

# TOWARD AN INTEGRATION OF LANDSCAPE AND FOOD WEB ECOLOGY: The Dynamics of Spatially Subsidized Food Webs

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## ABSTRACT

We focus on the implications of movement, landscape variables, and spatial heterogeneity for food web dynamics. Movements of nutrients, detritus, prey, and consumers among habitats are ubiquitous in diverse biomes and can strongly influence population, consumer-resource, food web, and community dynamics. Nutrient and detrital subsidies usually increase primary and secondary productivity, both directly and indirectly. Prey subsidies, by movement of either prey or predators, usually enhance predator abundance beyond what local resources can support. Top-down effects occur when spatially subsidized consumers affect local resources by suppressing key resources and occasionally by initiating trophic cascades. Effects on community dynamics vary with the relative amount of input, the trophic roles of the mobile and recipient entities, and the local food web structure. Landscape variables such as the perimeter/area ratio of the focal habitat, permeability of habitat boundaries, and relative productivity of trophically connected habitats affect the degree and importance of spatial subsidization.

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## INTRODUCTION

Food webs are a central organizing theme in ecology. The organisms that comprise food webs live in a spatially heterogeneous world where habitats vary

greatly in productivity, resource abundance, and consumer behavior and demography. Even local communities that appear discrete are open and connected in myriad ways to outside influences (75, 105, 135). The basic components of food webs—nutrients, detritus, and organisms—all cross spatial boundaries. Yet until recently, ecologists neglected to ask how spatial patterns and processes affect web structure and dynamics (135). The core themes of landscape ecology—spatial variation in habitat quality, boundary and ecotonal effects, landscape connections, scaling, and spatial context (187–189)—carry significant implications for food web ecology.

We focus on spatial flows among habitats as a key force in local web dynamics. We first synthesize a large literature documenting the ubiquitous movement of material and organisms among habitats. We then show how spatial subsidies influence consumer-resource and web dynamics, and we propose a preliminary framework to integrate landscape and food web ecology. By spatial subsidy, we mean a donor-controlled resource (prey, detritus, nutrients) from one habitat to a recipient (plant or consumer) from a second habitat which increases population productivity of the recipient, potentially altering consumer-resource dynamics in the recipient system.

## LANDSCAPE CONSIDERATIONS

Connectivity varies enormously among real systems, from near total isolation to strong mixing. Factors that influence exchange rate among spatial units are a central focus of landscape ecology (50, 66, 170, 186). “Flow rate” depends on a suite of environmental and organismal attributes (e.g. habitat geometry and area; similarity of, distance between, and relative productivity of interacting habitats; boundary permeability; and organism mobility).

The ratio of “edge” to “interior” (i.e. perimeter-to-area,  $P/A$ ) is a major determinant of input to a habitat (137), e.g. watershed, riparian, and shoreline to and from streams and lakes (62, 132, 184, 185); the ocean to coastal areas and islands (137); and forest edge to interior (4, 6, 189).  $P/A$  is a function of size (larger units have less edge per unit area), shape (e.g. compact vs elongated), and fractal irregularity or folding of the edge (62, 137, 184). Such edge effects are likely universal, governing input, productivity, and dynamics among juxtaposed habitats (135, 137).

The “river continuum concept” (172) illustrates landscape influences on flow rates at several spatial scales.  $P/A$  declines from headwater streams to large rivers, with a corresponding decline in the relative importance of local allochthonous inputs compared to in situ productivity. Local production is reduced downstream because of increased depth and turbidity, such that large rivers are net sinks for energy and material derived from smaller order streams; upstream subsidies drive downriver dynamics. Finally, the contribution of

allochthonous stream material to lakes or oceans is governed by landscape factors (e.g. small source streams or short rivers should contribute relatively more than longer or larger rivers).

## FLOW AND SPATIAL SUBSIDIES: DIRECT EFFECTS

Allochthonous input can influence greatly the energy, carbon (C), and nutrient budget of many habitats. In general, nutrient inputs (nitrogen [N], phosphorus [P], trace elements) increase primary productivity; detrital and prey inputs produce numerical responses in their consumers. Transport across boundaries occurs via either physical or biotic vectors. Wind and water are the primary physical vectors; they transport subsidies either by advection or diffusion (44). Mobile consumers transport nutrients and detritus when they forage in one habitat and defecate in another. We organize trophic flows by origin and destination using two comprehensive categories, water and land.

### *Movement of Nutrients and Detritus*

**WATER TO WATER** Water masses often differ substantially in productivity and organic biomass. Transport, both vertical (upwelling, pelagic detrital fallout to benthos) and horizontal (currents, tidal movement, eddy-diffusion), is generally a key determinant of local marine productivity and consequent food webs. In particular, pelagic-benthic coupling is a major route for energy and nutrient flow (7, 13, 14, 16, 90, 98, 140). Much shallow water benthos consists of sessile particle or detritus feeders that rely on settlement of food from the coastal fringe and production from overlying waters. In situ benthic productivity is relatively unimportant (most areas) or totally absent (aphotic zones). Worldwide, the biomass of benthic fauna reflects the productivity of overlying waters (13, 98, 140). Conversely, infusion of nutrients from bottom via both mixing and upwelling controls primary productivity of surface waters (13, 14, 98).

Benthic and pelagic lake habitats are connected via turnover, a process similar to upwelling whereby bottom nutrients, reinfused into photic waters, stimulate productivity. Lakes also receive many nutrients from streams, springs, precipitation, watershed soil and fertilizer runoff, shore vegetation, and litter fall (132, see below). In beaver ponds, biomass input from streams is three times greater than local production (116). One implication of the river continuum concept is that downstream communities are subsidized by upstream "inefficiencies" in C retention and processing (117, 179). In some systems, such input is quite important, e.g. in a Washington estuary, rivers contributed four to eight times more organic material than all local producers combined (165).

Plant detritus produced in one habitat and transported to a second can subsidize detritivores. Productive kelp and seagrass beds fuel dense detritivore

populations in the supralittoral (137), littoral (49), intertidal (32), and deep benthic zones (174).

Large consumers transport material among aquatic habitats. Seasonally and daily migrating fish are particularly important conduits. Anadromous fish (e.g. salmon) deposit great amounts of energy and nutrients of marine origin to lakes and nutrient-deficient headwater streams via reproductive products, excretion, and death (51). For example, dead salmon contribute 20–40% of total lake P (51); abundant ( $9 \times 10^8$  to  $4.4 \times 10^{10}$ /year) marine alewives leave up to 146 g/m<sup>2</sup> in freshwater when they die. Nutrients from dead anadromous fish appear critical to sustain productivity of many freshwater and riparian ecosystems (15a, 51, 192).

Daily movement by fish and zooplankton facilitates rapid nutrient translocation across boundaries in freshwater (35, 89, 152, 171) and marine systems (7, 108, 124, 145). Such movement transports great quantities of fecal matter rich in fertilizing nutrients within the water column (the “diel ladder”; 89), between benthic and pelagic waters (“nutrient pump mechanism”; 171), between onshore and offshore waters (22), and to refuge areas (108, 124). In lakes, P input via fish excretion can exceed all other inputs, greatly increasing primary productivity, altering the outcome of phytoplankton competition, and stimulating trophic cascades (34, 171). Detritivorous benthic fish facilitate energy flow through lake webs by infusing DOM and P into the water in forms useful to phytoplankton (171). Marine fish transport nutrients and energy from feeding to resting areas, e.g. N and P from seagrass beds into nutrient-poor waters over corals, which thus increases coral growth rates. These effects are likely general in many marine habitats (26, 109).

Seabirds feeding on fish and invertebrates concentrate and transport great quantities of nutrients in their guano. Guano, a powerful fertilizer, enhances nutrient status and primary production in the intertidal and nearshore marine and estuarine waters (19, 82, 195).

**LAND TO WATER** Aquatic and terrestrial systems are often linked functionally by flows of nutrients and organic matter via wind or water moving in the hydrologic cycle (67). In general, food webs in rivers, lakes, and estuaries are fueled by both local primary productivity and allochthonous detritus. Terrigenous input is a major factor (along with upwelling and an enhanced light regime) that promotes high primary and secondary productivity in coastal waters, both marine (13, 98) and freshwater (171, 185). Three major conduits shunt material from land to freshwater (67, 179, 185): detritus from leaf and litter fall; dissolved and particulate organic matter (DOM, POM) from soil runoff (107, 110, 113, 117, 170); and detritus, POM, and DOM from floods (64, 114, 178, 179).

The impact of such input on energy budgets and community structure depends on many landscape variables: location in a drainage, nature of the terrestrial surroundings, watershed size, amount of terrestrial runoff, and shoreline to water P/A ratio (40, 93, 109, 132, 152, 165, 172, 185). Often, input greatly exceeds in situ productivity (18, 58, 165). For example, primary production in ponds (2.4% of C budget), stream riffles (10%), and streams (4.2%, 16%) is substantially less than allochthonous input (respectively, 80%, 76%, 91%, 74%; 116, 117). Plants usually benefit greatly from nutrient and DOM input (58, 109, 113).

In floodplain ecosystems, great amounts of detritus, nutrients, and sediments rich in organics are exchanged reciprocally between the river channel and the riparian land via flooding (178, 179, 182). Materials produced on land during dry phases increase productivity of aquatic plants and are a rich food supply for detritivores that move onto the floodplain from the channel during floods (193). Annual floodplain input of total C to a river channel in Georgia was seven times greater than in situ production (55). Blackwater river productivity is powered by inputs from terrestrial systems (15, 64, 106). In Amazonian rivers, "... primary productivity is so low that a food chain could not be built up from endogenous sources alone to support a large biomass of animals" (63: p. 252). The web is based strongly on allochthonous input of organisms and detritus. "The rainforest, in its floodplain manifestation, has come to the trophic rescue of these aquatic ecosystems" (63, p. 252). An estimated 75% of market fish receive substantial input (50–90% of diet) from terrestrial origin (fruit, seeds, insects, small vertebrates).

Birds and mammals foraging on land can transport great quantities of detritus and nutrients to water, e.g. geese, gulls, and hippopotamuses defecate rich feces into water. Well-studied birds bring terrestrial nutrients to lakes via guano (27, 82); e.g. birds bring 36% of the annual P input into some ponds, increasing plant abundance (102). Beaver-transported trees add nutrients and much organic matter (1 ton/beaver/year) to ponds (85), establishing an entire food chain based on wood decomposition (111, 115, 116). In the Amazon Basin, many fish import great amounts of energy and nutrients from terrestrial habitats (riparian, flood forest, and floodplains) to rivers (63, 64).

**WATER TO LAND** Conversely, terrestrial organisms benefit from periodic nutrient enhancement from aquatic habitats. This water-land linkage is well known to humans and is exemplified by the agriculturally based cultures along the fertile bottom lands of major rivers (e.g. Nile, Mississippi). The area affected can be great: the Amazon floods 2% (70,000 km<sup>2</sup>) of its adjacent forest annually (63). Lake material is an important source of organic matter in bordering land habitats (132). Flooding and winds transport lake plants in quantities

(7.4 kg/m<sup>2</sup>/year of shoreline) 4.5 times greater than in situ terrestrial productivity. Such input produces an "edge effect," with greater diversity and densities in the riparian than surrounding habitats (36, 83, 132).

Coastal areas fringing oceans worldwide receive great amounts (10 → 2000 kg/m shoreline/year) of organic matter from the sea via shore wrack (algae and carrion) (32, 68, 69, 96, 137) and possibly from N-rich seafoam (78, 162). Seabirds transport substantial nutrients and organic material to land via guano, food scraps, eggs, feathers, and bodies of dead chicks and adults (82, 114, 137). Birds that feed on massive schools of Peruvian anchovetta deposit guano to mean depths of 5.4–28.5 m, with three offshore islands each containing 2.3–5.2 × 10<sup>6</sup> metric tons (76). Worldwide, seabirds annually transfer 10<sup>4</sup>–10<sup>5</sup> tons of P to land (114).

**LAND TO LAND** Surprisingly great amounts and variety of windborne detritus and nutrients arrive from near and far and may totally sustain or partially subsidize local webs (10, 53, 78, 97, 154, 162, 164). "Aeolian ecosystems" (162) fueled by windborne input (53, 78) include caves, mountaintops, snowfields, polar regions, new volcanic areas, phytotelmata, and barren deserts and islands. In these systems, local plant productivity is low or absent; yet diverse, detrital-based webs exist with abundant consumers at several trophic positions.

Such webs characterize high-altitude and snow-covered habitats worldwide (10, 53, 97). "Truly immense quantities of pollen grains of many different plants, spores of fungi and of Protozoa, seeds of a great variety of plants, . . . and nearly every conceivable group of winged and apterous insects, spiders, etc brought by the upper air currents, are frozen and entombed in the snow and glacier ice" (97, p. 70). Melted water carries detritus and carcasses to streams to provide a rich food for insects.

Worldwide, nutrient budgets of many terrestrial ecosystems depend on nutrients transported aurally (94). Such subsidies may compensate for low-nutrient soils in temperate forest communities (9). In much of the Amazon Basin, where soils are nutrient poor due to limited river deposition, airborne soils apparently are needed to achieve a nutrient balance (86, 176). Most P, a critical element that limits net primary production, is intercontinental: 13 million tons (13–190 kg/ha/year) is carried by dust blown from the African deserts 5000 km away (163)! Such input doubles the standing stock of P over 4.7–22 ky. Thus, the productivity of Amazon rainforests depends critically upon fertilization from another large ecosystem, separated by an ocean yet atmospherically coupled (163).

Consumers that redistribute large quantities of biomass include mammalian herbivores (e.g. grazers in the Serengeti; 103) and roosting or nesting birds (181). Bats, rats, birds, and crickets are major conduits of energy via guano into caves (42, 79, 82). Great quantities of fecal fruit and seeds from Peruvian

oil birds form the base of a diverse cave food web: bacteria, fungus, and >50 species of arthropods (47). Caves worldwide are similar; they receive all energy allochthonously via animals, root exudates, and water flow that deposits surface detritus; such input supports many detritivores, scavengers, fungivores, and a rich predator guild (42, 79, 99).

### *Movement of Prey*

Species produced in one habitat frequently end up as food elsewhere. Movement may be accidental (e.g. by winds), or a product of life history (e.g. migration, ontogenetic habitat switches) or interactions (e.g. interference).

**WATER TO WATER** The ubiquitous horizontal and vertical movement of water transports nutrients (see above) and prey. The prey of filter feeders may be produced locally, in adjacent habitats, or far away. Downstream movement of prey characterizes streams and rivers; generally, most productivity is fixed in riffles, yet most consumption occurs in ponds, often subsidizing resident predators (39, 116, 117).

Members of the "deep scattering layer" move 300–1500 m to feed at night in the photic zone and return to deeper waters during the day. These diel migrants carry much primary productivity to depths where they form the prey of large populations of fish and invertebrate predators (7). On deep seamounts in areas of very low in situ productivity, many fish species eat great amounts of prey carried to them by currents and vertical migrations; the population biomass of these fish is an order of magnitude higher than populations that do not receive allochthonous prey (90). Life history migrations of species at all trophic positions at several temporal scales connect food webs of marine pelagic and benthic habitats (the "jellyfish paradigm"; 16; but see 61). Diadromous migration of fish transport large numbers of potential prey between marine and freshwater habitats.

**LAND TO WATER** Some aquatic consumers eat terrestrial prey. Fish and aquatic insects eat insects and spiders that drop to streams (63, 193), often in great numbers (100). These amounts may surpass production of in situ aquatic insects. Many salmonids eat "an astonishing diversity" of terrestrial prey (80), at least seasonally; such prey can form >50% of annual energy uptake (80, 100). Land insects from 70 families provide  $\approx 10\%$  of fish diet in a Swedish lake (121).

An abundance of insects blow onto the ocean, both near and far from shore (21, 37, 38). On a typical summer day, an estimated 4.5 billion insects drift over the North Sea from a 30-km coastal strip (38). Greater numbers can occur. Off Nova Scotia, an estimated 800 billion budworm moths formed a floating slick  $100 \times 66$  km (21). An estimated mean of 2–17 million insects annually drop onto each  $\text{km}^2$  of ocean surface worldwide; this equals 2–17  $\text{kg}/\text{m}^2/\text{year}$ ,

or 0.01% of phytoplankton productivity (38). Although insects contribute little to the energetics of ocean ecosystems, they form 27%–60% of the prey volume of some fish and may have large impacts in low-productivity regions.

**WATER TO LAND** Many land consumers eat prey of aquatic origin. Emerging aquatic insects are eaten by terrestrial insects, arachnids, amphibians, reptiles, and birds; such consumers often occur in large populations at the margins of water (36, 70, 83, 118, 136, 137, 138, 146). Only  $\approx 3\%$  of emerging insect biomass remained in a desert stream, with  $23 \text{ g/m}^2/\text{year}$  ( $400\text{--}155,000$  individuals/ $\text{m}^2/\text{year}$ ) exported to the adjacent riparian zone (83). Such great export can be crucial to terrestrial predators, affecting abundance, territoriality, feeding behavior, and reproductive success (83). Seabirds and their associated ectoparasites are a major food of many consumers (48, 137).

Anadromous fish are important prey of diverse consumers in many terrestrial habitats, e.g.  $\approx 50$  species of birds and mammals eat salmon in Alaska (192). These fish “appear to be a keystone food resource for vertebrate predators and scavengers, forging an ecologically significant link between aquatic and terrestrial ecosystems” (192, p. 489) and appear critical to the success of many consumers. This interaction carries important conservation implications; the loss of such fish could exert major effects on these species and their community.

**LAND TO LAND** Winds frequently transport prey great distances. Windborne arthropods allow stable populations of predators to persist on barren volcanic fields and new volcanic islands (52, 54, 78, 166, 168). Insects also waft to mountain tops and snowfields (52, 53, 97, 162) where they are eaten by diverse and abundant predators. Over 130 species of arthropods, most from lowland habitats, can occur on barren snowfields (10). “Surprisingly large numbers” of diverse consumers in every trophic category “gorge” with foods “refrigerated in the snows” (97, p. 70). Webs with “every class of feeder” are driven by allochthonous foods (97). In these examples, airborne prey sustained predators (e.g. spiders, insects, lizards, birds, and small mammals) in a system lacking local primary productivity.

Prey movement among habitats often characterizes insect life cycles. Brown & Gange (28) give many examples of the generalized life-cycle of such insects: Females deposit eggs into the soil; larvae, which feed underground on roots or detritus, pupate there; and adults emerge to mate aboveground. Such a life cycle characterizes some of the most successful insects: Almost all termites, ants, cicadas, and many beetles, moths, and flies transport belowground organic material to aboveground consumers (112, 161). In the case of periodic cicadas (the land animal with the greatest biomass/area), predators feed to satiation on emergent adults (28).



Life-history migrations transport prey great distances. For example, monarch butterflies eat temperate milkweed but overwinter in Mexico where they are eaten by tropical birds (33). Similar transport occurs via other migratory animals, e.g. songbirds (92), mammalian grazers (150), and locusts.

### *Movement of Consumers*

Consumers' movement ranges from fine (e.g. local foraging paths) to broad scales (e.g. long-distance migration). Many mobile consumers, migrants, and age classes choose habitats based on relative profitability of forage intake (36, 155, 183). However, some consumers move into habitats with relatively low productivity to avoid interference or predation (73, 127). A vast number of species change feeding habitats during their lifetime (see 135 for examples and food web implications of ontogenetic habitat shifts by consumers).

**WATER TO WATER** Aquatic species exhibit a continuum of horizontal and vertical, short and long migrations. The "food availability hypothesis" for the evolution of diadromy in 128 species of fish (65) posits that relative productivity of marine and riverine environments at a given latitude determines if fish feed and grow in the ocean and move to freshwater to reproduce (anadromy) or vice versa (catadromy). Anadromy is more frequent when ocean productivity exceeds neighboring freshwater productivity (temperate, arctic). Many diadromous fish also feed in the less productive habitats and can exert great effects on prey in these places, e.g. anadromous steelhead in California rivers (141). Stable isotope analyses show the relative importance of coupled habitats on anadromous and estuarine fish (15a, 60).

Shorter migrations occur. Krill move annually from the Antarctic ice shelf, where they graze on algae, to pelagic zones, where they eat phytoplankton (157). This cycle may be central to southern oceans ecosystem dynamics. Feeding on ice algae (along with fat storage and cannibalism) allows krill to overwinter and be present in great numbers in the spring. Such seasonal and regional switches of food resources hypothetically explain two mysteries: the maintenance of very large populations and biomass of krill in this oligotrophic community, and the rapid suppression of phytoplankton during their exponential growth phase in spring.

In general, marine zooplankton, fish, birds, and mammals aggregate near regions of high productivity and food density (e.g. upwelling, frontal regions) (3, 14, 173). Crustacean densities inside frontal regions are 74.5 times greater than outside (14). Large populations of consumers migrate from deep water to feed on near-surface resources (7). Both marine and freshwater fish forage across habitats that vary in prey availability, e.g. pelagic and littoral zones (95, 111, 130), coral reef and sand flats (142), river and floodplain (63, 182).

**BETWEEN WATER AND LAND** Many species of land and seabirds eat both aquatic and land prey (29, 30, 156, 159). Sixteen Crozet Island species forage in the ocean, in freshwater, and on land (81). Predation by coastal seabirds significantly influences land invertebrates by consuming 24 tons/100 km<sup>2</sup>/year; land prey form 12%–25% of their total annual energy intake (156). Many land predators forage along shores (137, 146, 192). Along coasts worldwide, mammals and land birds eat living marine species and carrion (30, 126, 146). Such subsidies allow these species to maintain relatively large coastal populations that also forage on “typical” terrestrial prey (146).

**LAND TO LAND** Many taxa move at varying temporal and spatial scales (patches to continents) to use distinct habitats. The dependency on spatially and temporally variable resources (fruit, nectar, insects) necessitates that birds be highly mobile to track changes in resource abundance across geographic scales ranging from within trees to between altitudinal zones, and from intrahabitat shifts to intercontinental migrations (92). Many consumers move 200–500 m from the edge of adjacent fields to exploit forest birds (4, 6, 143, 189). Landscape considerations are important: Nest predation is greater in areas closer to the edge (6, 189) and is a function of P/A ratio of the forest (greater nest predation in smaller fragments; 4, 143). Predators entering habitat islands significantly affect the composition, abundance, and dynamics of avian communities.

Movement by parasitic and pathogenic consumers among “habitats” (hosts) is a key to parasite-host (17) and pathogen-resource dynamics (144, 177). Alternative hosts frequently support parasites (e.g. of humans; 17) or pathogens; infection occurs via movement of either the alternative host or infective stages of pathogens. A typical control measure is to eliminate “reservoir” species of alternative hosts. However, such measures are often only partially successful—e.g. local infection rates are influenced by spores from distant outbreaks (144, 177). Further, most parasites with complex life histories and many plant pathogens require “landscape complementation” (50) of resources. For example, some rust fungi must move among alternative hosts to develop, e.g. cedar-apple rust alternates between apples and eastern red cedar (144).

## FLOW AND SPATIAL SUBSIDIES: INDIRECT EFFECTS ON TROPHIC DYNAMICS

“Tropho-spatial” linkage is often a key factor in local dynamics. Recipient species almost always benefit from inputs. Food web effects depend on web configuration and the trophic roles of the mobile entity (e.g. nutrients, basal species, predators) and recipient (basal, intermediate, or top species) (1, 139).

### *Donor Control*

Interactions between consumers and allochthonous resources are typically donor controlled, i.e. consumers benefit from but do not affect resource renewal rate (i.e. no recipient control; 131, 135, 139). Donor control occurs whenever a resource population is spatially partitioned into subpopulations that occupy different compartments, only one of which is accessible to consumers (36, 139). For mobile consumers, some feedback is likely, i.e. recipient control of resources by consumers may occur in either habitat.

### *Movement of Nutrients*

We suggest that nutrient input is a major factor in open systems (and we argue that most systems are open); by contrast in closed systems, in situ herbivores and decomposers regulate nutrient recycling rates and availability to plants (171). If allochthonous nutrients enrich plants, primary productivity will increase, often dramatically (see earlier). Nutrient enrichment also increases plant quality. Herbivore survival and reproduction often depends more on host N concentration than on C availability (101, 139). Consequently, nutrient-subsidized systems often exhibit elevated densities of herbivores and higher-level consumers.

Mixing and upwelling of nutrients in the ocean stimulate phytoplankton blooms, followed by numerical responses through the web: Zooplankton increase, and nekton and vertebrates move to plankton concentrations (13, 14, 98). Upwelling drives oceanic production: Upwelling ecosystems account for just 0.1% of the ocean's surface, but 50% of the world's fish catch (13, 14). Cessation of upwelling sharply depresses pelagic productivity at all levels; e.g. El Niño events produce population collapses of seabirds, mammals, marine iguanas, and invertebrates off the Americas (14).

Exchange of nutrients between pelagic/littoral zones and intertidal zones can be quite important. Nutrient enhancement from coastal upwelling allows intertidal algae and higher-level consumers to increase productivity and standing stock (19). Nutrient input from oceanic waters may be a key "bottom up" factor in intertidal community structure (104). Fertilization effects of seabird guano on intertidal algae also can propagate up the web (25, 194): Invertebrate consumers grow faster and larger, reproduce more, and increase in density. The density of birds eating these invertebrates is 2–3.8 times greater than in unaffected areas (194). Conversely, nearshore productivity can increase secondary productivity of adjacent marine waters (98, 119).

In freshwater systems, large populations of herbivores/detritivores are fueled by detrital input from land and by aquatic plants using nutrients ultimately derived from terrestrial systems (40, 57, 147). Areas receiving P and N in runoff develop productive, "nutrient subsidized" phyto-benthic assemblages that then support a rich zoobenthic community (179). Anthropogenic nutrients (e.g. from

sewage, fertilizer, phosphate detergents) increase productivity, cause eutrophication, and significantly alter lake and estuarine communities (34, 44). A striking "dead zone" in the Gulf of Mexico is linked to fertilizer input from North America's agricultural regions (87).

Nutrient subsidies likewise affect terrestrial systems. Fixed N from atmospheric pollution arrives in sufficiently large quantity via rain to change plant species composition and productivity, alter the outcome of plant competition, and disrupt entire communities worldwide (56, 84, 175). Guano, rich in N and P, enhances the quality and quantity of land plants and underlies entire food webs in coastal and insular ecosystems worldwide (19, 31, 82, 91, 102, 137; WA Anderson, GA Polis, unpublished data). In inland Antarctica, allochthonous guano provides the only nutrients to sustain lichens, which then support microorganisms and arthropods (149). These communities occur only around bird colonies.

Nutrient enrichment subsidizes plants and also indirectly influences herbivores and predators (34, 35, 139, 171). Thus, although nutrient input increases productivity, effects on system stability are unclear (44, 45, 160). The "paradox of enrichment" (148) suggests that reducing nutrient limitation can destabilize plant-herbivore interactions—plant populations become susceptible to overgrazing by indirectly subsidized herbivores (44, 148). For example, bird guano increases N concentration and growth rates of mangroves; fertilized plants lose four times more tissue to abundant herbivorous insects than do unfertilized plants (129).

### *Movement of Detritus*

Cross-habitat flows of detrital subsidies (122, 164) often produce bottom-up effects in marine, freshwater, and terrestrial systems: Detritivores and their consumers increase throughout the web (see earlier). Diverse webs form even where local productivity is largely (or totally) absent: caves (42, 47, 79, 99), barren oceanic islands (74, 137, 138, 166, 167, 168) and deserts (154), light-limited zones of oceans and lakes (13, 174), blackwater rivers (15, 63, 64), and aeolian environments (162) such as lava flows (78, 168), mountaintops (53, 97), and polar areas (149, 164). The most biomass-rich community on earth is supported 100% by allochthonous detritus: 15–300 m mats of detrital surfgrass and kelp are converted into  $>1 \text{ kg/m}^3$  of benthic crustaceans (up to  $3 \times 10^6$  individuals/ $\text{m}^3$ ); large numbers of tropically distinct fish feed in these "hotspots" (174).

In other marine systems, detrital input allows species throughout the web to increase productivity and standing stock (20, 23, 32, 49, 104). Faunal biomass on beaches receiving various energy subsidies, from either upwelling or plankton blooms, is one to three orders of magnitude greater than on beaches without

subsidies (12). Islands receiving detrital shore wrack often support diverse and abundant consumers (68, 137, 138). Abundant beach detritus from a successful kelp restoration project allowed several seabird species that eat kelp detritivores to recover (23). Inputs from extremely productive marshes, estuaries, and seagrass and mangrove areas contribute substantially to secondary productivity in adjacent coastal waters; e.g. an estimated 3.5–8 metric tons/ha of mangrove detritus is exported offshore annually (123). Many stream consumers directly and indirectly rely heavily on terrestrially produced detritus as a major energy source (40, 41, 184, 185)

Numerical responses of subsidized detritivores can depress in situ resources. Intertidal grazers can occur at very high densities if they receive kelp detritus that originates sublittorally (32, 49, 105). These dense intertidal herbivores then graze noncoralline algae to low cover. Leaf fall is the major energy source producing great numbers of herbivorous stream snails; snails, so subsidized, depress in situ algae (147).

### *Movement of Prey*

Prey input allows predators to increase locally, as observed for diverse consumers in many habitats (see earlier). Top down effects occur when subsidized consumers increase densities and depress local resources. The dynamics of such donor-controlled interactions exhibit several features. First, because subsidized consumers cannot depress the renewal rate of imported prey, they are assured of a food supply that they cannot overexploit. Second, consumer success is decoupled at least partially from the constraints of local productivity and prey dynamics. Third, subsidized consumers can depress local resources below levels possible from isolated in situ consumer-resource dynamics in an interaction parallel to apparent competition (72, 77); however, instead of an alternative prey, an alternative habitat furnishes resources to consumers (or provides food for mobile consumers; see below). Thus, imported foods permit consumers to overexploit resident prey, even to extinction, without endangering the predator itself. Note that donor-controlled input decouples resource suppression from in situ productivity (73, 126, 127, 138, 139). Consequently, spatial subsidies can lead to dynamics and abundance patterns inconsistent with consumer-resource models (e.g. 8, 125) based solely on in situ productivity (135, 139). Fourth, effects are generally asymmetric: Prey in less productive habitats are affected more adversely than are those in more productive habitats.

We illustrate these dynamics. In a California vineyard, two-spotted mites move from grass to less productive grapevines. This prey input allows populations of predaceous mites on the vines to increase and suppress populations of an in situ pest, the Willamette mite, to lower densities than without spatial subsidy (59). In the Serengeti, nomadic herds track rainfall to forage in relatively

productive habitats (155). Migratory prey (e.g. wildebeest) are thought to allow resident lions to increase to the point that they depress resident species (e.g. warthogs, impala; 150). Heavy poaching of mobile Cape buffalo outside the Serengeti lowered their numbers in the game park, causing lions to decrease substantially, with increases in several alternative prey species (AR Sinclair, personal communication).

Subsidized consumers can influence entire communities if they suppress key species. Communities should be more stable if subsidies allow consumers to suppress species capable of explosive reproduction (e.g. sea otter example below). Subsidized predators can increase so much that they depress herbivores, thus allowing plants to be more successful—an “apparent trophic cascade”—apparent because energy sustaining high consumer densities is not from in situ productivity (as usually modeled) but arises outside the focal habitat (138).

We cite four examples of trophic cascades subsidized by allochthonous prey. Large numbers of lump sucker fish that migrate periodically from deeper waters are eaten by sea otters; such prey help maintain equilibrium densities of otters and allow control of sea urchins, thus releasing kelp from intense herbivory (180). Abundant coastal spiders eat many marine *Diptera* and suppress insect herbivores; plant damage is significantly less than on plants unprotected by subsidized spiders (136). Spiders along German rivers, subsidized by abundant aquatic insect prey, suppress herbivores, thus lessening damage to plants (J Henschel, personal communication). Detritivorous soil insects from gaps (herb/grass layer) in tropical forests are the major food of canopy anoles (46). Landscape considerations are important: Canopies immediately downwind from a gap support twice the flying insects and lizards as do closed canopies or those adjacent to, but upwind of, a gap. In subsidized areas, anoles depress resident herbivores, and plants show significantly less damage. Subsidized anoles also depress arboreal spiders, thus indirectly allowing small insects to increase. In each example above, prey import is donor controlled, spatially subsidized consumers exert recipient control on local prey, and such prey depression indirectly makes resources of these prey more successful.

Finally, prey movement can homogenize patches of differing productivity by linking predators with prey produced elsewhere. Prey flow from riffles to pools can be great: Drifting insects (50–1300/100 m<sup>3</sup>) subsidize resident pool predators and overwhelm predator effects on local prey populations (39). This process is a function of the number of prey moving, habitat isolation, and rates of immigration versus local depletion (41, 72). Thus, although predators may remove many prey individuals, prey input may make mask predator effects (39).

### *Movement of Consumers*

Consumer movement produces effects generally similar to those of prey movement (but see below): Consumers usually persist at densities higher than

possible in isolated habitats. We expect that cross-habitat foraging greatly affects resource dynamics at several spatial scales ranging from long-distance migrations of birds, marine and terrestrial mammals, and fish to short-distance foraging behaviors of predators among patches. Although such effects are undoubtedly widespread, few examples document how such movement facilitates resource depression or even how consumers benefit by cross-habitat foraging. This situation exists because the process is difficult to study and the question has not been well focused theoretically.

We focus on how consumer movement affects resources directly via consumption, and community structure indirectly via food web effects. If mobile consumers feed only in one area (e.g. migrating gray whales, predaceous stoneflies), they exert no top-down effects in alternative habitats (although they may fall prey to resident predators, e.g. tropical birds feeding on monarchs; 33). Feeding in two or more areas (e.g. songbirds, ungulates, diadromous fishes, metamorphic insects or amphibians) can sustain consumers in less productive habitats (e.g. summer breeding vs. winter feeding grounds). Movement may even maintain consumers in a habitat too small or unproductive to sustain the population solely on in situ resources.

Mobile consumers can depress prey: e.g. spiders and insects depressed by baboons traveling from productive riparian areas to adjacent desert dunes (24), halos in seagrass beds caused by intense herbivory from fish resident in adjacent reefs (142), coastal birds eating inland invertebrates (156, 159), pathogens among plant hosts (144, 177). Agricultural changes in southern wintering grounds favorable to lesser snow geese may have caused destruction of littoral vegetation on the shores of Hudson Bay; geese, subsidized to very high densities by crops, overgraze lawns of reeds and grass to near zero cover (88).

Consumer movement may influence the stability and structure of entire communities if subsidized consumers suppress key species or movement facilitates trophic cascades. In two well-studied freshwater cascades, fish predators are subsidized by noncascade, allochthonous prey to population levels that can suppress local prey. Adult and juvenile bass derive much food from littoral prey; bass predation on planktivorous fish tops the cascade in the pelagic zone of Wisconsin lakes (34, 152). Steelhead grow most in the ocean and migrate to California rivers, where they initiate strong cascades if conditions are suitable (141).

## CASE STUDY: ISLANDS AND THE OCEAN-LAND INTERFACE

We have shown how single inputs to specific trophic positions directly and indirectly influence dynamics. In nature, however, a variety of inputs are used by many species within a community. The significance of such inputs

on entire communities is well studied in two systems. Information on freshwater streams and lakes is presented throughout the paper. Here we describe the other system— island and coastal habitats affected greatly by multiple input from the sea. We suggest that the processes we describe occur worldwide along the ocean-land interface. This “coastal ecotone” forms a major ecosystem that occupies about 8% of the earth’s surface along 594,000 km of coastline (137).

We describe systems that, without marine input, would be fairly simple; in reality, myriad allochthonous inputs create a complex system. Primary productivity on Gulf of California islands off Baja California is low, yet material from the very productive ocean supports high densities of many consumers (135–138). Two features allow smaller islands in the Gulf (and elsewhere) to receive more marine subsidies than large islands and the adjacent mainland. First, seabirds frequently nest and rest on small islands (their predators are usually absent). Second, small islands exhibit a greater P/A ratio and are thus influenced relatively more by marine detritus along the shore.

Seabirds are one conduit by which nutrients, detritus, and prey enter islands. Seabirds deposit large quantities of N- and P-rich guano, which indirectly affects consumers (31, 82, 114, 137, 156, 158, 191). When coupled with adequate precipitation, these nutrients make terrestrial primary productivity on Gulf islands 13.6 times greater than on islands unaffected by seabirds. Plant quality also increases; plant tissue has three to four times more N and P (WA Anderson, GA Polis, unpublished data). The quantity and quality of plant detritus is likewise higher, thus indirectly allowing larger herbivore and detritivore populations (134). Seabirds also directly facilitate large populations of ectoparasitic and scavenger arthropods that eat bird tissue (48, 137). Overall, insects are 2.8 times more abundant on islands with seabirds (137). These prey stimulate large populations of higher-level consumers, e.g. on average, spiders are 4.1 times and lizards, 4.9 times more abundant on Gulf islands with seabirds. Ants, when present, appear to limit tick populations on islands worldwide; this cascades to produce more successful seabird breeding (48).

Algal wrack and carrion deposited on the shore form the second conduit. About 28 kg/year enter each meter of shore on Gulf islands (much lower than in many areas where seagrass and kelp contribute 1000 → 2000 kg/year/m; 137). The ratio of biomass from marine input (MI) to terrestrial productivity (TP) by plants is 0.5–22 on most islands; overall, 42 of 68 Gulf islands are predicted to have more MI than TP; five others have MI/TP ratios of 0.5 to 1.0. Many islands worldwide receive more energy from the sea than from land plants (30, 68, 69, 96, 137).

Marine input supports abundant detritivore and scavenger populations on the coast. Some of these consumers fall prey to local and mobile terrestrial predators. In the Baja system, insects, spiders, scorpions, lizards, rodents, and



coyotes are 3–24 times more abundant on the coast and small islands compared to inland areas and large islands (136, 137, 138, 146). (Coastal carnivores worldwide are often dense; 146.) In Baja, coastal spiders are six times more abundant than inland spiders;  $^{13}\text{C}$  and  $^{15}\text{N}$  stable isotope analyses confirm that their diet is significantly more marine based than is that of inland counterparts (5). Such analyses show that marine matter contributes significantly to the diet of many coastal taxa worldwide (5). On the Baja mainland, coastal coyotes eat  $\approx 50\%$  mammals and  $\approx 50\%$  marine prey and carcasses (146). Here, coastal rodent populations are significantly less dense than on islands lacking coyotes, suggesting that marine-subsidized coyotes depress local rodent populations.

Complex webs based on multiple allochthonous inputs are well studied in two other systems. On Marion Island (31, 156, 158, 191), manuring by penguins, seabirds, and seals significantly influences terrestrial processes. Guano and other material are deposited at 0.4 tons/ha/year, contributing 87% of all N to terrestrial plants; almost 1 ton of carcasses/km<sup>2</sup>/year are also deposited. Most carcasses are eaten by predatory and scavenger birds and mammals. Feral cats eat great numbers of seabirds: 2100 cats ate 400,000 petrels (35.4 tons; 1.7 kg/ha/year/cat; 30, 190).

On the Mercury Islands off New Zealand, guano from dense seabird populations adds K, N, and P (11, 43, 169). Enriched soils support luxuriant plant growth; abundant detritus is used by a trophically diverse and dense fauna. Three groups that eat detritivores and/or seabirds occur at very high densities and biomass: centipedes, lizards (10/m<sup>2</sup> supralittorally), and tuatara (densities as high as 2000/ha, with an immense population biomass, as individuals average 450 g). Tuatara eat many seabirds and terrestrially based prey indirectly supported by seabird nutrients (43).

In these systems, it is impossible to explain consumer dynamics solely by local productivity, and it is short-sighted to focus on one conduit of energy flow. The relative importance of each conduit varies due to the structure of the land-water interface (e.g. P/A ratios), temporal variability in climate (e.g. rain-stimulated plant growth decreases MI/TP on Gulf islands, 137, 138), and changes in marine productivity (e.g. depressed productivity due to El Niño events reduces kelp production, seabird populations, and marine input to islands; 14, 137, 138).

## DIRECT AND INDIRECT EFFECTS OF SPATIAL SUBSIDIES: THEORY

Spatial subsidies, in theory, influence all aspects of food web structure and dynamics (135). Theory of consumer-resource dynamics in spatially heterogeneous landscapes suggests key effects expected in natural systems. Some

predictions match empirical patterns; others need assessment. We focus on how spatial subsidies affect stability and abundance in stable systems. In unstable systems, effects of flows can be counterintuitive and are poorly explored.

For simplicity, consider a landscape where focal habitat A is coupled to a much larger or more productive habitat, with little or no reciprocal impact of A on the larger habitat. The influence of the larger habitat on A is represented by splicing input and emigration terms into standard predator-prey and food web models, such as this model for a food-limited predator eating a local prey:  $dN/dt = NF(N) - aPN + I_N - e_N N$ ,  $dP/dt = P[g(aN) - m] + I_P - e_P P$ , where N and P are prey and predator abundance in habitat A;  $F(N)$ , local prey growth rate;  $aN$ , predator functional response ( $a$  is the per-predator attack rate, per prey);  $g$ , local predator birth rate (an increasing function of  $aN$ );  $m$ , predator mortality. The input terms  $I_N$ ,  $I_P$  are spatial subsidies for prey and predator (in simple cases, constant input rates);  $e_P$  and  $e_N$  scale losses to the larger habitat (e.g. emigration, wash-out). Without immigration, predator persistence requires local prey abundance to exceed a threshold. In stable, isolated systems, increasing prey production sustains more predators, with large-amplitude oscillations possible at high productivities (195). This model is useful to examine a range of scenarios, e.g. direct density-dependence, or additional prey species.

### *Prey Flow, Specialist Predator ( $I_P = 0$ )*

Prey input, mimicking enhanced prey productivity (e.g. Schoener's [e.g. 153] models of competition in donor-controlled systems) can enhance predator numbers, but with little effect on equilibrium prey numbers. By contrast, prey emigrating in response to predator abundance (i.e.  $e = e'P$ ) can strongly reduce prey abundance and net productivity, indirectly depressing predator abundance. The openness of prey dynamics puts a floor of  $I_N/e$  on prey numbers and is analogous to incorporating a fixed-number refuge (74). Generally, refuges tend to stabilize unstable predator-prey interactions (e.g. 2, 75, 151). Even a low-productivity refuge with little effect on mean abundance can exert strong effects by damping the destabilizing impact of prey fluctuations in productive habitats (2, 151). This partially donor-controlled interaction involving allochthonous input makes less likely the classic "paradox of enrichment" (148).

### *Flow of Alternative Prey, Generalist Predator*

To model input of a second prey not recruited locally, we add an equation for the local dynamics of this second prey and express predator growth as a function of the abundance of both prey. This model is one of apparent competition between alternative prey of a generalist, food-limited predator (71, 72, 74, 77). The interaction between the second prey and predator is donor controlled. This allochthonous prey indirectly increases predation pressure on the local prey.

If input or quality of the second prey is sufficiently great, overconsumption can drive the local prey extinct. We suggest this model describes many of our empirical cases and illuminates how allochthonous input often depresses in situ prey.

The effects of consumer movement differ from those of nutrients, detritus, or prey: Consumers using one habitat can affect resource dynamics in another upon their return. General models suggest that predator dispersal in heterogeneous environments can stabilize otherwise unstable predator-prey systems (72).

### *Predator Flow, Resident Prey ( $I_N = 0$ )*

The rules a predator uses to select among habitats can greatly influence local dynamics. With passive immigration, as in the above model, the predator persists (at  $P^* = I_P/e_P$ ), even without local prey, and so can depress unproductive local prey populations. Predator immigration likewise tends to depress local prey; if  $r$  is prey intrinsic growth rate, when  $I/e > r/a$ , prey are eliminated. Sufficiently high predator flows destabilize at the community level, as resident prey in low-productivity environments can be eliminated; lower predator flows tend to stabilize, with depressed prey numbers. If the resident prey shows inverse density-dependence at low abundance, the system can also exhibit alternative stable states, with or without the prey (76).

Alternatively, predators may use optimal foraging rules to move among habitats. If consumers exhibit ideal free habitat selection, at equilibrium abundances of both, consumers and resources are those expected from local dynamics (72, 128). This prediction sometimes holds (armored catfish-algae; 128). However, the multiple examples of resource depression caused by predator subsidies (see above) suggest this is not the norm in nature.

### *Landscape Variables Influencing Immigration and Input Rates ( $I_X$ )*

Our models assume constant rates for  $I_N$  and  $I_P$ . However, input rates may vary both spatially and temporally. Immigration or input rates are undoubtedly a function of landscape variables such as perimeter and permeability of focal habitat A, and the distance between trophically connected habitats A and B. The probability that habitat A will intercept a subsidy or consumer moving from B is related directly to the perimeter ( $p$ ) of A and inversely to the distance ( $d$ ) between A and B. Furthermore, the probability that a moving entity will enter A once A is intercepted is a function of the boundary permeability ( $M$ ) of A. Thus,  $I_X = (p_A M_A/d_{AB})$  and is variable in time and among habitats. Such variability in input rates, although not incorporated into our models, likely exerts substantial impact on the dynamics in the recipient habitat.

## OVERVIEW

Ecologists are now aware that dynamics are rarely confined within a focal area and that factors outside a system may substantially affect (and even dominate) local patterns and dynamics. Local populations are linked closely with other populations through such spatially mediated interactions as source-sink and metapopulation dynamics, supply-side ecology, and source pool-dispersal effects (75, 135). The identification of landscape ecology as a specific discipline is recognition of multihabitat dynamics (50, 66, 170, 195). Here we dramatize the need to integrate landscape and food web ecology. This requires consideration of issues not in this paper: e.g. spatial scaling (186), landscape influences on food web assembly (75), and reciprocal effects of web dynamics on landscapes (e.g. large herbivores creating patchiness). However, the themes explored here will be central to an integrated discipline of landscape and food web ecology.

Our synthesis suggests several general principles: the movement of nutrients, detritus, prey, and consumers among habitats is ubiquitous in diverse biomes and is often a central feature of population, consumer-resource, food web and community dynamics. Bottom-up effects that increase secondary productivity are initiated frequently by inputs of nutrient to producers in the herbivore channel or detritus to decomposers in the saprovores channel. Top-down effects occur when spatially subsidized consumers affect *in situ* resources. These effects then can propagate indirectly throughout the entire web to affect species abundance and stability properties, often in complex ways (120). The strength of these effects depends on the flow rates of resources and consumers, each a function of landscape variables. A natural avenue of future work is to examine the relative impact of input when added to a landscape perspective and particular food web configurations.

One strong insight for applied ecology is that the dynamics of seemingly distinct systems are intimately linked by spatial flow of matter and organisms. Land management of local areas (e.g. agricultural and forestry practices, fragmentation, desertification) affects not only other terrestrial habitats (e.g. 6, 84, 88, 92, 163, 175, 188) but the productivity, food webs, and community structure of streams, rivers, lakes, estuaries, and oceans (67, 87, 165, 181, 183). Conversely, processes and policies in aquatic systems (e.g. eutrophication, fisheries) affect both aquatic (51, 165, 172) and terrestrial (23, 105, 137, 191) systems. The message is clear: Ecosystems are closely bound to one another, be they stream and lake, pelagic and intertidal zones, farms and the sea, forest and river, or ocean and desert.

We end by noting that "tropho-spatial" phenomena (movement of nutrients, food, and consumers; subsidized consumers; resource suppression in low-productivity habitats; altered stability properties) exert their influence at all

scales throughout ecology. Although most of our examples used distinct habitats, such dynamics can occur "sympatrically" among microhabitat patches (e.g. 46, 59) or at immense distances (e.g. 92, 163, 176). An integration of landscape perspectives with consumer-resource and food web interactions will enrich models, complement our understanding of the dynamics of populations and communities, help design better protocols for biological control of pest species, and improve techniques for the protection of critical habitats and endangered species.

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#### Literature Cited

1. Abrams PA. 1993. Effects of increased productivity on the abundance of trophic levels. *Am. Nat.* 141:351-71
2. Abrams PA, Walters CJ. 1996. Invulnerable prey and the paradox of enrichment. *Ecology* 77:1125-33
3. Ainley DG, Demaster DP. 1990. The upper trophic levels in polar ecosystems. In *Polar Oceanography*, ed. WO Smith, pp. 599-630. Orlando, FL: Academic
4. Ambuell B, Temple SA. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057-68
5. Anderson WA, Polis GA. 1997. Evidence from stable carbon and nitrogen isotopes showing marine subsidies of island communities in the Gulf of California. *Oikos*. In press
6. Andren H, Anglestam P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69:544-47
7. Angel MV. 1984. Detrital organic fluxes through pelagic ecosystems. In *Flows of Energy and Materials in Marine Ecosystems*, ed. MJR Fasham, pp. 475-516. New York: Plenum
8. Arditi R, Ginzburg LR. 1989. Coupling in predator-prey dynamics: ratio dependence. *J. Theor. Biol.* 139:311-26
9. Art HW, Bormann FH, Voigt G, Woodwell G. 1974. Barrier island forest ecosystem: role of meteorologic nutrient inputs. *Science* 184:60-62
10. Ashmole NP, Nelson JM, Shaw MR, Garside MR. 1983. Insects and spiders on snow fields in the Cairngorms, Scotland. *J. Nat. Hist.* 17:599-613
11. Atkinson IAE. 1964. The flora, vegetation and soils of Middle and Green Islands Group. *NZ J. Bot.* 6:385-402
12. Bally R. 1987. The ecology of sandy beaches of the Benguela ecosystem. *S. Afr. J. Mar. Sci.* 5:759-70
13. Barnes RSK, Hughes RN. 1988. *An Introduction to Marine Ecology*. Oxford, UK: Blackwell Sci.
14. Barry JP, Dayton PK. 1991. Physical heterogeneity and the organization of marine communities. In *Ecological Heterogeneity*, ed. J Kolasa, ST Pickett, pp. 270-320. New York: Springer Verlag
15. Benke AC, Wallace JB. 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology*. 78:1132-45
- 15a. Bilby RE, Fransen BR, Bisson PA. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evi-

- dence from stable isotopes. *Can. J. Fish. Aquat. Sci.* 53:164-73
16. Boero F, Belmonte G, Fanelli G, Piraino S, and Rubino F. 1996. The continuity of living matter and the discontinuities of its constituents: Do plankton and benthos really exist? *Trends Ecol. Evol.* 11:177-80
  17. Bogitsh, BJ, Cheng TC. 1990. *Human Parasitology*. Philadelphia, PA: Saunders Coll.
  18. Boling RH, Goodman E, VanSickle J, Zimmer J, Cummins K, et al. 1975. Towards a model of detritus processing in a woodland stream. *Ecology* 56:141-51
  19. Bosman AL, Hockey PAR. 1986. Seabird guano as a determinant of rocky intertidal community structure. *Mar. Ecol. Prog. Ser.* 32:247-57
  20. Bosman AL, Hockey PAR, Seigfried WR. 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. *Oecologia* 72:226-32
  21. Bowden J, Johnson CG. 1976. Migrating and other terrestrial insects at sea. In *Marine Insects*, ed. L Cheng, pp. 99-117. Amsterdam: North Holland
  22. Braband Å, Faafeng A, Nilssen JPM. 1990. *Can. J. Fish. Aquat. Sci.* 47:364-72
  23. Bradley RA, Bradley DW. 1993. Wintering shorebirds increase after kelp (*Macrocystis*) recovery. *Condor* 95:372-76
  24. Brain C. 1990. Spatial usage of desert environment by baboons. *J. Arid Environ.* 18:67-73
  25. Branch GM, Barkai A, Hockey PA, Hutchings L. 1987. Biological interactions: causes or effects of variability in the Benguela ecosystem. *S. Afr. J. Mar. Sci.* 5:425-46
  26. Bray RN, Miller AC, Geesey GG. 1981. The fish connection: a trophic link between planktonic and rocky reef communities. *Science* 214:204-05
  27. Brinkhurst RO, Walsh B. 1967. Rostherne Mere, England, a further instance of guanotrophy. *J. Fish. Res. Board Can.* 24:1299-309
  28. Brown VK, Gange AC. 1990. Insect herbivory below ground. *Adv. Ecol. Res.* 20:1-59
  29. Burger AE. 1982. Foraging behaviours of Lesser Sheathbills *Chionis* minor exploiting invertebrates on a sub-antarctic island. *Oecologia* 52:236-45
  30. Burger AE. 1985. Terrestrial food webs in the sub-Antarctic: island effects. In *Antarctic Nutrient Cycles and Food Webs*, ed. WR Siegfried, PR Condy, RM Laws, pp. 582-91. New York: Springer Verlag
  31. Burger AE, Lindebloom HJ, Williams AJ. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarctic Res.* 8:59-70
  32. Bustamante RH, Branch GM, Eekhout S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76:2314-29
  33. Calvert WH, Hedrick LE, Brower LP. 1979. Mortality of the monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. *Science* 204:847-51
  34. Carpenter SR, Kitchell JF. 1993. *The Trophic Cascade in Lakes*. Cambridge, UK: Cambridge Univ. Press
  35. Carpenter SR, Kraft CE, Wright R, He X, Soranno PA, Hodgson JR. 1992. Resilience and resistance of a lake phosphorus cycle before and after a food web manipulation. *Am. Nat.* 140:781-98
  36. Charnov EL, Orians GH, Hyatt K. 1976. Ecological implications of resource depression. *Am. Nat.* 110:247-59
  37. Cheng L, Birch MC. 1977. Terrestrial insects at sea. *J. Mar. Biol. Assoc. UK* 57:995-97
  38. Cheng L, Birch MC. 1978. Insect flotsam: an unstudied marine resource. *Ecol. Entomol.* 3:87-97
  39. Cooper SD, Walde SJ, Peckarsky BL. 1990. Prey exchange rates and the impact of predators on prey populations. *Ecology* 71:1503-14
  40. Covich AP. 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. *J. N. Am. Bent. Soc.* 7:361-86
  41. Covich AP, Crowm T, Johnson S, Varza D, Certain D. 1991. Post-hurricane Hugo increases in atyidshrimp abundances in a Puerto Rican montane stream. *Biotropica* 23:448-54
  42. Culver D. 1982. *Cave Life*. Cambridge, MA: Harvard Univ. Press
  43. Daugherty CH, Towns DR, Atkinson IAE, Gibbs GW. 1990. The significance of the biological resources of New Zealand islands for ecological restoration. In *Ecological Restoration of the New Zealand Islands*, ed. DR Towns, CH Daugherty, IAE Atkinson, pp. 9-21. *Conserv. Sci. Publ., No. 2*

44. DeAngelis DL. 1992. *Dynamics of Nutrient Cycling and Food Webs*. London: Chapman & Hall
45. DeAngelis DL, Loreau M, Neergaard D, Mulholland PJ, Marzolf ER. 1995. Modelling nutrient-periphyton dynamics in streams: the importance of transient storage zones. *Ecol. Model* 80:149-60
46. Dial R. 1992. *A food web for a tropical rain forest: the canopy view from Anolis*. PhD diss. Stanford, CA: Stanford Univ.
47. Dourojeanni M, Tovar A. 1974. Notas sobre el ecosistema y la conservacion de la cueva de las Lechuzas (Pargue Nacional de Tingo Maria, Peru). *Rev. For. Peru* 5:28-45
48. Duffy D. 1991. Ants, ticks, and nesting seabirds: dynamic interactions. In *Bird-Parasite Interactions*, ed. J Loye, M Zuk, pp. 242-57. New York: Oxford Univ. Press
49. Duggins DO, Simenstad CA, Estes JA. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170-73
50. Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-75
51. Durbin AS, Nixon SW, Oviatt CA. 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. *Ecology* 60:8-17
52. Edwards JS. 1986. Derelicts of dispersal: arthropod fallout on Pacific Northwest volcanoes. In *Insect Flight, Dispersal and Migration*, ed. W Dantharyana, pp. 186-203. Berlin: Springer-Verlag
53. Edwards JS. 1987. Arthropods of alpine aeolian ecosystems. *Annu. Rev. Entomol.* 32:163-79
54. Edwards JS, Crawford RL, Sugg PM, Peterson M. 1986. Arthropod colonization in the blast zone of Mt. St. Helens: five years of progress. In *Mt. St. Helens: Five Years Later*, ed. S Keller. Spokane, WA: E. Wash. Univ. Press
55. Edwards RT, Meyer JL. 1987. Metabolism of a sub-tropical low gradient blackwater river. *Freshwater Biol.* 17:251-63
56. Field CB, Chapin FS III, Matson PA, Mooney HA. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annu. Rev. Ecol. Syst.* 23:201-35
57. Fisher SG, Likens GE. 1972. Stream ecosystem: organic energy processes. *BioScience* 22:33-37
58. Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecol. Monogr.* 43:421-39
59. Flaherty DL. 1969. Ecosystem trophic complexity with Willamette mite, *Eotetranychus willamettei* Ewing (Acarina: Tetranychidae), densities. *Ecology* 50:911-15
60. France R. 1995. Stable nitrogen isotopes in fish: literature synthesis on the influence of ecotonal coupling. *Estuar. Coast. Shelf Sci.* 41:737-42
61. France RL. 1996. Benthic-pelagic uncoupling of carbon flow. *Trends Ecol. Evol.* 11:471
62. Gasith A, Hasler AD. 1976. Airborne litterfall as a source of organic matter in lakes. *Limnol. Oceanogr.* 21:253-58
63. Goulding M. 1980. *The Fishes and the Forest*. Berkeley, CA: Univ. Calif. Press
64. Goulding M, Carvalho ML, Ferreira EG. 1988. *Rio Negro: Rich Life in Poor Water*. The Hague, The Netherlands: SPB Academic
65. Gross MR, Coleman RM, McDowall RM. 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science* 239:1291-93
66. Hansen AJ, di Castri F, eds. 1992. *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. New York: Springer Verlag
67. Hasler AD, ed. 1975. *Coupling of Land and Water Systems*. New York: Springer-Verlag
68. Heatwole H. 1971. Marine-dependent terrestrial biotic communities on some cays in the coral sea. *Ecology* 52:363-66
69. Heatwole H, Levins R, Byer M. 1981. Biogeography of the Puerto Rican Bank. *Atoll Res. Bull.* 251:1-62
70. Henschel J, Stumpf H, Mahsberg D. 1996. Increase in arachnid abundance and biomass at water shores. *Rev. Suisse Zool* Vol. hors serie:269-78
71. Holt RD. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12:197-229
72. Holt RD. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* 124:377-406
73. Holt RD. 1985. Population dynamics of two patch environments: some anomalous consequences of an optimal habitat

- distribution. *Theor. Popul. Biol.* 28:181-208
74. Holt RD. 1987. Prey communities in patchy environments. *Oikos* 50:276-90
  75. Holt RD. 1993. Ecology at the meso-scale: the influence of regional processes on local communities. In *Community Diversity: Historical and Biogeographical Perspective*, ed. R Ricklefs, D Schuller, pp. 77-88. Chicago, IL: Univ. Chicago Press
  76. Holt RD. 1996. Food webs in space: an island biogeographic perspective. See Ref. 139a, pp. 313-23
  77. Holt RD, Lawton JH. 1994. The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.* 25:495-520
  78. Howarth FG. 1979. Neogeoaeolian habitats on new lava flows on Hawaii island: an ecosystem supported by windborne debris. *Pac. Insects* 20:133-44
  79. Howarth FG. 1983. Ecology of cave arthropods. *Annu. Rev. Entomol.* 28:365-89
  80. Hunt RL. 1975. Use of terrestrial invertebrates as food by salmonids. See Ref. 67, pp. 137-52
  81. Hureau JC. 1985. Interactions between antarctic and sub-antarctic marine, freshwater and terrestrial organisms. In *Antarctic Nutrient Cycles and Food Webs*, ed. WR Siegfried, PR Condy, RM Laws, pp. 626-29. New York: Springer-Verlag
  82. Hutchinson GE. 1950. Survey of existing knowledge of biogeochemistry: 3. The biogeochemistry of vertebrate excretion. *Bull. Am. Mus. Nat. Hist.* 96:554p
  83. Jackson JK, Fisher SG. 1986. Secondary production, emergence and export of aquatic insects of a Sonoran Desert stream. *Ecology* 67:629-38
  84. Jefferies RL, Maron JL. 1997. The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. *Trends Ecol. Evol.* 12:74-78
  85. Johnston CA, Naiman RJ. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecol.* 1:47-57
  86. Jordan CF. 1985. *Nutrient Cycling in Tropical Forest Ecosystems: Principles and Their Application in Management and Conservation*. New York: Wiley & Sons
  87. Justic D, Rabalais NN, Turner RE, Wiseman WJ Jr. 1993. Seasonal coupling between riverborne nutrients, net productivity, and hypoxia. *Mar. Pollut. Bull.* 26:184-89
  88. 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. Anim. Ecol.* 27:242-58
  89. Kitchell JF, O'Neill RV, Webb D, Gallepp GW, Bartell SM, et al. 1979. Consumer regulation of nutrient cycling. *BioScience* 29:28-34
  90. Koslow JA. 1997. Seamounts and the ecology of deep-sea fisheries. *Am. Sci.* 85:168-76
  91. Leevantaar P. 1967. Observations in guanotrophic environments. *Hydrobiologia* 29:441-89
  92. Levey DJ, Stiles FG. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *Am. Nat.* 140:447-76
  93. Likens GE. 1984. Beyond the shoreline: a watershed-ecosystem approach. *Int. Ver. Theor. Angew. Limnol.*, Ver. 22:1-22
  94. Likens GE, Bormann FH. 1975. An experimental approach in New England landscapes. See Ref. 67, pp. 7-29
  95. Lodge DM, Barko JW, Strayer D, Melack JM, Mittlebach GG, et al. 1988. Spatial heterogeneity and habitat interactions in lake communities. In *Complex Interactions in Lake Communities*, ed. SR Carpenter, pp. 181-208. New York: Springer Verlag
  96. Lord WD, Burger JF. 1984. Arthropods associated with Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*Larus marinus*) carrion on islands in the Gulf of Maine. *Environ. Entomol.* 13:1261-68
  97. Mani MS. 1968. *Ecology and Biogeography of High Altitude Insects*. The Hague, The Netherlands: Junk
  98. Mann KH, Lazier JRN. 1991. *Dynamics of Marine Ecosystems*. London: Blackwells
  99. Martin JL, Oromi P. 1986. An ecological study of Cueva de los Roques lava tube (Tenerife, Canary Islands). *J. Nat. Hist.* 20:375-88
  100. Mason CF, MacDonald SM. 1982. The input of terrestrial invertebrates from tree canopies to a stream. *Freshw. Biol.* 12:305-11
  101. Mattson WJ. 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.* 11:119-61
  102. McColl JG, Burger J. 1976. Chemical input by a colony of Franklin Gulls nesting in cattails. *Am. Mid. Nat.* 96:270-80



103. McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 55:259-94
104. Menge B. 1992. Community regulation: Under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755-65
105. Menge BA. 1995. Joint 'bottom-up' and 'top-down' regulation of rocky intertidal algal beds in South Africa. *Trends Ecol. Evol.* 10:431-32
106. Meyer JL. 1990. A blackwater perspective on riverine ecosystems. *Bioscience* 40:643-51
107. Meyer JL, Schultz ET. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnol. Oceanogr.* 30:146-56
108. Meyer JL, Schultz ET, Helfman GS. 1983. Fish schools: an asset to corals. *Science* 220:1047-49
109. Meyer JL, Tate CM. 1983. The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. *Ecology* 64:33-44
110. Minshall GW. 1967. Role of allochthonous detritus in the trophic structure of a woodland stream. *Ecology* 48:139-49
111. Mittelbach GG, Osenberg CW. 1993. Stage structured interactions in bluegill: consequences of adult resource variation. *Ecology* 74:2381-94
112. Moran VC, Southwood TRE. 1982. The guild composition of arthropod communities in trees. *J. Anim. Ecol.* 51:289-306
113. Mulholland PJ. Organic carbon flow in a swamp-stream ecosystem. *Ecol. Monogr.* 51:307-22
114. Murphy GI. 1981. Guano and the anchovetta fishery. *Res. Man. Environ. Uncert.* 11:81-106
115. Naiman RJ, Melillo JM. 1984. Nitrogen budget of a subarctic stream altered by beaver. *Oecologia* 62:150-55
116. Naiman RJ, Melillo JM, Hobbie JE. 1986. Ecosystem alteration of boreal forest streams by beaver. *Ecology* 67:1254-69
117. Naiman RJ, Melillo JM, Lock MA, Ford TE, Reice SR. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology* 68:1139-56
118. Nelson JM. 1965. A seasonal study of aerial insects close to a moorland stream. *J. Anim. Ecol.* 34:573-79
119. Newell RC. 1984. The biological role of detritus in the marine environment. In *Flows of Energy and Materials in Marine Ecosystems*, ed. MJR Fasham, pp. 317-43. New York: Plenum
120. Nisbet RM, Briggs CJ, Gurney WSC, Murdoch WW, Stewart-Oaten A. 1993. Two-patch metapopulation dynamics. In *Patch Dynamics*, ed. SA Levin, TM Powell, JH Steele, pp. 125-35. Berlin: Springer-Verlag
121. Norlin A. 1967. Terrestrial insects on lake surfaces, their availability and importance as fish food. *Rep. Inst. Freshwater Res. Drottningholm* 47:39-55
122. Odum EP. 1971. *Fundamentals in Ecology*. Philadelphia, PA: Saunders. 3rd ed.
123. Odum WE, Heald EJ. 1975. Mangrove forests and aquatic productivity. See Ref. 67, pp. 129-36
124. Ogden JC, Gladfelter EA. 1983. Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean. *UNESCO Rep. Mar. Sci.* 23:1-130
125. Oksanen L, Fretwell S, Arruda J, Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240-61
126. Oksanen L, Oksanen T, Ekerholm P, Moen J, Lundberg P, et al. 1996. Structure and dynamics of arctic-subarctic grazing webs in relation to primary productivity. See Ref. 139a, pp. 231-42
127. Oksanen T. 1990. Exploitative ecosystems in heterogeneous habitat complexes. *Evol. Ecol.* 4:220-34
128. Oksanen T, Power ME, Oksanen L. 1995. Ideal free habitat selection and consumer-resource dynamics. *Am. Nat.* 146:565-85
129. Onuf CP, Teal JM, Valiela I. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. *Ecology* 58:514-26
130. Osenberg CW, Mittelbach GG, Wainwright PC. 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology* 73:255-67
131. Persson L, Bengtsson J, Menge BA, Power ME. 1996. Productivity and consumer regulation: concepts, patterns, and mechanisms. See Ref. 139a, pp. 396-434
132. Pieczynska E. 1975. Ecological interactions between land and the littoral zones of lakes. See Ref. 67, pp. 263-76
133. Deleted in proof
134. Piñero FS, Polis GA. 1997. Marine donor controlled dynamics on islands in the Gulf of California: subsidy of de-

- tritivore tenebrionid beetles by seabirds. *Ecology*. Submitted
135. Polis GA, Holt RD, Menge BA, Winemiller K. 1996. Time, space and life history: influences on food webs. See Ref. 139a, pp. 435–60
136. Polis GA, Hurd SD. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proc. Natl. Acad. Sci. USA* 92:4382–86
137. Polis GA, Hurd SD. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* 147:396–423
138. Polis GA, Hurd SD. 1996. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. See Ref. 139a, pp. 275–85
139. Polis GA, Strong D. 1996. Food web complexity and community dynamics. *Am. Nat.* 147:813–46
- 139a. GA Polis, KO Winemiller, eds. 1996. *Food Webs: Integration of Patterns and Dynamics*. London: Chapman & Hall
140. Pomeroy LR. 1979. Secondary production mechanisms of continental shelf communities. In *Ecological Processes in Coastal and Marine Systems*, ed. RJ Livingston, pp. 163–86. New York: Plenum
141. Power ME. 1990. Effects of fish in river food webs. *Science* 250:811–14
142. Randall JE. 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255–60
143. Robbins CS. 1980. Effect of forest fragmentation on breeding bird populations in the piedmont of the Mid-Atlantic region. *Am. Nat.* 33:31–36
144. Roberts DA, Boothroyd CW. 1972. *Fundamentals of Plant Pathology*. San Francisco: WH Freeman
145. Roger C, Grandperrin R. 1976. Pelagic food webs in the tropical Pacific. *Limnol. Oceanogr.* 21:731–35
146. Rose M, Polis GA. 1997. The distribution and abundance of coyotes: the importance of subsidy by allochthonous foods coming from the sea. *Ecology*. In press
147. Rosemond AD, Mulholland PJ, Elwood JW. 1993. Top down and bottom up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264–80
148. Rosenzweig MLK. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–87
149. Ryan PG, Watkins BP. 1989. The influence of physical factors and ornithogenic products on plant and arthropod abundance at an island group in Antarctica. *Polar Biol.* 10:152–60
150. Schaller GB. 1972. *The Serengeti Lion*. Chicago, IL: Univ. Chicago Press
151. Scheffer M, de Boer RJ. 1995. Implications of spatial heterogeneity for the paradox of enrichment. *Ecology* 76:2270–77
152. Schindler DE, Carpenter SR, Cottingham KL, He X, Hodgson JR, et al. 1996. Food-web structure and littoral zone coupling to pelagic trophic cascades. See Ref. 139a, pp. 96–105
153. Schoener TW. 1976. Alternatives to Lotka-Volterra competition: models of intermediate complexity. *Theor. Popul. Biol.* 10:309–33
154. Seely MK. 1991. Sand dune communities. In *The Ecology of Desert Communities*, ed. GA Polis, pp. 348–82. Tucson, AZ: Univ. Ariz. Press
155. Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, et al. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–99
156. Siegfried WR. 1981. The role of birds in ecological processes affecting the functioning of the terrestrial ecosystem at sub-antarctic Marion Island. *Com. Natl. Francais Rech. Antarct.* 51:493–99
157. Smetacek V, Scharek R, Nothig EM. 1990. Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. In *Antarctic Ecosystems: Ecological Change and Conservation*, ed. KR Kerry, G Hempel, pp. 103–14. New York: Springer Verlag
158. Smith VR. 1979. The influence on seabird manuring on the phosphorus status of Marion island (sub-Antarctic) soils. *Oecologia* 41:123–26
159. Stahl JC, Weimerskirch H. 1982. Le ségrégation écologique des deux espèces de sternes des Iles Crozet. *Com. Natl. Francais Rech. Antarct.* 51:449–56
160. Stone L, Gabric A, Berman T. 1996. Ecosystem resilience, stability, and productivity: seeking a relationship. *Am. Nat.* 148:892–903
161. Stork NE. 1991. The composition of the arthropod fauna a Bornean lowland rain forest trees. *J. Trop. Ecol.* 7:161–80
162. Swan LW. 1963. Aeolian zone. *Science* 140:77–78

163. Swap R, Garstang M, Greco S, Talbot R, Källberg P. 1992. Saharan dust in the Amazon Basin. *Tellus B* 44:133-49
164. Teeri JA, Barrett PE. 1975. Detritus transport by wind in a high arctic terrestrial system. *Arctic Alpine Res.* 7:387-91
165. Thom RM. 1981. *Primary productivity and carbon input to Grays Harbor estuary*. Washington. US Army Corps Eng., Seattle Dist., Seattle, WA
166. Thornton IWB, New TR. 1988. Krakatau invertebrates: the 1980's fauna in the context of a century of recolonization. *Philos. Trans. R. Soc. London Ser. B* 322:493-522
167. Thornton IWB, New TR, McLaren DA, Sudarman HK, Vaughan PJ. 1988. Air-borne arthropod fall-out on Anak Krakatau and a possible pre-vegetation pioneer community. *Philos. Trans. R. Soc. Lond. B* 322:471-79
168. Thornton IWB, New TR, Zann RA, Rawlinson PA. 1990. Colonization of the Krakatau islands by animals: a perspective from the 1980s. *Philos. Trans. R. Soc. Lond. B* 328:131-65
169. Towns DR. 1975. Ecology of the black shore skink, *Leiopisma suteri* (Lacertilia: Scincidae), in boulder beach habitats. *NZ J. Zool.* 2:389-408
170. Turner MG. 1989. Landscape ecology: the effect of pattern on processes. *Annu. Rev. Ecol. Syst.* 20:171-97
171. Vanni MJ. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. See Ref. 139a, pp. 81-95
172. Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37:130-37
173. Veit RR, Silverman ED, Everson I. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *Ecology* 62:551-64
174. Vetter E. 1994. Hotspots of benthic production. *Nature* 372:47
175. Vitousek PM. 1994. Beyond global warming: ecology and global change. *Ecology* 75:1861-76
176. Vitousek PM, Sanford RL. 1986. Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17:137-67
177. Walker JC. 1969. *Plant Pathology*. New York: McGraw-Hill. 3rd ed.
178. Ward JV. 1988. Riverine-wetland interactions. In *Freshwater Wetlands and Wildlife*, ed. RR Sharitz, JW Gibbons. Oak Ridge, TN: Off. Sci. Tech. Info., US Dep. Energy
179. Ward JV. 1989. The four dimensional nature of lotic ecosystems. *J. N. Am. Benth. Soc.* 8:2-8
180. Watt J, Siniff DB, Estes JA. 1997. Diet and foraging behavior of an "equilibrium density" sea otter population: the influence of episodic oceanic subsidies. *J. Anim. Ecol.* Submitted
181. Weir JS. 1969. Importation of nutrients into woodlands by rooks. *Nature* 221:487-88
182. Welcomme R. 1979. *Fisheries Ecology of Floodplain Rivers*. London: Longmans
183. Werner E, Gilliam J. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. System.* 15:393-426
184. Wetzel RG. 1983. *Limnology*. Philadelphia, PA: WB Saunders. 2nd ed.
185. Wetzel RG. 1990. Land-water interfaces: metabolic and limnological regulators. *Int. Ver. Theor. Angew. Limnologie, Ver.* 24:6-24
186. Wiens JA. 1992. Ecological flows across landscape boundaries: a conceptual overview. In *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*, ed. AJ Hansen, F di Castri, pp. 217-35. New York: Springer Verlag
187. Wiens JA. 1995. Landscape mosaics and ecological theory. In *Mosaic Landscapes and Ecological Processes*, ed. L Hansson, L Fahrig, G Merriam, pp. 1-26. London: Chapman & Hall
188. Wiens JA. 1997. Metapopulation dynamics and landscape ecology. In *Metapopulation Biology: Ecology, Genetics and Evolution*, ed. I Hanski, M Gilpin, pp. 43-62. San Diego, CA: Academic
189. Wilcove DS, McLellan CH, Dodson AP. 1986. Habitat fragmentation in the temperate zone. In *Conservation Biology*, ed. ME Soule, pp. 237-56. Sunderland, MA: Sinauer Assoc.
190. Williams AJ. 1978. Mineral and energy contributions of petrels (Procellariiformes) killed by cats, to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res* 8:49-53
191. Williams AJ, Burger AE, Berruti A. 1978. Mineral and energy contributions of carcasses of selected species of seabirds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.* 8:53-59

192. Willson MF, Halupka KC. 1995. Anadromous fish as keystone species in vertebrate communities. *Conserv. Biol.* 9:489-97
193. Winemiller KO. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* 60:331-67
194. Wootton JT. 1991. Direct and indirect effects of nutrients on intertidal community structure: variable consequences of seabird guano. *J. Exp. Mar. Biol. Ecol.* 151:139-53
195. Yodzis P. 1989. *Introduction to Theoretical Ecology*. New York: Harper & Row