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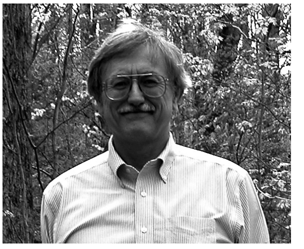
IJEE SOAPBOX:
CULTURAL AMNESIA IN THE ECOLOGICAL SCIENCES



ROBERT D. HOLT
Department of Zoology,
University of Florida, Gainesville, Florida 32611-8525, USA

PREAMBLE

> "Whatever we say, it is bound to be dependent on what has been said before" (James, 2007, p. xxv).

With the explosion of knowledge all around us, it is becoming increasingly difficult for any of us in science to keep up with the latest ideas and findings of our disciplines. Maybe more importantly, the incessant pressure of dealing with the "new" at times threatens to submerge any appreciation we may have of the broader historical intellectual context from which current concerns in our disciplines emerge. This issue is aggravated by the fact that intellectual history is seldom a straight run across a smooth and obvious landscape. Rather, it is more like a braided tangle of trails, with many intersecting and merging paths and byways.

I was reminded of this dilemma of the modern condition recently when preparing a lecture for an advanced course in Fribourg, Switzerland, focused on the theme of metacommunities. The organizer, Professor Louis Bersier, asked me to kick off the course with a lecture on the historical context of metacommunity ecology. In putting this lecture together, I came across some little-known quotes from one of the founding figures of ecology, Charles Elton, which resonated with the concerns of this course, more broadly with the increasing emphasis on spatial aspects of ecology (Levin, 1993), and to an uncanny extent, some themes in my own work.

So as not to lose some readers, I should start with a few definitions. If a "community" is "a collection of species found in a particular place" (Morin, 1999), a "metacommunity" is "a set of local communities linked by dispersal of multiple potentially interacting species" (Wilson, 1992). The metacommunity perspective is increasingly important in many different theoretical approaches in ecology, from neutral models (Hubbell, 2001) to niche- and patch-centered perspectives on community organization (Leibold et al.,

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E-mail: rdholt@zoo.ufl.edu

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Robert D. Holt is our first invited ***IJEE Soapbox*** essayist. Bob is Professor of Zoology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

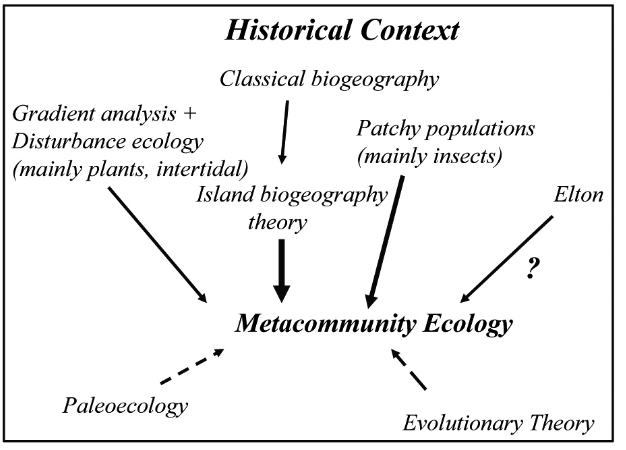

Fig. 1. A schematic depiction of the distinct lines of thought that converged into the contemporary metacommunity perspective.

2004; Holyoak et al., 2005). In this essay, I will first attempt to lay out what seem to me to be some of the main strands of thought that laid a historical foundation for metacommunity theory, then focus on a largely forgotten contribution by Charles Elton.

Figure 1 shows schematically my conception of the intellectual antecedents and parallel developments that fed into the current metacommunity framework. I will not walk through each of these in the detail they deserve, but mention a few high points.

The most obvious intellectual ancestor to metacommunity ecology is the theory of island biogeography (MacArthur and Wilson, 1967), mediated through metapopulation biology. The term "metapopulation" was coined by Richard Levins (1969). Levins was a close friend of MacArthur and carried out island studies of his own (e.g., Heatwole and Levins, 1973). MacArthur and Wilson (1967) themselves in their opening pages noted that in continental settings, many species inhabit naturally patchy habitats (e.g., fallen logs, caves, bogs), and that with increasing habitat destruction and fragmentation, insularity may become the norm, not the exception, in the natural world. In his 1970 paper, "Extinction" (Levins, 1970), Levins states that "a species can be regarded as a population of populations."

But the metapopulation concept crystallized in part because Levins was concerned with other important directions in ecology and evolution, such as the debate swirling around group selection and population structure in evolutionary theory (Levins, 1970). Evolutionary biology in the 1960s was in a state of ferment, concerned with topics such as altruism that seemed difficult to explain by the usual mechanisms of natural selection (Dugatkin, 2006). Sewall Wright (1945) early on argued that spatial structure, with localized selection and limited dispersal, could lead to altruism. Levins argued that extinction could in some circumstances lead to group selection, which might favor traits that reduce extinction rates, even if they impose a cost on individuals. Even in the absence of extinction, spatial structure can modify the action of natural selection, a theme taken up and elaborated by David Sloan Wilson (1975, 1980), among many others (e.g., van Ballegooijen and Boerlijst, 2004). Wilson (1992) later coined the term "metacommunity", and argued that complex interspecific interactions create a rich opportunity for heterogeneity in selection pressures and the emergence of *de facto* "coalitions" of species, even in homogeneous landscapes.

The rhetorical warfare over group selection has largely died out in recent years. There is now widespread agreement that what really matters is that population structure and dispersal can profoundly affect the direction of selection in heterogeneous landscapes. Indeed, an exciting direction in current metacommunity work is fusing evolutionary processes into metacommunity dynamics (e.g., Urban and Skelly, 2006).

Levins (1970) also noted that extinction is "fundamental to any theory of pest control". A robust school of insect ecology had long emphasized the patchy nature of many insect species. For instance, Andrewartha and Birch (1984) updated their 1954 monograph titled *The Distribution and Abundance of Animals* and wrote "The natural population comprises many local populations … the local population is the unit in which individuals interact with one another… most local populations are doomed to extinction." It is interesting that Andrewartha and Birch do not use the word "metapopulation". Indeed, they only cite MacArthur and Wilson (1967) once, to sniffingly state that "nature seems to abhor these simple models" (pp. 304–305). Nicholson and Bailey (1935) had much earlier suggested that natural host-parasitoid interactions persist, despite the violent oscillations predicted by their models, because "the interacting animals exist in numerous disconnected small groups, within each of which interspecific oscillations follows its course independently of that in the other groups." Huffaker's celebrated orange experiments with predatory mites chasing prey mites (e.g., Huffaker et al., 1963) provided an empirical demonstration that patchiness could promote persistence. This theme over time has developed into a rich body of spatially explicit population theory (nicely reviewed in Hassell, 2000). So the metapopulation perspective fed naturally into the issue of understanding the persistence of strong interspecific interactions, which is a core question in community ecology.

Another significant current of thought leading to metacommunity ecology came from studies of sessile organisms such as plants and intertidal invertebrates, where competition for space tends to foster competitive dominance and exclusion. Understanding regional coexistence requires analysis of species sorting along environmental gradients and the impact of disturbance regimes (Levin and Paine, 1974; Whittaker and Levin, 1977). Whittaker and Levin (1977) state that "in a sense, the fugitive is the general, and not the special case, for most species are to some degree locally ephemeral." This is a robust statement of the "patch dynamics" perspective on metacommunities (Leibold et al., 2004). Other intellectual currents doubtless facilitated the emergence of the metacommunity perspective, in particular the paleoecological insight that few local communities hang together as tight assemblages over long time scales. Viewed over a "sufficiently" long time scale, all members of a local community arrived via dispersal from somewhere else. So, the structure of local communities can reflect dispersal limitation as well as the imprint of processes that operate at large spatial scales (e.g., speciation) (Ricklefs and Schluter, 1993). The assemblage of species found together today in local communities may not even have been in the same general region at times in the past (Graham, 1986; though see McGill et al., 2005 for a contrary view).

Back to Charles Elton. Did Elton have any intellectual input into the metacommunity perspective? Leibold and Wootton do note in their introduction to the reprinted issue (2000) of Elton's classic 1927 volume *Animal Ecology* that Elton in Chapter III discussed succession as a kind of patch mosaic, with different patches at different stages in a landscape. And then Chapter X on dispersal (which is largely filled with anecdotes) further speaks to an early concern with the spatial connection of habitats and communities. Most ecologists know about Elton's book (Elton, 1958) *The Ecology of Invasions by Animals and Plants*, which can be viewed as the founding document of invasion biology, and which moreover laid out arguments related to general ecological issues, such as the relationship between diversity and stability or invisibility. So in a very general sense, the answer to my question may be "yes".

But I suspect few ecologists at present are familiar with Elton's later book, *The Pattern of Animal Communities* (Elton, 1966), a 432-page-long tome full of detailed descriptions of his observations during a two-decade ecological survey of Wytham Woods. This is the kind of book that few people, at least scientists, read—much less write—these days. I had never looked at it myself, even though I had picked up a copy at a second-hand bookstore a few years ago. I was curious to see if Elton continued any of these spatial themes evident in his earlier works into his later years, so as I put my lecture for Fribourg together, I thumbed through the tome. The first thing I noticed was that the frontispiece of the book is an aerial photo, showing a complex mosaic of habitat patches, which hints at a spatial perspective. Then, the final chapter of the book, titled "The Whole Pattern" is organized around a series of "propositions" (in effect, inductive generalizations from Elton's personal experience in Wytham Woods). These turn out to contain many indications of Elton's abiding concern with spatial processes.

His very first such "proposition" is that "The pyramid of numbers, really a pyramid of consumer layers, is matched by… the inverse pyramid of habitat." Essentially, the spatial range defining populations increases with trophic rank. I, myself, (Holt, 1996) in a piece on the spatial dimensions of food web ecology, had reflected on how communities are comprised of organisms that experience the world at vastly different spatial scales, and Holt and Hoopes (2005) (modifying fig. 29.1 in Holt 1996) schematically indicated how these might vary with trophic rank with a figure, as shown in Fig. 2. Figure 2A shows a standard non-spatial rendition of a simple food web, with trophic linkages between species indicated by lines. Figures 2B–D place this food web in space, and display three different kinds of communities that differ in the spatial scale pertaining to different trophic ranks. In Fig. 2B, the square at the base is the spatial scale of a study area, and this area contains three producer species confined to different habitats, with two layers of consumers. The ovals in Fig. 2B indicate increasing mobility with increasing trophic rank. So, I had just reinvented for myself Elton's notion of an "inverse pyramid of habitat" as a function of trophic rank!

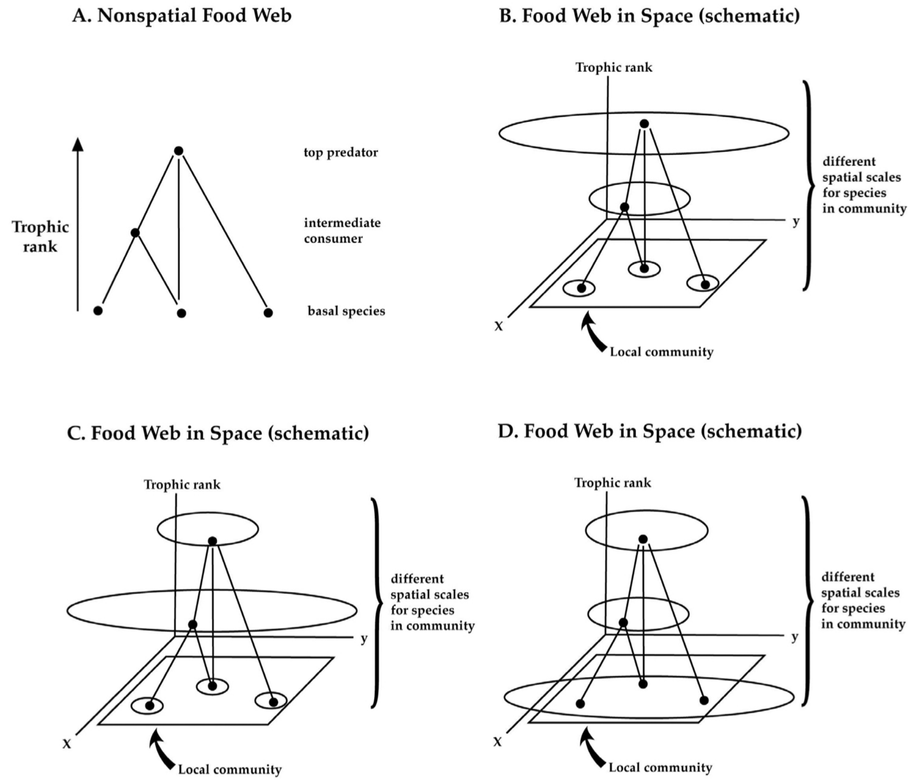

Fig. 2. Schematic depiction of how the spatial scale describing population processes varies with trophic rank (from Holt and Hoopes, 2005). A. Typical non-spatial food web. B. Spatial scale increase with trophic rank (the "inverse habitat pyramid" suggested by Elton). C. Spatial scale is greatest at intermediate trophic ranks. This may describe systems where top predators are resident, but intermediate prey are migratory (e.g., lions and wildebeest in the Serengeti). D. The spatial scale is greatest at the low trophic level. This could describe intertidal systems, where planktonic fluxes determined by large-scale oceanographic processes feed sessile filter-feeders like mussels and barnacles, which in turn sustain more mobile consumers like starfish.

Other humbling thoughts followed, as I read through others of Elton's propositions. Combining elements of Propositions 8 and 9 leads to "no habitat component with its animal community is a closed system… they are constantly passed by population movement… every community unit is partly interlocked with others, not necessarily its nearest neighbors". Likewise, for Propositions 13 and 14, we read: "the ecological machinery of any community, or any habitat component… is kept going by the movements of animals… These continual movements may have a considerable effect on the efficiency of any community."

In 1997, Several friends and I published a lengthy review (Polis et al., 1997) on the integration of landscape and food web ecology. In our Introduction to that paper, we noted that "even local communities that appear discrete are open and connected in myriad ways to outside influences. The basic components of food webs… all cross spatial boundaries. Yet until recently, ecologists neglected to ask how spatial pattern and processes affect web structure and dynamics." We focused on "spatial flows among habitats as a key force in local web dynamics [and synthesized] a large literature documenting the ubiquitous movement of material and organisms among habitats". Elton, in his own way, seems to have presaged these thoughts, some forty years earlier.

Charles Elton may not have directly influenced any of the individuals noted above who directly contributed to the recent emergence of metacommunity themes in ecology, and I know for a fact that I was not directly influenced by reading his 1966 book. But at the very least, his own synthesis of a lifetime of careful natural history observations led to a perspective that is philosophically sympathetic with metacommunity ideas. I now wish I had looked at this work much earlier, to have given it its due.

I suspect this kind of story could be repeated with some frequency across our science. John Lawton and I, in a review of shared predation effects (Holt and Lawton, 1994), were somewhat disconcerted to discover that numerous authors had independently come up with parallel sets of ideas, and so we titled a section of our paper "Rediscovering the wheel". This is not an entirely bad thing, since convergence provides evidence for a kind of robustness in certain ways of thinking about complex ecological systems. It nonetheless does indicate a kind of looseness in the conceptual structure of our discipline, as reflected in particular in the enormous heterogeneity one finds in the training of people who call themselves "ecologists".

To return to the initial concern I expressed above, it may be impossible to maintain a sense of historical continuity and context in the face of the deluge of information that besieges us. But I think that it is important to try, because it allows us to embed our own particular studies in much larger currents of thought, which in turn may help us carry out work that transcends particular systems and speaks to much broader issues. And an appreciation of the efforts of past thinkers may even provide an appropriate modicum of humility. I end with a quote from Ludwig Wittgenstein (1953) that seems pertinent to this basic idea—"*all progress looks bigger than it is*."

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