MIGRATORY SPECIES AND ECOLOGICAL PROCESSES

BY

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By definition, migratory species are members of multiple ecological communities separated in space and time. We examine this attribute of migratory species in terms of the ecological roles played by migrants in ecosystems. Using the Millennium Ecosystem Assessment's framework for classifying the services provided to humans by ecosystems, we provide an overview of the community- and ecosystem-level effects of migratory species, considering those effects that lead to human well-being (ecosystem services) as well as effects that pose threats to human well-being (e.g., disease transmission). Ecosystem services and disservices are in many cases a function of abundance, raising the argument that rarity as a traditional threshold of species protection fails to preserve key ecological roles. While this argument applies to all species, migratory species provide instructive case studies.

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I. INTRODUCTION

Migration of animal species, defined as the periodic movement between two sites,[1] has been well recognized for millennia and subject to intense

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scientific interest for over 150 years. Most scientific attention has been focused on the physiology, behavior, or population dynamics of particular migratory species.[2] Yet like all species, migratory species are members of ecological systems (ecosystems)—assemblages of plants, animals, and microbes that interact with one another and with the physical and chemical environment. The capture and transformation of energy and nutrients by organisms within ecosystems, through photosynthesis, nitrogen fixation, feeding, defecation, pollination, and decomposition among myriad other processes and activities, results in an array of life-supporting goods and services without which human life could not be sustained.[3] Food, fiber, and timber production; recreational and aesthetic experiences; the provision of life-saving drugs and other pharmaceuticals; and the supply of fresh air and water are just a few of the ecosystem services provided by nature's "green infrastructure."[4] The activities of organisms in ecosystems can also result in disservices to humans, such as sustaining and spreading pests and disease.

From this ecological perspective, migratory species are of interest as components of two or more ecosystems and vectors for energy and matter transfer between them. The distance and frequency that migratory species travel in space and time can vary widely, from the diurnal movements of tiny krill (e.g., *Euphausia superba*) through a few hundred vertical feet of ocean water[5] to the annual circumpolar navigations of Arctic Terns (*Sterna paradisaea*).[6] Despite these differences in scale, all migratory species share the distinction of being regular participants in multiple ecosystems encountered throughout the migration route.

An important rationale for the conservation of species, including migratory species, is rarity. Rare species are more likely to go extinct because of demographic fluctuations or loss of critical habitat.[7] However, the ecosystem services provided by species may be a positive function of their abundance, such that the greater the number of individuals the greater

1 DAVID S. WILCOVE, NO WAY HOME: THE DECLINE OF THE WORLD'S GREAT ANIMAL MIGRATIONS 3 (2008).

2 Hugh Dingle & V. Alistair Drake, *What Is Migration?*, 57 BIOSCIENCE 113, 113 (2007); *see, e.g.*, EVOLUTION OF INSECT MIGRATION AND DIAPAUSE (Hugh Dingle ed., 1978) (collection of articles on physiology and ecology of migration of insects); S. Kimura, K. Tsukamoto & T. Sugimoto, *A Model for the Larval Migration of the Japanese Eel: Roles of the Trade Winds and Salinity Front*, 119 MARINE BIOLOGY 185, 185–186 (1994) (discussing a hypothetical model for larval transport and adult spawning migration of Japanese eels "from a physical and environmental point of view").

3 *See* Gretchen C. Daily, *Introduction: What Are Ecosystem Services?*, *in* NATURE'S SERVICES: SOCIETAL DEPENDENCE ON NATURAL ECOSYSTEMS 1, 3 (Gretchen C. Daily ed., 1997).

4 Gretchen C. Daily et al., *Ecosystem Services: Benefits Supplied to Human Societies by Natural Ecosystems*, ISSUES ECOLOGY, no. 2, Spring 1997, at 2, 2 (describing various services provided through natural ecosystems that "help sustain and fulfill human life").

5 WILCOVE, *supra* note 1, at 2.

6 *Id.*

7 *See* KEVIN J. GASTON, RARITY 137, 139 (1994) (explaining that rarity is a "major determinant of a species' risk of extinction" and thus contributes to the risk of extinction posed by environmental factors).

amount of ecosystem services they provide.[8] Animal migrations provide especially clear examples of this relationship because they are often phenomena of abundance[9] and their periodic and often discrete nature facilitates measurement of species effects. For example, the more salmon migrate upstream to their spawning grounds, the more marine nutrients are transported inland to fertilize stream and forest ecosystems.[10] Likewise, the larger a population of migratory pollinators, the more plants will be pollinated.[11] Thus, valuation of migratory species based on their capacity to provide ecosystem services may be the inverse of their valuation based on rarity. This represents an alternative paradigm to rarity-based conservation and instead provides a strong rationale for conserving and protecting abundant migratory species because of the magnitude of their ecosystem services.

Using the framework of ecosystem services and disservices our focus here is to consider the functional roles of migratory species as members of multiple ecosystems and to highlight novel implications for conservation policy that arise from this functional perspective. In Part II, we discuss the Millennium Ecosystem Assessment framework for ecosystem services and provide examples of the ecosystem services and disservices of migrating species. In Part III, we present case studies in order to explore more fully the services and disservices of migratory species and their relationship to abundance. In Part IV, we consider the implications that a functional perspective brings to conservation policy, with special attention to migratory species.

II. OVERVIEW

Ecosystem services are the life-supporting and life-enhancing benefits provided to people by the world's ecosystems,[12] or "natural capital."[13]

8 F. S. Chapin, III et al., *The Functional Role of Species in Terrestrial Ecosystems*, *in* GLOBAL CHANGE AND TERRESTRIAL ECOSYSTEMS 403, 403, 406 (Brian Walker & Will Steffen eds., 1996); Patricia Balvanera et al., *Applying Community Structure Analysis to Ecosystem Function: Examples from Pollination and Carbon Storage*, 15 ECOLOGICAL APPLICATIONS 360, 361 (2005); *see also* J.P. Grime, *Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects*, 86 J. ECOLOGY 902, 903 (1998) (noting that a plant species's abundance, or "mass ratio," in an ecosystem is closely related to its impact on the overall functions of the ecosystem); Claire Kremen, *Managing Ecosystem Services: What Do We Need to Know About Their Ecology?*, 8 ECOLOGY LETTERS 468, 474 (2005) (emphasizing conversely that when a species loses its abundance within an ecosystem, it loses its function in that ecosystem).

9 *See* David S. Wilcove & Martin Wikelski, *Going, Going, Gone: Is Animal Migration Disappearing?*, 6 PLOS BIOLOGY 1361, 1361–62 (2008) (noting that as the number of migrants decreases, so does the ecological importance of the migration).

10 Robert J. Naiman et al., *Pacific Salmon, Nutrients, and the Dynamics of Freshwater and Riparian Ecosystems*, 5 ECOSYSTEMS 399, 400–01 (2002).

11 *See* Carol A. Kearns et al., *Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions*, 29 ANN. REV. ECOLOGY & SYSTEMATICS 83, 86 (1998).

12 Daily et al., *supra* note 4, at 2.

Animals provide a variety of important ecosystem services with direct economic benefits to humans. For example, coffee, one of the world's most important export commodities, is highly dependent on pollination by natural insect populations.[14] An estimated one-third of global crop production is dependent on wild animal pollinators.[15] The economic value of commercial plus wild pollinator services is estimated to be $100–$200 billion annually on a global basis.[16] Food production from wild marine systems (overwhelmingly animal based) was estimated to have an annual worth of nearly one trillion dollars per year.[17]

We use the Millennium Ecosystem Assessment (MA) classification of ecosystem services.[18] Initiated in 2001 by the United Nations, the MA is a working group of over 1300 leading scientists and other experts from more than 100 nations that provides scientific assessment of the health and condition of the world's ecosystems and ecosystem services and analyzes options for enhancing human well-being through the conservation and sustainable use of ecosystems and their associated services.[19] Associated services are categorized into four general groups: supporting, provisioning, regulating, and cultural.[20] Supporting services include biogeochemical processes that are foundational to all other services and may occur over time scales longer than those of human decision-making.[21] Examples of these supporting services include soil formation, soil renewal through nutrient cycling, and the development and maintenance of an oxygen-containing atmosphere.[22] Provisioning services are the products of ecosystems such as crops, game, timber, fiber, or fresh water and are typically well integrated into human economic markets.[23] Regulating services modulate the quality and quantity of environmental conditions within ranges that promote human well-being, and include disease control, pollination, water purification, and the regulation of climate at local to global scales.[24] Cultural services

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13 Robert Costanza & Herman E. Daly, *Natural Capital and Sustainable Development*, 6 CONSERVATION BIOLOGY 37, 38 (1992).

14 Taylor H. Ricketts, *Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee Crops*, 18 CONSERVATION BIOLOGY 1262, 1264 (2004).

15 Alexandra-Maria Klein et al., *Importance of Pollinators in Changing Landscapes for World Crops*, 274 PROC. ROYAL SOC'Y B 303, 306 (2007).

16 Claire Kremen et al., *Pollination and Other Ecosystem Services Produced by Mobile Organisms: A Conceptual Framework for the Effects of Land-Use Change*, 10 ECOLOGY LETTERS 299, 305 (2007).

17 Robert Costanza et al., *The Value of the World's Ecosystem Services and Natural Capital*, 387 NATURE 253, 256 tbl.2 (1997).

18 CONCEPTUAL FRAMEWORK WORKING GRP., MILLENNIUM ECOSYSTEM ASSESSMENT, ECOSYSTEMS AND HUMAN WELL-BEING: A FRAMEWORK FOR ASSESSMENT 56, 57 fig.2.1 (2003).

19 *Id.* at x–xi; CONDITION & TRENDS WORKING GRP., MILLENNIUM ECOSYSTEM ASSESSMENT, ECOSYSTEMS AND HUMAN WELL-BEING: CURRENT STATE AND TRENDS, VOLUME 1, at x (2005).

20 CONCEPTUAL FRAMEWORK WORKING GRP., *supra* note 18, at 56.

21 *Id.* at 59–60.

22 *Id.* at 60.

23 *Id.* at 56, 57 fig.2.1.

24 *Id.* at 57–58.

encompass the intangible benefits of ecosystems to human spirit, intellect, expression, recreation, and heritage.[25]

From the perspective of human welfare, community and ecosystem effects of migrating species can be categorized as positive, insofar as ecosystem services are provided, or negative, insofar as human welfare is harmed. Examples of ecosystem services provided by migratory species are described in Part II.A. below. In Part II.B. we discuss ecosystem disservices of migratory species, such as dispersal of human pathogens and invasive species or the movement and accumulation of toxins.

Table 1. Examples of ecological processes associated with migration, classified by ecosystem services (benefits to humans). Supporting services are foundational to provisioning, regulating, and cultural services. This table is meant to be illustrative, not exhaustive.

Ecosystem Service	Type	Ecological Processes	Migration Example
Supporting	Nutrient supply	Excretion, predation, decomposition	Salmon,[26] Alewives[27]
	Nutrient supply	Excretion	Seabirds[28]
	Nutrient cycling	Grazing, excretion	American Buffalo,[29] African Serengeti ungulates[30]

25 *Id.* at 58–59.

26 Morgan D. Hocking & Thomas E. Reimchen, *Salmon Species, Density and Watershed Size Predict Magnitude of Marine Enrichment in Riparian Food Webs*, 118 OIKOS 1307, 1307 (2009); David J. Janetski et al., *Pacific Salmon Effects on Stream Ecosystems: A Quantitative Synthesis*, 159 OECOLOGIA 583, 584 (2009).

27 Annika W. Walters et al., *Anadromous Alewives* (Alosa pseudoharengus) *Contribute Marine-Derived Nutrients to Coastal Stream Food Webs*, 66 CANADIAN J. FISHERIES & AQUATIC SCI. 439, 439 (2009).

28 Wendy B. Anderson & Gary A. Polis, *Nutrient Fluxes from Water to Land: Seabirds Affect Plant Nutrient Status on Gulf of California Islands*, 118 OECOLOGIA 324, 325 (1999); Katherine Griffiths et al., *Comparing Nitrogen Isotopic Signals Between Bulk Sediments and Invertebrate Remains in High Arctic Seabird-Influenced Ponds*, 44 J. PALEOLIMNOLOGY 405, 405–07 (2009).

29 Douglas A. Frank, *Ungulate Regulation of Ecosystem Processes in Yellowstone National Park: Direct and Feedback Effects*, 26 WILDLIFE SOC'Y BULL. 410, 416 (1998); Douglas A. Frank & R. David Evans, *Effects of Native Grazers on Grassland N Cycling in Yellowstone National Park*, 78 ECOLOGY 2238, 2238 (1997); Douglas A. Frank et al., *Consumer Control of Grassland Plant Production*, 83 ECOLOGY 602, 604 (2002); Alan K. Knapp et al., *The Keystone Role of Bison in North American Tallgrass Prairie*, 49 BIOSCIENCE 39, 41 (1999).

30 Douglas A. Frank et al., *The Ecology of the Earth's Grazing Ecosystems*, 48 BIOSCIENCE 513, 518 (1998); S. J. McNaughton, *Ecology of a Grazing System: The Serengeti*, 55 ECOLOGICAL MONOGRAPHS 259, 269–70 (1985) [hereinafter McNaughton, *Ecology*]; S. J. McNaughton et al., *Promotion of the Cycling of Diet-Enhancing Nutrients by African Grazers*, 278 SCI. 1798, 1800 (1997) [hereinafter McNaughton et al., *Promotion*]; S. J. McNaughton et al., *Ecosystem Catalysis: Soil Urease Activity and Grazing in the Serengeti Ecosystem*, 80 OIKOS 467, 468 (1997) [hereinafter McNaughton et al., *Ecosystem Catalysis*].

Supporting (cont.)	Maintenance of biodiversity	Wallowing, grazing, excretion	American Buffalo[31] African Serengeti ungulates[32]
Provisioning	Food	Predation (fishing)	Salmon[33]
	Food	Predation (hunting)	American buffalo,[34] African Serengeti ungulates[35]
Regulating	Engineering	Spawning	Salmon[36]
	Engineering	Wallowing, grazing	American Buffalo,[37] African Serengeti ungulates[38]
	Seed dispersal	Seed dispersal	American Buffalo[39]
	Seed dispersal	Seed dispersal	African Serengeti ungulates[40]
	Pollination	Pollination	Bats[41]
	Pollination	Pollination	Hummingbirds[42]

31 Bryan R. Coppedge & James H. Shaw, *American Bison* Bison bison *Wallowing Behavior and Wallow Formation on Tallgrass Prairie*, 45 ACTA THERIOLOGICA 103, 104 (2000); Samuel D. Fuhlendorf et al., *Pyric Herbivory: Rewilding Landscapes Through the Recoupling of Fire and Grazing*, 23 CONSERVATION BIOLOGY 588, 596 (2009); Knapp, *supra* note 29, at 44–45.

32 N. Thompson Hobbs, *Modification of Ecosystems by Ungulates*, 60 J. WILDLIFE MGMT. 695, 696 (1996).

33 Xanthippe Augerot & Courtland L. Smith, *Comparative Resilience in Five North Pacific Regional Salmon Fisheries*, 15 ECOLOGY & SOC'Y, no. 2, 2010, *available at* http://www.ecologyandsociety.org/vol15/iss2/art3/ES-2009-3247.pdf; Sarah K. Campbell & Virginia L. Butler, *Archaeological Evidence for Resilience of Pacific Northwest Salmon Populations and the Socioecological System over the Last ~7,500 Years*, 15 ECOLOGY & SOC'Y, no. 1, 2010, *available at* http://www.ecologyandsociety.org/vol15/iss1/art17/ES-2009-3151.pdf.

34 Curtis H. Freese et al., *Second Chance for the Plains Bison*, 136 BIOLOGICAL CONSERVATION 175, 178 (2007).

35 Kathlee A. Galvin et al., *Human Responses to Change: Modelling Household Decision Making in Western Serengeti, in* SERENGETI III: HUMAN IMPACTS ON ECOSYSTEM DYNAMICS 325, 333–34 (A. R. E. Sinclair et al. eds., 2008).

36 Jonathan W. Moore et al., *Biotic Control of Stream Fluxes: Spawning Salmon Drive Nutrient and Matter Export*, 88 ECOLOGY 1278, 1279 (2007); Daniel E. Schindler et al., *Pacific Salmon and the Ecology of Coastal Ecosystems*, 1 FRONTIERS ECOLOGY & ENV'T 31, 31 (2003).

37 Coppedge & Shaw, *supra* note 31, at 108; Knapp, *supra* note 29, at 45.

38 Hobbs, *supra* note 32, at 696.

39 Claudia A. Rosas et al., *Seed Dispersal by* Bison bison *in a Tallgrass Prairie*, 19 J. VEGETATION SCI. 769, 776 (2008).

40 Suzanne J. Milton & W. R. J. Dean, *Seeds Dispersed in Dung of Insectivores and Herbivores in Semi-Arid Southern Africa*, 47 J. ARID ENVIRONMENTS 465, 480 (2001).

41 Laura López-Hoffman et al., *Ecosystem Services Across Borders: A Framework for Transboundary Conservation Policy*, 8 FRONTIERS ECOLOGY & ENV'T 84, 86 (2010).

42 Eric S. Menges, *Factors Limiting Fecundity and Gremination in Small Populations of* Silene regia (Caryophyllaceae)*, a Rare Hummingbird-Pollinated Prairie Forb*, 133 AM. MIDLAND

Regulating (cont.)	Pest Control	Insectivory	Bats[43]
	Pest Control	Insectivory	Birds[44]
	Carbon Sequestration	Grazing, excretion (maintains grassland primary productivity)	African Serengeti ungulates[45]
Cultural	Spiritual, aesthetic, or intellectual fulfillment; cultural expression; recreation		Salmon,[46] Whales,[47] Monarch Butterflies,[48] African Serengeti ungulates[49]

Table 2. Examples of ecological processes associated with migration that have negative consequences for humans.

Ecosystem Disservice	Ecological Process	Migration Example
Disease	Dispersal of human pathogens	West Nile Virus/birds[50]

NATURALIST 242, 245 (1995); Richard J. Reynolds et al., *Pollinator Specialization and Pollination Syndromes of Three Related North American* Silene, 90 ECOLOGY 2077, 2081–82, 2082 tbl.2 (2009).

43 Cutler J. Cleveland et al., *Economic Value of the Pest Control Service Provided by Brazilian Free-Tailed Bats in South-Central Texas*, 4 FRONTIERS ECOLOGY & ENV'T 238, 238, 242 (2006).

44 Russell Greenberg et al., *The Impact of Avian Insectivory on Arthropods and Leaf Damage in Some Guatemalan Coffee Plantations*, 81 ECOLOGY 1750, 1750, 1753 (2000). Russell Greenberg & Javier Salgardo Ortiz, *Interspecific Defense of Pasture Trees by Wintering Yellow Warblers,* 111 AUK 672, 674, 678–80 (1994).

45 Andy Dobson, *Food-Web Structure and Ecosystem Services: Insights from the Serengeti*, 364 PHIL. TRANSACTIONS ROYAL SOC'Y B 1665, 1677 (2009).

46 Daniel L. Bottom et al., *Reconnecting Social and Ecological Resilience in Salmon Ecosystems*, 14 ECOLOGY & SOC'Y, no. 14, 2009, *available at* http://www.ecologyandsociety.org/vol14/iss1/art5/ES-2008-2734.pdf; Augerot & Smith, *supra* note 33.

47 Mason Weinrich & Claudio Corbelli, *Does Whale Watching in Southern New England Impact Humpback Whale* (Megaptera novaeangliae) *Calf Production or Calf Survival?*, 142 BIOLOGICAL CONSERVATION 2931, 2931 (2009) (discussing concerns about potential impacts to humpback whales from whale-watching tourism).

48 López-Hoffman et al., *supra* note 41, at 87.

49 Dobson, *supra* note 45, at 1677.

50 Kurt D. Reed et al., *Birds, Migration and Emerging Zoonoses: West Nile Virus, Lyme Disease, Influenza A and Enteropathogens*, 1 CLINICAL MED. & RES. 5, 8–9 (2003).

Disease (cont.)	Dispersal of pathogen vectors	Ticks/birds[51]
Invasion	Biological invasion by exotic species	Sea lampreys[52]
		Exotic plants/ungulates[53]
Herbivory	Migration of agricultural pests	Fall Armyworm[54]
		Migratory locusts[55]
Chemical pollution	Transport of toxins	Seabirds[56] Fish[57]

A. Ecosystem Services of Migratory Species

Migratory species can provide all four categories of ecosystem services: supporting, provisioning, regulating, and cultural (Table 1). For example, migratory fish (e.g., salmon,[58] alewives[59]), seabirds,[60] and hoofed grazing mammals (ungulates) of the American plains or African Serengeti[61] are well known avenues by which large quantities of nutrients are recycled via excretion, predation, and decomposition, thus enriching the fertility of

51 Muhammad G. Morshed et al., *Migratory Songbirds Disperse Ticks Across Canada, and First Isolation of the Lyme Disease Spirochete,* Borrelia burgdorferi*, From the Avian Tick,* Ixodes auritulus, 91 J. PARASITOLOGY 780, 781, 786 (2005).

52 *See generally* T.C. Pratt et al., *Balancing Aquatic Habitat Fragmentation and Control of Invasive Species: Enhancing Selective Fish Passage at Sea Lamprey Control Barriers*, 138 TRANSACTIONS AM. FISHERIES SOC'Y 652 (2009) (discussing the effectiveness of control barriers designed to allow passage of native fish, while obstructing passage of invasive sea lamprey).

53 Mason W. Kulbaba et al., *Morphological and Ecological Relationships Between Burrs and Furs*, 161 AM. MIDLAND NATURALIST 380, 380, 384 (2009) (noting high rates of adherence to bison and deer fur by certain seeds of invasive plant species).

54 E. R. Mitchell et al., *Seasonal Periodicity of Fall Armyworm, (*Lepidoptera: Noctuidae*) in the Caribbean Basin and Northward to Canada*, 26 J. ENTOMOLOGICAL SCI. 39, 48–49 (1991).

55 David M. Hunter, *Advances in the Control of Locusts (*Orthoptera: Acrididae*) in Eastern Australia: From Crop Protection to Preventive Control*, 43 AUSTRALIAN J. ENTOMOLOGY 293, 293 (2004).

56 Andrea H. Buckman et al., *Organochlorine Contaminants in Seven Species of Arctic Seabirds from Northern Baffin Bay*, 128 ENVTL. POLLUTION 327, 327, 334, 336 (2004); Jules M. Blais et al., *Arctic Seabirds Transport Marine-Derived Contaminants*, 309 SCIENCE 445, 445 (2005); Neal Michelutti et al., *Seabird-Driven Shifts in Arctic Pond Ecosystems*, 276 PROC. ROYAL SOC'Y B 591, 594–95 (2009).

57 Sara Hardell et al., *Levels of Polychlorinated Biphenyls (PCBs) and Three Organochlorine Pesticides in Fish from the Aleutian Islands of Alaska*, 5 PLOS ONE, no. 8, Aug. 2010, at 1–2, 9–10, *available at* http://www.plosone.org/article/fetchObjectAttachment.action?uri=info%3Adoi%2F10.1371%2Fjournal.pone.0012396&representation=PDF.

58 Schindler et al., *supra* note 36, at 31–32.

59 Walters et al., *supra* note 27, at 439; Derek C. West et al., *Nutrient Loading by Anadromous Alewife (*Alosa pseudoharengus*): Contemporary Patterns and Predictions for Restoration Efforts*, 67 CANADIAN J. FISHERIES & AQUATIC SCI. 1211, 1212 (2010).

60 Griffiths et. al., *supra* note 28, at 405.

61 *See generally* Frank et al., *supra* note 30 (describing functional similarities between the grazing ecosystems of the Serengeti and Yellowstone).

ecosystems and providing a key supporting ecosystem service.[62] Another supporting service is the maintenance of biodiversity. The wallowing and grazing activities of ungulates provide this supporting service by creating different types of microhabitats that sustain distinct assemblages of plant species.[63] As a provisioning ecosystem service, migratory species are fished and hunted, providing humans with food and materials.[64] Migratory species can also provide important regulating ecosystem services such as ecosystem engineering, modulation of climate, seed dispersal, pollination, and pest control. For example, migratory birds and bats are important pollinators and seed dispersers in many systems and thereby directly influence the structure and dynamics of plant communities, including agricultural crops and species of conservation concern.[65] Additionally, migratory species provide a variety of cultural services, often intertwined with fishing, hunting, or other food provisioning services.[66] The willingness of people to travel and expend significant amounts of money for things like bird watching, observing marine mammals and turtles, and African safari adventures is evidence of the important cultural services of migratory species.[67] Migratory species provide especially valuable cultural services because their migration pathways are typically predictable in time and space so that ecotourists are virtually guaranteed to see them.[68]

B. Negative Effects of Migratory Species

While most attention focuses on the various advantages accruing to migratory species and their resident ecosystems as a result of migrations, we also recognize that there can be significant negative consequences of migration for humans and ecosystems (Table 2). One of the most dramatic

62 Costanza et al., *supra* note 17, at 254 tbl.1.

63 Knapp et al., *supra* note 29, at 40–41, 45.

64 *See* Campbell & Butler, *supra* note 33, at 9 (noting that native populations in the Northwest utilized the migratory salmon populations as food and trade resources); *see also* Evolutionary Distinct & Globally Endangered (EDGE), Sperm Whale (*Physeter macrocephalus*), http://www.edgeofexistence.org/mammals/species_info.php?id=109 (last visited Mar. 27, 2011) (noting that sperm whales, a migratory species, have long been hunted for the oil contained in their bodies).

65 *See* Theodore H. Fleming et al., *Sonoran Desert Columnar Cacti and the Evolution of Generalized Pollination Systems*, 71 ECOLOGICAL MONOGRAPHS 511, 512–513 (2001) (noting that migratory bats and birds are important pollinators for columnar cacti—a species of conservation concern—in the Sonoran Desert, and that these migratory species directly influence the development of the cacti's specialization mechanisms); X. J. Ge et al., *Population Structure of Wild Bananas, Musa balbisiana, in China Determined by SSR Fingerprinting and cpDNA PCR-RFLP*, 14 MOLECULAR ECOLOGY 933, 933–935 (2005) (asserting that the genetic viability of the wild banana populations—an important agricultural crop in China—is dependent on pollinantion and seed dispersal functions from migratory bats).

66 Bottom et al., *supra* note 46.

67 Joanna Burger et al., *Ecotourism and Birds in Coastal New Jersey: Contrasting Responses of Birds, Tourists, and Managers*, 22 ENVTL. CONSERVATION 56, 56, 59 (1995); Dobson, *supra* note 45, at 1677.

68 Burger et al., *supra* note 67, at 57.

examples is the spread of infectious disease by migratory species. For example, West Nile Virus and Avian Influenza Virus have been distributed widely by birds, and have resulted in many human deaths.[69] The dispersal of pathogens by migratory species is more significant with longer distance migrations and where the pathogen has a broad host range, potentially infecting many species along the migration route.[70] Migratory species can also serve to move and concentrate toxic chemicals such as heavy metals or pesticides.[71] Likewise, invasive species, which can disrupt resident communities and ecosystems, can be dispersed by migratory species[72] or may be migratory themselves and self-spread into new areas.[73] For example, sea lamprey (*Petromyzon marinus*) normally live in the ocean and spawn in fresh water, but their shift to a Great Lakes–feeder streams-based migration has had a huge negative impact on native fish stocks and fisheries that provision human food supply.[74] Agriculture may also be severely impacted by migratory species. A good example of this is the fall armyworm (*Spodoptera frugiperda*), which forms permanent populations in the Caribbean region, but migrates northwards over the growing season and can cause substantial damage to grass crops like rice and corn.[75] In summary, significant negative consequences can result from abundant migratory species that are pests or disease vectors, to the extent humans intervene to prevent migration or eliminate the migrants.[76] In that sense, migration is no different than other ecological processes such as predation where there are both costs and benefits, and the net value depends on the eye of the beholder.

III. CASE STUDIES

Here we present case studies that illustrate the ecosystem services and disservices of migratory species for a taxonomically diverse set of animal species. We highlight the relationships between the abundance of migratory species and their services or disservices.

69 Anne-Laure Brochet et al., *The Potential Distance of Highly Pathogenic Avian Influenza Virus Dispersal by Mallard, Common Teal and Eurasian Pochard*, 6 ECOHEALTH 449, 452, 545–55 (2009); Robert J. Dusek et al., *Prevalence of West Nile Virus in Migratory Birds During Spring and Fall Migration*, 81 AM. J. TROPICAL MED. HYGIENE 1151, 1151, 1155 (2009).

70 Reed et al., *supra* note 50, at 6–7.

71 *See* Blais et al., *supra* note 56, at 445.

72 Kulbaba et al., *supra* note 53, at 380 ("Local and intercontinental movement of livestock and humans has created ideal circumstances for long-range [external seed transportation by animals] that has been responsible for the introduction of invasive plant species to many parts of the world.").

73 Pratt et al., *supra* note 52, at 653.

74 IND. DEP'T OF NATURAL RES., AQUATIC INVASIVE SPECIES: SEA LAMPREY (2005), *available at* http://www.in.gov/dnr/files/SEA_LAMPREY1.pdf.

75 Mitchell et al., *supra* note 54, at 39–40, 43.

76 IND. DEP'T OF NATURAL RES., *supra* note 74; Hunter, *supra* note 55, at 293–94.

A. Serengeti Ungulates

The African Serengeti supports the largest migratory populations of hoofed grazing mammals (ungulates) left in the world, including about 1.3 million wildebeest (*Connochaetes taurinus*), 200,000 zebra (*Equus burchelli*), 440,000 Thompson's Gazelle (*Gazella thomsoni*), and 15,500 eland (*Taurotragus oryx*).[77] The Serengeti is one of the last examples of a "grazing ecosystem," defined by abundant migratory ungulates and their grazing activities, once characteristic of the Earth's grasslands before the expansion of industrial agriculture and cattle ranching.[78] Wildebeest and other migratory ungulates provide the supporting ecosystem service of nutrient cycling. These animals have coevolved with grasses in such a way that ungulate grazing and subsequent excretion (primarily urine) rapidly recycles essential nutrients, like nitrogen, between plant and soil pools.[79] Both the abundance of wild ungulates and their migratory nature are keys to these dynamics.[80] High herbivore biomass in the Serengeti—the highest of any terrestrial ecosystem—results in high plant consumption rates, on average about 60% of available foliage per year, and correspondingly high nutrient recycling and plant growth rates.[81] When grasses develop in a "green wave" across the Serengeti with the advance of the rainy season, herds migrate as they track the most nutrient rich grasses, plants have adequate time to regrow between bouts of grazing, and overgrazing is avoided.[82]

The rapid nutrient recycling promoted by the Serengeti's abundant migratory ungulates contributes to the lushness and fecundity of the entire ecosystem.[83] As a result, migratory ungulates support other important ecosystem services for humans, including the cultural service of ecotourism, a major economic engine for the region, and the climate regulating service of carbon sequestration.[84] A traditional ecosystem service provided by migratory ungulates for hunter-gatherers was food and materials (e.g. furs, skin, bone).[85] Some groups that benefitted from this ecosystem service still exist in the Serengeti today.[86] However, human population pressure associated with shifts to settled pastoralist and agriculturalist ways of life is now too great to allow sustainable hunting, and poaching by poor villagers

77 A. R. E. Sinclair et al., *Historical and Future Changes to the Serengeti Ecosystem*, *in* SERENGETI III: HUMAN IMPACTS ON ECOSYSTEM DYNAMICS, *supra* note 35, at 7, 19; Simon A. R. Mduma & J. Grant C. Hopcraft, *The Main Herbivorous Mammals and Crocodiles in the Greater Serengeti Ecosystem*, *in* SERENGETI III: HUMAN IMPACTS ON ECOSYSTEM DYNAMICS, *supra* note 35, app. tbl.A.1.

78 Frank et al., *supra* note 30, at 513.

79 McNaughton, *Ecology*, *supra* note 30, at 285; McNaughton et al., *Ecosystem Catalysis*, *supra* note 30, at 467; McNaughton et al., *Promotion*, *supra* note 30, at 1798.

80 McNaughton, *Ecology*, *supra* note 30, at 281–82; Frank et al., *supra* note 30, at 516–17.

81 Frank et al., *supra* note 30, at 514.

82 *Id.* at 513, 515, 518–19.

83 McNaughton, *Ecology*, *supra* note 30, at 285–86.

84 Dobson, *supra* note 45, at 1675–77.

85 *Id.* at 1676.

86 *Id.*

results in declines in wildebeest populations.[87] Other threats posed to migratory ungulates are habitat destruction and degradation from encroaching agriculture[88] and climate change.[89] In the absence of migratory ungulates, grassland structure and function is dramatically altered, with slowed recycling of nutrients and decreases in average grass production.[90]

B. Pacific Salmon

Perhaps one of the most famous and mysterious of migrating species are Pacific salmon (*Oncorhynchus*), a complex of seven species native to the North Pacific rim, collectively ranging from California north to Canada and Alaska, and south again to Russia, Japan, and Korea.[91] Pacific salmon are anadromous, doing most of their feeding, growth and maturation in the ocean before migrating back to the freshwater stream, river or lakeshore in which they originally hatched, where they breed and lay their own eggs (spawn), and then die.[92] For millennia, this life history has brought millions of adult salmon to coastal freshwater systems in late summer through early winter, providing a food provisioning service to indigenous coastal and near-coastal peoples.[93] As an integral part of spiritual tradition and cultural heritage, Pacific salmon also provide cultural services.[94] After colonization and rise of European cultures, the provisioning services of Pacific salmon were adopted by European settlers and led to major commercial and national fishing industries for domestic and export markets and to new forms of cultural services, including sport fishing.[95] The food provisioning

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87 Stephen Polasky et al., *Larger-Scale Influences on the Serengeti Ecosystem: National and International Policy, Economics, and Human Demography*, *in* SERENGETI III: HUMAN IMPACTS ON ECOSYSTEM DYNAMICS, *supra* note 35, at 347, 353, 367–68.

88 Sinclair et al., *supra* note 77, at 34–35 (noting that much of the land around the Seregenti has been converted to farm land interrupting the wildebeest migration); Mike Norton-Griffiths et al., *Land Use Economics in that Mara Area of the Serengeti Ecosystem*, *in* SERENGETI III: HUMAN IMPACTS ON ECOSYSTEM DYNAMICS, *supra* note 35, at 379, 379, 397, 402; William D. Newark, *Isolation of African Protected Areas*, 6 FRONTIERS ECOLOGY & ENV'T 321, 321, 322 (2008).

89 Dobson, *supra* note 45, at 1677; *see also* Mark E. Ritchie, *Global Environmental Changes and Their Impact on the Serengeti*, *in* SERENGETI III: HUMAN IMPACTS ON ECOSYSTEM DYNAMICS, *supra* note 35, at 183, 184.

90 Frank et al., *supra* note 30, at 520.

91 C. Groot & L. Margolis, *Preface* to PACIFIC SALMON LIFE HISTORIES, at ix, ix (C. Groot & L. Margolis eds. 1998).

92 *Id.*

93 Campbell & Butler, *supra* note 33.

94 Bottom et al., *supra* note 46.

95 *See* NAT'L RESEARCH COUNCIL, UPSTREAM: SALMON AND SOCIETY IN THE PACIFIC NORTHWEST 46–47 (Nat'l Acad. Press ed. 1996) (noting that the arrival of Euro-American settlers transformed the culture and industry of the Pacific region); *id.* at 49 (discussing the rise of commercial fishing in the Pacific region after the arrival of settlers, and its relationship to a national fishing industry); Augerot & Smith, *supra* note 33, at 5 (noting the import and export markets for Pacific salmon); *see generally* Robert W. Adler, *Restoring the Environment and Restoring Democracy: Lessons From the Colorado River*, 25 VA. ENVTL. L.J. 55, 89–90 (2007)

service of Pacific salmon is clearly a phenomenon of abundance, and as human population pressure has grown, overfishing and habitat loss have led to great reductions in the numbers and varieties of wild salmon stocks[96] and subsequent loss of livelihood and cultural services.[97]

Recent ecological studies reveal that, in addition to provisioning and cultural services, Pacific salmon also provide substantial supporting and regulating services to coastal freshwater and terrestrial ecosystems in the form of nutrient subsidies and ecosystem engineering.[98] Because virtually all of their feeding and growth occurs during their time at sea, the migration of millions of salmon back to the freshwaters of their birth to spawn and die entails large transfers of energy and nutrients from marine to coastal systems in the form of excretory waste, eggs and sperm, and carcasses.[99] These subsidies stoke the growth and productivity of many other organisms throughout coastal food webs, including other fish, bear, insects, birds, phytoplankton, and plants.[100] By digging shallow nests in gravel areas during spawning, Pacific salmon also act as ecosystem engineers as their activity alters many physical and biological variables, from particle size and water flow to algal cover and bottom-dwelling invertebrates.[101] These services vary in space and time, influenced by factors such as watershed area and

(discussing stocking of western rivers with non-native fish in the late 1800s, and that some of this stocking was fueled by settler pressure to expand the types of fish available for sport fishing); James K. Hein, Note, *The "Sound Science" Amendment to the Endangered Species Act: Why it Fails to Resolve the Klamath Basin Conflict*, 33 B.C. ENVTL. AFF. L. REV. 207, 211 (2005) (noting that fish in Oregon's Klamath River Basin historically supported tribal livelihood, but that when settlers arrived, a vibrant sports fishery sprung up).

96 NAT'L RESEARCH COUNCIL, *supra* note 95, at 73; Ted Gresh et al., *An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem*, 25 FISHERIES 15, 15 (2000); *see also* NW. Reg'l Office, Nat'l Oceanic & Atmospheric Admin., Salmon Populations, http://www.nwr.noaa.gov/ESA-Salmon-Listings/Salmon-Populations/Index.cfm (last visited Mar. 10, 2011).

97 Irene E. Martin, *Resilience in Lower Columbia River Salmon Communities*, 13 ECOLOGY & SOC'Y, no. 2, 2008, *available at* http://www.ecologyandsociety.org/vol13/iss2/art23/ES-2008-2609.pdf; Bottom et al., *supra* note 46.

98 Hocking & Reimchen, *supra* note 26, at 1307–08; Janetski et al., *supra* note 26, at 584; Schindler et al., *supra* note 36, at 31.

99 Schindler et al., *supra* note 36, at 31–34.

100 Katie S. Christie & Thomas E. Reimchen, *Presence of Salmon Increases Passerine Density on Pacific Northwest Streams*, 125 AUK 51, 51–52 (2008) (discussing the effects of large amounts of salmon biomass transported to forests and speculating that salmon biomass increases density and diversity of songbird populations adjacent to salmon streams); Hocking & Reimchen, *supra* note 26, at 1307 (discussing salmon biomass subsidies to insect and plant populations); Janetski et al., *supra* note 26, at 583–84 ("Nutrients delivered by salmon can increase the abundance and growth rates of aquatic biota several fold."); T. E. Reimchen et al., *Isotopic Evidence for Enrichment of Salmon-Derived Nutrients in Vegetation, Soil, and Insects in Riparian Zone in Coastal British Columbia*, 34 AM. FISHERIES SOC'Y SYMPOSIUM 59, 68 (2002) (discussing salmon as nutrient source for bears and insects such as the blowfly and carabid beetle).

101 Schindler et al., *supra* note 36, at 33; *see also* Janetski et al., *supra* note 26, at 584 ("Disturbance during [salmon nest] construction can reduce the abundance of benthic organisms . . . as well as increase sediment export from watersheds.").

sediment size, but also strongly by the biomass of returning salmon.[102] Indeed, analyses suggest that severe declines in salmon abundances in the Pacific Northwest (Washington, Oregon, Idaho, and California) over the past century has led to a greater than 90% reduction in the original marine nutrient subsidy reaching those coastal ecosystems,[103] which raises concerns whether the loss of this supporting service could prevent system recovery.[104]

C. Long-Nosed Bats and Hummingbirds

Bats provide an important regulating service as pollinators of many night-blooming plant species, including economically important agaves of the New World deserts. Bat-pollinated plants have a characteristic syndrome of characters including robust flowers, light flower colors, protein rich pollen, copious nectar produced primarily at night and odors like ripening fruit.[105] In particular, *Agave* species produce profuse floral displays with typical characteristics of bat pollination.[106] The large floral displays, simultaneous flowering, and dense plant populations serve to attract abundant pollinator populations.[107] Agaves are ecologically important[108] and support significant economic interests in Mexico, notably as the base ingredient of tequila and mezcal.[109] Two species of long-nosed bats (*Leptonycteris curasoae* and *L. nivalis*) feed primarily on agave species and columnar cacti, consuming pollen and nectar, and dispersing pollen from plant to plant to effect pollination.[110] The two species of *Leptonycteris* are

102 Janetski et al., *supra* note 26, at 586, 588; Hockings & Reimchen, *supra* note 26, at 1307, 1312, 1315–16.

103 *See* Gresh et al., *supra* note 96, at 15, 18 (explaining that only 5% to 7% of the marine-derived nitrogen and phosphorus previously delivered to the rivers of the Pacific Northwest now reach those waters); Bottom et al., *supra* note 46.

104 *See* Bottom et al., *supra* note 46 ("[Some authors] hypothesize that disruption of the marine feedback loop to coastal rivers could cause a downward spiral in freshwater ecosystems and a shift to a persistent low-productivity regime that is resistant to salmon recovery.").

105 K. FÆGRI & L. VAN DER PIJL, THE PRINCIPLES OF POLLINATION ECOLOGY 154 tbl.8 (2nd ed. 1971.).

106 Liz A. Slauson, *Pollination Biology of Two Chiropterophilous Agaves in Arizona*, 87 AM. J. BOTANY 825, 825 (2000).

107 *See* Martha Rocha et al., *Reproductive Ecology of Five Sympatric* Agave littaea *(Agavaceae) Species in Central Mexico*, 92 AM. J. BOTANY 1330,1330 (2005) (arguing that agaves have "one of the most spectacular floral displays in nature," and that the specie's floral traits "suggest adaptation to bat pollination").

108 Alejandro Martínez-Palacios et al., *Genetic Diversity of the Endangered Endemic* Agave victoriae-reginae *(Agavaceae) in the Chihuahuan Desert*, 86 AM. J. BOTANY 1093, 1093 (1999).

109 *See* Emilio Godoy, *Tequila Leaves Environmental Hangover*, INTER PRESS SERVICE, Aug. 9, 2009, http://ipsnews.net/print.asp?idnews=47999 (last visited Feb. 11, 2011) (detailing the economic importance of tequila to Mexico, including the country's 118 tequila factories and 715 brands); Ryan Thomas, *Tequila—A Bit of History*, LOS CABOS MAG., Oct. 2002, http://www.loscabosguide.com/tequila/tequila-history.htm (last visited Feb. 11, 2011) (explaining that mezcal is the "sister beverage" of tequila).

110 *See* Sara V. Good-Avila et al., *Timing and Rate of Speciation in* Agave *(Agavaceae)*, 103 PROC. NAT'L ACAD. SCI. 9124, 9127 (2006) (documenting that these two species of bats feed off agave plants); Rocha et al., *supra* note 107, at 1335; Slauson, *supra* note 106, at 825 (explaining

the major pollinators of Blue Agave (*Agave tequilana*) which is the primary ingredient of tequila.[111] Along with the Mexican Long-tongued Bat (*Choeronycteris mexicana*), they represent the primary nectarivorous bats in North America that migrate from the southwestern United States to the Mexican plateau during winter.[112] During migrations, long-nosed bats follow the so-called "nectar corridor" that provides a dependable supply of flowers and nectar.[113] The primary threats to endangered long-nosed bats include the disruption or destruction of caves where they roost.[114] The decline of long-nosed bats and their pollination services represents a threat to the genetic diversity and persistence to several agave species, including species important for the tequila industry.[115] Tequila is an important economic product in Mexico for both large corporate producers as well as a growing number of smaller, artisan producers who use a greater genetic and species diversity of agave.[116] At present, corporate tequila producers propagate agave vegetatively and do not depend on pollination services by bats.[117] However, genetic monocultures of agave are susceptible to pathogen epidemics, unlike genetically diverse agave resulting from cross-pollination by bats.[118]

Migratory hummingbirds provide similar regulatory ecosystem services, in this case by pollinating wildflowers. Fire pink (*Silene virginica*) is one of the most recognizable and beloved wildflowers of the eastern United States.[119] Several experimental studies have demonstrated that the ruby-throated hummingbird is the major pollinator of fire pink.[120] Seed set is

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that the columnar cacti and agave form a "nectar corridor" for bats, including the lesser long-nosed bat, that provide essential sustenance during migration).

111 López-Hoffman et al., *supra* note 41, at 86.

112 Santiago Arizaga et al., *Pollination Ecology of* Agave macroacantha *(Agavaceae) in a Mexican Tropical Desert. II. The Role of Pollinators*, 87 AM. J. BOTANY 1011, 1015 (2000); *see also* Rodrigo A. Medellín & Steve Walker, *Nightly Wings, Nectar Sips*, 28 ENDANGERED SPECIES BULL., no. 3, May/June 2003 at 16, 16–17 (explaining that the migration is a complex one, in which not all of the species migrate at the same time).

113 Arizaga et al., *supra* note 112, at 1015.

114 *See* López-Hoffman et al., *supra* note 41, at 86 (explaining that millions of the bats have been barred from their roosts by ranchers—who mistake them for vampire bats—and highway construciton, vandals, and urban development have destroyed bat caves).

115 *See* Hector T. Arita & Don E. Wilson, *Long-Nosed Bats and Agaves: The Tequila Connection*, 5 BATS MAG., no. 4, Dec. 1987, at 3, *available at* http://www.batcon.org/archives/batsmag/v5n4-4.html (detailing the Mexican tequila industry).

116 López-Hoffman et al., *supra* note 41, at 86 (explaining that although corporate producers are seeking to replace bat pollination with technological solutions, smaller-scale artisan tequila producers are "interested in collaborating with conservation biologists to develop long-term solutions to bat conservation in Mexico and the U.S.").

117 *See id.*

118 *See id.* (detailing a devastating loss to homogenous agave crops in the 1980s and in 1996–1997 brought on by pathogens).

119 *See* Charles B. Fenster & Michele R. Dudash, *Spatiotemporal Variation in the Role of Hummingbirds as Pollinators of* Silene virginica, 82 ECOLOGY 844, 845 (2001).

120 *See, e.g.*, *id.* at 845, 848 (finding that humingbirds are the most important pollinator at study sites, but their importance varies across years and between sites); Charles B. Fenster & Michele R. Dudash, *Nectar Reward and Advertisement in Hummingbird-Pollinated* Silene virginica *(Caryophyllaceae)*, 93 AM. J. BOTANY 1800, 1801 (2006) (describing *Silene virginica* as

greatly reduced if hummingbirds are excluded.[121] A congeneric species, Royal Catchfly (*Silene regia*), is an endangered species of prairie habitats,[122] which have been largely lost due to agriculture.[123] Experimental exclusion of hummingbirds sharply reduced fruit and seed production of this rare species.[124] Thus, loss of pollination services provided by migratory hummingbirds could result in population losses or extinctions of dramatic native wildflowers, which themselves provide cultural ecosystem services.

D. Manatees

Marine mammals such as manatees provide numerous cultural services, including recreational, spiritual, and aesthetic benefits. The opportunity to observe manatees, whales and other marine mammals up close and in person holds tremendous appeal as judged by the amount of money people are willing to spend for these activities, which generate significant ecotourism revenues.[125] The Florida manatee (*Trichechus manatus latirostris*), a subspecies of the West Indian manatee,[126] was one of the original seventy-eight species on the endangered species list.[127] A major threat to their survival is injury from impacts with propeller-driven boats.[128] Florida manatees can be found in rivers and coastal areas of Florida, near the northern limit of their distribution.[129] In addition to cultural services, they also provide a valuable regulating service by eating aquatic weeds in

"[h]ummingbird-pollinated"); Reynolds et al., *supra* note 42, at 2084 (finding that *Silene virginica* is "specialized to pollination by hummingbirds").

121 *See* Fenster & Dudash, *supra* note 120, at 847–48 (explaining that in the authors' five-year study, hummingbirds were responsible for "12–67% of the amount of seed set per fruit").

122 Menges, *supra* note 42, at 243.

123 Ctr. for Plant Conservation, Silene regia, http://www.centerforplantconservation.org/collection/cpc_viewprofile.asp?CPCNum=4005 (last visited Feb. 14, 2011) (listing "conversion of its habitat to farmland" as one of the threats to the plant).

124 Menges, *supra* note 42, at 248.

125 *See* Kasey A. Stamation et al., *Behavioral Responses of Humpback Whales* (Megaptera novaeangliae) *to Whale-Watching Vessels on the Southeastern Coast of Australia*, 26 MARINE MAMMAL SCI. 98, 99 (2010) (noting that whale watching generates millions of dollars in eco-tourism revenue each year). *See generally* Weinrich & Corbelli, *supra* note 47, at 2931 (highlighting the rapid worldwide increase in eco-tourism in recent years).

126 *See* Charles J. Deutsch et al., *Seasonal Movements, Migratory Behavior, and Site Fidelity of West Indian Manatees Along the Atlantic Coast of the United States*, 67 J. WILDLIFE MGMT. (WILDLIFE MONOGRAPHS, NO. 151) 1, 3 (2003); *see also* Marine Mammal Comm'n, Florida Manatee (*Trichechus manatus latirostris*), http://www.mmc.gov/species/floridamanatee.html (last visited Feb. 11, 2011).

127 Endangered Species, 32 Fed. Reg. 4001, 4001 (Mar. 11, 1967) (outlining the list of original endangered species, including the Florida Manatee); *see* Oliver A. Houck, *The Endangered Species Act and Its Implementation by the U.S. Departments of Interior and Commerce*, 64 U. COLO. L. REV. 277, 282, 282 n.23 (1993) (confirming that 32 Fed. Reg. 4001 was the first published list of endangered species by the U.S. government).

128 Keith Rizzardi, *Toothless? The Endangered Manatee and the Florida Manatee Sanctuary Act*, 24 FLA. ST. U. L. REV. 377, 384 (1997).

129 Deutsch et al., *supra* note 126, at 3.

waterways that otherwise would have to be dredged.[130] Manatees are very sensitive to cold water and during winter months they migrate to warmer water refugia.[131] A common refuge is spring-fed rivers in central Florida that run at a constant temperature year-round. For example, more than three hundred manatees use the Crystal River during winter months.[132] The Marine Mammal Commission estimates that every year 100,000 tourists visit Crystal River, Florida to participate in manatee-watching activities.[133] In historical times, warmer water released from electrical power plant cooling towers has also attracted manatees.[134]

The migratory behavior of manatees seeking warmer water during the winter months is key to their wildlife-based tourism for several reasons. Large numbers of animals often congregate in relatively small areas near springs, making it easy to view multiple animals at the same time.[135] Manatees can often be viewed from the shoreline so observations do not require boats or scuba equipment, and the spring fed waters are typically crystal clear, making observations easier.[136] Also, manatees are relatively gregarious and friendly, so close encounters (swimming, touching) are easily attained.[137] Some people are concerned that these encounters might harm the manatees themselves.[138] In Central America, manatees are also subject to poaching but the warmer water temperatures do not result in the seasonal migrations and dense aggregations found in Florida[139] and so do not

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130 Barry D. Soloman et al., *The Florida Manatee and Eco-Tourism: Toward a Safe Minimum Standard*, 50 ECOLOGICAL ECON. 101, 112 (2004) (noting the amount of money not spent by Citrus County, Florida on mechanical and herbicidal treatment of vegetation in waterways because of manatee consumption and also detailing the cultural and economic benefits of manatees to the county).

131 Deutsch et al., *supra* note 126, at 3, 50 (explaining that Florida Manatees migrate to warmer water areas during the winter, and that the animals are sensitive to water temperature changes).

132 Michael G. Sorice et al., *Managing Endangered Species Within the Use-Preservation Paradox: The Florida Manatee* (Trichechus manatus latirostris) *as a Tourism Attraction*, 37 ENVTL. MGMT. 69, 72 (2006).

133 *Id.*

134 Joel T. Bell, Characterization and Analysis of Artificial Warmwater Refugia and Their Use by the Florida Manatee (*Trichechus manatus latirostris*) on the East Coast of Florida 1 (May 1, 2000) (unpublished Master of Environmental Mangement thesis, Duke University) (on file with Pearse Memorial Library, Duke University).

135 Jill M. King & Joel T. Heinen, *An Assessment of the Behaviors of Overwintering Manatees as Influenced by Interactions with Tourists at Two Sites in Central Florida*, 117 BIOLOGICAL CONSERVATION 227, 228 (2004).

136 *See* Sorice et al., *supra* note 132, at 72 (noting that the clear water and open bay in Crystal River makes viewing manatees easy). *But cf. id.* (explaining that although the clear waters and open bay allow for easy viewing from public places, because much of the shoreline in the bay is private property, many viewers choose to go on encounters instead).

137 *Id.* at 72–73 (emphasizing the friendly nature of manatees and the intimacy that can occur between a manatee and a human who is snorkeling on an encounter).

138 King & Heinen, *supra* note 135, at 228 (noting the potential detrimental impacts on manatee behavior that these encounters might have).

139 Benjamín Morales-Vela et al., *Distribution and Habitat Use by Manatees (*Trichechus manatus manatus*) in Belize and Chetumal Bay, Mexico*, 95 BIOLOGICAL CONSERVATION 67, 73 (2000) (highlighting the issue of manatee poaching in Central America); *see* Joseph P. Healey

provide the same cultural services as Florida manatees. The reduction or extinction of manatees in Florida would have a negative impact on manatee-based tourism.[140]

E. Migratory Birds

By definition, ecosystem services contribute positively to human well-being.[141] It should also be recognized that migratory species can directly harm human well-being. Migratory birds that disperse human pathogens or their vectors over long distances provide a dramatic case of ecosystem disservices. The spread of global infectious disease by migratory birds is analogous to aircraft travel, where human pathogens can be carried very long distances in short periods of time.[142] For example, the rapid global spread of H5N1 avian influenza has been linked to migratory birds.[143] Molecular analyses of the H5N1 virus indicate that isolates of the virus throughout Eurasia are highly related to a strain identified in northwestern China where an outbreak killed 6000 wild birds in 2005.[144] The World Health Organization issued a report suggesting that the pathogenic H5N1 virus is adapted to some species of waterfowl and is traveling with them along their migratory routes.[145] This conclusion is strengthened by research demonstrating that genetically similar viruses have been isolated from mainland China and Hong Kong,[146] again suggesting that this virus is

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Library, Univ. of Mass. Bos., Protecting Manatee Populations, http://www.lib.umb.edu/node/3974 (last visited Feb. 11, 2011) (explaining that Central American manatees do not migrate because of consistently warm water in the region).

140 *See generally* King & Heinen et al., *supra* note 135, at 233 (suggesting that a reduced manatee population could have a negative economic impact on eco-tourism); Sorice et al., *supra* note 132, at 69–70 (noting the positive correlation between manatee numbers and tourism revenue).

141 MILLENNIUM ECOSYSTEM ASSESSMENT, ECOSYSTEMS AND HUMAN WELL-BEING: SYNTHESIS, at v (2005), *available at* http://www.maweb.org/documents/document.356.aspx.pdf (defining "ecosystem services" as the benefits people obtain from ecosystems).

142 *See* Reed et al., *supra* note 50, at 8–9 (noting the impact migratory birds had in quickly spreading diseases like West Nile Virus across the United States in a period of less than three years).

143 *See* Brochet et al., *supra* note 69, at 450 (linking the spread of the disease to migratory birds, including wild ducks).

144 Guihua Wang et al., *H5N1 Avian Influenza Re-emergence of Lake Qinghai: Phylogenetic and Antigenic Analyses of the Newly Isolated Viruses and Roles of Migratory Birds in Virus Circulation*, 89 J. GEN. VIROLOGY 697, 698–701 (2008) (noting that the QH05 strain responsible for the 2005 outbreak in China has been disseminated by migratory birds throughout Eurasia).

145 WORLD HEALTH ORG., AVIAN INFLUENZA AND HUMAN PANDEMIC INFLUENZA 5, 10 (2005), *available at* http://www.who.int/entity/mediacentre/events/2005/avian_influenza/summary_report_Nov_2005_meeting.pdf.

146 *See* Doan C. Nguyen et al., *Isolation and Characterization of Avian Influenza Viruses, Including Highly Pathogenic H5N1, from Poultry in Live Bird Markets in Hanoi, Vietnam, in 2001*, 79 J. VIROLOGY 4201, 4210 (2005), *available at* http://jvi.asm.org/cgi/reprint/79/7/4201.pdf (explaining that several strains of H5N1 virus have circulated throughout the globe, including genetically similar strains in Hong Kong and mainland China).

circulating among migratory birds. It has also been suggested that the initial spread of West Nile Virus in the United States along the eastern seacoast occurred along a major migratory corridor for birds,[147] although the inland spread of West Nile Virus may not be consistent with patterns of bird migration.[148]

Migratory birds can also be dispersal agents for disease vectors. Ticks are blood-sucking arthropods that serve as vectors for a wide range of human and wildlife diseases.[149] They are ectoparasites carried on the bodies of their vertebrate hosts, including birds.[150] Of over 50 species of birds surveyed for ticks during spring and fall migrations on Appledore Island, Maine, 2.4% of all spring migratory birds carried at least one tick—0.6% in fall—with at least seven species of ticks represented in previous New England studies.[151] Studies conducted in Canada also demonstrate that migratory birds are important dispersal agents of Lyme disease-infected ticks from the United States and Central America.[152] The causal agent of Lyme Disease is the bacterium *Borrelia burgdorferi*.[153] Over 40% of trapped birds in a Czech Republic study were infested with ticks, and over 20% of these ticks were infected with various subspecies of *Borrelia burgdorferi*.[154] The researchers concluded that during migration periods birds may transfer millions of *Borrelia*-infected ticks that could establish new endemic foci of Lyme disease in southwest Europe and Northern Africa.[155] Migrating birds may also play a role in the dispersal of encephalitis virus-infected ticks in Europe.[156] While more research is needed, it stands to reason that the greater the number of migrating birds, the more pathogens and pathogen-vectors will be dispersed.[157]

147 Reed et al., *supra* note 50, at 8.

148 *See* J. H. Rappole & Z. Hubálek, *Migratory Birds and West Nile Virus*, J. APPLIED MICROBIOLOGY (SYMP. SUPPLEMENT) 47S, 53S (2003) (noting that the disease, which took months to spread over a few hundred kilometers, would likely have done so in a matter of days if transported by migratory birds).

149 David T. Dennis & Joseph P. Peisman, *Overview of Tick-Borne Infections of Humans*, *in* TICK-BORNE DISEASES OF HUMANS 3, 3 (Jesse L. Goodman, et al. eds., 2005).

150 *Id.*; Sara R. Morris et al., *The Incidence and Effects of Ticks on Migrating Birds at a Stopover Site in Maine*, 14 NORTHEASTERN NATURALIST 171, 171 (2007).

151 Morris et al., *supra* note 150, at 171–72, 176.

152 John D. Scott et al., *Birds Disperse Ixodid (Acari: Ixodidae) and* Borrelia burgdorferi-*Infected Ticks in Canada*, 38 J. MED. ENTOMOLOGY 493, 495–96 (2001); Morshed et al., *supra* note 51, at 786.

153 Morshed et al., *supra*, note 51, at 780.

154 Lenka Dubska et al., *Differential Role of Passerine Birds in Distribution of* Borrelia *Spirochetes, Based on Data from Ticks Collected from Birds During the Postbreeding Migration Period in Central Europe*, 75 APPLIED & ENVTL. MICROBIOLOGY 596, 597 (2009).

155 *Id.* at 601.

156 Jonas Waldenström et al., *Migrating Birds and Tickborne Encephalitis Virus*, 13 EMERGING INFECTIOUS DISEASES 1215, 1217 (2007).

157 R. Jory Brinkerhoff et al., *Do Birds Affect Lyme Disease Risk? Range Expansion of the Vector-Borne Pathogen* Borrelia burgdorferi, 9 FRONTIERS ECOLOGY & ENV. 103 (2011).

IV. CONCLUSION

Traditional approaches to conservation, as exemplified in the federal Endangered Species Act,[158] take rarity as the threshold for concern that triggers protective action for species. More holistic approaches to conservation have since developed, such as the Fish and Wildlife Service's Policy on Maintaining the *Biological Integrity, Diversity, and Environmental Health* of the National Wildlife Refuge System.[159] Such system-based approaches to conservation implicitly recognize the interdependence of species with one another and with the physical and chemical environment of soil, water, and atmosphere. Yet shifting the emphasis from individual species protection to whole system integrity can also risk too coarse a lens, a missing of the "trees for the forest," to invert an old adage. Consideration of the functional role of species in ecosystems presents an intermediate perspective that we advance as an important complement to species-versus system-based endpoints of the conservation spectrum. Attention to species functional roles is consistent with the emerging recognition that species, as components of ecosystems, provide many life-supporting services to humans.[160] This functional perspective promotes a widening of the focus of conservation concern to include abundance in addition to the traditional focus on rarity.

To be sure, there are many valid reasons to conserve species, not least for their intrinsic value, apart from any instrumental value to humans.[161] Moreover, rare species may be essential to ecosystem services, either because they contribute disproportionately to current ecosystem functioning or because they provide insurance against a loss of functioning in the face of environmental changes. For example, so-called keystone species have effects on current ecosystem functioning disproportionate to their abundance.[162] Such keystone effects might arise because of particularly high per capita efficiencies[163] or from interactions with other species that in turn have strong effects on ecosystem functioning.[164] Rare species that

158 Endangered Species Act of 1973, 16 U.S.C. §§ 1531–1544 (2006).

159 *Id.* § 1531(b); Policy on Maintaining the Biological Integrity, Diversity, and Environmental Health of the National Wildlife Refuge System, 66 Fed. Reg. 3810, 3810 (Jan. 16, 2001).

160 *See* CONCEPTUAL FRAMEWORK WORKING GRP., *supra* note 18, at 52–53, 128 (noting the interrelated nature of ecosystems and their value in satisfying human material and nonmaterial needs).

161 Lawrence H. Goulder & Donald Kennedy, *Valuing Ecosystem Services: Philosophical Bases and Empirical Methods*, *in* NATURE'S SERVICES: SOCIETAL DEPENDENCE ON NATURAL ECOSYSTEMS, *supra* note 3, at 23, 31–34.

162 Mary E. Power et al., *Challenges in the Quest for Keystones*, 46 BIOSCIENCE 609, 609 (1996).

163 *See* Balvanera et al., *supra* note 8, at 361–63 (discussing efficiencies of species).

164 *See* James A. Estes & John F. Palmisano, *Sea Otters: Their Role in Structuring Nearshore Communites*, 185 SCI. 1058, 1060 (1974) (describing how sea otters affect the size of nearshore and intertidal kelp beds and associated communities by feeding on sea urchins); J. A. Estes et al., *Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems*, 282 SCIENCE 473, 474–75 (1998) (analyzing how increased killer whale predation causes other species' populations to decline).

make relatively small contributions to current ecosystem functioning might also provide insurance against environmental change. For example, a currently rare species may be pre-adapted to climate change-induced drought, the invasion of a new pathogen, or any number of other human-caused or natural environmental changes, while currently common species may be unable to cope with such changes and decline in abundance, resulting in compensation by the previously rare species and stability of ecosystem services.[165]

Yet abundance is a neglected aspect in the study of biodiversity and ecosystem services.[166] New conceptual frameworks, modeling, and empirical data are pointing to abundance as a critical factor in predicting ecosystem functioning and associated services.[167] Migratory species can provide especially clear examples of species' roles, and the importance of abundance, in providing life-supporting and life-enhancing ecosystem services. This perspective adds support to a proactive, rather than a reactive, approach to biodiversity protection.[168]

165 Shigeo Yachi & Michel Loreau, *Biodiversity and Ecosystem Productivity in a Fluctuating Environment: The Insurance Hypothesis*, 96 PROC. NAT'L ACAD. SCI. 1463, 1466–67 (1999) (using modeling to show insurance effect of biodiversity in ecosystems); D. U. Hooper et al., *Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge*, 75 ECOLOGICAL MONOGRAPHS 3, 4 (2005) (reviewing current literature and concluding that more species are needed to ensure stable supply of ecosystem goods and services); Michel Loreau, *Linking Biodiversity and Ecosystems: Towards a Unifying Ecological Theory*, 365 PHIL. TRANSACTIONS ROYAL SOC'Y B 49, 53–54 (2010) (discussing how asynchrony of species's responses to environmental stresses allows some species to compensate for a decline in another species at the ecosystem level).

166 Kremen, *supra* note 8, at 472 (asserting that most diversity–function research has focused solely on the role that species richness plays in ecosystem functioning).

167 Claire Kremen & Richard S. Ostfeld, *A Call to Ecologists: Measuring, Analyzing, and Managing Ecosystem Services*, 3 FRONTIERS ECOLOGY & ENV'T 540, 542–43 (2005) (discussing different approaches to measuring ecosystem variability); Balvanera et al., *supra* note 8, at 361 (discussing the benefits of measuring gradual changes in abundence); Trond H. Larsen, Neal M. Williams & Claire Kremen, *Extinction Order and Altered Community Structure Rapidly Disrupt Ecosystem Functioning*, 8 ECOLOGY LETTERS 538, 539 (2005) (discussing the critical need to properly measure abundance in future studies).

168 Wilcove & Wikelski, *supra* note 9, at 1363.