CASCADING CONSEQUENCES OF INTRODUCED AND INVASIVE SPECIES ON IMPERILED INVERTEBRATES

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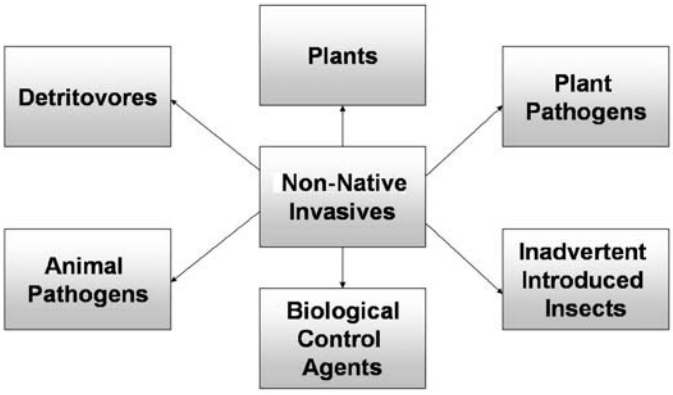
The address began with a review of three lists of insects of conservation importance: the U. S. Fish and Wildlife Service's list of 57 federally endangered and threatened insects native to North America (USFWS 2006); Connecticut's Endangered, Threatened and Special Concern Species (CT DEP 2004); and the 26 species of conservation importance identified in Connecticut's recently completed Butterfly Atlas Project (O'Donnell et al. 2007). In addition to the above, information on rare species was extracted from NatureServe (2007), the Red List of Pollinator Insects of North America (Shepherd et al. 2005), and Globally Rare Butterflies and Macro-moths (Lepidoptera) of Forests and Woodlands in the Eastern United States (Schweitzer et al., in prep.).

Non-native invasive species threaten 25 (44%) of the 57 insects listed by USFWS as endangered or threatened, and are second only to development/habitat loss as a threat to listed insects. Invasive species are regarded as the primary threat for 14 of these: 12 Hawaiian *Drosphila*, 1 Hawaiian sphingid moth (*Manduca blackburni* (Butler)), and 1 Californian sphingid moth (*Euproserpinus euterpe* Hy. Edwards). Fire ecology plays an important role in the welfare of many federally listed species, especially among the protected Lepidoptera. Three important threats for vertebrates—overharvesting, pollution, and disease—the third, fourth, and fifth most important factors for imperiled vertebrates (Wilcove et al. 1998), appear to be of minimal importance for insects (but see below).

Principal threats to Connecticut's state-listed insects include a host of factors but two have clear primacy: (1) development + habitat loss and (2) succession + afforestation. Overgrazing by deer was identified as an important but second-order threat. In Connecticut, non-native invasives were regarded to be of tertiary importance, roughly on the same level as excessive ATV and ORV traffic and global warming.

The above approach, focused on state and federally listed taxa, does not take into account that even widespread and common species can become rare and face extinction as a result of biological introductions. A heralded example is that of the apparent displacement of the C-9 lady beetle (*Coccinella novemnotata* Herbst) by the C-7 lady beetle (*Coccinella septempunctata* L.), which in turn appears to have lost ground to the Asian lady beetle (*Harmonia axyridis* (Pallas)) (Stephens and Losey 2003). The recent catastrophic collapse of members of the subgenus Bombus—*Bombus occidentalis* Greene and *B. franklini* (Frisson) in the West and its congener *B. affinis* Cresson in the East, as well as their social parasite, *Psithyrus ashtoni* Cresson—following an epizootic of *Nosema bombi*, that swept through commercial bumblebee hives (Thorp and Shepherd 2005; John Ascher, pers. comm.)[1], was held as a particularly alarming case, illustrating that no species is safe.

The remainder of the talk considered classes of threats to native insects, i.e., those stemming from biological introductions of plants, plant pathogens, inadvertently introduced insects, biological control agents, animal pathogens, and detritovores.



[1]N. American *Bombus* were brought to Europe and reared with European species where transfer of the *Nosema* likely occurred.

The two invasive plants most widely recognized to be threats to state-listed insects in the Northeastern States are common reed (*Phragmites australis*) and purple loosestrife (*Lythrum salicaria*) (Wagner 2007b). Over vast acres New Englanders are witnessing the ecological erasure of diverse wetland communities by these non-natives. A new threat in northeastern woodlands is Japanese stilt grass (*Microstegium vimineum*): from Tennessee to New Jersey, rich forest understories are being replaced by monocultures of stilt grass.

An important invasive plant in non-forested landscapes in the Northeast affecting imperiled insects is autumn olive (*Elaeagnus umbellata*). The shrub is a pernicious invader of early successional habitats, such as sandplains, where many of the region's most imperiled invertebrates are eking out their existence: tiger beetles, ground-nesting bees, sand wasps, ground beetles, and numerous other arenicolous taxa. In part because autumn olive is a nitrogen-fixer, it too often proves to be an early and successful invader of non-vegetated landscapes and accelerates succession.

Partly tongue-in-cheek and partly serious, I introduced the idea of Malcolm effects[2]: Small changes in complex systems that create chain reactions that throw a system from one state into another, the consequences of such are difficult to predict (or control). Citing one example of a Malcolm effect, I talked about instances where exotics have proven to be "egg traps" for rare and declining species: females of the federally endangered sphinx, *Euproserpinus euterpe*, oviposit on filigree (*Erodium cicutarium*) (Family Geraniaceae), a plant on which the larvae have no chance of survival (its normal host is *Camissonia contorta)* (Family Onagraceae)). In the East, garlic mustard (*Alliaria petiolata*) is perceived to be a primary threat to populations of the West Virginia white (*Pieris virginiensis* (W. H. Edwards)) —as garlic mustard invades woodlands, the butterfly disappears.

Introduced plant pathogens are a perennial and chronic threat to our native flora. Five forest diseases that have garnered great attention in eastern North America include beech bark disease, chestnut blight, dogwood anthracnose, Dutch elm disease, and Sudden Oak Death. While all have the potential to change forest stand characters and impact biodiversity, only chestnut blight has been linked to the extinction of insect herbivores. Opler (1978) listed seven American chestnut-feeding lepidopterans as extinct: *Coleophora luecochrysella* Clemens, *Ectoedemia castaneae* Busck, *Ectoedemia phleophaga* Busck, *Synanthedon castaneae* (Busck), *Tischeria perplexa* Braun, *Swammerdamia castaneae* Busck, and *Argyresthia castaneella* Busck. While two of these have since been rediscovered (*Synanthedon castaneae* and *Coleophora leucochrysella*), and the taxonomic validity of two others is in question (*Tischeria perplexa* and *Swammerdamia castaneae*), the remaining three species appear to have been driven to extinction as a consequence of the rangewide collapse of their foodplant, chestnut.

Inadvertently established herbivorous, predatory, and parasitic insects pose great threats to biological communities, especially to those on remote islands and other disharmonic biotas. Hundreds of exotic herbivores have established in the United States—their economic and/or community-level effects range from largely positive such as honey bee (*Apis mellifera* L.) to potentially devastating such as Mediterranean fruit fly (*Ceratitis capitata*) (Wiedemann) and emerald ash borer (*Agrilus planipennis* Fairmaire). In eastern forests, the gypsy moth (*Lymantria dispar* (L.)) has had no equal in its biological, economic, and even social impacts. Efforts to control this pest are thought to have had direct and indirect consequences for our native lepidopteran fauna.

Other herbivores of great importance to the forests of eastern North America include the hemlock woolly adelgid (*Adelges tsugae* (Annand)) and balsam woolly adelgid (*Adelges piceae* (Ratzeburg)). The destruction of the high-elevation Fraser fir (*Abies fraseri*) forests of the southern Appalachians has been catastrophic. These boreal sky-island communities are home to many endemics, glacial disjuncts (e.g., Scholtens and Wagner 2007), and otherwise globally imperiled species (Keith Langdon, pers. comm.) that are threatened by the changes in forest structure and composition underway as a result of balsam woolly adelgid infestations.

[2]Ian Malcolm was the mathematician in Michael Crichton's Jurassic Park who wove fractal and chaos theory into the drama that unfolded on Isla Nublar.

Among three of North America's newest arrivals, the Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky)), winter moth (*Operophtera brumata* (L.)), and emerald ash borer, the latter is the most worrisome to the conservation community. Early reports suggest the buprestid has the potential to eradicate or greatly reduce ash (*Fraxinus*) from woodlands and forest community types across North America. If the insect's spread and impacts go unchecked, and ash mortality continues to hover near 100%, as many as 21 ash-feeding Lepidopterans could be threatened with extinction (Wagner 2007a). Other indirect effects—cascading consequences—will surely occur. For example, as black ashes are removed from wooded swamps of the Upper Midwest, buckthorn (*Rhamnus cathartica*) is expected to gain a stronger foothold in natural communities.

While much has been written about the impacts of non-native predatory insects on native species, no place has suffered more than Hawaii. Ants, wasps, and insect parasitoids have wreaked havoc on the islands' biota. Forty-seven species of ants have established in Hawaii--included are several of the world's most aggressive pest species. Eighteen percent of the wasps reared by Henneman and Memmott (2001) from native caterpillars retrieved from a high elevation swamp forest represented parasitoid species believed to have been inadvertently established in the Hawaiian Islands.

Purposefully introduced biological control agents have had wide ranging impacts on native species and communities. C.V. Riley's introduction of the Vedalia beetle (*Rodolia cardinalis* (Mulsant)) is held as one of the most successful examples of biological control—the beetle saved California's citrus industry, and impacts to native species appear to have been minimal. In contrast, purposeful introductions of the mongoose to control snakes have proven disastrous for island bird and reptile populations worldwide. Examples of biological control efforts that have impacted indigenous plants and animals have been discussed by Howarth (1991), Van Driesche and Van Driesche (2003), Berenbaum (2004), and others. Several studies have documented consequences of introduced herbivores to our native flora (e.g., Louda and O'Brien 2002). Much recent research has been focused on the non-target impacts of "sanctioned" introductions of parasitoids. In Henneman and Memmot's (2001) study of the natural enemies of a Hawaiian caterpillar community, introduced biological control agents accounted for 83% of the parasitoids reared from wild, non-target caterpillars. Empirical studies by Benson et al. (2003a,b) provide evidence that the introduced braconid, *Cotesia glomerata* (L.), is at least partially, if not wholly responsible, for the collapse of mustard white (*Pieris napi* (L.)) populations in Massachusetts. Many in New England's conservation community are looking at the tachinid fly (*Compsilura coccinata* Meigan), a generalist and prolific parasitoid of Macrolepidoptera, introduced to control the gypsy moth, as a contributor to the regional decline of silkmoths (Boettner et al. 2000), sphingids, and Datanas.

The ecological impacts of introduced predators, such as lady beetles and vespid wasps, are poorly understood and largely unstudied. Given the millions of Asian lady beetles that turned up in homes throughout the Northeast around the turn of the century, there can be little question that this phenomenally prolific insect had a direct impact on the population dynamics of native predators such as aphelinines, chrysopids, hemerobiids, and even butterflies such as the harvester butterfly, *Feniseca tarquinius* (Fabr.), that were competing for the same food.

Introduced animal pathogens also pose a threat to North American insect biodiversity. A well-documented example was the sudden decline of feral hives of the (introduced) honey bee (*Apis mellifera* L.) across the whole of North America, caused by infestations of the hemolymph-feeding varroa mite (*Varroa jacobsoni* Oudemans). The recent and phenomenally rapid declines of *Bombus franklini* and *B. occidentalis* Greene in western North America and *Bombus affinis* and *B. terricola* Kirby in eastern North America have been linked to a 1998 epizootic of *Nosema bombi* [Microsporidian] introduced through commercial movement of bumblebee queens and colonies for pollination of greenhouse tomatoes (Thorp 2005, Thorp and Shephard 2005).

There is growing concern that even detritovores, and in particular exotic earthworms, dramatically change the terrestrial communities where they establish and proliferate. North America is now home to nearly four dozen exotic earthworm species, some of which (e.g.,

Lumbricus rubellus Hoffm.) are becoming exceedingly abundant and widespread, especially north of the last glacial maximum where native earthworms do not occur. High earthworm densities eliminate surface litter, release elevated amounts of nitrogen, calcify soil, and mix layers that would have otherwise remained largely distinct (Frelich et al. 2006 and references therein). The ecology of the forest understory is fundamentally changed: e.g., studies have documented impacts to understory ferns and herbs (Gundale 2002, Hale 2004, Hale et al. 2006) and amphibians (Migge-Kleiam et al. 2006; John Maerz, pers. comm.).

Some general patterns were then addressed in the talk. Foremost among these was that invasives often loom as focal threats in disharmonic communities, which tend to be ecologically unchallenged and vulnerable to invasion. Remote islands and cave biotas were mentioned as being particularly threatened. Similarly, trophically simplified communities, such as freshwater ecosystems and early successional communities, bear great risk. Conversely, complex and/or ecologically stressful communities —tropical rainforests, tundra, desert, many marine systems—while far from free of non-native invasive species problems, appear to face fewer challenges. Given the above, it is somewhat surprising that our eastern forests ecosystems have so many invasives —perhaps it is just a matter of our forests being challenged by very large species pools, drawing from nearly the whole of Europe and Asia.

In summary, for USWFS-listed species invasives pose the second greatest threat to imperiled insects, second only to development and habitat loss. Invasives are the principal threat facing federally protected species listed from Hawaii. In Connecticut, for both state-listed terrestrial and imperiled butterflies, non-native invasives are of tertiary importance, following afforestation/ succession and deer, and perhaps even global warming in importance. Once exotics are established, expect the unexpected (Malcolm effects): consequences of biological introductions often are complex, indirect, and unpredictable, with problems trickling in and trickling out to other trophic levels. Disharmonic biotas and simple communities are especially threatened by non-native invasives. Exotics pose their greatest threat to biodiversity in those instances where their presence catalyzes changes in basic ecosystem properties—two egregious examples include the impact of the balsam woolly adelgid on the sky island biotas of the southern Appalachians and the changes brought on by introduced earthworms to forest understory communities. If the spread of the emerald ash borer continues unchecked, its ecological consequences will be catastrophic for the many specialist herbivores that rely on ash and the ecological communities where ash is a co-dominant.

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