

Mobile Link Organisms and Ecosystem Functioning: Implications for Ecosystem Resilience and Management

Jakob Lundberg* and Fredrik Moberg

Natural Resources Management, Department of Systems Ecology, Stockholm University, SE-106 91 Stockholm, Sweden

ABSTRACT

Current natural resource management seldom takes the ecosystem functions performed by organisms that move between systems into consideration. Organisms that actively move in the landscape and connect habitats in space and time are here termed “mobile links.” They are essential components in the dynamics of ecosystem development and ecosystem resilience (that is, buffer capacity and opportunity for reorganization) that provide ecological memory (that is, sources for reorganization after disturbance). We investigated the effects of such mobile links on ecosystem functions in aquatic as well as terrestrial environments. We identify three main functional categories: resource, genetic, and process linkers and suggest that the diversity within functional groups of mobile links is a central component of ecosystem resilience. As the planet becomes increasingly dominated by humans, the magnitude, frequency, timing, spatial extent, rate,

and quality of such organism-mediated linkages are being altered. We argue that global environmental change can lead to (a) the decline of essential links in functional groups providing pollination, seed dispersal, and pest control; (b) the linking of previously disconnected areas, for example, the spread of vector-borne diseases and invasive species; and (c) the potential for existing links to become carriers of toxic substances, such as persistent organic compounds. We conclude that knowledge of interspatial exchange via mobile links needs to be incorporated into management and policy-making decisions in order to maintain ecosystem resilience and hence secure the capacity of ecosystems to supply the goods and services essential to society.

Keywords: mobile links; ecosystem functioning; global environmental change; ecosystem services; ecological memory; biodiversity; functional groups; resilience; management; invasive species.

INTRODUCTION

In addition to the ecosystem services of direct value to human society, such as the production of food, timber, and recreational services, there are indirect services that are of crucial importance for ecosystem functioning and the delivery of goods and services over the long term (Chapin and others 2000; Costanza and others 1997; Daily 1997; Folke 1991;

Odum 1989). Organisms that actively move between habitats and ecosystems are important providers of such services. We refer to these organisms, which support essential functions by connecting areas to one another and contribute to ecosystem resilience (Holling 1973), as “mobile link species” or “mobile links” (Gilbert 1980; Moberg and Folke 1999; Myers 1993). Mobile links provide a multitude of different functions, such as pollination (Allen-Wardell and others 1998; Buchmann and Nabhan 1996), seed dispersal (Hutchins and others 1996), the translocation of nutrients (Meyer and

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*Corresponding author; e-mail: jakob@system.ecology.su.se

Schultz 1985; Polis and others 1997), and grazing (Carpenter 1986; Walker 1993). Therefore, they often have pivotal effects on ecosystem processes, especially following disturbance, through their input of, for example, seeds, pollen, mycorrhiza, as well as essential processes such as grazing. Furthermore, they are essential components of ecological memory (Bengtsson and others forthcoming; Nyström and Folke 2001).

Organisms that have mobile link functions can have substantial effects on ecosystem functioning and structure (Mills and others 1993). In this sense, they often provide functions analogously to keystone species (Paine 1969). However, the classic keystone species concept has focused on the experimental manipulation of less mobile top-level carnivores and their top-down effects. Hence, studies of the functional role of biological diversity have traditionally concentrated on single habitats or ecosystems, often in small experimental plots or enclosures, and have typically dealt with only one or two trophic levels (Chapin and others 2000; Naeem and others 1994; Schindler 1998; Tilman and Downing 1994). The effect of biodiversity loss on ecosystem dynamics and species interactions across system boundaries has received less attention (Peterson and others 1998). The study of animal migration is certainly not a new phenomenon, and much has been learned since 1555, when the archbishop of Uppsala, Sweden, proclaimed that swallows spent the winter under water (Baker 1980). In recent years, the study of the migration of animals or their movement between patches in the landscape has become one of the central themes of theoretical ecology and applied conservation biology (Ormerod and Watkinson 2000).

Thus far, these biotic vectors have not been considered to the same extent in terms of their role in the functioning and dynamics of ecosystems, but the situation is changing. There is a growing appreciation among ecologists that flows of matter and organisms can link seemingly isolated systems and exert a substantial influence on local patterns and dynamics (Hilderbrand and others 1999; Huxel and McCann 1998; Polis and others 1997). In a human-dominated environment (Vitousek and others 1997b), the influence of surrounding systems often becomes more conspicuous. The various components of global environmental change (for example, land-use change, habitat fragmentation, climate change, pollution, exploitation) have both a direct impact on ecosystem processes (for example, through altered disturbance regimes) (Paine and others 1998) and indirect effects mediated through changes in ecosystem composition and diversity

(Tilman 1998). Thus, global environmental change may lead to both qualitative and quantitative shifts in a variety of ecosystem processes (Chapin and others 2000; Tilman 1998; Vitousek and others 1997a).

The rate, timing, duration, frequency, and spatial extent of a mobile link function could all be affected (Dukes and Mooney 1999; Harrington and others 1999; Hughes 2000), leading to profound changes in local ecosystems (Post and others 1998). For example, the lack of pollinators and seed dispersers might lead to recovery failures and phase shifts after disturbances (Buchmann and Nabhan 1996; Cox and others 1991). In addition, so that an existing organism-mediated link could contribute to the spread of aggressive alien species (Larosa and others 1985; Simberloff and von Holle 1999; Woodward and others 1990), genetically modified organisms (Scheffler and Dale 1994), disease (Epstein 1999), pathogens (Olsen and others 1995), or pollutants (Ewald and others 1998).

In this article, we identify different functions provided by mobile links and analyze a number of cases where human-induced global environmental change has altered their functioning. We focus on how the altered functioning of mobile links could affect ecological or ecosystem resilience (Holling 1973). Ecosystem resilience provides insurance to societies, in terms of sustaining a flow of ecological goods and services (Costanza and others 2000; Folke and others 1996). Consequently, we conclude that knowledge of the exchange among spatial units via mobile links should be integrated into natural resources management and policy making. This is an important measure that can secure ecosystem functioning and reduce the risk of unnecessary surprises for human societies due to the loss of resilience.

MOBILE LINKS AS IMPORTANT COMPONENTS OF ECOLOGICAL MEMORY AND ECOSYSTEM RESILIENCE

A mobile link is an animal connecting either two different kinds of patches or two patches of the same kind with some kind of "barrier" between them. The patches may be ecosystems in the landscape, or smaller biotopes within a habitat, or other types of interacting landforms.

In this article, we assess the functional role of mobile link organisms, and especially their role in maintaining the resilience and dynamic functioning of ecosystems. Ecosystem resilience is the magnitude of disturbance that can be absorbed by a sys-

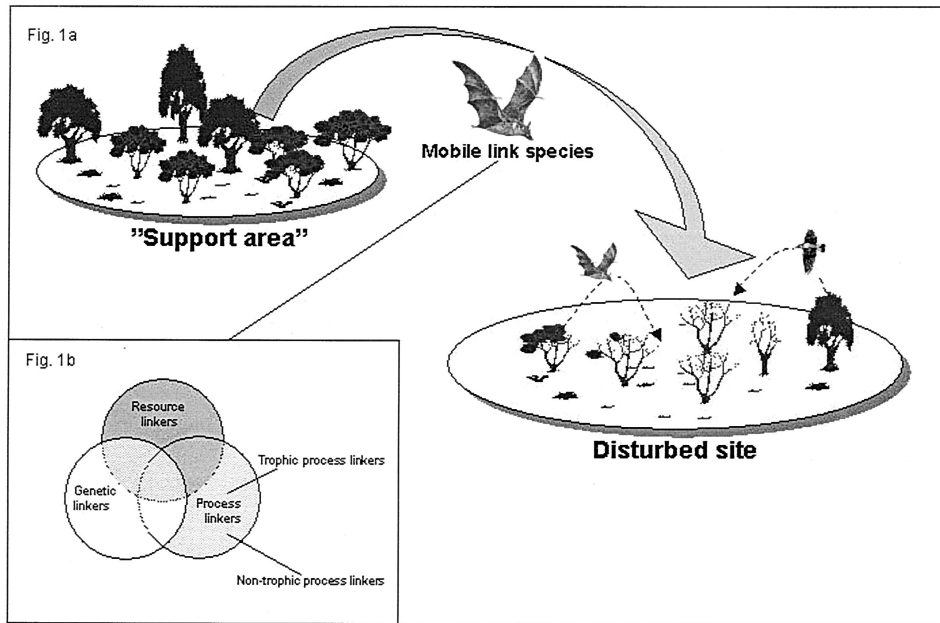


Figure 1. (a) As providers of external ecological memory (for example, by carrying seeds and pollen, or by grazing), mobile link species are important for resilience. This is of special concern after a disturbance has reduced internal ecological memory (biological legacies). Mobile links can also link patches within the disturbed site and reallocate internal ecological memory (*dotted arrows*). (b) A mobile link species can provide several functions simultaneously or at different life stages. Hence, the functional categories of mobile links (resource, genetic, and process linkers) are not mutually exclusive.

tem before it shifts from one stable state (or stability domain) to another (Holling 1973). Ecosystem resilience entails not only the capacity to reorganize and reestablish following disturbance, but also the ability of a system to renew itself through the maintenance of a diversity of options for development and evolution (Holling and others 1995).

After disturbance, an ecosystem is open for new successional pathways, allowing for chance events and new species compositions and interactions. Which pathway the system will follow is the product of several features. These features, which determine the capacity of ecosystems to reestablish their former functions and avoid phase shifts following disturbance (Scheffer and others 2001), have been termed “ecological memory”, which is the historical component of resilience (Bengtsson and others forthcoming; Nyström and Folke 2001). Following the disturbance of an ecosystem, biological legacies (internal ecological memory) include surviving organisms (residuals), organic materials, and the organically generated environmental patterns that persist through a disturbance and serve as foci for regeneration and recolonization (T. Elmqvist and others unpublished; Franklin and MacMahon 2000; Thompson and others 2001). External ecological memory is the availability of assemblages (refugia) of plants and animals outside the disturbed area that act as sources for its recolonization. The larger a disturbance and the more damage it causes within an ecosystem, the greater its relative dependence on external ecological memory for the reestablish-

ment of ecosystem functions (Duncan and Chapman 1999) (Figure 1a).

Mobile links are key components of external ecological memory, acting, as vectors for seeds, pollen, eggs, larvae, mycorrhiza, nutrients, and even other organisms through their trophic and nontrophic interactions with other species surviving at the disturbed site. In this sense, they are important factors in determining the direction of ecosystem development after disturbance (Cox and Elmqvist 2000; Nyström and Folke 2001). For the components of ecological memory (biological legacies, mobile links, refugia, and support areas), the degree of diversity found within functional groups and their redundancy seem to be factors that play a major role in sustaining critical ecosystem processes (Nyström and Folke 2001; Peterson and others 1998). A “functional group” (for example, herbivores and pollinators) is defined as a set of species that performs similar but not identical ecological roles (Levin 1998; Walker and others 1999). Peterson and others (1998) have suggested that resilience is generated by diverse, overlapping function within a scale and by redundant species that operate at different scales.

As an illustrative example of the importance of diversity within functional groups of mobile links, we will consider the fruit-eating flying foxes native to Samoa and several other Pacific islands. Due to the impact of human activities they are more or less the only remaining species capable of pollinating and dispersing the seed of a large proportion of the

islands' canopy tree species (Steadman and Kirch 1990). Flying foxes enhance recolonization after disturbances and can therefore be regarded as key components of ecosystem dynamics and development (Cox and Elmqvist 2000; Cox and others 1991). However, the pollination and seed dispersal functions seem fragile because there is little redundancy due to the low diversity within this functional group.

FUNCTIONAL GROUPS OF MOBILE LINKS

There are three different categories of mobile link organisms: *Resource linkers* are animals that transport and translocate essential resources, such as organic material, nutrients, and minerals. *Genetic linkers*, such as seed dispersers and pollinators, are organisms that carry genetic information between habitats. *Process linkers* include organisms that connect habitats by providing, or supporting, an essential process (for example, grazers, which structure the development of plant communities, or insect-eating birds, which control noxious pests); however, process linkers can also be involved in non-trophic interactions, hence influencing the physicochemical environment rather than the trophic web (see Table 1).

These three categories are not mutually exclusive. Often a species may perform several functions simultaneously or at different times (for example, during different life stages) (Figure 1b). For each category, we will illustrate, with a few examples from terrestrial as well as aquatic systems, how these mobile links influence ecosystem functioning and resilience.

Resource Linkers

Fluxes across habitats often bring both nutrient and energy resources from areas of higher productivity into areas of low productivity. These inputs can alter the consumption rates of consumer and predator species in the recipient food webs, thereby influencing food web stability and sometimes leading to cascading effects (Huxel and McCann 1998).

Seabirds deposit large quantities of nutrient-rich guano on land, thereby reallocating large amounts of nutrients from sea to land. Locally, this process can substantially increase terrestrial primary production and result in small-scale "nutrient-subsidized systems," with significant effects on species diversity and abundance higher up the food web (Polis and others 1997; Stapp and others 1999). According to estimates by Murphy (1981), seabirds worldwide transfer 10^4 – 10^5 tons of phosphorus to

land annually. The activities of dense aggregations of wetland birds such as geese and ducks can lead to substantial nutrient loading, affecting water quality and vegetation growth, as well as fostering disease outbreaks (Post and others 1998). Such resource linkers contributed, for example, 27% of all nitrogen, 69% of all carbon, and 70% of all phosphorus that entered Wintergreen Lake in southwestern Michigan from external sources (Manny and others 1994).

Hilderbrand and others (1999) also described the important role played by two interacting mobile link species, spawning salmon and brown bear (*Ursus arctos*), in transporting marine nitrogen into forest ecosystems in the Kenai Peninsula, Alaska. They estimated that over 15% of the total nitrogen in spruce foliage within 500 m of the stream was derived from marine systems via salmon. Of that amount, bears had distributed more than 80%. Similarly, migrating fish in coral reefs may, through excretion and defecation, transfer essential nutrients and minerals from adjacent ecosystems to primary producing corals in nutrient-poor areas; in addition, they can transport limiting nutrients from one part of a coral reef to another (Geesey and others 1984; Meyer and Schultz 1985). However, massive nutrient enrichment originating from mobile links can also be harmful to vegetation and lead to long-term changes in species composition and community structure (Leenetaar 1967; Onuf and others 1977).

Genetic Linkers

Genetic information linkers are animals that move genetic material such as pollen, eggs, mycorrhizal fungi, seeds, larvae, and even other organisms in the landscape or seascape. Seeds, pollen, and larvae can be important food resources for many animals, but here we emphasize the genetic information component.

Of the estimated 240,000 species of flowering plants, about 90% are pollinated by animals (Nabhan and Buchmann 1997; Renner 1995). It has even been suggested that the reproductive success of plants is often more limited by pollinator scarcity than resource scarcity (Burd 1994). The arrival of seeds from off-site through mobile links is of special importance on human-disturbed land where the resources for succession (the internal ecological memory) are impoverished (Duncan and Chapman 1999). Long-distance dispersal by birds is important for remote and isolated areas where other means of dispersal are relatively limited. Several Pacific Island floras contain disproportionate numbers of animal-dispersed fruits (Carlquist 1966; Ridley 1930;

Table 1. Examples of the Three Main Categories of Mobile Link Species (Genetic, Resource, and Process Linkers) and Examples of Human Health Effects Caused by Mobile Links

Reference	Organism	Function/ Effect of Link	Geographic Setting	Habitat/System	Human Impacts	Effect on Link
Resource Linkers						
Geesey and others (1984)	Coral fishes	Transport of minerals and nutrients from feeding to resting areas	US Virgin Islands	Coral reef	Overfishing, eutrophication	↓
Stapp and others (1999)	Seabirds	Guano-mediated energy and nutrient transport	Baja California, Mexico	Terrestrial environment on small islands	Global climate change altering El Nino events?	Altered frequency
Hilderbrand and others (1999)	Bear and salmon	Nutrient transport from sea to forest	Kenai Peninsula, Alaska	Sea, river and spruce forest	Damming, overharvesting	↓
Genetic Information Linkers						
Cox and others (1991)	Flying foxes	Seed dispersal, pollination	Samoa Islands	Tropical forest	Hunting, habitat loss, introduction of exotic predators	↓
Duncan and Chapman (1999)	Bats and birds	Seed dispersal	Western Uganda	Deforested agricultural area	Deforestation, fragmentation	↓
Harrington and others (1999)	Various	Pollination	Various	Various	Increased carbon dioxide concentration in atmosphere	Decoupled timing of flowering and pollination
Process Linkers						
a. Trophic process linkers						
Hughes (1994)	Coral fishes	Grazing off algae	Jamaica	Coral reef	Overfishing	↓
Walker (1993)	Cattle	Grazing	Various	Semi-arid rangeland	Increased live stocks	↑ Pulsed grazing becomes chronic
b. Nontrophic process linkers						
Post and others (1998)	Lesser snow geese	Grazing, grubbing for roots, creating patches of barren ground	New Mexico	Temperate wetland	Habitat fragmentation, reduced hunting pressure, expansion of agriculture	↑ (Increased evaporation on bare patches leading to salination)
McClanahan and Muthiga (1988)	Sea urchins	Erosion of coral reef	Kenya	Coral reef	Overfishing of predator fishes	↑ Population outbreaks of urchins
Mobile Links and Human Health Effects (Carriers of Pests, Disease, or Toxic Compounds)						
Ewald (1998)	Salmon	Vectors for persistent organic compounds	Arctic	Ocean	Emission of toxic compounds	Carrier of harmful compounds
Epstein (1999)	Insects	Vector for diseases	Various	Various	Climate change, land-use change (e.g., dams and irrigation)	Increased spatial extent

For each example, human-induced environmental change affecting the link is also indicated. The last column describes how human impacts alter the functioning of the link. Arrows up indicate an increase in the magnitude of the linking function; arrows down indicate a decreased magnitude.

Taylor 1954). An additional function of some genetic information linkers is that seed passage through vertebrate frugivores may enhance or even be critical for germination (Temple 1977; Traveset and Willson 1997). Many species of trees with large seeds and fruits for example, *Fagus*, *Quercus* *Corylus*), and depend largely on animals that transport and cache their diaspores. The jay (*Garrulus glandarius*), for example, is essential for the regeneration of temperate oak stands (*Quercus robur*). The jays hide acorns in the soil for future consumption and scatter their storage sites over large areas. Regeneration is favored by burying the acorns at a suitable depth and on a suitable substrate for germination and by protection from drying, freezing, and predation by seed-eaters (Bossema 1979; J. Lundberg unpublished).

In temperate forests, small mammals often spread mycorrhizal fungi that are critical to the survival of many higher plants (Wilcox and Murphy 1985). Such an input of mycorrhizal fungi might enhance recolonization after a disturbance, in particular after a severe disturbance (for example, intense fire) that has eradicated predisturbance mycorrhiza.

Process Linkers

Process linkers are organisms that connect and move into habitats by providing, or supporting, an essential process. This category can be further divided into *trophic process linkers* and *nontrophic process linkers*.

Trophic Process Linkers. This category includes organisms that play a role in food webs across habitats—that is, cross-habitat foragers and prey.

Mobile link grazers can influence plant species composition, biomass, productivity, and nutrient cycling in aquatic as well as terrestrial environments by, for example, maintaining the vegetation in early successional stages of high productivity and selective cropping of otherwise superior competitors (Carpenter 1986; Hobbs and Huenneke 1992; McNaughton 1985; Tansley and Adamson 1925). Also important as trophic process linkers are birds, mammals, and predator insects that provide natural pest control, an important ecosystem service that is often replaced by expensive pesticides, leading to ecosystem damage and health impairment (Naylor and Ehrlich 1997). Mobile links providing such pest control can be actively managed. In Germany, for example, hedgerows have been planted along the borders of fields to attract predator insects that control the potential damage of aphids on the cereals in surrounding fields (Schulze and Gerstberger 1993). A similar practice is also followed by the Warils of India, who place tree branches in their paddy fields

to attract birds that control noxious insects (Pereria 1992). Details for the design of such natural pest control systems for agriculture can be found in Altieri (1991).

In coral reefs, herbivorous fishes and invertebrates that migrate between different reef sites and adjacent seagrass beds and mangroves are important mobile links (Moberg and Folke 1999). Sufficient grazing intensity is necessary to keep the substrate in a suitable state for coral larvae to settle after disturbance (Hixon and Brostoff 1996; Pearson 1981) and avoid phase shifts from coral to algal dominance (Done 1992; Hughes 1994). In coral reefs, grazing occurs at several different spatiotemporal scales (Carpenter 1990). The distribution of functional groups across scales is thought to promote the resilience of ecological processes, and thus the ecosystems that are maintained by these processes (Peterson and others 1998).

Nontrophic Process Linkers. Another type of process linkers influence the physicochemical environment rather than the trophic web. In the terminology of Jones and others (1994), these are mobile “allogenic engineers” that change the environment by transforming living or nonliving material from one physical state to another, via mechanical processes or other means. These nontrophic process linkers include sediment operators, nest builders, and other organisms that trample, scrape, and cut (but do not eat) plants and organisms to form trails, mounds, burrows, and wallows or that move, mix, and structure soils (Huntly 1995; Naiman and others 1988; Snodgrass 1997). Nontrophic process linkers can alter habitat suitability and facilitate the recolonization of species when ecosystems reorganize after disturbance (Hobbs and Huenneke 1992). A recently discovered nontrophic process linker, the coral reef “eunicid” worm, gathers and glues together small lumps of coral to extend its home, potentially spreading rock and coral structures. The introduction of these worms could facilitate the establishment of reefs on sandy and muddy bottoms and even help to restore degraded reefs (Chisholm and Kelley 2001).

Mobile Links as a Part of Disturbance Regimes

Disturbances triggered by events such as intense pulses of grazing or insect pests are an inherent part of the internal dynamics of ecosystems; they serve to foster renewal and to promote and maintain species diversity (Holling and others 1995). Some resource linkers and nontrophic linkers act to create such important pulses, for example, by grazing intensely for short periods or by altering the accessi-

bility of prey or nutrients. When these pulses are transformed by human activities, they can have profound ecosystem-level effects. For example, the domestication of cattle on the semiarid savannah, introducing fenced, sedentary livestock, has transformed a pulse disturbance to persistent grazing pressure, leading to changes in species composition and a reduced capacity to buffer against environmental fluctuations that may lead to phase shifts (Walker 1993). Similar examples of loss of resilience due to altered mobile link-mediated pulses have been reported for grazing sea urchins in coral reefs (McClanahan and Muthiga 1988), bird grazing in temperate wetlands (Kerbes and others 1990), and reindeer grazing in the Scandinavian alpine regions (Danell and others 1999).

Altered Mobile Link Functions Due to Ecosystem Effects. Global environmental change can indirectly affect ecosystem processes through changes in ecosystem composition, community structure, and diversity (Tilman 1998). If the diversity within functional groups of mobile links is affected, this can result in altered resilience, changes in ecosystem functioning, and the potential for shifts into other stability domains (Chapin and others 2000; Cox and others 1991; Nyström and others 2001). Changes in the diversity of mobile links can alter the rate, timing, duration, magnitude, spatial extent, quality, and frequency of their linking functions, thereby altering ecosystem dynamics and development (see Table 1). Altered functioning of mobile links can either mitigate or exacerbate the effects of global environmental change. Therefore, it is important to consider the role of mobile links in ecosystem dynamics and their effects on ecosystem resilience if we are to reduce the risk of undesirable shifts between stability domains. These shifts can entail the loss of organisms that support ecosystem function and the provision of ecological services, with both direct and indirect social and economic consequences (Brock and others 2001; Folke and others 1996).

Habitat fragmentation and increased pesticide use are among the major drivers behind what has been termed “the pollination crisis” (Allen-Wardell and others 1998). The fragmentation of habitats can affect the frequency of flower visitation by pollinators, pollen loads, and the possibility of large-scale movements (Law and Lean 1999). The timing of pollination can be altered due to global environmental change; for example, Harrington and others (1999) have suggested that increased carbon dioxide in the atmosphere could lead to a decoupling of the phenology of flowering plants and their pollinators.

Diseases and parasites suppress pollinator populations in many parts of the world. For example, the tracheal mite (*Acarapis woodi*), a parasite on bees, has resulted in an \$80 million annual loss in managed bee colonies (NASDA 1991). During the past few years, almond farmers in the United States have experienced the loss of almost all wild honeybees, with consequent deprivation of their service as pollinators. To mitigate this loss and restore the pollination service managed honeybees have been trucked to California from other states (Watanabe 1994). Other wild pollinators, such as bumblebees, orchard mason bees, and leafcutter bees, have also declined due to pesticide misuse and loss of habitat. This is a case where nearly an entire functional group of genetic linkers has vanished, with disastrous impacts on ecosystem productivity and vulnerability.

Land-use changes in one area may, through mobile link populations, affect remote areas in unpredictable ways, altering the basic conditions of entire ecosystems and undermining the delivery of the ecosystem goods and services (Holling 1988). For example, the expansion of a group of important resource linkers in the Bosque del Apache National Wildlife Refuge, New Mexico, where over 40,000 lesser snow geese (*Chen caerulescens caerulescens*) and Ross's geese (*Chen rossii*) winter annually, has led to increased grazing pressure on the shores of Hudson Bay, resulting in the fundamental destruction of salt marsh vegetation and a loss of resilience in the wetland system (Kerbes and others 1990). The density of the geese populations has increased sharply over the last decades, primarily due to the large amounts of food made available to the geese by spring sowing and land-use alterations. The two species of geese contribute up to 40% of total nitrogen and 75% of total phosphorus import to the main wetland where the geese roost (Kitchell and others 1999; Post and others 1998). However, due to their foraging behavior, these geese populations also function as trophic process linkers with system-level effects.

Overexploitation of natural resources can lead to unexpected cascading effects in habitats far from the overharvested area per se due to the activity of mobile links. For example, in the North Pacific, overfishing has changed the foraging behavior of killer whales. In the absence of fish prey, killer whales moved closer to shore and switched their diet from fish to sea otters. Because sea otters are keystone predators on sea urchins, the altered feeding behavior of the killer whales triggered outbreaks of sea urchins, leading in turn to the defor-

estation of kelp beds in the nearshore community (Estes and others 1998).

Mobile Links and Biological Invasions. Animals transporting seeds, pollen, larvae, and eggs can also act as vectors for alien species, and the introduction of such invasive species can have far-reaching consequences for ecosystem functioning and resilience. Of the 199 representative invasive species listed by Cronk and Fuller (1995), 25% are known to be dispersed by birds, 14% by mammals, and 1% by ants (Richardson and others 2000). Some introduced plant species, particularly ficus and orchid species, also require the introduction of their specific pollinators to become successful invaders. For example, 60 ficus species did not become invasive in New Zealand and Florida until the accidental introduction of their specific wasp pollinators (Nadel and others 1992). Such alien/alien synergism can lead to acceleration in both invasion and impact, a process called “invasional meltdown” (Simberloff and von Holle 1999). In the Hawaiian forest, the introduced fleshy-fruited tree *Myrica faya* has spread steadily with the help of alien birds that carry their seeds (Larosa and others 1985). Richardson and others (2000) believe that such complexes are widespread and that, coupled with our continued movement of species around the world and other components of human-induced global environmental change, ecosystems are becoming increasingly susceptible to invasion. Such components include temperature variability, fragmentation or breakdown of barriers, and increased proportion of early successional stages (Dukes and Mooney 1999). Introductions of exotic species have to a large extent occurred in human-altered and simplified ecosystems, presumably with a smaller number of competitors and predators. Ahead of us we may have a “weedy world” suffering from “ecological homogenization” where invasive species are increasingly successful in outcompeting native species (Culotta 1991; Enserink 1999).

Mobile Links and Their Effects on Human Health. Climate change can have unexpected effects on human health caused by vectors such as mosquitoes and mobile link–spread ticks. These vectors may transmit a variety of diseases, including dengue fever, malaria, yellow fever, and tick-borne encephalitis, to higher altitudes and latitudes as the planet warms (Epstein 1999; Lindgren and others 2000). In addition, accidental introductions of alien species can have severe effects on human health. For example, passive transport in aircrafts and ships has led to the spread of dengue fever and malaria (Epstein 1999).

Mobile links may also become carriers of deleterious

material emitted by humans. Ewald and others (1998) reported that migrating salmon transport polychlorinated persistent organic compounds such as PCBs and DDT to pristine subarctic and arctic areas. Other contaminants that can be transported by fishes include methyl mercury, pesticide residues, and flame-retardants such as PBDEs (GAO 2001). Hence, fishes harvested in relatively pristine areas could contain high levels of pollutants deleterious to human health.

The rapid increase in genetically modified crops has resulted in growing concern over the health and the environmental impacts of these crops. In Great Britain, agricultural fields with genetically modified organisms are said to be protected from cross-pollination and from spreading into surrounding systems by a 200–600-m buffer zone (MAFF 2000). Without a small buffer zone, there is a possibility that dispersal by wind, water, and mobile links might contribute to the escape of transgenes or genetically modified organisms (Scheffler and Dale 1994; Snyder and others 1998).

DISCUSSION

The case studies reviewed here suggest that the effects of mobile link species on ecosystem functioning can be substantial. Consequently, mobile links, and their associated habitats, should be considered more extensively in our approach to ecosystem management and biodiversity conservation. They play significant roles in ecosystem dynamics and help to sustain the capacity of ecosystems to supply the ecological services essential for social welfare and economic development. Furthermore, resource, genetic, and process linkers often have pivotal effects on ecosystem processes, especially following disturbance, because they act as mediators of recolonization through the input of seeds, pollen, mycorrhiza, and the performance of other essential processes such as grazings. Hence, in human-dominated landscapes, management plans need to take the functional roles of mobile links in sustaining ecosystems and contributing to ecosystem resilience into account. The function of a particular mobile link may not be evident until an infrequent disturbance occurs and other species with similar functions have become lost. Such “creeping” loss of resilience due to our lack of ecological knowledge could cause serious social and economic problems as we experience the loss of critical ecosystem services and support.

It is critical that we expand our understanding of the ways in which global environmental change could alter the fundamental processes that deter-

mine ecosystem structure, dynamics, and functioning. Most studies on the effects of global environmental change on ecosystems emphasize the direct effects of climate, pollution, and other abiotic factors on selected species (Kingsolver and others 1993). However, as we have argued here, and as other studies of invasions have indicated, the introduction of alien species, the fragmentation of landscapes, and indirect changes to community composition are serious problems (Carpenter and others 1993; Kingsolver and others 1993; Tilman 1998). Although most ecological experimentation is small in scale and short in duration, ecologists increasingly acknowledge that if we want to understand the dynamics and patterns of ecosystems, we must take factors outside the system being studied into consideration and study interactions across scales (Peterson and others 1998). The approach of management has broadened in the last few decades from focusing mainly on a single habitat or species to examining abiotic flows of water, nutrients, and sediment within a watershed or drainage basin perspective (Downs and others 1991). Unfortunately, this newly revised approach is not always enough as species interactions by mobile links across system boundaries are seldom considered. Even when they are, the focus tends to be on the conservation of particular species and populations, rather than on sustaining ecosystem functioning and the capacity of ecosystems to generate services. The newly formed Millennium Ecosystem Assessment Project (see Ayensu and others 1999), which represents three international conventions, is a promising effort that represents a step in the right direction.

We do not mean to suggest that mobile links are inherently good or bad. In many cases, mobile links support ecosystem resilience (for example, pollinators and seed dispersers), whereas in other cases, they may be problematic. However, because this group of species has significant effects on ecosystem functioning, it is crucial to consider their role in ecosystem management and biodiversity conservation if we are to avoid surprises resulting from management policies.

Several international conventions have as their explicit aim the conservation and management of migratory species—for example, the Convention on the Conservation of Migratory Species of Wild Animals and the Ramsar Wetland Convention. There are numerous difficulties associated with the design of management strategies for highly mobile organisms because they use a spatially dispersed mosaic of sites. In addition, our understanding of the dynamic relationships between mobile links and ecosystem functioning is not complete. Indeed, it may

never be complete. Nevertheless, we cannot afford to wait until we have perfect scientific information. In the management of mobile link species, general scientific knowledge often has to be complemented by local ecological knowledge (Johannes 1998; Olsson and Folke 2001). There are several examples from the literature that show how local ecological knowledge can complement limited scientific information so that managers can respond appropriately to pulses and surprises (Berkes and others 2000; Costanza and others 1998; Johannes 1998). In some cases, local knowledge about pollinators and other mobile links is extensive (P. A. Cox personal communication; Nabhan 2000) and could be used to greater advantage, for example, in co-management designs involving local users (Colding and Folke 2001).

CONCLUSION

We have emphasized the importance of the functions provided by mobile link species and argued that they need to be taken into account in ecosystem management and biological conservation schemes, especially in human-dominated environments with altered disturbance regimes or in landscapes simplified by land-use transformations. We believe that conservation efforts need to focus on mobile link species to a greater extent than has been the case and to consider their key role in promoting ecosystem resilience and ecosystem functioning. In landscapes drastically transformed by human activities, internal and external ecological memory is often low (Bengtsson and others forthcoming). In such circumstances, land-use transformation and altered disturbance regimes often open the area to the invasion of exotic species, leading to phase shifts, irreversible changes, and the loss of ecosystem services. Mobile links often provide an important source of external memory to sites that have little internal memory available for recolonization (Duncan and Chapman 1999). Consequently, when ecosystem resilience is the ultimate objective, management should consider the role of mobile link species more explicitly and conduct studies to determine which species function as mobile links and what their impacts will be on the managed landscape or system.

We cannot simply manage passively, or for maximal diversity; we must be selective and design management strategies for specific goals and determine which species to encourage. Finally, we must acknowledge that effective management and policy making will require crossing the borders of ecosystems, scientific disciplines, and nations.

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REFERENCES

- Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox PA, Dalton V, Feinsinger P, Ingram M, and others. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv Biol* 12(1):8–17.
- Altieri MA. 1991. How best can we use biodiversity in agroecosystems? *Outlook Agric* 20(1):15–23.
- Ayensu E, Claassen DV, Collins M, Dearing A, Fresco L, Gadgil M, Gitay H, Glaser G, Lohn CL, Krebs J, and others. 1999. Ecology: international ecosystem assessment. *Science* 286(5440):685–686.
- Baker R. 1980. The mystery of migration. London: Macdonald Futura. 256 p.
- Bengtsson J, Angelstam P, Elmqvist T, Emanuelsson E, Folke C, Ihse M, Moberg F, Nyström M. Reserves, resilience and dynamic landscapes. *Ambio*. Forthcoming.
- Berkes F, Colding J, Folke C. 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecol Appl* 10(5):1251–1262.
- Bossema I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. *Behavior* 70:1–118.
- Brock WA, Mäler KG, Perrings C. 2001. Resilience and sustainability: the economic analysis of nonlinear dynamic systems. In: Gunderson LH, Holling CS, editors. *Panarchy: understanding transformations in human and natural systems*. Washington (DC): Island Press.
- Buchmann SL, Nabhan GP. 1996. The forgotten pollinators. Washington (DC): Island Press. 292 p.
- Burd M. 1994. Bateman principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Bot Rev* 60(1):83–139.
- Carlquist S. 1966. The biota of long-distance dispersal. I. Principles of dispersal and evolution. *Q Rev Biol* 41(3):247–270.
- Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56(4):345–363.
- Carpenter RC. 1990. Title mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population dynamics and coral reef algal communities. *Mar Biol* 104(1):67–77.
- Carpenter SR, Frost TM, Kitchell JF, Krantz TK. 1993. Species dynamics and global environmental change: a perspective from ecosystem experiments. In: Kareiva PM, Kingsolver JG, Huey RB, editors. *Biotic interactions and global change*. Sunderland (MA): Sinauer. p 267–279.
- Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, and others. 2000. Consequences of changing biodiversity. *Nature* 405(6783):234–242.
- Chisholm JRM, Kelley R. 2001. Marine ecology: worms start the reef-building process. *Nature* 409(6817):152.
- Colding J, Folke C. 2001. Social taboos: “invisible” systems of local resource management and biological conservation. *Ecol Appl* 11(2):584–600.
- Costanza R, Andrade F, Antunes P, van den Belt M, Boersma D, Boesch DF, Catarino F, Hanna S, Limburg K, Low B, and others. 1998. Principles for sustainable governance of the oceans. *Science* 281(5374):198–199.
- Costanza R, Daly M, Folke C, Hawken P, Holling CS, McMichael AJ, Pimentel D, Rapport D. 2000. Managing our environmental portfolio. *BioScience* 50(2):149–155.
- Costanza R, D’Arge R, De-Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O’Neill RV, Paruelo J, and others. 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387(6630):253–260.
- Cox PA, Elmqvist T. 2000. Pollinator extinction in the Pacific Islands. *Conserv Biol* 14(5):1237–1239.
- Cox PA, Elmqvist T, Pierson ED, Rainey WE. 1991. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conserv Biol* 5(4):448–454.
- Cronk QCB, Fuller JL. 1995. Plant invaders: the threat to natural ecosystems. London: Chapman & Hall. 241 p.
- Culotta E. 1991. Biological immigrants. *Science* 254:1444–1447.
- Daily G, editor. 1997. Nature’s services: societal dependence on natural ecosystems. Washington (DC): Island Press. 392 p.
- Danell Ö, Staaland H, Nieminen M. 1999. Rennäring i Nordvästeuropa (reindeer husbandry in northwest Europe). In: Dahle HK, Danell Ö, Gaare E, Nieminen M, editors. *Reindrift i Nordvest-Europa 1998: biologiske muligheter och begränsningar*. Copenhagen: Nordisk Ministerråd, Tema Nord. p 19–30.
- Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132.
- Downs PW, Gregory KJ, Brookes A. 1991. How integrated is river basin management? *Environ Manage* 15(3):299–309.
- Dukes JS, Mooney HA. 1999. Does global change increase the success of biological invaders? *Trends Ecol Evol* 14(4):135–139.
- Duncan RS, Chapman CA. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecol Appl* 9(3):998–1008.
- Enserink M. 1999. Predicting invasions: biological invaders sweep in. *Science* 285(5435):1834–1836.
- Epstein PR. 1999. Perspectives: medicine—climate and health. *Science* 285(5426):347–348.
- Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282(5388):473–476.
- Ewald G, Larsson P, Linge H, Okla L, Szarzi N. 1998. Biotransport of organic pollutants to an inland Alaska lake by migrating sockeye salmon (*Oncorhynchus nerka*). *Arctic* 51(1):40–47.
- Folke C. 1991. The societal value of wetlands. In: Folke C, Kåberger T, editors. *Linking the natural environment and the economy: essays from the Eco-Eco Group*. Dordrecht (The Netherlands): Kluwer Academic. p 141–172.
- Folke C, Holling CS, Perrings C. 1996. Biological diversity, ecosystems, and the human scale. *Ecol Appl* 6(4):1018–1024.
- Franklin JF, MacMahon JA. 2000. Messages from a mountain. *Science* 288(5469):1183–1185.
- Geesey GG, Alexander GV, Bray RN, Miller AC. 1984. Fish fecal

- pellets are a source of minerals for inshore reef communities. *Mar Ecol Progr Ser* 15:19–25.
- Gilbert LE. 1980. Food web organization and the conservation of neotropical diversity. In: Soulé ME, Wilcox BA, editors. *Conservation of neotropical biology: an evolutionary-ecological perspective*. Sunderland (MA): Sinauer. p 11–33.
- Harrington R, Woiwod I, Sparks T. 1999. Climate change and trophic interactions. *Trends Ecol Evol* 14(4):146–150.
- Hilderbrand GV, Hanley TA, Robbins CT, Schwartz CC. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121(4):546–550.
- Hixon MA, Brostoff WN. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol Monogr* 66(1):67–90.
- Hobbs RJ, Huenneke LF. 1992. Disturbance, diversity, and invasion: implications for conservations. *Conserv Biol* 6(3):324–337.
- Holling CS. 1973. Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23.
- Holling CS. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. *Mem Entomol Soc Can* 146:21–32.
- Holling CS, Schindler DW, Walker BW, Roughgarden J. 1995. Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perrings CA, Mäler K-G, Folke C, Holling CS, Janson BO, editors. *Biodiversity loss: ecological and economical issues*. Cambridge (England): Cambridge University Press. p 44–83.
- Hughes L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol* 15(2):56–61.
- Hughes TP. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Huntly N. 1995. How important are consumer species to ecosystem functioning? In: Jones CG, Lawton JH, editors. *Linking species and ecosystems*. New York: Chapman & Hall. p 73–83.
- Hutchins HE, Hutchins SA, Liu BW. 1996. The role of birds and mammals in Korean pine (*Pinus koraiensis*) regeneration dynamics. *Oecologia* 107(1):120–130.
- Huxel GR, McCann K. 1998. Food web stability: the influence of trophic flows across habitats. *Am Nat* 152(3):460–469.
- Johannes RE. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol Evol* 13(6):243–246.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69(3):373–386.
- Kerbes RH, Kotanen PM, Jefferies RL. 1990. Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *J Appl Ecol* 27(1):242–258.
- Kingsolver JG, Huey RB, Kareiva PM. 1993. An agenda for population and community research on global change. In: Kareiva PM, Kingsolver JG, Huey RB, editors. *Biotic interactions and global change*. Sunderland (MA): Sinauer. p 480–486.
- Kitchell JF, Schindler DE, Herwig BR, Post DM, Olson MH, Oldham M. 1999. Nutrient cycling at the landscape scale: the role of dial foraging migrations by geese at the Bosque del Apache National Wildlife Refuge, New Mexico. *Limnol Oceanogr* 44(3):828–836.
- Larosa AM, Smith CW, Gardner DE. 1985. Role of alien and native birds in the dissemination of firetree (*Myrica-faya* Ait-Myricaceae) and associated plants in Hawaii. *Pacific Sci* 39(4):372–378.
- Law BS, Lean M. 1999. Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rain-forest. *Biol Conserv* 91(2–3):201–212.
- Leenetaar P. 1967. Observations in guantrophic environments. *Hydrobiologia* 29:441–489.
- Levin SA. 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1(5):431–436.
- Lindgren E, Talleklint L, Polfeldt T. 2000. Impact of climatic change on the northern latitude limit and population density of the disease-transmitting European tick *Ixodes ricinus*. *Environ Health Perspec* 108(2):119–123.
- [MAFF] Ministry of Agriculture Fisheries and Food. 2000. Review of the use of separation distances between genetically modified and other crops. London: MAFF.
- McClanahan TR, Muthiga NA. 1988. Changes in Kenyan coral reef community structure due to exploitation. *Hydrobiologia* 166:269–276.
- McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol Monogr* 55:259–294.
- Manny BA, Johnson WC, Wetzel RG. 1994. Nutrient additions by waterfowl to lakes and reservoirs: predicting their effects on productivity and water quality. *Hydrobiologia* 280:121–132.
- Meyer JL, Schultz ET. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnol Oceanogr* 30(1):146–156.
- Mills LS, Soule ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43(4):219–224.
- Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. *Ecol Econ* 29(2):215–233.
- Murphy GI. 1981. Guano and the anchovetta fishery. *Res Man Environ Uncert* 11:81–106.
- Myers N. 1993. Biodiversity and the precautionary principle. *Ambio* 22(2–3):74–79.
- Nabhan GP. 2000. Interspecific relationships affecting endangered species recognized by O’odham and Comcaac cultures. *Ecol Appl* 10(5):1288–1295.
- Nabhan GP, Buchmann SL. 1997. Services provided by pollinators. In: Daily G, editor. *Nature’s services: societal dependence on natural ecosystems*. Washington (DC): Island Press. p 133–150.
- Nadel H, Frank JH, Knight RJ. 1992. Escapees and accomplices: the naturalization of exotic figs and their associated faunas in florida. *Fla Entomol* 75(1):29–38.
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368(6473):734–737.
- Naiman RJ, Johnston CA, Kelley JC. 1988. Alteration of North American streams by beaver. *BioScience* 38(11):753–762.
- [NASDA] National Association of State Departments of Agriculture. 1991. Honey bee pest: a threat to the vitality of U.S. agriculture. Washington (DC): NASDA. 1–14 p.
- Naylor RL, Ehrlich PR. 1997. Natural pest control services and agriculture. In: Daily GC, editor. *Nature’s services: societal dependence on natural ecosystems*. Washington (DC): Island Press. p 151–176.
- Nyström M, Folke C. 2001. Spatial resilience of coral reefs. *Ecosystems* 4(5):406–417.
- Nyström M, Folke C, Moberg F. 2001. Corals and phase shifts. *Trends Ecol Evol* 16(3):127.

- Odum EP. 1989. Ecology and our endangered life-support systems. Sunderland (MA): Sinauer. 283 p.
- Olsen B, Jaenson TGT, Bergstrom S. 1995. Prevalence of borrelia-Burgdorferi Senu late-infected ticks on migrating birds. Appl Environ Microbiol 61(8):3082–3087.
- Olsson P, Folke C. 2001. Local ecological knowledge and institutional dynamics for ecosystem management: a study of Lake Racken Watershed, Sweden. Ecosystems 4(2):85–104.
- Onuf CP, Teal JM, Valiela I. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58: 514–526.
- Ormerod SJ, Watkinson AR. 2000. Large-scale ecology and hydrology: an introductory perspective from the editors of the *Journal of Applied Ecology*. J Appl Ecol 37:1–5.
- Paine RT. 1969. A note on trophic complexity and community stability. Am Nat 103:91–93.
- Paine RT, Tegner MJ, Johnson EA. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1(6):535–545.
- Pearson RG. 1981. Recovery and recolonization of coral reefs. Mar Eco Progr Ser 4:105–122.
- Pereria W. 1992. The sustainable lifestyle of the Warils. In: Sen G, editor. Indigenous vision: peoples of India attitudes to the environment. New Dehli: Sage.
- Peterson G, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1(1):6–18.
- Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316.
- Post DM, Taylor JP, Kitchell JF, Olson MH, Schindler DE, Herwig BR. 1998. The role of migratory waterfowl as nutrient vectors in a managed wetland. Conserv Biol 12(4):910–920.
- Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmanek M. 2000. Plant invasions: the role of mutualisms. Biol Rev Cambridge Philos Soc 75(1):65–93.
- Ridley HH. 1930. The dispersal of plants throughout the world. Ashford (England): L. Reeve. 744 p.
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. Nature 413(6856):591–596.
- Scheffler JA, Dale PJ. 1994. Opportunities for gene transfer from transgenic oilseed rape (*Brassica napus*) to related species. Transgen Res 3(5):263–278.
- Schindler DW. 1998. Replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1(4):323–334.
- Schulze E-D, Gerstberger P. 1993. Functional aspects of landscape diversity: a Bavarian example. In: Schulze E-D, Mooney HA, editors. Biodiversity and ecosystem function. Berlin: Springer-Verlag. p 453–466.
- Simberloff D, von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol Inv 1:21–32.
- Snodgrass JW. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American landscape. J Appl Ecol 34(4): 1043–1056.
- Snyder WE, Tonkyn DW, Kluepfel D. 1998. Insect-mediated dispersal of the rhizobacterium *Pseudomonas chlororaphis*. Phytopathology 88(12):1248–1254.
- Stapp P, Polis GA, Pinero FS. 1999. Stable isotopes reveal strong marine and El Nino effects on island food webs. Nature 401(6752):467–469.
- Steadman DW, Kirch PV. 1990. Prehistoric extinction of birds on Mangaia, Cook Islands, Polynesia. Proc Natl Acad Sci USA 87(24):9605–9609.
- Tansley AG, Adamson RS. 1925. Studies of the vegetation of the English chalk. III. The chalk grassland of the Hampshire–Sussex border. J Ecol 13:177–223.
- Taylor BW. 1954. An example of long-distance dispersal. Ecology 35:569–572.
- Temple SA. 1977. Plant–animal mutualism: co-evolution with dodo leads to near extinction of plant. Science 197:885–886.
- Thompson JN, Reichman OJ, Morin PJ, Polis GA, Power ME, Sterner RW, Couch CA, Gough L, Holt R, Hooper DU, and others. 2001. Frontiers of ecology. BioScience 51(1):15–24.
- Tilman D. 1998. Species composition, species diversity, and ecosystem processes: understanding the impacts of global change. In: Pace ML, Groffman PM, editors. Successes, limitations, and frontiers in ecosystem science. New York: Springer-Verlag. p 453–469.
- Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. Nature 367(6461):363–365.
- Traveset A, Willson MF. 1997. Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. Oikos 80(1):89–95.
- Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R. 1997a. Introduced species: a significant component of human-caused global change. NZ J Ecol 21(1):1–16.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997b. Human domination of Earth's ecosystems. Science 277:494–499.
- Walker B, Kinzig A, Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2(2):95–113.
- Walker BH. 1993. Rangeland ecology: understanding and managing change. Ambio 22(2–3):80–87.
- Watanabe ME. 1994. Pollination worries rise as honey-bees decline. Science 265(5176):1170.
- Wilcox BA, Murphy DD. 1985. Conservation strategy: the effects of fragmentation on extinction. Am Nat 125:879–887.
- Woodward SA, Vitousek PM, Matson K, Hughes F, Benvenuto K, Matson PA. 1990. Use of the exotic tree *Myrica faya* by native and exotic birds in Hawaii Volcanoes National Park. Pacific Sci 44:88–93.