**Rachael Winfree**
**Selected publication abstracts**

**Winfree, R**., N. M. Williams, J. Dushoff, and C. Kremen. Accepted pending minor revisions. Wild bees provide insurance against ongoing honey bee losses. Ecology Letters

One of the values of biodiversity is that it may provide "biological insurance" for services currently rendered by domesticated species or technology. We used crop pollination as a model system, and investigated whether the loss of a domesticated pollinator (the honey bee) could be compensated for by native, wild bee species. We measured pollination provided to watermelon crops at 23 farms in New Jersey and Pennsylvania, USA, and used a simulation model to separate the pollination provided by honey bees and native bees. Simulation results predict that native bees alone provide sufficient pollination at >90% of the farms studied. Furthermore, empirical total pollen deposition at flowers was strongly, significantly correlated with native bee visitation but not with honey bee visitation. The honey bee is currently undergoing extensive die-offs due to Colony Collapse Disorder. We predict that in our region native bees will buffer potential declines in agricultural production due to honey bee losses.

**Winfree, R**., N. M. Williams, H. Gaines, J. Ascher, and C. Kremen. Accepted pending minor revisions. Wild pollinators provide majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology

**1.** Concern about a global decline in wild pollinators has increased interest in how pollinators are affected by human land use, and how this in turn affects crop pollination.
**2.** We measured wild bee visitation to four summer vegetable crops, and investigated associations between flower visitation rates and land use intensity at local and landscape scales. We studied 29 farms in New Jersey and Pennsylvania, U.S.A. Over two years we recorded >7400 bee visits to crop flowers and identified 54 species of wild bees visiting crops.
**3.** Wild bees were the dominant flower visitors at three of the four crops we studied; domesticated honey bees *Apis mellifera* L. provided the remainder of visits.
**4.** Ordination of the two best-studied crops showed that the wild bee species visiting tomato *Solanum lycopersicum* L. were distinct from those visiting watermelon *Citrullus lanatus* (Thunb.) Matsum. & Nakai.
**5.** Crop visitation by wild bees was not associated with organic farming, nor with natural habitat cover at either the local or the landscape scales.
**6.** *Synthesis and applications*. The extent of crop visitation by wild bees observed in this study is among the highest recorded. In contrast to previous studies of crop visitation by wild bees, we did not find negative effects of conventional farming or natural habitat loss. In our study system, organic and conventional farms differ little in field size, crop diversity and weedy flower diversity, unlike some systems where organic farms have smaller fields with greater crop and weed diversity. Such variables may be more important than organic versus conventional farming practices. Second, small patches of natural habitat are dispersed throughout our entire study system, and this habitat heterogeneity may support high bee abundance even in landscapes with a low proportion

of natural habitat overall. Our findings suggest that agri-environment schemes and similar programs, which work through local habitat restoration, should target farms in intensively agricultural (i.e., homogeneous) landscapes to gain maximum conservation benefits.

Greenleaf, S.S., N.M. Williams, **R. Winfree** and C. Kremen.2007. *Bee foraging ranges and their relationship to body size.* Oecologia 152: XX

Bees are the most important pollinator taxon; therefore, understanding the scale at which they forage has important ecological implications and conservation applications. The foraging ranges for most bee species are unknown. Foraging distance information is critical for understanding the scale at which bee populations respond to the landscape, assessing the role of bee pollinators in affecting plant population structure, planning conservation strategies for plants, and designing bee habitat refugia that maintain pollination function for wild and crop plants. We used data from 96 studies of 62 bee species to determine whether body size predicts foraging distance. We regressed maximum and typical foraging distances on body size and found highly significant and explanatory nonlinear relationships. We used a second data set to: (1) compare observed reports of foraging distance to the distances predicted by our regression equations and (2) assess the biases inherent to the different techniques that have been used to assess foraging distance. The equations we present can be used to predict foraging distances for many bee species, based on a simple measurement of body size

Kremen, C., N. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, D. Vazquez, **R. Winfree**, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A. Klein, J. Regetz, T. Ricketts. 2007. *Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land use change.* Ecology Letters 10: 299-314

Many ecosystem services are delivered by organisms that depend on habitats that are segregated spatially or temporally from the location where services are provided. Management of mobile organisms contributing to ecosystem services requires consideration not only of the local scale where services are delivered, but also the distribution of resources at the landscape scale, and the foraging ranges and dispersal movements of the mobile agents. We develop a conceptual model for exploring how one such *mobile-agent-based ecosystem service* (MABES), pollination, is affected by land use change, and then generalize the model to other MABES. The model includes interactions and feedbacks among policies affecting land use, market forces, and the biology of the organisms involved. Animal-mediated pollination contributes to the production of goods of value to humans such as crops; it also bolsters reproduction of wild plants on which other services or service-providing organisms depend. About one-third of crop production depends on animal pollinators, while 60 – 90% of plant species require an animal pollinator. The sensitivity of mobile organisms to ecological factors that operate across spatial scales makes the services provided by a given community of mobile-agents highly contextual. Services vary, depending on the spatial and temporal distribution of resources surrounding the site, and on biotic interactions occurring locally,

such as competition among pollinators for resources, and among plants for pollinators. The value of the resulting goods or services may feed back *via* market-based forces to influence land use policies, which in turn influence land management practices that alter local habitat conditions and landscape structure. Developing conceptual models for MABES aids in identifying knowledge gaps, determining research priorities, and targeting interventions that can be applied in an adaptive management context.

**Winfree, R.**, C. Kremen and T. Griswold. 2007. *Effect of human disturbance on bee communities in a forested ecosystem.* Conservation Biology 21: 213-223.

It is important for conservation biologists to understand how well species persist in human-dominated ecosystems because protected areas constitute a small fraction of the Earth's surface and because anthropogenic habitats may offer more opportunities for conservation than has been previously thought. We investigated how an important functional group, pollinators (bees; Hymenoptera: Apiformes), are affected by human land use at the landscape and local scales in southern New Jersey (U.S.A.). We established 40 sites that differed in surrounding landscape cover or local habitat type and collected 2551 bees of 130 species. The natural habitat in this ecosystem is a forested, ericaceous heath. However, bee abundance and species richness within forest habitat decreased with increasing forest cover in the surrounding landscape. Similarly, bee abundance was greater in agricultural fields and suburban and urban developments than in extensive forests, and the same trend was found for species richness. Particular species groups that might be expected to show greater sensitivity to habitat loss, such as floral specialists and bees of small or large body size, did not show strong positive associations with forest habitat. However, 18 of the 130 bee species studied were positively associated with extensive forest. One of these species is a narrow endemic that was last seen in 1939. Our results suggest that at least in this system, moderate anthropogenic land use may be compatible with the conservation of many, but not all, bee species.

Dobson, A., D. Lodge, J. Alder, G. Cumming, J. Keymer, J. McGlade, H. Mooney, J. A. Rusak, O. Sala, V. Wolters, D. Wall, **R. Winfree**, and M. Xenopoulos. 2006. *Habitat loss, trophic collapse and the decline of ecosystem services.* Ecology 87: 1915-1924

The provisioning of sustaining goods and services that we obtain from natural ecosystems provide a strong economic justification for the conservation of biological diversity. Understanding the relationship between these goods and services and changes in the size, arrangement, and quality of natural habitats is a fundamental challenge of natural resource management. In this paper, we describe a new approach to assessing the implications of habitat loss by examining the ways in which the provision of different ecosystem services is dominated by species from different trophic levels. We then develop a mathematical model that illustrates how declines in habitat quality and quantity lead to sequential losses of trophic diversity. The model suggests that declines in the provisioning of services will initially be slow but will then accelerate as species from higher trophic levels are lost at faster rates. Comparison of these patterns with empirical examples of ecosystem collapse (and assembly) suggests that similar patterns occur in natural systems impacted by anthropogenic change. In general, ecosystem goods and

services provided by species in the upper trophic levels will be lost before those provided by species lower in the food chain. The decrease in terrestrial food chain length predicted by the model parallels that observed in the oceans following overexploitation. The large area requirements of higher trophic levels make them as susceptible to extinction as they are in marine systems where they are systematically exploited. Whereas the traditional species-area curve suggests that 50% of species are driven extinct by an order-of-magnitude decline in habitat abundance, this magnitude of loss may represent the loss of an entire trophic level and all the ecosystem services performed by the species on this trophic level.

**Winfree, R**., S.K. Robinson, D. Bengali and J. Dushoff. 2006. *A Monte Carlo model for estimating the reproduction of a generalist brood parasite across multiple host species.* Evolutionary Ecology Research 8: 213-236.

Questions: How can the productivity of a generalist brood parasite be estimated? Does an invasive brood parasite have greater productivity (defined as fledglings / egg and fledglings / area) in a recently invaded habitat, compared to a habitat similar to its original range?
Features of model: We developed a simulation model that uses Bayesian and Monte Carlo methods to integrate brood parasite productivity across multiple host species over the entire breeding season.
Organisms: We use the model to estimate the productivity of the brown-headed cowbird (*Molothrus ater*) in two host communities, one breeding in deciduous forests (a recently invaded habitat) and one in old fields (a grassland habitat more similar to the cowbird's original range). We parameterize the model with data from 616 nests of 14 cowbird host species, containing 428 cowbird eggs and young.
Results and Conclusions: We developed methods for estimating the productivity of a brood parasite with an entire community of host species. We found that cowbirds have higher productivity in the recently invaded habitat, deciduous forest. Our findings are consistent with the rapid spread of the cowbird once it invaded the forested eastern U.S.

**Winfree, R**., J. Dushoff, E. Crone, C. Schultz, R. Budny, N. Williams and C. Kremen. 2005. *Testing simple indices of habitat proximity*. The American Naturalist 165: 707-717

Simple measures of habitat proximity based primarily on land cover are widely used in the ecological literature to infer habitat connectivity, or the potential for animal movement among resource patches. However, such indices have rarely been tested against observations of animal movement, or against more detailed biological models. We developed a priori expectations as to the types of study systems and organisms for which various habitat proximity indices would be best suited. We then used data from three study systems and four species to test which, if any, of the indices were good predictors of population-level responses. Our a priori expectations about index performance were not upheld. The indices that consider both habitat area and distance from the focal patch were highly correlated with each other, suggesting that they do index

similar quantities. However, none of the indices performed well in predicting population response variables. The results suggest that the pattern of habitat cover alone may be insufficient to predict the process of animal movement.

Chace, J., C. Farmer, **R. Winfree**, D. Curson, W. Jensen, C. Goguen, and S.K. Robinson. In press 2005. *Cowbird ecology: a review of factors affecting the distribution and abundance of cowbirds across spatial scales*. Ornithological Monographs

Brown-headed Cowbirds (Molothrus ater) provide one of the best case studies for demonstrating the need to consider multiple spatial scales in the management of a species and in the design of conservation strategies. An adaptive management program to reduce cowbird parasitism levels through reducing cowbird abundance should mirror the multiple spatial scales to which cowbirds respond. At the continental scale (>50 km), cowbirds are widespread across most of North America, and their abundance declines with distance from the center of their distribution in the Great Plains and Midwest. Generally, parasitism rates are highest in, and decline with distance from, the Midwest; however abundance at this broad scale is by no means indicative of parasitism rates at the local level because regional, landscape and local factors play a significant role in cowbird abundance, distribution and parasitism levels. At the regional scale (10-50 km) cowbird abundance and the cowbird/host ratio declines with increasing forest cover resulting in lower parasitism levels in the Midwest, where most of this work has been conducted. Underrepresented are studies from forested regions of the East and Far West, and from non-forested systems; nevertheless it is clear that increasing the spatial extent of contiguous habitat for host species is a key priority in cowbird management. Within the landscape scale (< 10 km) the density and dispersion of feeding sites has a strong influence on cowbird distribution and abundance. Cowbirds are known to commute over 10 km between feeding and breeding habitats; removing feeding opportunities for cowbirds near targeted management areas is a key directive. Feeding sites have traditionally considered livestock and managed for their removal during the breeding season. However, cowbirds also use agriculture fields, residential back yards and recreational areas, these feeding opportunities need to be considered during the process of land use planning and zoning. Locally, cowbird breeding abundance and distribution is strongly influenced by habitat type, vegetative structure, and passerine richness. Local management should strive to protect habitat for large host populations while reducing habitat edges and, in grasslands, cowbird perching sites. Comparative studies of cowbird breeding site use are needed in most regions, and there is a need for consistent use of standardized protocol of vegetative measurement (e.g., BBIRD) to aid future comparisons.

**Winfree, R**. 2004. *High offspring survival in an invaded habitat for the brown-headed cowbird.* Animal Conservation 7: 445-453.

The brood parasitic brown-headed cowbird (Molothrus ater) is considered an important threat to bird conservation in North America because it reduces the reproduction of its numerous host species. Prior to the colonisation of America by Europeans, the cowbird

was largely confined to the North American prairie region, but it has since invaded forests and other habitats and is now one of the continent's most abundant breeding passerines. The objective of this study was to examine cowbird reproduction with different host communities to determine whether habitat-specific reproduction might contribute to the cowbird's population expansion. Cowbird offspring survival was estimated with hosts breeding in fragmented deciduous forest (a newly invaded habitat) and old fields (a habitat more similar to the cowbird's original range). Offspring survival was 1.8–3.1 times higher in forest compared to old fields and was high enough to cause the cowbird population to increase with most forest hosts. The results suggest that increased offspring survival in an invaded habitat facilitates cowbird population growth. Land management for extensive, continuous forests, which cowbirds are known to avoid, could help control the cowbird population and reduce parasitism levels for the >140 species of cowbird hosts.

Dobson, A.P., S. Kutz, M. Pascual and **R. Winfree**. 2003. *Pathogens and parasites in a changing climate.* Pages 33-38 in L. Hannah and T. Lovejoy, eds, Climate Change and Biodiversity: Synergistic Impacts. Advances in Applied Biodiversity Science 4. Washington, DC: Center for Applied Biodiversity Science, Conservation International

The world is changing. It has always changed. Without long-term evolutionary change, it would not be possible to write (or read) this article. However, current rates of change are unprecedented. The increase in the size of the human population and the huge increases in our demand for natural resources have led to significant changes in a wide number of ecological processes. Climate is warming. Natural habitat is eroding into agricultural land while also being invaded by alien species. The stocks of most exploited fi sh species have declined, and huge increases have occurred in the levels of nitrogen, phosphorus, and other elements in both our rivers and oceans, as well as in the atmosphere. Elucidating the long-term societal and environmental impact of these changes is arguably the greatest scientific and economic challenge facing humans. Paradoxically, most of the world's political agenda is currently focused on resolving conflicts that are emergent epiphenomena of this larger economic crisis. This chapter focuses on two aspects of global change: what role do pathogens and invasive species play in ecological processes and how will these roles be modified by global climate change? This focus on parasites is warranted by the fact that more than half of biodiversity is parasitic upon the remaining half. Invasive species have similar population dynamics to many pathogens; such species are one of the greatest and fastest growing threats to biodiversity. The insights derived from comparative studies of parasitic and invaded systems shed important light on future threats to biodiversity in a changing world. Many interesting parallels and interactions exist between these two groups of organisms.

**Winfree, R.** 1999. *Cuckoos, cowbirds, and the persistence of brood parasitism*. Trends in Ecology and Evolution 14: 338-343

Brood parasites provide a particularly good opportunity for the study of host–parasite evolution because they directly affect the reproductive success of their hosts. Two parasitic species, the common cuckoo (*Cuculus canorus*) and the brown-headed cowbird (*Molothrus ater*), differ widely in their relationships with their hosts, yet share the attribute of having been particularly well studied by biologists. Recent work on the cuckoo and the cowbird has resulted in new answers to the question begged by all brood parasites: why do host species raise parasitic young?