

Box A

Additional Model Complexity Reduces Fit to Complex Food-Web Structure

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Cattin et al. (2004) assert that the simple “niche model” (N) of food-web structure (Williams and Martinez 2000) “fail[s] to adequately describe recent and high-quality data” and that, in contrast, their more complex version of the niche model called the “nested-hierarchy model” (NH) yields “food webs whose structure is very close to real data” and “better reflects the complexity” of ecosystems. However, we suggest that Cattin et al.’s results actually support a different conclusion: that N, the simpler model, more accurately predicts the structure of complex food webs than NH.

Cattin et al. compare both models against 14 network properties of 7 food webs (Williams and Martinez 2000). Degree distribution and two small-world properties that N predicts well (Camacho et al. 2002b; Williams et al. 2002; Dunne et al. 2004) were not included. Cattin et al. assert both models perform equally for three properties, N better predicts five properties, and NH better predicts six properties. Even without further analysis, it is already apparent that their claim that N fails

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to adequately describe recent food-web data is a mischaracterization, since there is little difference in this coarse-grained assessment of overall performance of the two models. A closer look shows that two of the six properties that NH predicts better were chosen to characterize related aspects of intervality, an assumption of N that was acknowledged to not match empirical data in the original study (Williams and Martinez 2000). In sum, the link distribution rules of N create webs that are interval, while the rules of NH (like the cascade model before it) do not. It has long been known that most large webs ($S > 30$) are not interval (Cohen and Palka 1990). Cattin et al. have clearly made contributions by quantifying intervality, creating a model that does not generate intervality, and including intervality in a quantitative comparison of models. However, by introducing two measures related to intervality, and by ignoring other common properties of food webs that N is known to fit well, Cattin et al. bias their results in a way that overemphasizes the non-intervality fit to data of NH.

Going beyond the coarse-grained assessment, a careful look at Cattin et al.'s results paint a picture that differs from their characterization of their results (table 1). Both models perform similarly for mean chain length. N better predicts the fraction of species at the top, intermediate, and basal trophic levels, looping, and the variability of food-chain length, while NH better predicts the fraction of omnivores. More importantly, N fits three properties, I, Lo, and Ch_{sd} , significantly better than NH and NH fails to fit any property significantly better than N ($P < 0.05$, Wilcoxon paired-sample test). N and NH are more frequently closer to the reference webs for 8 and 5 of the 14 properties, respectively, which become 8 and 4 of 13 properties, respectively, when 1 of the 2 intervality-related properties is excluded. Considering each individual prediction for properties of each reference web, N is closer to 47 observed properties while NH is closer to 43. Excluding Cy_4 (an intervality property that N predicts more poorly relative to NH), N and NH more closely predict 47 and 39 properties, respectively. Overall, this means that N performs slightly better than NH even when analyses are biased toward intervality measures. When only one intervality measure is considered, NH underperforms compared to N. The increased complexity of NH, while allowing a better fit to intervality measures, decreases its performance on other properties compared to the niche model.

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Further exploration should study more properties and employ the more rigorous statistical methodology (Williams and Martinez 2002; Dunne et al. 2004) that considers variability of stochastic network models in addition to the models' means discussed above. Based on the results of Cattin et al. (2004), it is difficult to judge the nested-hierarchy model's fit to particular food-web properties because the variability of the model is not specified, important information that has been provided for the niche and cascade models (Williams and Martinez 2000; Dunne et al. 2004). We note that although natural food webs are generally not interval, they are close enough to interval that the niche model is very successful in its overall characterization of food-web structure. While Cattin et al.'s new measures of intervality do highlight a limitation of the niche model, the empirical evidence presented by Cattin et al. (2004) suggests that the more complicated nested-hierarchy model provides a worse fit to empirical data, rather than a better fit, as was claimed.

TABLE 1 Summary of table 1 in Cattin et al. (2004) indicating a better fit of the niche (N) or nested-hierarchy (NH) model.

	Skipwith Pond	Little Rock Lake	Bridge Brook Lake	Chesa- peake Bay	Ythan Estuary	Coachella Desert	St. Martin Island
T	N	NH	N	NH	N	N	N
I*	N	NH	N	N	N	N	N
B	N	N	N	NH	NH	N	NH
Gen _{sd}	NH	NH	NH	N	N	N	N
Vul _{sd}	N	NH	N	NH	NH	NH	NH
M _{sim}	N	N	N	NH	NH	N	NH
Ch _{mean}	NH	x	NH	N	N	N	NH
Ch _{sd} *	N	x	N	N	N	N	N
Ch _{log}	NH	x	NH	NH	NH	N	NH
Lo*	N	x	N	NH	N	N	N
Can _{sp}	N	N	NH	NH	N	N	NH
O	NH	x	NH	NH	N	NH	N
Cy ₄	=	NH	=	=	NH	NH	NH
D _{diet}	NH	NH	N	NH	NH	NH	NH

Entries indicate whether the means (medians for Cy₄) of the niche (N) or nested-hierarchy (NH) models are closer or equally close (=) to the observed properties of the empirical food webs (x indicates properties not calculated due to computational limits). Three properties* were better fit by one model (N) at $P < 0.05$. Properties and food webs are fully described elsewhere (Williams and Martinez 2000, Cattin et al. 2004). Briefly, the properties are the fractions of trophic species that are omnivores (O), cannibals (Can_{sp}), or are found in loops (Lo) or at top (T), intermediate (I), or basal (B) trophic levels; the variability of generality (Gen_{sd}), vulnerability (Vul_{sd}), and food-chain length (Ch_{sd}); and the mean length (Ch_{mean}) and log number (Ch_{log}) of food chains. Cy₄ and D_{diet} indicate the degree to which food webs are "interval" in that each species' diet can be represented as an unbroken segment of a fixed sequence of species.