An Overview of Ecological and Evolutionary Research on Disease in Natural Systems: An Annotated Reference List

Helen M. Alexander[1]

Background

The Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry (July 31-August 5, 2011) included a session on "Ecology and Evolutionary Biology of Resistance and Tolerance, Natural Systems." Within this session, I gave a talk entitled "An overview of ecological and evolutionary research on disease in 'natural' systems" that reviewed research on disease that is primarily in ecology and evolutionary biology journals (as opposed to forestry and plant pathology journals). Several people requested that I provide details of the references listed in that talk, and this annotated reference list is the result.

To reduce the length of this document, I note that several of the references in my talk were cited in a recent review article (Alexander 2010). Thus, instead of writing the full reference, I have simply listed "PD" next to the names of the authors for citations included in this review.

Overview and a Brief Timeline of Studies of Disease by Ecologists/Evolutionary Biologists

Most work on plant disease has been done by plant pathologists working in agriculture or forestry. In contrast, ecologists and evolutionary biologists working in less applied settings have historically largely ignored disease (but see Haldane 1949, PD). Harper, a well-established British ecologist, was one of the first to focus attention on disease when he included a chapter on pathogens in his classic book on plant population biology (Harper 1977 PD). The 1970s and 1980s were also a time when many researchers compared disease levels in crops and wild plants (e.g., Thresh 1981 PD). Burdon's (1987 PD) book on the interactions between pathogens and the ecology and genetics of plant populations stimulated considerable work. Since the 1980s, studies of plant disease by ecologists and evolutionary biologists in natural/unmanaged systems have become increasingly common.

The reference to plant disease in "natural" systems is potentially confusing. Realistically, there are no plant communities on earth that are not in some way impacted by humans and, of course, indigenous people have always interacted with plant communities. It is useful, however, to recognize that there is a continuum of landscapes from "managed" on one hand to "unmanaged/natural" on the other hand. An example of the former is row crops in western agriculture where there is reduced plant species diversity, high uniformity within plant populations (low genetic diversity, even-age age structure, regular plant spacing), and a lack of linkage in plant dynamics from year to year (i.e., plants growing at a site are not the result of seeds produced at the site in the previous year). In contrast, unmanaged systems typically have higher species diversity, more complex structure within a plant population, and a linkage in plant dynamics from year to year. Unmanaged systems can include apparently pristine settings, but also apply equally well to disturbed environments such as roadside weed communities.

[1] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045. halexander@ku.edu.

Overview of Talk: Studies of Disease in Relation to Plant Population Dynamics, Evolutionary Interactions Between Plants and Pathogens, Plant Community Composition, and Global Change and Ecosystem Function

Within these areas there are biases, with more research on the effects of pathogens on plants than vice versa and more emphasis on fungal pathogens than other types of pathogens.

Plant Population Dynamics

Research in this area examines how pathogen populations affect the size and spatial distribution of plant populations. A variety of approaches are used; excellent examples include experimental approaches (such as pesticide applications; Roy et al. 2011) and long-term surveys of plant and pathogen numbers (research on anther-smut disease; Antonovics 2004 PD, Antonovics et al. 1998 PD). Both of these examples also have a strong modeling component. Other examples of research in disease/plant population dynamics include:

a. Effects of disease on plant age/stage composition (Davelos and Jarosz 2004).

b. Effects of pathogens on seed populations and seed bank persistence (Beckstead et al. 2010, Eviner and Chapin 2003 PD, Meyer et al. 2007 PD).

c. Density-dependent effects of disease and the degree to which plants and plant populations can compensate for disease losses (Alexander and Mihail 2000 PD, Lively et al. 1995 PD).

d. Examining plant-pathogen interactions on landscape spatial scales; effects on plant metapopulation dynamics (Antonovics 1999 PD, Antonovics 2004 PD, Antonovics et al. 1994 PD).

e. Temporal and spatial variation in disease (19–year-study over large number of Swedish islands; Smith et al. 2011).

Other examples include: Alexander et al. 2007 PD, Antonovics 2004 PD, Antonovics et al. 1994 PD, Augspurger and Kelly 1984 PD, Carlsson et al. 1990, Carlsson-Granér and Thrall 2002 PD, Koslow and Clay 2010, Laine and Hanski 2006, Reinhart and Clay 2009, Smith et al. 2003 PD, Thrall et al. 2001 PD.

Evolutionary Interactions Between Plants and Pathogens: Genetic Variation in Resistance, Virulence, and Tolerance

Studies of genetic interactions between plants and pathogens have a long history, and were the primary focus of talks by B. Roy and J. Burdon at this conference. The references below provide examples of this kind of work: Antonovics et al. 2010, Barrett et al. 2007 PD, Barrett et al. 2009, Burdon and Thrall 2009, Burdon et al. 2002 PD, Carr et al. 2003, Carr et al. 2006, Dinoor 1977 PD, Gilbert and Parker 2010, Harry and Clarke 1986, Inglese and Paul 2006 PD, Jarosz and Burdon 1991, Koslow and Clay 2007, Laine 2004 PD, Laine et al. 2011, Roy 1993 PD, Roy and Bierzychudek 1993, Roy and Kirchner 2000 PD, Roy et al. 2000 PD, Roux et al. 2010, Simms 1993, Springer 2007 PD, Thompson and Burdon 1992 PD, Thrall et al. 2002 PD.

Of particular importance is research that links ecology and genetics; examples include:

a. Links between resistance structure and disease levels and plant dynamics: Alexander et al. 1996 PD, Thrall and Burdon 2000 PD, Thrall and Jarosz 1994 PD, Laine 2004 PD, Springer 2007 PD.

b. Passive resistance – heritable traits other than resistance genes affect field disease levels: Alexander 1989 PD, Alexander et al. 1993, Biere and Antonovics 1996 PD, Giles et al. 2006 PD.

c. Links between community ecology and population genetics/phylogeny

1. Host shifts: Antonovics et al. 2002 PD, López-Villavicencio et al. 2005 PD, Roy 2001 PD.

2. Use of metagenomics to determine viral prevalence (70 percent and 25 percent of samples across tropical forest and prairie communities, respectively, have viral RNA): Muthukumar et al. 2009 PD, Roossinck et al. 2010.

3. Role of phylogeny in host range: Gilbert and Webb 2007 PD, Webb et al. 2006.

Plant Community Composition

Research in this area includes work examining the direct and indirect effects of pathogens on the number of plant species in an area and their relative frequency. Many of the classic studies in this area come from work in forest systems, such as research on mortality centers caused by *Phellinus weirii* in mountain hemlock forests (Hansen and Goheen 2000 PD) and work on sudden oak death in California forests (Rizzo and Garbelotto 2003 PD, Rizzo et al. 2005 PD).

Three subdisciplines of community ecology have been of major interest in recent years:

1. Interactions of pathogens with multiple hosts: apparent competition and pathogen spillover. Generalist pathogens may lead to the development of "apparent competition" where increases in pathogen populations on tolerant hosts may "spill over" and lead to increased disease on less tolerant hosts (Holt 1984 PD, Power and Mitchell 2004 PD). In addition to forestry examples (e.g., sudden oak death), another classic example of this phenomenon is work on barley yellow dwarf virus in California, where increases in virus prevalence and aphid vector numbers on exotic grasses can lead to adverse viral impacts on nearby native grasses (Malmstrom et al. 2005 PD). Recent work by Cronin et al. (2010) suggests that host physiological phenotypes may be predictive of pathogen reservoir potential.

2. Soil microbial community: feedback studies, Janzen-Connell studies. Several models and research groups have examined similar questions such as the following: Consider plant species "A:" Does the presence or high density of plant species A contribute to the development of a soil microbial community that leads to low survival for individuals of species A (but not species B, C, D, etc.)?. Such processes may be important in the maintenance of plant species diversity. Research examples include: Bagchi et al. 2010, Bever 2003 PD, Bever et al. 1997 PD, Diez et al. 2010, Holah and Alexander 1999, Klironomos 2002 PD, Mangan et al. 2010, Mills and Bever 1998 PD, Packer and Clay 2000 PD, Petermann et al. 2008 PD, Reinhardt et al. 2003 PD, Reynolds et al. 2003 PD, Swamy and Terborgh 2010, Van der Putten et al. 1993 PD. Many of the studies provide general support for the theories noted above, but there are major gaps in our knowledge. In particular, there is a tendency in previous work to treat the microbial community as a "black box" in most experiments. Further, most theory in this area focuses on specialist pathogens, yet most soil pathogens are generalists.

3. Invasion ecology and disease. A major issue in ecology and conservation biology is the unprecedented movement of species around the world due to both intentional and nonintentional introductions. One mechanism that may be important is the idea of "enemy release," where pathogens regulate plant populations in native sites, but the reduced pathogen presence or pressure in introduced sites allow for an expansion of the plant population. There is supporting evidence for this mechanism, but results are variable and can depend on the system being studied (Agrawal et al. 2005, Diez et al. 2010, Mitchell et al. 2006 PD, Mitchell et al. 2010, Parker and Gilbert 2007 PD, Reinhart et al. 2003 PD, Roy et al. 2011, van Kleunen and Fisher 2009 PD). Current work on invasion ecology and disease have focused on a) plant demography and dynamics (Chun et al. 2010, Roy et al. 2011), b) role of generalists versus specialist enemies (Halbritter et al. 2012), c) variation among species in enemy release (Blumenthal et al. 2009), and d) accumulation of pathogens on invasive plants and evolutionary responses (Diez et al. 2010, Gilbert and Parker 2010, Mitchell et al. 2010).

Global Change and Ecosystem Function

In recent years, there is increasing emphasis on how global change variables may affect pathogen populations and communities, and in turn, how pathogens may alter the functioning of ecosystems. Due to time limitations in my talk, I did not cover this area deeply. Examples of work, however, include:

a. Effects of temperature, carbon dioxide, and nutrients on plant disease: Mitchell et al. 2003 PD, Nordin et al. 1998 PD, Nordin et al. 2009, Roy et al. 2004 PD, Strengbom et al. 2002 PD, Strengbom et al. 2006, Tylianakis et al. 2008.

b. Genetic variation in pathogen populations in response to environmental change: Laine 2007 PD.

c. Effects of disease on ecosystem function: Eviner and Likens 2008 PD, Mitchell 2003 PD, Lovett et al. 2006 PD.

Conclusions

As we contemplate the future, it is important to emphasize that natural areas are increasingly fragmented and occur within a mosaic of human impacted biomes (see concept of "anthropogenic biomes," Ellis and Ramankutty 2008 PD). An area worthy of increased emphasis is studies of disease at the interface between agriculture/forestry and "natural" habitats (Burdon and Thrall 2008 PD, Fabiszewski et al. 2010 PD).

Literature Cited

As noted earlier, to save space on references, many citations above have the letters "PD" after them. This means that the full reference can be found in a recent review article in the journal Plant Disease (Alexander 2010); such PD references are not listed below.

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