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Synthesis, part of Special Feature on Pollinator Decline

Causes and Extent of Declines among Native North American Invertebrate Pollinators: Detection, Evidence, and Consequences

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ABSTRACT

Ecosystem health and agricultural wealth in North America depend on a particular invertebrate fauna to deliver pollination services. Extensive losses in pollinator guilds and communities can disrupt ecosystem integrity, a circumstance that today forces most farmers to rely on honey bees for much fruit and seed production. Are North America's invertebrate pollinator faunas already widely diminished or currently threatened by human activities? How would we know, what are the spatiotemporal scales for detection, and which anthropogenic factors are responsible? Answers to these questions were considered by participants in a workshop sponsored by the National Center for Ecological Analysis and Synthesis in October of 1999, and these questions form the nucleus for the papers in this special issue. Several contributors critically interpret the evidence for declines of bee and fly pollinators, the pollination deficits that should ensue, and their economic costs. Spatiotemporal unruliness in pollinator numbers, particularly bees, is shown to hinder our current insights, highlighting the need for refined survey and sampling designs. At the same time, two remarkable studies clearly show the long-term persistence of members of complex bee communities. Other authors offer new perspectives on habitat fragmentation and global

warming as drivers of pollinator declines. Bees and lepidopterans are contrasted in terms of their natural genetic variation and their consequent resilience in the face of population declines. Overall, many ecologists and conservation biologists have not fully appreciated the daunting challenges that accompany sampling designs, taxonomy, and the natural history of bees, flies, and other invertebrate pollinators, a circumstance that must be remedied if we are to reliably monitor invertebrate pollinator populations and respond to their declines with effective conservation measures.

KEY WORDS: Apiformes, Apoidea, Insecta, conservation, diversity, land-use change, native invertebrate pollinators, North America, pollination, pollinator declines.

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INTRODUCTION

That human activities can decimate or impoverish local and regional biotas is indisputable. In the past few decades, disturbing continental, oceanic, and global trends have emerged that show accelerating losses of biodiversity in such species-rich groups as marine fishes (Safina 1997), birds (Terborgh 1989), amphibians (Alford and Richards 1999), and reptiles (Gibbons et al. 2000), to name but a few. The causes can include habitat loss and degradation, pollution, overharvesting, invasive species, disease, and climate change. The impact of such losses can multiply beyond mere direct effects if the endangered organisms deliver vital community services, such as pollination (Kevan and Collins 1974, Kearns et al. 1998). In these cases, additional taxa within the community may suffer reproductive losses that could ultimately disrupt community function.

Invertebrates, particularly native bees, are the pollinators whose loss is most likely to have far-reaching effects in North America, the focus of this issue. They are the primary and essential "go-betweens" for the flowers of most wild and agricultural plants that require a pollinator. During their flights between flowers of conspecific plants in search of nectar, pollen, oil, or mates, bees and other insects often move pollen to floral stigmas, thereby enhancing fruit set and size, seed production and viability, seedling vigor, and the genetic diversity of plant populations.

Has this essential ecosystem service come into recent jeopardy in North America, as some have concluded (Buchmann and Nabhan 1996, Allen-Wardell et al. 1998)? Perhaps, if human activities are indeed causing widespread declines in pollinator abundance, shifts in pollinator community composition, or accelerated rates of pollinator extinction. Depauperate pollinator faunas may offer less of the redundancy that can buffer fruit and seed set against the inevitable and sometimes chaotic population swings of individual pollinator species (Cane and Payne 1993, Roubik 2001), with repercussions for humans and other animal species dependent on the regular production of those plants for food (Kevan and Collins 1974). Declining pollinator abundance could soon translate into less frequent flower visitation and abrupt or gradual diminution of seed and fruit production. In addition, self-compatible flowering plants that rarely receive floral visitors could suffer greater risks of inbreeding, because visitors encountering the rich resources accumulated in individual flowers would be more likely to remain with the plant than to move on in search of more profitable nectar and pollen sources.

The consequences of such lingering pollinators can extend to self-incompatible plants, too. In this case, rather than receiving beneficial pollen from other conspecifics, their stigmas may become clogged with self-pollen from neighboring flowers (Waser 1978), which can hasten pistil senescence (Scribailo and Barrett 1994). Chronic agricultural shortfalls in native pollinator abundance in many fruit and seed crops is widespread, especially among self-incompatible crop species (Kevan and Phillips 2001), which has forced the United States to rely on migratory beekeeping. That service has been recently jeopardized by Old World parasitic mites and larval diseases. But how frequent, prolonged, and severe are pollination deficits in nature, and when do pollination deficits signal actual pollinator declines (Thomson 2001)?

POSSIBLE CAUSES OF POLLINATOR DECLINE

Human activities are apparent everywhere, and their potential effects on beneficial insect populations would seem to be obvious. Claims for widespread declines of invertebrate pollinators are plausible but inadequately documented, at least in North America. For instance, insecticides are applied not only on agricultural fields but also in backyards and on rangelands, golf courses, parks, forests, and mosquito-ridden marshes and swamps. The broad-spectrum insecticides that are commonly used (and abused) are often as toxic to beneficial insects as they are to the target species (Johansen and Mayer 1990). On the other hand, it may be that plant losses from chronic herbicide use are, in fact, driving losses of pollinator species, and not vice versa.

Agriculture increasingly replaces natural plant communities with monocultures, some of which are incapable of sustaining pollinator populations. For instance, grains such as wheat and corn, which are planted every year across 6% of the continental U.S. land area and in up to 20% of some midwestern states (http://www.nass.usda. gov), do not provide for the nectar or pollen needs of any bee species. Undocumented acreages of hedgerows, field margins, embankments, and other "waste places" provide nesting habitat for some native bees. Removal of these often unappreciated habitats has been associated with dramatic declines in Germany's native bee fauna since the 1960s (Westrich 1989). Conversely, retention of some of these features has been associated with persistently rich native bee faunas in some Polish agricultural landscapes (Banaszak 1995, 1997).

In addition, more than 3% of the U.S. land area has been urbanized (http://usda.mannlib.cornell.edu:80/usda/), converting rich arrays of habitats into highways, houses, strip malls, office complexes, and industrial parks. Urbanization not only removes habitat directly but also isolates and fragments the land that it does not degrade or assimilate. The attributes, extent, and permanence of fragmentation effects for native bee faunas and their flowers, however, are barely understood (Cane 2001).

However, the effect of human industry on pollinators may not be so clear-cut (Bohart 1972*a*). Where humans have taken, they have also, quite unintentionally, given in return. The clearing of American forests has opened up previously shaded, humid habitats for many sun-loving pollinators and their plants. Roadsides, with their partially compacted soils, are frequently favored nesting sites for bees and wasps. In deserts, highway pavement channels rainfall runoff to road edges, inadvertently irrigating linear populations of native wildflowers (Lightfoot and Whitford 1991). Wooden fences, barns, and even stone walls provide substrates for bees that nest above ground (Westrich 1989). Where native plants and their flowers have been removed or displaced, they have sometimes been replaced, in equal or greater numbers, by introduced species in flower and vegetable gardens, waste places, and disturbed areas. Although some of these flowers are nothing more than the sterile fabrications of plant breeders, in other cases exotic plant species supply novel resources to pollinators with unknown consequences. Berlin, Germany, for instance, with its patchwork of waste places populated by ruderal floras, retains a bee fauna of 262 native bee species (Saure 1996).

By the same token, brief bursts of flowering (e.g., by orchard crops) may provide superabundant resources for one life stage of a pollinator, but be unable to support all the stages of its life cycle. Such short-lived bonanzas may also favor one species at the expense of others. For instance, the alkali bee (*Nomia melanderi*), a native of the dry basins of the U.S. intermountain west, proliferates wherever blooming seed alfalfa combines with subirrigated alkali flats for nesting (Bohart 1972*b*). Clearly, some of North America's fauna of invertebrate pollinators, probably the vast majority, are not inextricably linked to pristine parks and reserves, but what balance, extent, and kind of human activities are compatible with their persistence?

INVERTEBRATE POLLINATOR DECLINES: EXTENT AND EVIDENCE

Researchers from the United States and Canada came together during an October 1999 workshop at the National Center for Ecological Analysis and Synthesis (NCEAS) in Santa Barbara, California, to evaluate a single question: Is there evidence to support the claim by some (Buchmann and Nabhan 1996, Allen-Wardell et al. 1998) of widespread invertebrate pollinator declines, or a loss of species diversity in pollinator community composition, in North America? How would we know? The obvious auxiliary question—Has pollination service suffered as a consequence?—was secondary to our objective, but was discussed more fully at an earlier conference briefly

described in Tepedino and Ginsberg (2000). In the nine papers that arose from the NCEAS workshop, participants explored the evidence for, and the likelihood of detecting, declines in native invertebrate pollinators. Evidence was mustered from studies of population dynamics, genetic diversity, and species composition in pollinator communities. Accessory papers evaluated the issue of pollination deficits in plants or explored several of the anthropogenic factors that could elicit declines, such as global warming and habitat fragmentation.

Three papers address the magnitude of the spatial and temporal turnover of relatively undisturbed natural populations and communities of bees. When confronted with these natural vagaries in bee community abundance and composition, can we ever hope to detect the shifts and changes in pollinator faunas that may arise from human activity? One answer comes from Roubik (2001), who presents an unrivaled data set of 22 consecutive years of unbiased samples of an orchid bee (Euglossinae) fauna in Panama. Orchid bees were sampled from Parque Soberania, a protected lowland rain forest site in Panama famed for its bird diversity (http://www.nps.gov/centralamerica/panama/bio.html). No aggregate trends were detected in the nearly 2000 samples, although two- to fourfold annual swings in the population densities of individual species were common in this and the other faunal studies that he reviews.

Williams et al. (2001) extend Roubik's insights with a quantitative analysis of the spatiotemporal variation of bee faunas worldwide. They find, as did Roubik, that populations and local diversity are characterized by daunting variability, especially among the numerous rarer species. In light of this, they review and evaluate a number of protocols to help develop improved, standardized, systematic sampling efforts for detecting true declines in native bee faunas.

An exemplary study from Marlin and LaBerge (2001) summarizes data for the bee fauna that they sampled at 24 flowering plant species in the vicinity of Carlinville, Illinois, USA. Carlinville is the site of the world's first published example of an exhaustively sampled local bee fauna and its floral associations, which was begun by Charles Robertson late in the 19th century. The authors found that Carlinville's diverse native bee fauna was remarkably persistent when resampled nearly a century later, in the 1970s, despite the continued dominance of row-crop agriculture in that locale and the diverse arsenal of insect control tools used over the decades.

Bees are not the only invertebrate pollinators whose potential decline is poorly understood. Kearns (2001) marshals evidence to suggest that flies are more important pollinators than we currently allow. They are persistent visitors of flowers, particularly those that are easy to access and manipulate, and, despite their relative hairlessness, are likely to be important pollinators of some flowering species in some ecosystems. However, flies are enmeshed in ecosystems in different, more complicated ways than bees. Although floral products feeds all life stages of bees, those flies that do use flower products do so mostly as adults; their immature progeny typically eat unrelated foodstuffs. This perhaps makes it harder to study them, because we must examine two very different life associations, and also makes them more unpredictable as flower visitors. As a result, their role in pollination and the spatiotemporal patterns in their diversity are even less well known than those of bees.

Two papers address select issues of global change as they impinge on invertebrate floral visitors of North America. Using GIS, Kerr (2001) successfully correlates the geographic distribution of Canadian butterfly diversity (292 species) with contemporary biotic and climatic parameters, particularly habitat heterogeneity and potential evapotranspiration, which is a measure of climatic energy. Warmer, more heterogeneous habitats host more butterfly species. The spatial distribution of climate energy is of particular interest, because it will shift with global warming. Kerr's method holds promise for other well-sampled faunas of floral visitors, especially if it proves to be a valid link between remotely sensed surface features and pollinator biodiversity on the ground.

Cane (2001) reviews the worldwide literature of habitat fragmentation as it pertains to native bees. Contrary to some reviews and more popular accounts, it is evident that the few extant studies of bees all have features that limit their interpretation and general applicability. Conclusions linking habitat fragmentation with pollinator demise are premature. In particular, Cane advocates that future studies need to consider the habitat needs for nesting by bees when evaluating the effects of fragmentation.

Declining abundance in a pollinator species can hasten its demise, because a decline in numbers is frequently accompanied by a decline in genetic variability via genetic drift, which increases the likelihood that populations and species will become extinct (Barrett and Kohn 1991). Fragmentation and habitat destruction can add to the rate of genetic erosion by reducing gene flow between demes. But what is the "natural" genetic diversity and

heterozygosity for taxa of invertebrate floral visitors? Packer and Owen (2001) compare genetic variation among species of two important higher taxa of invertebrate pollinators, bees and lepidopterans. Bees are renowned for their limited natural genetic variability because of factors such as their haplodiploid genetic system, aggregated nesting, central-place foraging habits, viscous population structure, and, perhaps, sociality. Packer and Owen suggest that bee populations may consequently be more genetically resilient in the face of declining population size than are butterflies and moths.

An alternative and less direct way of seeking evidence for pollinator declines is to examine pollination deficits. If pollinators are in decline, the thinking goes, then we should be able to measure the results of their absence as reductions in fruit or seed production in natural or agricultural ecosystems. Thomson (2001) critically reviews this idea, the thinking that educes it, and some of the work that has been used to support it. He concludes that expectations are really more complicated than we currently allow and that, although valuable if conducted properly, studies using pollination deficits to make the case for pollinator declines need to be interpreted with caution. Kevan and Phillips (2001) examine the case for pollination deficits in agroecosystems from the perspective of an economic market analysis. Although shortfalls in agricultural production stemming from pollination deficits may spawn both short-term winners and losers in the producer and trade economies, in all cases the consumer will pay higher prices for a depleted cornucopia of food products in the retail marketplace.

CONCLUSION AND FUTURE CHALLENGES

We conclude that we do not presently know the net effect of these confounding factors on native North American invertebrate pollinator faunas. We suspect that anthropogenic activities will be detrimental to some species but beneficial to others, with sometimes subtle and counterintuitive causal linkages (Thomas and Jones 1993, Benedek 1996). Obviously, if we have so far been unable to detect broad-scale declines in invertebrate pollinator taxa in North America, then we are even less able to draw conclusions about expected shortfalls in their services as pollinators. However, this lack of evidence is no cause for complacency. Instead, taking action now in response to these early alarms might allow North Americans to avert the very real and widespread declines that are now being detected among central European bee faunas (Westrich 1996). A concerted and scholarly multidisciplinary effort is needed to answer the critical questions, lest we embark on mistaken solutions extrapolated from other animal taxa and fail in our endeavors to conserve, let alone restore, communities of native invertebrate pollinators in North America.

Our conference highlighted several critical challenges that must be met if we are to make meaningful headway in understanding and addressing the conservation needs of invertebrate pollinators (see also Tepedino and Ginsberg 2000).

1) *Sampling.* Variable abundance is the natural norm for invertebrate pollinators. For sampling to faithfully represent the composition of a local bee community, it must accommodate or control for differing patterns of daily activity, weather, seasonal patterns of emergence, and annual fluctuations in abundance. No currently available sampling method should be presumed to be objectively representative; this is especially true of some of the passive methods such as pan-trapping (e.g., with Moericke traps). A representative passive sampling method would be very desirable indeed. If detected spatiotemporal patterns in pollinator faunas are to be generalized to spatial scales as large as or larger than a watershed, then the sampling regime must include the different habitats available from the pollinator's perspective, not our own.

Replicate stratified sampling is essential. Roubik (2001) recommends at least four years of samples to detect trends. Williams et al. (2001) advocate multiyear samples as well, to bracket variability before evaluating differences between modern and historical samples. The less dramatic the disturbance, the less likely that its influence will be detected against this background of natural stochasticity. Unfortunately, most species in samples of invertebrate pollinator communities and guilds are uncommon or rare. They are the least likely ones to reveal declines, as they are often represented by just one or a few specimens (Williams et al. 2001). Nevertheless, traditionally we worry most about rare taxa in conservation biology. Rare bee species might be profitably monitored if they are floral specialists, whose absence can more readily be confirmed by focal surveys if their flowering hosts are discretely distributed. For the general case, however, we must rely on the more common

invertebrate pollinator species for the detection of declines.

2) *Taxonomy.* Commonly encountered, species-rich bee genera contain many species that are difficult to identify. Like the Asteraceae, Orchidaceae, and Poaceae among plants, their identification is not for the tyro. Just 10 of the 119 or so bee genera of North America contain two-thirds of the estimated 4000 known species (T. Griswold, *personal communication*). Although representatives of these species-rich genera often predominate in samples of local bee communities such as Carlinville (Marlin and LaBerge 2001), it is ironic that many of these species are notoriously difficult to distinguish. Even if their genera have received formal taxonomic revision, individual identifications still often benefit from comparison with authoritatively identified pinned specimens in collections. Correct identifications are important, because congenerics of these bees often differ in terms of their habitat requirements for immatures, seasonality, sociality, floral associations, pollination value, geographic range, and other factors. Circumstances for anthophilous flies are comparable. Close collaboration between ecologists and museum taxonomists is essential, not just as an afterthought but in the planning stages of a project.

3) *Habitat delimitation.* We cannot assume a priori that we know what constitutes "habitat" from the perspective of an invertebrate pollinator. The important invertebrate pollinators have holometabolous life cycles, with discrete larval stages whose mobility and habitat requirements are dramatically different from those of the winged adult. Conservation initiatives have sometimes been slow to consider the needs of different life-cycle stages. For example, many conservation-minded researchers advocate planting nectar plants for butterflies but then fail to foster their larval host plants. Bees pose a slightly different problem: immatures have no dispersal potential, whereas adults are expert, vagile navigators. Although we lack evidence for the flight range potentials of smaller bodied bee species, we know that those of honey bee size can, if necessary, readily forage at a distance of 1 km or more from their nesting sites. Hence, invertebrate pollinators do not need continuously favorable habitats to persist, just a suitably scaled patchwork that meets adult and larval needs. The concepts of "habitat complementarity" (Dunning et al. 1992) or "partial habitats" (Westrich 1996, Tepedino et al. 1997) are therefore broadly applicable to invertebrate pollinators. Immature stages of invertebrate pollinators are generally difficult to find and impractical to sample, but, in surveys of adults, the requirements of immatures must be understood and borne in mind when classifying habitat diversity, mapping habitat "fragments," and evaluating change in *their* habitats.

RESPONSES TO THIS ARTICLE

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Acknowledgments:

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