Species Interactions and Biodiversity Conservation

Introduction

In the last couple of lectures we've begun to explore some of the ways in which a single-species focus on conservation is incomplete. First, we pointed out that the vast number of species threatened with extinction and our vast ignorance about most of them means that we can only hope to save many of them if we can save the systems on which they depend. "Hotsposts" may or may not be the best way to identify those larger systems, but clearly we're going to have to have some means of protecting many species at once if we are to prevent the extinction of the vast majority of species. Kareiva and Marvier [5] point out that there are several other reasons for conservationists to be concerned about systems, not just individual species:

- Relatively natural, undisturbed systems provide a benchmark against which we can measure human impacts.
- Biotic systems provide a variety of services necessary for human health and welfare. Part of our concern about the loss of biological diversity stems from the potential impacts of losing those services.
- Wild places inspire the human spirit.

We're going to continue in this vein for several more weeks. Today we'll step back a bit from the ecosystem- or landscape-scale perspective associated with the diversity-stability debate and focus on the many ways in which species interactions are vital to conserving the structure and function of ecological systems.

Keystone species

A *keystone species* is one whose impact on its community or ecosystem is disproportionately large relative to its abundance [8]. The classic example is a starfish (*Pisaster ochraceus*) in

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the rocky intertidal of the Pacific Northwest:

- *Pisaster ochraceus* is an efficient predator of the common mussel, *Mytilus californicus*.
- It reduces abundance of *M. californicus*, allowing other macroinvertebrates to persist.
- Experimental removal of *P. ochraceus* results in near total dominance of intertidal by *Mytilus* to the exclusion of other intertidal macroinvertebrates.
- *Pisaster* present $\Longrightarrow$ diverse intertidal community
- *Pisaster* absent $\Longrightarrow$ depauperate intertidal community dominated by *M. californicus*.

Kangaroo rats (members of the genus *Dipodymys*) play a similar role in the Chihuahuan desert of southeastern Arizona [2].

- Kangaroo rats are the largest of the seed-eating desert rodents. James Brown and collaborators excluded them from experimental plots starting in 1977.
- From 1977–1995 energy use by rodents on plots without kangaroo rats averaged only 14% of the energy use by kangaroo rats on matched control plots.
- The density of small seed-eating rodents averaged almost two times higher on plots without kangaroo rats.
- In 1996 a pocket mouse, *Chaetodipus baileyi*, colonized the plots, and by 1999 energy use increased to 80% of the energy use by kangaroo rats.

If we're going to focus on conserving whole systems, it might make sense to begin with a focus on keystone species. After all, ensuring that they persist and, more importantly, that their ecological role persists would, it seems, guarantee that the system as a whole will persist relatively intact. Although the idea of keystone species is intuitively appealing, it has been much criticized in the ecological literature.[1] Why?

- Even a disproportionately large impact may be small if the species is very rare.
- How "disproportionately large" is disproportionate enough for something to be considered a keystone?

[1] See [7] for a particularly thorough review of the keystone concept as it applies to *Pisaster* and *Mytilus*.

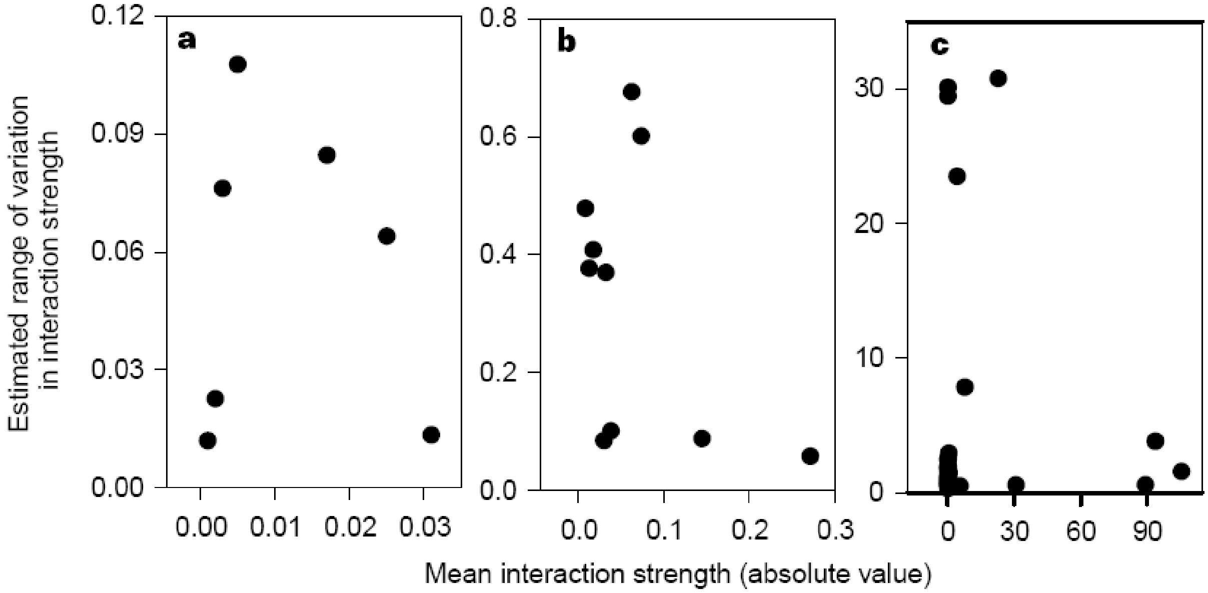

Figure 1: Interaction strength *versus* range of interaction strength for (a) six rock intertidal grazers on kelp, (b) praying mantids feeding on arthropods, and (c) six predators on six benthic invertebrates in the Ythan river estuary, Scotland (from [1]).

- More importantly, investigators tend to identify keystone species as those that have a large and consistent impact on the dynamics of other species. "Large" makes sense, but does "consistent"?
  - Berlow [1] points out that species effects identified as "weak" are often extremely variable among replicates, with variation on the order of the strongest mean effects observed (Figure 1).
    1. It is important to distinguish among effects that are strong, but variable (in magnitude and direction), those that are consistently weak, and those that are consistently strong (and in a single direction). Strong effects that differ in direction from one circumstance to the next might, on average, appear to have no effect.
    2. By identifying species with "strong" effects, we may simply be identifying those that have low variance.
  - He goes on to illustrate how important "weak," but variable, interactions might be in a simple experimental system.

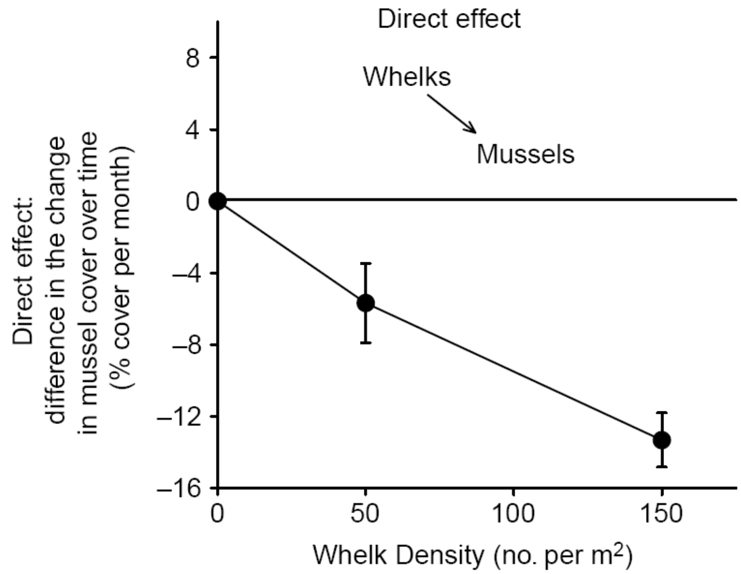

Figure 2: Direct effect of whelks (*Nucella emarginata*) on mussels (*Mytilus californicua*) on the rocky, central coast of Oregon (from [1]).

∗ Whelks (*Nucella emarginata* and *N. canaliculata*) prey on our old friend *Mytilus californicus*. By manipulating the density of whelks in three experimental treatments (0, 50, and 150 per square meter), he showed that the *Mytilus* declines linearly with increasing density of *Nucella* (Figure 2). In this experiment, Berlow transplanted mussels to experimental plots and used enclosures to manipulate whelk density.

∗ In a second experiment, Berlow manipulated whelk density (none, low, and high) and the abundance of an alternative prey (acorn barnacles, *Balanus glandula*). The experimental plots were scraped bare, mussels and barnacles were allowed to colonize, barnacles were then removed monthly from half of the plots, and whelk density was maintained with enclosures. In the barnacle removal plots, both low- and high-density predation have a negative effect on mussels (Figure 3a,b,c). Unlike the transplant experiment above, the strong negative effect of whelks is seen even at low density in the absence of barnacles. Mussel colonization is low in the absence of barnacles, so whelks essentially eliminated the few that managed to settle.
When barnacles are present, mussel recruitment is enhanced. So not only

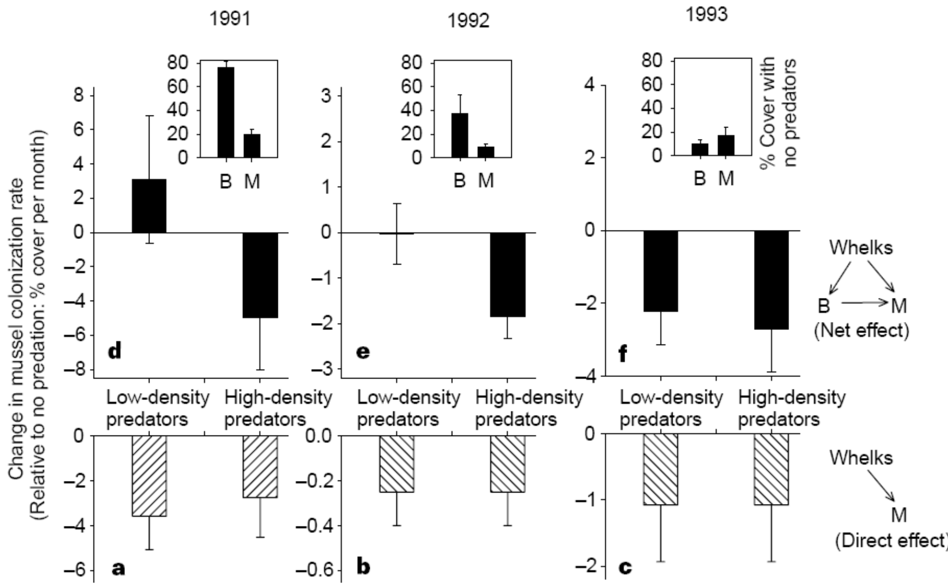

Figure 3: Effects of whelks on mussel density when newly settled barnacles are removed monthly (a-c) or allowed to remain (d-f) (from [1].)

do barnacles provide an alternate food source for whelks, they increase the chancels that mussels will become established. When whelks are abundant, however, they reduce the abundance of mussels regardless of the barnacle density — not too surprising. But when whelks are rare, they enhance mussel abundance when barnacles are very common, have no detectable effect when barnacles are only moderately common, and decrease mussel abundance when barnacles are uncommon (Figure 3d,e,f).

∗ Clearly whelks have an important influence on the abundance of mussels. It's just that the influence they have depends on the environmental context, i.e., the abundance of mussels. And yet, if we simply took the average effect across years, we'd be tempted to conclude that whelks don't have much effect.

McCann et al. [6] also point out that it may be the *weak* trophic interactions that are most important in stabilizing food webs. Weak links dampen the oscillations in population size characteristically associated with resource-consumer dynamics, which tends to keep both resource population sizes and consumer population sizes bounded away from zero and decreasing the chance they will become extinct. Thus, strong links may have the greatest influence on overall community dynamics and structure, but it's the abundance of weak links that allow communities to persist.

In spite of its limitations, the keystone species concept has some usefulness in the same way that elasticity coefficients in a Leslie or Lefkovitch matrix are useful. It directs attention to those aspects of the system where management efforts are likely to have the greatest impact. Of course, identifying those aspects is not an easy task.

Evolutionary consequences of species interactions

John Thompson [10] argues that species interactions must be an integral part of conservation efforts directed at maintaining communities that will be viable. Four properties of species interactions seem particularly important.

1. *Many species are composed of populations specialized to different interactions.* Even if the same two species are interacting across a broad geographical range, the details of that interaction (e.g., its genetic basis) may differ from population to population. Thus, minimizing the extinction of populations within species is important (compare [4, 3]). Moreover, long-term persistence of the interaction may depend on time lags and asynchronous responses in different populations, as appears to be the case in some gene-for-gene interactions between plants and fungal pathogens.

2. *Some interactions can evolve rapidly under changed ecological conditions.* Host-pathogen interactions may evolve particularly rapidly,[2] but we also saw an example with the checkerspot butterfly in the Sierra Nevada. Populations occupying clear-cut meadows, which were created in the late 1960s, switched their food plant preferences from *Pedicularis semibarbata* and *Castilleja disticha* to *Collinsia torreyi*. The Hawaiian i'iwi provides a particularly striking example [9].

    - The i'iwi has a long, curved bill, presumably to match the long, curved corollas of lobeliod flowers that used to be common in the Hawaiian understory.
    - They now feed predominantly on ohia (*Metrosideros polymorpha*, Myrtaceae), which has relatively flat open flowers.
    - The upper mandible of contemporary i'iwis appears to be detectably shorter than that of i'iwis collected in the late 19th century.

[2] The myxoma virus introduced to control rabbit populations in Australia is an example you should learn about if you don't already know it.

3. *There is no inherent directionality in how interactions will evolve.* Because the genetic basis of interactions may differ from one population to the next and because the ecological details of the interaction are likely to differ from one population to the next, natural selection is likely to produce different results in populations that evolve independently of one another. Habitat fragmentation may contribute to evolutionary divergence among populations that were once similarly adapted.

4. *The impacts of interaction often depend on the density of the interactors.* The more frequently individuals encounter one another, the more intense their interactions. Pathogens tend to evolve greater virulence in dense populations with high rates of horizontal transmission, for example, than in sparse populations with high rates of vertical transmission.

As Thompson argues, these effects reinforce the importance of conserving large, relatively undisturbed tracts of land. Only over these broad expanses can we study and understand how species interactions evolve in relatively unmanipulated conditions. Only by understanding how they evolve in those circumstances can we discover how to manage them more effectively in human-dominated landscapes.

References

[1] E. L. Berlow. Strong effects of weak interactions in ecological communities. *Nature*, 398:330–334, 1999.

[2] S. K. Morgan Ernest and J. H. Brown. Delayed compensation for missing keystone species by colonization. *Science*, 292:101–104, 2001.

[3] R. J. Hobbs and H. A. Mooney. Broadening the extinction debate: population deletions and additions in California and western Australia. *Conservation Biology*, 12:271–283, 1998.

[4] J. B. Hughes, G. C. Daily, and P. R. Ehrlich. Population diversity: its extent and extinction. *Science*, 278:689–692, 1997.

[5] Peter Kareiva and Michelle Marvier. Conserving biodiversity coldspots: recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. *American Scientist*, 91:344–351, 2003.

[6] K. McCann, A. Hastings, and G. R. Huxel. Weak trophic interactions and the balance of nature. *Nature*, 395:794–798, 1998.

[7] B. A. Menge, E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, 64:249–286, 1994.

[8] R. T. Paine. A note on trophic complexity and community stability. *American Naturalist*, 103:91–93, 1969.

[9] T. B. Smith, L. A. Freed, J. K. Lepson, and J. H. Carothers. Evolutionary consequences of extinctions in populations of a Hawaiian honeycreeper. *Conservation Biology*, 9:107–113, 1995.

[10] John N. Thompson. Evolutionary ecology and the conservation of biodiversity. *Trends in Ecology & Evolution*, 11:300–303, 1996.

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