

## On nestedness in ecological networks

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### ABSTRACT

**Questions:** Are interaction patterns in species interaction networks different from what one expects by chance alone? In particular, are these networks nested – a pattern where resources taken by more specialized consumers form a proper subset of those taken by more generalized consumers?

**Organisms:** Fifty-nine and 42 networks of mutualistic and host–parasitoid interactions, respectively.

**Analytical methods:** For each network, the observed degree of nestedness is compared with the distribution of nestedness values derived from a collection of 1000 random networks. Those networks with nestedness values lower than 95% of all random values are considered ‘unusually nested’. The analysis considers two different metrics of nestedness and five different network randomization algorithms, each of which differs in the ecological assumptions imposed.

**Results:** Most ecological networks are unusually nested when compared with loosely constrained random networks. Comparisons with highly constrained networks temper these findings, but we still report a significant preponderance of nested networks (typically those with the most species).

**Conclusions:** Bascompte *et al.* (2003) previously showed most observed mutualistic networks to be unusually nested. Later work using more ecologically realistic randomization algorithms cast doubt on those results. Across the largest set of species interactions considered to date, we conclude that an unexpectedly large number of interaction networks are patterned in a non-random manner.

*Keywords:* ecological network, food web, host–parasitoid, mutualism, nestedness, null model.

### INTRODUCTION

Inspired by physical analogies, Atmar introduced the idea of *nestedness* to describe the incidence matrix of the presence of different species on different islands. A nested pattern is where the species composition on islands with fewer species is a proper subset of those on

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