying theory of microbial biodiversity (5). Although our predictions of S were similar in magnitude to values expected

from the scaling of S with N of samples and entire microbiomes (3), Willis argues that our approach is not appropriate for predicting S (1).

Here, we address the concern of predictive power (1) by testing our approach in a global-scale system where S is known with a relatively high degree of certainty. Specifically, it is estimated that there are up to $4 \cdot 10^{11}$ birds on Earth belonging to $\sim 10,500$ species (6). The most abundant of these is the red-billed quelea ($N_{max} = 3.0 \cdot 10^9$) and the rarest is the New Caledonian owlet-nightjar ($N_{min} = 25$). Using these values of N_{max} and N_{min} , and assuming global avian abundance (N) of $3 \cdot 10^{11}$ individuals, the lognormal model predicts that Earth is home to 11,114 species of bird, a difference of 6% from observed global avian S . Our richness-abundance scaling relationship (3) based on bird datasets predicts a somewhat smaller number of 9,740 bird species, an 8% difference compared with observed global avian S . These predictions are reasonable given the few inputs needed and that confidence intervals for global estimates of abundance and diversity can span an order of magnitude, as discussed in ref. 3. If the example from avian systems is indicative of the overall success of our approach (3), then intersecting predictions from scaling relationships and biodiversity theory would indeed provide powerful predictions of biodiversity, especially when the data required by more sophisticated statistical estimators are not available.

- 1 Willis A (2016) Extrapolating abundance curves has no predictive power for estimating microbial biodiversity. *Proc Natl Acad Sci USA*, 10.1073/pnas.1608281113.
- 2 Willis A, Bunge J (2015) Estimating diversity via frequency ratios. *Biometrics* 71(4):1042–1049.
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- 4 Curtis TP, Sloan WT, Scannell JW (2002) Estimating prokaryotic diversity and its limits. *Proc Natl Acad Sci USA* 99(16):10494–10499.
- 5 Shoemaker WR, Locey KJ, Lennon JT (June 8, 2016) A unifying ecological theory of microbial biodiversity. *PeerJ Preprints* 4:e1450v3. Available at <https://peerj.com/preprints/1450/>.
- 6 Gaston KJ, Blackburn TM (1997) How many birds are there? *Biodivers Conserv* 6(4):615–625.

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The authors declare no conflict of interest.

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