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# 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.

## 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

289

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 esturary, 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$^2$ 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. Terriginous 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$^2$) 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

$(7.4 \text{ kg/m}^2/\text{year}$ 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 $(10 \longrightarrow 2000$ 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–$5.2 \times 10^6$ metric tons (76). Worldwide, seabirds annually transfer $10^4$–$10^5$ 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 aerially (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 ≈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 × 66 km (21). An estimated mean of 2–17 million insects annually drop onto each $km^2$ of ocean surface worldwide; this equals 2–17 $kg/m^2/year$,

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 ≈3% of emerging insect biomass remained in a desert stream, with 23 g/m$^2$/year (400–155,000 individuals/m$^2$/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. ≈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 signifi-
cantly influences land invertebrates by consuming 24 tons/100 km$^2$/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, mam-
mals 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 (pat-
ches 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). Land-
scape 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 is-
lands 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). Al-
ternative 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 alter-
native 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" phytobenthic assemblages that then support a rich zoobenthic community (179). Anthropogenic nutrients (e.g. from

sewage, fertilizer, phosphate detergents) increase productivity, cause eutroph-
ication, 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 atmo-
spheric 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, al-
lochthonous 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 herbi-
vores 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 over-
grazing 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 $>1$ kg/m$^3$ of benthic crustaceans (up to
$3 \times 10^6$ individuals/m$^3$); large numbers of trophically 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 plank-
ton 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 sea-grass 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. Leaffall 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 vinyard, 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 lumpsucker 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$^3$) 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 fresh-water 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 pro-ductivity 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 pre-cipitation, 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 popu-lations (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 $\longrightarrow$ 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; $^{13}$C and $^{15}$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 ≈50% mammals and ≈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$^2$/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 poulations 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$^2$ 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: $dN/dt = NF(N) - aPN + I_N - e_NN$, $dP/dt = P[g(aN) - m] + I_P - e_PP$, 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 equilibrial 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 saprovore 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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