Excerpts from: **Impacts of Invasive Species on Food Webs: A Review of Empirical Data by P. David, E. Thebault, O. Anneville, P.-F. Duyck, E. Chapuis and N. Loeuille. 2017.** ***Advances in Ecological Research 56:*** **1-60** **https://doi.org/10.1016/bs.aecr.2016.10.001**

Text in Italics indicates material added to provide context or summary statements.

Over the past half century there has been increased concern about the impacts of biological invasions *including* invasions studies detailing spectacular impacts of invasions on whole ecosystems. The impacts are diverse and, depending on the variables considered, not necessarily negative. For example, while introduced filter-feeding species deplete planktonic communities, they improve water quality and create substrates that may favor benthic invertebrates and macrophytes. Invasive species must also exploit the resources available in the recipient ecosystem, and thus establish trophic interactions with
the resident species.

The term "invasive" is often used for nonnative species whose expansion can cause economic or environmental harm and/or has negative effects on public health. Although species invasions are often considered to be an anthropogenic disturbance linked to growing commercial transportation and *human impacts on* habitats, species distributions have always changed in time and colonization is also a natural component of ecological systems. When introduced, a species may persist only *if it is able to thrive under the environmental conditions in the new habitat.* This includes all the abiotic conditions that determine the range of physicochemical properties, often called the fundamental niche, that make a new habitat suitable for a species to complete its life cycle.

Networks to Study Impacts. Food webs are complex structures, which can be summarized as *diagrams with arrows (links) between nodes* with species or groups of species as nodes connected by trophic links ("is eaten by" or, sometimes, "is parasitized by"), possibly with some quantification of the intensity of transfer of energy or matter through these links. *For trophic cascades, the arrows are directional.* The idea of the species-centered approach is to study just the trophic links through which an invasive species A influences a resident species B, focusing on particular species known to have changed in frequency, abundance, or diet after invasion. Experimental approaches of this kind include comparisons of diet and abundance of focal species before and after an invasion into the community, and manipulative addition or depletion of populations in controlled environments or in situ.

A food-web-centered approach *to study invasive species impact*s is to compare food webs before and after invasion, or to compare the position of invasive species to that of residents in a food web. Research on ecological networks has underlined the role of some general characteristics of food webs such as the distribution of the interaction strength, diversity, or connectance, in controlling the productivity and stability of food webs. Sophisticated algorithms are now available to measure such variables and undertake cross-network comparisons.

Networks that have high ***nestedness (****a node's neighborhood is a subset of the neighborhood of nodes with more connections) or high* ***modularity*** *(network has multiple subsets or modules in which there are lots of connections within each module but sparse connections between modules) tend to be more resistant to invasions. Also called more stable networks. See Figure 1 below for examples.*

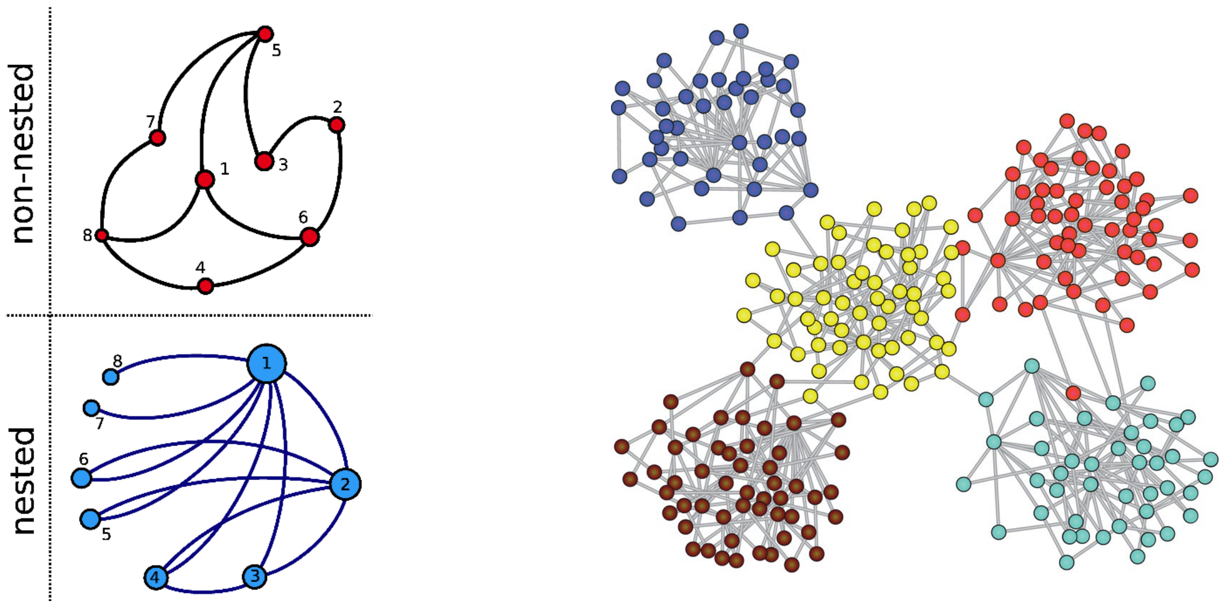

Figure 1. Left: An illustration of nestedness – in the bottom, node 2's neighborhood is nested within node 1's neighborhood (From: Mariana et al. 2019 https://doi.org/10.1016/j.physrep.2019.04.001). Right: Illustrates modularity; colors may indicate different attributes of the nodes (agents, specie) with each module from: Wikipedia.

Effects of Invaders. Introduced species inevitably create new trophic links because they eat and/or are eaten by resident species. Through these links, they affect the demography and abundance of other species and these effects may propagate at two or more steps of distance in the network (e.g. to the prey of their prey, the predator of their predator). Based on this simple premise, there is an abundant literature examining the impacts of an invasive species on one or more resident species. These studies examine local impacts on the resident food web. … A common theme in all these examples is that strong impacts occur because of "prey inexperience". The invader may be a formerly absent type of predator (i.e., tree-climbing snakes in Guam, predatory snails in Moorea) against which local species have no defense, or a large-bodied species that eats the previously top predators. Prey inexperience exists both in an ecological and in an evolutionary sense. … Invasive species seem to exploit their prey more rapidly and efficiently than natives and can reduce more severely native prey than do native predators. …. [Likely because] inefficient predators simply fail to invade. Invasive predators are often generalists: indeed, specialists have less chance to find exploitable prey outside their area of origin, and more often fail to invade.

Note that, effects of invasions can propagate through food webs and strongly modify food web structure. This occurs not only through species extinctions but also through changes in relative abundance of trophic levels

Trophic Cascades.

Top-down effects – this is when a species at or near the top of a food web cases changes in the species just below it when in turn has effects on the one below it and so on i.e., **has cascading effects**. Top-down impacts of an introduced predator may propagate several steps and have even been proposed as a method for lake management, called biomanipulation. The idea would be to increase piscivore *[those who eat fish]* fish, which will decrease planktivore [*eat plankton*] biomass, increase herbivore biomass, and decrease phytoplankton, resulting in higher water transparency. Planktivorous fish would be removed by intensive netting and the lakes then restocked with piscivorous fish. Although strong effects of piscivorous fish have been observed, the results from this method have been mixed and its success requires a particular set of conditions (shallow lake, macrophytes, etc.) and a deep understanding of local aquatic communities.

<u>Bottom-up effects</u> – this is when one or more species at the very base of the food web causes **cascading effects that move up the web**. Invasive species represent a new, often abundant, resource to local predators or parasites. As such, they are expected to have direct positive consequences on resident species at higher trophic levels, and the residents may change their diet to exploit them. For example, endangered endemic water snakes from Lake Erie seem to draw large benefit from the introduction of gobies, which now make up more than 90% of their diet. Another common example is the introduction of a new algal or plant species to an ecosystem that benefits some herbivorous resident species and perhaps other residents can consume it. The new resource may also attract other herbivorous species that may or may not be invasive but may be non-residents formerly.

Food Web Resistance to Invasion

Diversity is believed to often be positively related to robustness to invasion. Specifically, this is horizontal diversity in a food web i.e., more than one food resource (species) at a specific trophic level. Theory predicts that species rich communities are less invasible due to a more complete use of available resources by diverse species (niche packing), leaving less resources for potential invaders. Experiments on plant communities generally support this prediction. However, most studies have focused on the basal trophic level, and fewer on higher trophic levels. Discrepancies between experiments and observational studies may reflect correlations between diversity and other factors affecting invasions in natural systems. *Except for disturbances, many of the other factors that were once believed (or have been theorized) to provide resistance have not been definitely shown to do so*.

Effects of Invasions on Food Web Structure

Invasive species may simply modify a food web by adding a node to the trophic network but this could have subsequent effects on other nodes (species) including extinction or local extirpation and changes in the strength of interactions among species. Largest impacts are when the invader is an ecosystem engineer, that is a species that changes the environment such as beaver, carp, some corals, and others. Impacts are also great when the invader affects a keystone species, that is a species that has a disproportionate impact (relative to its abundance) on others such as starfish on rocky shores who keep mussels and barnacles in check.

Management to Minimize Invasion

Repeated <u>removal of the invaders</u> is however very common and if resources are available to continue this for a long time then this strategy is often used. If, however, the invader can be completely eradicated, it is important to try this strategy. It seems that whatever the aptness of the eradication plan, invasive species have traits that make it possible for them to adapt. Indeed, most eradication programs fail. Even on islands, and for invasive species that are quite large (e.g. cats), only a small minority of the eradication programs attempted have succeeded. Eradication programs may also interfere with the evolution of resident species. Resident species, where they do not go extinct, often adapt to the invasion. *The success may depend on how long the invader has been established* *and how much the food web has changed* Low diversity webs inherently attract invaders, and invasive removal itself is unlikely to solve the problem, as long as niche opportunities persist.

Diversity-oriented management is particularly important in the case of well defined, isolated systems, such as lakes or islands. In such instances, empty niches may exist, for example, abundant prey without predator, due to dispersal limitation. … "Vaccinating" such a system with an invader with mild effect that fills an empty niche, thus preventing subsequent invasions by higher impact invaders might be more suitable in the long run. On a related note, any success at removing an invasive may indicate that the removed invader was not very high on the fast reproduction/high competitive ability scale. Its removal may open the door for faster or more competitive invaders that may not be so easily removed. … From the observed importance of top-down controls and indirect competitive effects, it can be inferred that maintaining healthy populations of top predators as well as omnivore predators is an important management target as they reduce the probability of invasion. … More generally, in order to avoid or limit the impacts of invasions, functional diversity may matter more than species diversity. Indeed, if an invader creates a new functional group within the receiving network, this invasion will by definition modify the overall functioning of the web. … if it were possible to *maintain ecological networks that contain a large set of functions* (i.e., a high level of functional diversity), any incomer would likely be redundant with species already present. This would reduce the probability that the impact of the invasive species is large. *Removing stressors that enhance invasibility is extremely important.*

Managing bottom-up and down-down control. Species competition for resources is the dominant force determining the distribution of biomass within networks with bottom-up control. Increasing resources allows for a general increase in biomass and food chain length. As a consequence, increased nutrient or energy availability facilitates the maintenance of invasive predators; and, for management, it may be important to focus on the interaction between biological invasions and nutrient imbalance (e.g., eutrophication) rather than on invasion per se. In such instances, the long-term solution may be to reduce the primary production in the system. Another option might be to allow another invasive predator with mild effect to occupy the niche. … Much of biological control uses local or introduced predators to fight the invasion of a species in a given ecosystem. Much of this literature is devoted to the management of pests in agroecosystems, but in several instances, biological control has been used in natural ecosystems to limit the growth of an invasive species. As biological control requires the introduction of a predator to limit the focal species, decisions for which predator to use have to be made. *But traits of the predators have to be carefully considered and there are many cases where unintended consequences have been serious. This is also the case for efforts in which attempts to reduce basal food resources involve the introduction of a herbivore.*