

Modeling trophic dynamics in the CAP area

Christofer Bang¹, Stanley H. Faeth¹ & J. Marty Anderies²

¹School of Life Sciences, POB 874501, Arizona State University, Tempe AZ 85287-4501
²School of Human Evolution and Social Change, POB 872402, Arizona State University, Tempe AZ 85287

Summary

Water is usually the limiting resource for plant productivity in the Sonoran Desert. In the Central Arizona Phoenix area (CAP), urbanization generally leads to increased and more stable water availability, resulting in increased plant productivity. Several research projects are presently underway that explore how this changing water availability affects ecological communities, with emphasis on plant productivity, arthropod and bird species diversity, and composition. We explore these issues using simple mathematical models. These models will be later integrated and validated with data from CAP empirical studies. The models assume water as the limiting resource, thereby directly influencing plant carrying capacity. The simplest model is a tri-trophic system with a linear functional response on herbivore and predator level. The second model is similar, but with a type II functional response on the same levels. The third model consists of producer, herbivore and an omnivore level, the two last with type II functional response. All models are able to incorporate bird predation on both consumer levels. The models are compared using bifurcation analysis, focusing on plant carrying capacity, trophic biomass and predation by birds. The models give results that are easily testable in field experiments, and this work provides a good foundation for integrating empirical data from the CAP urban ecosystem.

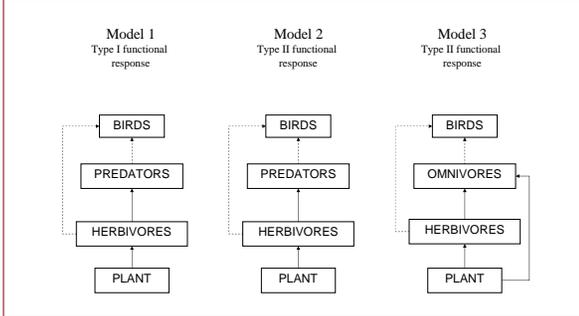


Figure 1: Three food webs explored by mathematical models. The arrows indicate the direction of energy. The dashed arrows indicate that bird predation is optional to simulate exclusion experiments.

Background

Our knowledge about control of food web structure in urban communities is limited, despite it being the most rapidly expanding type of ecosystem in the world. However, in Phoenix and other LTER sites we start to learn more about trophic dynamics in cities. In dry arid environments like the CAP area, habitat productivity increases with urbanization as a result of irrigated lawns and parks, and arthropod species diversity and composition are altered (Rango 2002, Shochat et al. 2004, Faeth et al. 2005, Cook and Faeth 2006, Shochat et al. 2006). Urbanization affects trophic structure partly by removing members of higher trophic levels (Cook and Faeth 2006), but the complex dynamics are not predictable based only on species composition (Shochat et al. 2006). Conflicting results from estimating the risk of predation of and on birds in urbanized areas raise a question of how important is top predation in regulating trophic dynamics (Shochat et al. 2006).

Mathematical models have been used for decades to explain relationships within populations, communities and trophic levels. Despite the many assumptions and simplifications they make, simple models can make it easier to understand complicated ecosystems (e.g. Hilborn and Mangel 1997, Murdoch et al. 2003). We believe that mathematical models can contribute to the understanding of complex trophic dynamics in urbanized communities. We compare three different tri-trophic model systems based on parameter values assumed to be appropriate for the CAP LTER area. Our goal is to integrate empirical data in the best fit model.

Parameter	Value	Meaning	Parameter	Value	Meaning
r	0.7	Intrinsic plant growth	b_0	0.2	Handling time by omnivore eating herbivores
a_1	1.667	Plants consumed per grams of herbivore	c_1	1	Herbivores produced per gram plant eaten
a_2	0.05	Herbivores consumed per grams of predators	c_2	1	Predators produced per grams herbivores eaten
a_3	1.667	Herbivore attack rate	c_3	1	Omnivores produced per grams plant eaten
a_4	0.05	Predator attack rate	c_4	1	Omnivores produced per grams herbivores eaten
a_5	0.005	Omnivore attack rate on plant	d_1	0.4	Minimum herbivore death rate
a_6	0.05	Omnivore attack rate on herbivore	d_2	0.005	Minimum predator death rate
h_1	0.2	Handling time by herbivore	d_3	0.005	Minimum omnivore death rate
h_2	10	Handling time by predator	D	0.005	Death rate caused by bird predation
h_3	10	Handling time by omnivore eating plant	K	0.7	Carrying capacity

$$\begin{aligned} \text{Model 1} & \left\{ \begin{aligned} \frac{dB}{dt} &= rB \left(1 - \frac{B}{K} \right) - \alpha_1 BH \\ \frac{dH}{dt} &= H(c_1 \alpha_1 B - \alpha_2 P - d_1 - D) \\ \frac{dP}{dt} &= P(c_2 \alpha_2 H - d_2 - D) \end{aligned} \right. \\ \text{Model 2} & \left\{ \begin{aligned} \frac{dB}{dt} &= rB \left(1 - \frac{B}{K} \right) - \frac{\alpha_1 BH}{1 + a_1 h_1 B} \\ \frac{dH}{dt} &= H \left(\frac{c_1 \alpha_1 B}{1 + a_1 h_1 B} - \frac{\alpha_2 P}{1 + a_2 h_2 H} - d_1 - D \right) \\ \frac{dP}{dt} &= P \left(\frac{c_2 \alpha_2 H}{1 + a_2 h_2 H} - d_2 - D \right) \end{aligned} \right. \\ \text{Model 3} & \left\{ \begin{aligned} \frac{dB}{dt} &= rB \left(1 - \frac{B}{K} \right) - \frac{\alpha_1 BH}{1 + a_1 h_1 B} - \frac{\alpha_3 BO}{1 + a_3 h_3 B} \\ \frac{dH}{dt} &= H \left(\frac{c_1 \alpha_1 B}{1 + a_1 h_1 B} - \frac{\alpha_2 O}{1 + a_2 h_2 H} - d_1 - D \right) \\ \frac{dO}{dt} &= O \left(\frac{c_3 \alpha_3 B}{1 + a_3 h_3 B} + \frac{c_4 \alpha_4 H}{1 + a_4 h_4 H} - d_3 - D \right) \end{aligned} \right. \end{aligned}$$

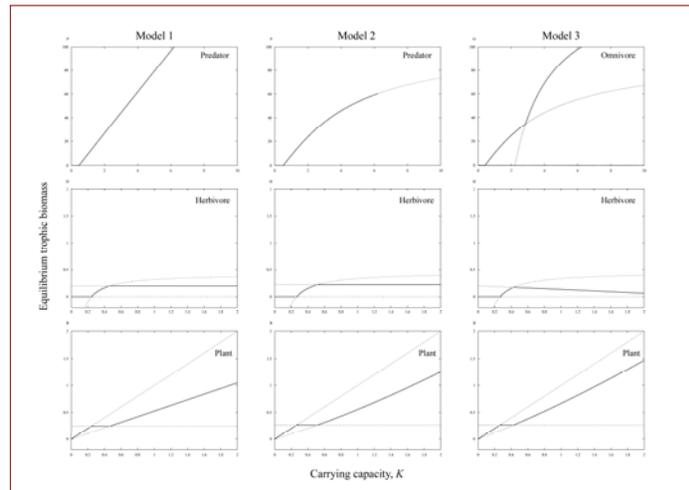


Figure 2: Solution branch diagrams of the three different models. Change in trophic biomass is on the second axis, while carrying capacity varies along the first axis. Solid lines indicate stable conditions, while the dashed lines indicate unstable conditions. Notice different scale on the top trophic level.

Results

All models were run until stable conditions were reached. At this equilibrium, we plotted the equilibrium biomass as a function of carrying capacity (Figure 2). This revealed several bifurcation points, which were analyzed with two parameters, bird predation and carrying capacity. Some of these analyses are shown in Figure 3.

Not surprisingly, the dynamics of all the models are relatively similar. Typically, low carrying capacity supports only the plant trophic level, and the plant biomass follows the growth in carrying capacity linearly. As the carrying capacity increases, the system supports more trophic levels. The plant biomass level stagnates when the herbivores enter the system, but then continues to increase when the carrying capacity is high enough to support either predators or omnivores.

The differences between the models are most easily detected at the top trophic level, where predator biomass increases linearly in Model 1, reaches a saturation level in Model 2, and the omnivores in Model 3 get a second bifurcation point. Notice however, that the top level response is only visible outside the realistic boundaries of the model. The other differences lie in the slopes of herbivore and plant biomass after the introduction of the third trophic level, where the plant biomass increases more rapidly and herbivore biomass decreases slowly in Model 3.

The two-parameter bifurcations show the boundaries for all three levels to co-exist, as carrying capacity and bird predation vary. The models show the same boundaries, with some variation in complexity.

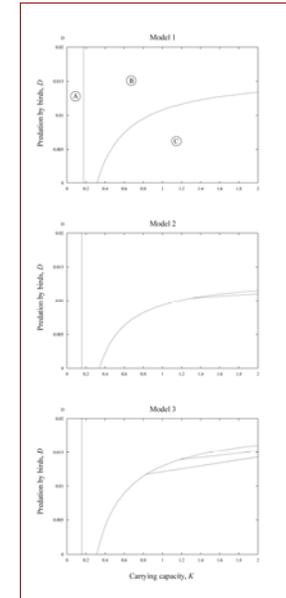


Figure 3: Two-parameter bifurcation diagrams of the three models. Three different areas, A, B and C are similar for all the models: A) Only the plant level can exist, B) plants and herbivores co-exist, and C) all three levels coexist.

Discussion

While the dynamics of these models have been studied by e.g. Rozenzweig (1973), Yodzis and Innes (1992), Abrams and Roth (1994), McCann and Yodzis (1995), we aim to extend this theoretical work and apply it to an actual system to learn more about what takes place in the real world. The work introduced here represents the first step in that direction, as we show that different simple models can predict almost identical dynamics within reasonable parameter boundaries. Varying the carrying capacity indirectly reflects different levels of water availability, which is typical for the CAP area. All the models give predictions that will be simple to measure empirically in controlled field experiments. For example, all the models show the same response to variation in carrying capacity, which may be reflected by different degrees of urbanization. At intermediate levels of water availability we may expect to find low levels of plant biomass, and almost no predators. In a natural system, arthropod predators have a higher motility and can move between plants. This is not considered in these models, and may explain individuals of predators on plants even if the water availability is low. In urban areas with high water availability, we may expect to find high abundances of predators. The models do not distinguish significantly between predators and omnivores, thus the complexity of Model 3 may be superfluous for later analyses.

The two-parameter bifurcations confirm that bird predation and carrying capacity limits the degree of co-existence in the analyzed system. Exclusion experiments along with different water treatments on plants are currently being carried out, and will tell us if these predictions are reliable. Experiments to determine functional responses for herbivores, arthropod predators and birds are being developed.

We have demonstrated that we can make sense of theoretical mathematical models in the context of urban ecology. Some or all of these three models can contribute greatly to further exploration of questions we may have about trophic dynamics, not only in the CAP area, but also other urban systems.

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