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Research

Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order

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Ecologists have found many patterns in food-web structure. Some, like the constant connectance hypothesis, lack definitive explanatory mechanisms. In response, we investigated whether community assembly mechanisms could explain why trophic complexity consistently scales with species richness among ecosystems. We analyzed how food-web structure developed during the community assembly recorded in Simberloff and Wilson's classic biogeography experiment. Using their arthropod surveys, we constructed six time series of food-webs from pre- and post-defaunation censuses of six experimental islands, and synthesized trophic information for 250 species from the literature and expert sources. We found that the fraction of specialist species increased and the fraction of generalists decreased during food-web assembly. Directed connectance initially declined over time, despite an increase in species richness, but eventually leveled off as predicted by the constant connectance hypothesis of diversity-complexity scaling. The initial decline was explained by later colonization by trophic specialists, probably due to limited resource availability during early colonization. Late-colonizing super-generalists maintained constant connectance at later dates. This relationship between colonization success and trophic breadth helps explain food-web patterns and corroborates assertions that community assembly is systematically influenced by species' trophic breadths.

Community assembly research has formulated generalities or assembly rules to predict community structure (Diamond 1975, Belyea and Lancaster 1999, Keddy and Weiher 1999). However, explaining factors responsible for assembly patterns and community structure can be complicated by environmental factors that act simultaneously (Weiher and Keddy 1995), or obfuscated by the temporal changes of multiple factors. Stochastic processes have emerged as an alternative explanation for species associations and community assembly (Ulrich 2004), however others have recognized repeated patterns during community assembly which argues for further research into biotic mechanisms (Diamond 1975, Belyea and Lancaster 1999, Gotelli and McCabe 2002, Fukami 2004). Our research addresses the role of species' trophic breadth in community assembly.

Ecologists now look to community assembly processes and patterns to detect mechanisms responsible for complex community structure and effects (Keddy 1992, Weiher and Keddy 1995, Holt et al. 1999, Fukami 2004). With MacArthur and Wilson's (1967) first description of the Equilibrium theory of island biogeography, investigators began to examine community assembly mechanisms like colonization and extinction dynamics, and how such factors as island size and degree of isolation became important to community structure, including trophic structure. For example, Heatwole and Levins (1972) added trophic information to mangrove arthropod survey data (Simberloff and Wilson 1969) to demonstrate that trophic structure does return to an equilibrium-like state, or a state similar to one observed before a major disturbance (e.g. defaunation) (Heatwole and Levins 1972). However, Simberloff (1976) discounted any biotic effects during arthropod re-colonization, claiming that Heatwole and Levins' trophic classifications were too broad, and because randomly generated or "null" species collections also exhibited patterns of trophic equilibrium.

Though understanding constancy within multi-species communities constitutes a rather complex analysis, examining trophic structure during community assembly is a simpler approach which can suggest mechanisms that operate during the assembly process. For example, Holt et al. (1999) assert that a species' ability to colonize an island is likely constrained by the presence of its food resources. That is, predators show 'sequential dependence' on their prey. Holt et al. (1999) constructed a conditional incidence function model which predicted that specialist predators at high trophic levels were less likely to be present on small, species-poor islands than on large, species rich islands because their prey were less likely to be present on smaller islands. They also mentioned that opportunistic