

Connectivity at the Land-Water Interface

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Introduction:

There is a growing appreciation in ecology and conservation that even those habitats and ecosystems (we will use these terms interchangeably) traditionally considered “insular” are in fact reticulately-connected (Polis and Strong 1996). These connections are mediated by both physical and biological processes spanning a wide range of spatial and temporal scales (Polis and Strong 1996). This is clearly true of linkages between similar habitat types, such as fragmented systems, or patchily-distributed communities (e.g., see DiBacco et al. Chp. 9; Moilanen and Hanski Chp. 3). However, linkages are also critically important between very distinct habitats, such as forests and grasslands, freshwater and marine habitats, or aquatic and terrestrial ecosystems. In fact, as we will discuss in this chapter, if connected habitats are dissimilar we believe there is at least as much potential for movement of materials to influence the connected systems than when habitats are similar.

Interhabitat connectivity has been formally recognized at least since 1923 (Summerhayes and Elton 1923), but recognition of the importance of linking systems for altering their productivity goes back much further (e.g., to ancient irrigation schemes, such as those in the Nile Delta of Egypt). Recently, an integration of the landscape and ecosystem ecology concepts of connectivity, and their potential to structure ecosystems, has begun to be examined in detail (e.g., Polis and Hurd 1996). We provide an overview of these linkages, but like Ricketts et al. (Chp. 11) and Paquet et al. (Chp. 6) we do not address connectivity between similar habitats across an intervening matrix (which are reviewed in the literatures on e.g., corridors, metapopulations, island biogeography, etc.). Instead, we concentrate on the mechanisms and importance of connectivity at the boundaries between two very different habitats: aquatic and terrestrial ecosystems. A huge variety of critical functional connections exist between aquatic and terrestrial habitats. These include diseases spreading to marine systems from terrestrial habitats thousands of kilometers away, large marine vertebrates altering terrestrial plant communities, and changes in watersheds altering nearshore benthic communities (Polis et al. 1997a). Linkages can also be demographic (e.g., source-sink dynamics, metapopulations), physical (e.g., sedimentation), trophic (“spatial subsidies”—food resources arriving from other habitats), or informational (behavioral). This large diversity creates the need for an organizing framework for land-water connections. Our main aim is to describe such a framework.

In this chapter, we demonstrate that habitat connectivity is a process of overarching importance at the land-water interface. We present several possible

frameworks in which to view habitat linkages generally (and those at the land-water interface specifically), and use one of them to provide examples of how these linkages have ramifying effects that can fundamentally structure both aquatic and terrestrial ecosystems. We will then demonstrate the importance of recognizing these connections for both theoretical and conservation biology, including examples of “lost connections” due to anthropogenic changes.

Defining habitat linkages

For the purposes of this chapter, we will consider two systems to be functionally linked (or “connected”) when one system, including biotic and abiotic factors, significantly affects another distinct system. This definition leaves both the question of what constitutes “significant effects” and what constitutes “distinct systems” intentionally vague. We feel this flexibility is appropriate because these terms depend on the system and the spatial and temporal scale of interest. Note also that we will use the terms “linkage” and “connectivity” synonymously.

Habitat linkages in general occur across a wide range of temporal and spatial scales. For instance, for marine fauna connectivity between juvenile and adult habitats has been shown to range from a few meters to thousands of kilometers (Gillanders et al. 2003), and to have a broad range of potential effects on population dynamics for the species considered. Examples of connectivity at the aquatic-terrestrial boundary range from short time periods (e.g., lizards foraging in intertidal zones over tidal time scales) to decadal periodicity, such as wind-blown deposition of terrigenous (land-derived) sediments into the ocean. The effects of these linkages range from minor, likely sub-population level effects (e.g., iguanas occasionally foraging on ghost crabs, Arndt 1999), to being dominant factors structuring ecosystems (e.g., seabird effects on some terrestrial ecosystems, Anderson and Polis 1999).

The heterogeneity among the examples that we have discussed illustrates why we need a way to classify habitat linkages. This need is augmented by the realization that our perception of linkages may also change depending on the system and species studied (e.g., see Crooks and Sanjayan Chp. 1). For instance, if the system under consideration is a salt marsh, then a land-water linkage might be the effects of marine isopods eroding creek-banks, thus changing the shape of the terrestrial landscape (Talley et al. 2001). If that same marsh were being viewed relative to large marine mammals that do not use this marsh habitat, there would arguably be no connectivity at all. Therefore our classification scheme needs to be sensitive to this context-dependence of linkages.

A conceptual framework for habitat connectivity

We propose a framework for evaluating habitat connectivity that comprises three different factors: units of flux, primary effects, and dynamical features.

Units of flux

Habitat linkages result from the movement of four basic units: organisms, energy, materials (nutrients, chemicals, inorganic materials, etc.), and information. Three of these potential forms of linkage involve physical entities crossing boundaries—movement of energy, material, or organisms between habitats—while the fourth involves only information crossing boundaries, such as when potential prey assess nearby habitats for predation risk.

These units of flux represent the basic currency through which connectivity occurs. These movements are not necessarily independent, and in many cases multiple fluxes will be important simultaneously (and sometimes with opposite signs). For example, inorganic material such as sediment may be moving from the land to the water at the same time emergent insects are moving in the opposite direction. Also note that the structure of the boundary can alter the fluxes between the habitats. Boundaries may be reflecting, absorbing, transforming or neutral for the different units, potentially affecting each unit type differently (Cadenasso et al. 2003; Strayer et al. 2003).

Primary effects

Mere movement of material or information across boundaries does not *de facto* create connectivity between two ecosystems, as defined here. A functional connection exists only when that movement in some (significant) way alters one of the systems. These alterations can take the form of almost any physical or biological interaction, but they can be broadly characterized as belonging to one or more of five classes of primary effect, with strongly overlapping and ramifying indirect effects on communities and ecosystems:

- *Trophic*—Here the linkage between two habitats involves the transfer of food resources, and the primary effect is a change in feeding status. This connection can be formed through the movement of either consumers or resources between habitats – for example, insects emerging from streams can become prey for terrestrial web-building spiders (Collier et al. 2002), or terrestrial consumers can move into aquatic habitats to forage (Carlton and Hodder 2003).
- *Demographic*—Demographic or “population” linkages are those that involve a change in population structure or population dynamics resulting from connecting two habitats. These comprise some of the more commonly studied classes of connectivity, and include issues such as metapopulations, source-sink dynamics, island biogeography, nursery or breeding habitats, and wildlife

- corridors. At the terrestrial-aquatic interface, demographic connections frequently involve ontogenetic (developmental) habitat changes, such as movement of amphibians between water and land.
- *Environmental*—Linkages for which the primary alteration involves a change of abiotic factors in the recipient and donor habitats. For example, woody debris from terrestrial plants can alter flow and sediment properties in rivers and streams (Naiman and Decamps 1997), or terrestrial land-use changes increasing sedimentation to coastal waters (Thrush et al. 2004).
 - *Behavioral*—Here the primary effect on the habitat involves a change in behavior of an organism based on the state of another habitat. Most examples in the literature involve changes in habitat use related to predation risk or prey availability. Examples at the land-water interface often include changes in fish behavior in response to avian predator presence (e.g., fishes moving to sub-optimal habitat to avoid terrestrial predators: Power 1984; Crowder et al. 1997). However, theoretically we would expect that behaviors such as optimal foraging and habitat selection (review: Rosenzweig 1991) could create many other kinds of land-water behavioral linkage.
 - *Genetic*—In some cases, the primary effect of connectivity of individuals (or gametes) will not be a change in population structure, density, or presence/absence, but rather a change in gene frequency or genetic structure of the connected populations. While this is an important aspect of habitat linkages generally (Rodriguez-Lanetty and Hoegh-Guldberg 2002, Frankham Chp. 4), we can find no examples of this form of connectivity at the land-water interface. However, on evolutionary time scales the land-water interface could have profound influences through either acting as a barrier (impeding gene flow) or by creating a corridor for increased genetic exchange between otherwise isolated populations. It is also feasible that there will be cases where correlated life history traits cause an adaptation in one habitat (e.g., land) to represent a maladaptation in another (e.g., aquatic habitat). There are currently no examples that we are aware of that apply to land-water interfaces. In terrestrial systems there are examples where bird breeding in one “source” habitat is timed to match peak resource availability; birds then disperse to another “sink” habitat where they breed at the same time as in the source habitat, but this is not the time of peak resource availability in the sink habitat, and reduced reproductive success results (Dias 1996).

There are numerous secondary and indirect effects that may cascade from the initial “primary effect”. Secondary effects may include individual, population, community, or environment-level impacts (see also Huxel et al. 2004). We define secondary effects as being of lower magnitude than primary effects, whereas

indirect effects can be of smaller or larger magnitude than direct effects. Essentially, almost any biological or physical interaction that can occur in nature can be modified, primarily or secondarily, by connectivity. As we present examples of connectivity at the aquatic-terrestrial interface in this chapter, we will make reference to the mechanisms and effect(s) involved in each example illustrated.

Dynamical features

Habitat linkages can also be classified on the basis of their dynamical features, and it is on this framework that we will focus our examination of connectivity in this chapter. The specific features of habitat linkages can be evaluated across four main axes—three dichotomous and one continuous.

- *Directionality.* The actual transport of material, organisms, or information can be either unidirectional or bidirectional. As will be seen in the examples that follow, this is in part a scale-dependent feature—often, processes that appear unidirectional at one temporal or spatial scale may be bidirectional across other scales. There is also an observer bias that affects the perception of directionality, which will be addressed later. Known examples mainly involve fluxes of energy, organisms, or materials, but there are also fluxes of information that create connectivity. For example, as described above, prey in one habitat may alter their behavior due to perceived predation risk in an adjoining habitat (Crowder et al. 1997).
- *Feedback.* Linkages can also be assessed for feedback—are the connections wholly controlled by one habitat, or are there feedbacks in place between the two interacting systems, whereby the recipient system(s) can affect the linkage from the donor system(s)? The original work on ecosystem subsidy assumed no feedback ("donor control", DeAngelis 1992), whereas recent empirical work (e.g., Nakano and Murakami 2001) and theory about "meta-ecosystems" include feedback (Loreau et al. 2003). A meta-ecosystem is defined as a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries (Loreau et al. 2003).
- *Temporal variation.* While all linkages are dynamic when viewed over long enough time periods, it is useful to ask to what extent does the link vary through time and over what time periods does this variation occur (e.g., diel, seasonal, interannual, interdecadal cycles). For example, Nakano and Murakami (2001) discuss a seasonal flux of insects emerging from freshwater streams passing to terrestrial bird communities, whereas some scavengers show diel foraging patterns in

visiting beaches to feed on washed up prey in Baja California (Rose and Polis 1998).

- *Biotic/abiotic mediation.* Connectivity between systems can be mediated by either biotic or abiotic factors. While there are numerous examples of each form of mediation, there are systematic differences between the mediation operating when terrestrial systems are donors versus recipients of linkages with aquatic systems (Box 1). Biotic and abiotic mediation are not always mutually exclusive or independent of each other.

The interaction among these dynamical features allows for the development of a conceptual framework in which to study linkages among habitats. We propose to use the first two axes (directionality and feedback) as a framework to illustrate various connectivities at the land/water interface (Figure 1). In addition we will present examples of linkages across mediation types (physical and biological), and will address where the linkage fits into this framework, which unit of flux is producing the linkage, and the primary effects, mediating forces, and time scales associated with the connection.

Box 1. Differences in mediation of linkages between freshwater, marine, and terrestrial habitats

The movement of material or organisms mediated by biotic vectors is equally frequent in either direction—organisms, whether prey or predators, will often actively move between terrestrial and aquatic systems (Polis et al. 2004). Abiotic mediation, however, more often moves materials, organisms, or nutrients from terrestrial to aquatic systems than in the other direction. One reason for this is that aquatic systems are generally lower in elevation than the terrestrial habitats that border them, and therefore gravity will tend to move material downslope and into the water. Yet this asymmetry of abiotic mediation differs between marine-terrestrial and freshwater-terrestrial habitats. This is due to two important factors. First, in most freshwater systems, land area is greater than inundated area; and terrestrial production outweighs aquatic production (Power 2001), which further increases the probability of the passive (abiotically-forced) movement of material from terrestrial to aquatic ecosystems. In most marine-terrestrial ecotones, the area inundated is clearly much larger than the terrestrial area, with a commensurate increase in production. The second factor relates to the physical forcing involved. At the freshwater-terrestrial boundary, physical forcing of material from the aquatic to terrestrial habitats is less frequent, as the dominant force driving the movement of water is gravity. This means that at shorter time scales (e.g., tidal), the passive transport of material from the aquatic to the terrestrial system is less common than at the marine-terrestrial boundary, where physical forcing is also strongly driven by winds, tides and waves. At longer time scales (e.g., annual or seasonal), freshwater flooding events are often of overarching importance to terrestrial ecosystems, providing nutrients and sediments to terrestrial habitats (e.g., see Likens and Bormann 1974 and references therein). In combination, these factors suggest that abiotic forcing will be less important when examining terrestrial-aquatic connectivity when the donor ecosystem is aquatic, and that at short time scales this is more true in freshwater than marine systems.

Examples of habitat linkages at the land-water interface

Here we present examples of habitat connectivity at the aquatic-terrestrial interface, paying particular attention to how they fit into the framework described in Figure 1. It should be emphasized that the dichotomization of the processes in Figure 1 is a convenient theoretical construct that simplifies description of real systems. The real world is likely to lie on a continuum between unidirectionality and bidirectionality, and between full and no feedback between connected habitats. Nonetheless, setting aside issues of scale and accepting a dichotomous framework is useful for suggesting a simplified categorization of linkages that serve to illustrate some common types of land-water connection. We describe examples in this simplified framework and then in the next section draw on some common features that aid thinking about linkages in a more flexible framework.

Cell A. Unidirectional movement of organisms, material or energy, without feedback

Many of the habitat linkages at the land-water interface presented in the literature are in this category, with a vast number of them being either donor-

controlled subsidies (Polis and Strong 1996), or connectivity involving changes to the physical structure of the recipient system. Note, however, that in some cases it is possible that there are actually feedbacks that have gone unrecognized. For example, decades of study were required before the feedbacks between streams and terrestrial systems were fully appreciated.

A clear example of donor controlled subsidy comes from Gary Polis's work on islands in the Gulf of California, which receive a trophic subsidy from the marine ecosystem. In this region, the terrestrial habitats possess very low productivity, while production in the adjacent marine system can be anywhere from 4 to 40 times as high (Polis and Hurd 1996). There are two main conduits through which this marine productivity subsidizes the terrestrial community—through shoredrift (material deposited onshore by tides and waves) of algae and carrion, and through seabird colonies. In this section, we will focus on shoredrift. Trophic subsidy through shoredrift has been shown to lead to densities of terrestrial arthropods nearshore that are as much as 560 times higher than for inland populations (Polis and Hurd 1996). These effects, though, are felt throughout the ecosystem, leading to increased densities of herpetofauna (Barrett et al. 2003) and mammals (Stapp et al. 1999). The primary effect of this subsidy is a trophic one, with food resources that originated from marine production moving unidirectionally to the terrestrial ecosystem. This primary effect leads to a host of ecosystem-wide secondary and tertiary effects, including changes in population persistence (Polis et al. 1997a), source-sink relationships with inland populations (Polis et al. 2004), diversity (Anderson and Wait 2001), or competitive interactions (Polis et al. 2004). This particular subsidy is donor-controlled because in this ecosystem the terrestrial habitat will generally not affect the timing or flow of material, which prevents feedback to the marine system. The unidirectionality of the effect comes about because there is little material produced on the islands to flow to the sea, and the sea is vast in size by comparison to the islands. The dominant dynamics here are at time scales that are tidal, seasonal, and interannual: the tidal time scale arises because more marine material will be washed ashore on high tides, in particular spring high tides; time scales are seasonal because storms and die-offs of marine plants and animals show seasonal periodicity (Bodkin and Jameson 1991); and time scales are interannually related to changes in marine productivity associated with El Niño events. Further, this example is generally an abiotically-mediated form of connectivity, in that it is the physical forcing of tides and waves that is moving dead and dying organisms onto the terrestrial landscape.

There are myriad other examples of trophic connectivity at the land-water interface involving unidirectional flow with no feedback. One of the more commonly examined linkages is the input of terrestrial organic matter fueling lake (Gasith and Hasler 1976), stream or riverine (Grimm 1987, Naiman et al. 1987, Wallace et al. 1997a), and marine (Odum 1980, Mann and Lazier 1991) production. In these examples, terrestrial organic matter influences productivity in entire aquatic ecosystems. Here again, the trophic connection is unidirectional, without clearly-demonstrated feedback, but in these cases the dominant dynamics

occur over time scales more closely tied to production of terrestrial biomass and flooding events (e.g., seasonal and interannual time scales). The mediating factors in these examples are also abiotic, being forced by the gravity-driven flow of water and materials.

A very common non-trophic example of unidirectional flow without feedback at the terrestrial-aquatic interface involves the movement of sediment from land to water. In many cases, changes in the terrestrial habitat lead to increased sedimentation, with effects ranging from altering or destroying coral communities (Cortes and Risk 1985) to filling lakes or wetlands (Luo et al. 1999) and changing the supply of sand for intertidal and subtidal systems hundreds of kilometers away (Inman in press). These examples cover a broad range of time scales, from seasonal to geologic, and are generally abiotically mediated, although biotic activity (e.g., plant growth stabilizing sediments) clearly plays a role.

An example that includes marine habitats dramatically altering terrestrial ecosystems comes from studies of the effects of seagrass litter on Saharan desert geomorphology (Hemminga and Nieuwenhuize 1990). Seagrass cast ashore during high tides alters the transport of sand, ultimately leading to the formation of sand dune habitats. Here again there is an interaction between abiotic (tides, wind) and biotic (seagrass growth) mediation of the connection, which occurs over tidal and geologic time scales.

Cell B. Unidirectional movement of organisms, material, or energy, with feedback

This is a form of habitat connectivity with few specific examples in the literature applying to the land-water interface. This form of connectivity *does* occur across other habitat boundaries, for example songbirds may disperse to other habitat types only when there is a vacant territory in the alternate habitat type, which causes density dependent feedback in movement (e.g., Marra and Holmes 1997). More generally this form of movement may involve diffusion with organisms moving from areas of high abundance to areas of lower abundance as a forcing function that creates feedback. Density dependent dispersal could also lead to this kind of linkage (as in the songbird example above). The commonness of these mechanisms leads us to expect that this will be a frequent form of terrestrial-aquatic linkage if researchers search for it.

One example at the aquatic-terrestrial interface involves large storm events washing woody debris into streambeds (see Naiman and Decamps 1997 and references therein). This in turn can alter the subsequent flow into the stream from the surrounding watershed and may cause damming. There may in fact be an additional feedback from the stream to the terrestrial environment if the damming causes additional flooding, increasing erosion and the likelihood of further deposition of materials causing further blockage. Here the mediation is biotic (vegetation altering flow) and abiotic (gravity-driven movement of water), with

dominant temporal signals at seasonal (rainfall or snowmelt) and interannual (El Niño) time scales.

Cell C. Bidirectional movement of organisms, material, or energy, without feedback

This interaction requires materials to be moved bidirectionally across boundaries, but in such a way that the movements are decoupled from each other. While there are relatively few examples at the land-water interface, there is a fairly well-studied form of connectivity that potentially fits this category, which we now discuss.

This connection involves the bidirectional movement of nutrients across the land-water interface. Seabirds have been shown to be effective conveyors of marine nutrients into the terrestrial ecosystem, often with dramatic consequences for the recipient communities, such as increases in production or alteration of diversity (Anderson and Polis 1999, Anderson and Wait 2001). In a reciprocal fashion, those nutrients (in the form of guano) have been shown to impact marine intertidal communities when they flow seaward (Bosman and Hockey 1988, Wootton 1991, Wainright et al. 1998). However, there is no evidence for any substantial feedback between these two pathways: guano additions to the terrestrial system have not been shown to increase the rate of bird-derived (ornithogenic) nutrient input, and increased production in the intertidal zone probably has little if any effect on seabird feeding. Note that the water to land component of this movement is biotically mediated, while the reciprocal movement from land to sea is generally physically mediated. The primary effects in both cases involve an enhancement of primary production in the recipient habitat.

Despite the relative paucity of examples of bidirectional flux without feedback at the land-water interface, there are numerous good examples of these uncoupled movements across habitats within terrestrial or aquatic systems. For example, larval exchange between embayments and the open ocean may be completely decoupled from each other, with oceanic larval supply being strongly driven by oceanic adult population dynamics, and movement from the embayment seaward being driven by dynamics of reproduction within the bay (DiBacco and Chadwick 2001).

Cell D. Bidirectional movement of organisms, material, or energy, with feedback

This quadrant represents another major portion of the habitat connectivity at the land-water interface studied to date. One common form of connection involves organisms undergoing changes in habitat use through development (ontogenetic habitat shifts). Amphibians provide an excellent example of this connectivity.

Anurans (frogs and toads) have complex life cycles, with ontogenetic habitat shifts between aquatic and terrestrial systems. Here, the larval stage is spent in

aquatic systems, while many adult anurans dwell largely in terrestrial habitats. This can lead to direct effects on population dynamics between the two systems, where changes to the population in either habitat affects densities in the other (Wilbur 1980). Further, both larval (e.g., tadpole) and adult populations can significantly impact their respective aquatic and terrestrial ecosystems (e.g., Kupferberg 1997, Anderson et al. 1999). Consequently, these connections can lead to ecosystem-wide effects of connectivity. In this example, the bidirectional movement of organisms drives the linkage between habitats, at temporal scales focusing around seasonal (breeding) or interannual time scales. In a case like this one, where the bidirectional flux involves different life-stages of the same species, there are necessary limits to the extent to which bidirectionality can occur when viewed over long time periods. Specifically, the lack of flux of larvae to terrestrial systems would eventually lead to a loss of terrestrial adults that could return to aquatic habitats to breed.

The anuran example is representative of the broader case of organisms that alternately use the land and the water at different life-history stages, which is a common form of bidirectional connectivity with feedback at the land-water boundary. Other examples at both freshwater and marine interfaces include sea turtles, seabirds, some marine mammals, parasites, and countless insect species (insect ontogenetic shifts are particularly prevalent at the freshwater-terrestrial interface; Cheng 1976). These connections can also be mediated by physical transformation of habitat, such as anurans or insects breeding in pools created by other vertebrates (Gerlanc and Kaufman 2003).

There are also examples of bidirectional movement with feedback that do not require ontogenetic shifts in habitat use. Probably one of the best studied is the connectivity formed by the activities of beavers (*Castor canadensis*). Beavers move back and forth between the terrestrial and aquatic habitats. Through their feeding and dam-building they have been shown to alter hydrology, water biochemistry, and diversity and abundance patterns of plants, birds, fishes, and insects (Wright et al. 2004 and references therein). These alterations cause a suite of changes to habitat suitability for beaver populations, often leading to a cyclic pattern of use and disuse of the area by beavers, as food resources are depleted, beavers emigrate or die, and then recolonize as vegetation re-grows. This feedback between the terrestrial and aquatic habitats cycles over scales on the order of several years (Wright et al. 2004).

From this framework, we begin to see patterns that indicate that the land-water interface has a number of constraints that are not seen elsewhere, with the exception of saltwater-freshwater connections. The land-water interface represents a strong physiological barrier that limits biotic movement between the two habitats. Over evolutionary time scales, overcoming these barriers from land to water or vice-versa has resulted in major evolutionary revolutions in some lineages (such as amphibians, or in the invasion of land by arthropods in the Silurian, 425 million years ago). For most species, however, the land-water interface still represents a strong barrier influencing population size and gene flow. These

limitations on the movement of organisms reduce the biotic influence of these linkages and increase the importance of abiotic physical processes (Witman et al. 2004). However, many strong biotic linkages do exist and are of great significance in particular systems. In the “Factors promoting and limiting habitat linkages” section below we discuss other factors that enhance or reduce the strength of biotically driven land-water linkages.

Some common features of the different types of linkages

Scale-dependence of connectivity. It is important to note that many linkages will switch between compartments of the matrix depending upon the temporal or spatial scale over which they are observed. A good example comes from the work of Nakano and Murakami (2001), who examined the food web in a deciduous forest and stream ecotone. They quantitatively and painstakingly measured the biomass of invertebrate prey and vertebrate predators in both terrestrial and stream habitats, cross-habitat prey fluxes, and the percentage contribution of aquatic and terrestrial prey items to terrestrial and stream consumers. Their results showed that reciprocal, across-habitat prey flux alternately subsidized both forest birds and stream fishes (Nakano and Murakami 2001; Figure 2). However, short term within season observations (e.g., Nakano et al. 1999) revealed largely unidirectional flow with no feedback: during the summer, the net flow was from terrestrial to aquatic systems, while during spring the flow was in the opposite direction (Nakano and Murakami 2001). It was only by looking across longer time scales (years) that they observed a bidirectional flow with potential feedback between the two habitats (Figure 3).

Scale dependence of linkages is not limited to temporal shifts in perspective. For example, a study of wading birds in wetlands in the Delta of the Colorado River found that some nesting birds received no trophic subsidy from adjacent waters on the scale of tens to hundreds of meters, but birds were instead feeding in waters kilometers away (D. Talley, E. Mellink, G. Huxel, S. Herzka, and P. Dayton, unpublished data). Thus, at small spatial scales, connectivity was absent, while at larger scales, it was intense. Such scale-dependence is a common feature of habitat connectivity, and requires that investigators pay particular attention to the spatial and temporal scales over which they are assessing connectivity.

Perspective-dependence of connectivity. The effect of temporal scale on perceived connectivity patterns brings up a larger issue of the importance of perspective-dependence of connectivity studies. The appropriate categorization of effects within our theoretical framework may vary depending on which species, units of flux, and habitats are considered. This applies to all of the aspects of connectivity presented here, including dynamical features, primary effects, or even the existence of connectivity between systems. It is important to ask what are the appropriate time and spatial scales for the process of interest and how do these differ from the scales of observation of that process. For example, one of the best documented forms of connectivity at the land-water interface involves the

movement of vertebrate predators and scavengers into the intertidal zone to feed, with hundreds of cases documented across a broad range of taxa and habitats (Willson et al. 1998, Carlton and Hodder 2003). If viewed from the perspective of a littoral prey population, terrestrial vertebrates feeding in the intertidal represent a linkage from terrestrial to aquatic systems, with the primary effect being mortality or changes in abundance for intertidal prey items (e.g., shorebird predation alters intertidal invertebrate communities, Thrush et al. 1994). This could reasonably be classified as belonging in Cell A in our scheme for categorizing linkages (Figure 1), with the directionality being terrestrial to aquatic. This perspective results from considering the predator foraging process over short time scales and not considering the longer term or larger spatial scale dynamics of the invertebrate prey. However, if this same example is viewed from the perspective of a terrestrial predator taking advantage of a periodically-available prey resource, the connectivity created by terrestrial vertebrates foraging in the littoral zone represents a trophic subsidy from the aquatic to the terrestrial ecosystem. This creates the potential for feedback, presuming that the predators alter prey availability (Cell D, Figure 1). Again, the literature is rich with examples, including coyotes (*Canis latrans*), bears (*Ursus* spp.), and lizards receiving trophic subsidy from aquatic organisms, leading to population-level responses of the terrestrial consumers (Rose and Polis 1998, Gende et al. 2002b, Sabo and Power 2002). This second perspective results from focusing on the population dynamics and controls of abundance of the invertebrate prey over longer time scales than those considered in the first perspective. While a holistic perspective would recognize both aspects of these linkages, it is often necessary to restrict one's attention to a particular facet of a linkage. Even in those restricted cases it is nonetheless important to identify the ecological framework in which the connection is embedded, as it profoundly influences the interpretation of the strength, direction, and other parameters of connectivity.

Ramifying and multiple effects. The examples presented in this chapter show that habitat connectivity can yield not only multiple primary effects, but can have impacts that spread reticulately throughout ecosystems. For instance, in the case of trophic subsidies to islands in the Gulf of California, the trophic subsidy provided by the input of guano initially leads to greater terrestrial primary productivity on islands which are heavily used by birds (Anderson and Polis 1999). These initial changes in productivity then have cascading effects that can alter structure, abundance, or even population persistence at all levels of the ecosystem (Stapp et al. 1999, Sanchez-Piñero and Polis 2000).

Various studies of the influence of salmon (*Oncorhynchus* spp.) on terrestrial environments in Alaska have found wide-ranging impacts on terrestrial organisms including brown bears (*Ursus arctos*), wolves (*Canis lupus*), riparian plants, bald eagles (*Haliaeetus leucocephalus*), and song birds (Gende et al. 2002b, Darimont et al. 2003, Willson et al. 2004). Many of the impacts are indirect. For example, brown bears feed on salmon carcasses, then defecate nutrients in the upland riparian habitats. This in turn increases riparian vegetation growth providing

shelter, nesting sites, and food resources for songbirds (Willson et al. 2004, Gende et al. 2002). Similar pathways can be followed from bald eagles to riparian trees to riparian insects to songbirds.

Although the focus has been on direct linkages between land and water habitats, one must recognize that these habitats and habitat boundaries often contain large, reticulate and highly connected food webs (Polis and Strong 1996, Polis et al. 2004 and chapters therein). These linkages can have profound influences on the dynamics of the two habitats that extend well beyond the initial linkage pathways (Polis et al. 1997a, Huxel and McCann 1998, McCann et al. 1998, Huxel et al. 2002, 2004). Below we focus on the initial mechanisms and pathways of habitat linkages.

Factors promoting and limiting habitat linkages

There is a suite of factors that alter the likelihood of connectivity between any two habitats. These include characteristics of the organisms that cross a boundary, of the environment, and of the boundary itself. We consider each of these in turn.

A number of biological parameters may increase the likelihood of connectivity between terrestrial and aquatic habitats. One critical trait involves ontogenetic habitat shifts that allow or require an organism to use aquatic and terrestrial habitats at different life stages. This is a common feature of many insects, birds, mammals, and reptiles, and is a defining characteristic of amphibians (Wilbur 1980). Further, some organisms, such as the many terrestrial vertebrates listed in Carlton and Hodder (2003), have behavioral and/or physiological plasticity and adaptations that allow foraging in either terrestrial or aquatic habitats. In some cases, such as the Galapagos marine iguana (*Amblyrhynchus cristatus*), these cross-boundary foraging excursions are obligate (Wikelski and Thom 2000). Where species exhibiting these habitat shifts are present, additional factors such as home range size, dispersal ability, or trophic position should affect how far the connection penetrates into the recipient habitat. On longer time scales, life-history patterns are expected to be intimately related to linking biological traits and our next category, traits of the environment (e.g., Roff 2002).

Traits of the habitat or environment can also affect the probability of habitat connectivity. It has been proposed that, at least as a null model, strong asymmetries in productivity would be expected through physical processes (such as the Second Law of Thermodynamics) alone to increase cross-boundary connectivity (Laurance et al. 2001). Further, large temporal changes in abiotic conditions and physical forcing (waves, currents, winds) should also increase connectivity. This is demonstrated by sea foam and dust transporting nutrients and bacteria between the land and the sea, (Blanchard and Syzdek 1970, Griffin et al. 2002), or sedimentation under flooding regimes (e.g., Naiman and Decamps 1997 and references therein). Unpredictability of habitats is also expected to lead to

selection for dispersal under certain sets of conditions (Southwood 1962, McPeck and Kalisz 1998).

Note that many of these factors, both biological and physical, increase the likelihood of connectivity by creating an inequality between habitats' ability to provide all of the fundamental requirements for an organism—inequality can be a driving force in connectivity. Strong asymmetry between habitats might be expected to decrease biological connectivity (in contrast to the physical mechanisms described above) by decreasing the likelihood of cross-habitat movement of organisms (Laurance et al. 2001). However, asymmetries which create trade-offs in habitat function for various life-history or biological needs of an organism may actually increase the likelihood of movement. As we have seen in the examples of allochthonous inputs (resources arriving from outside the system) and ontogenetic shifts in habitat use presented here (Polis et al. 1997b, Wikelski and Thom 2000, Nakano and Murakami 2001), inequality between habitats can be a driving force promoting connectivity depending on the interaction between biological and physical traits.

Features of the boundary between habitats will also influence the strength of linkages, therefore necessitating examination of the role of boundaries in understanding the importance of habitat linkages (Cadenasso et al. 2003, Strayer et al. 2003). Most studies of habitat linkages treat boundaries as passive entities. This may be appropriate in many situations such as in linkages between near shore and pelagic habitats, but for land-water linkages the boundary may play an important active role in processing of resources and acting as a zone of absorption, reflection or transformation of the resources (Strayer et al. 2003). Thus, models of boundaries as diffusion zones across which materials are passed unaltered may not be appropriate. For instance, on the islands of Baja California, marine algal wrack (shore-deposited vegetation) may be actively buried in the beach material (the boundary) by heavy wave action and subsequently utilized and converted by the detrital-based communities in the intertidal zones before entering the terrestrial environment. This active incorporation through wave action on beaches contrasts with passive reflection by cliffs, or washing up (often temporarily) on beaches.

Generally, “harder” or less permeable boundaries will tend to lower connectivity between systems, because low permeability will impede the flow of organisms, materials, and information across the boundaries. For example, the transport of marine nutrients to the terrestrial ecosystem by Galapagos sea lions (*Zalophus wollebaecki*) is restricted to shorelines with elevations low enough that sea lions are able to access the land—thus the nature of the boundary between the land and the sea determined the degree of connectivity between the marine and terrestrial system (Farina et al. 2003). Boundary permeability (and thus connectivity) is species- and habitat-specific, in that what forms a hard boundary for one organism or connection may not represent a boundary at all for another. In a study of the permeability to shoredrift at the land-sea boundary in the Gulf of California, we examined stable isotopes and terrestrial faunal community data

from both hard boundaries (cliffs) and soft boundaries (beaches). Sloping beaches were much more permeable to allochthonous inputs in the form of shoredrift, (Figure 4, Talley et al., in prep). Conversely, marine inputs that are mediated by cliff-roosting seabirds would be expected to show the opposite trend, and seabirds which nest inland would have some level of connectivity that is largely independent of the boundary type at the land-water interface (Figure 4). This shows that there is a complex interaction between the form of connectivity (or mediation) and the boundary, which prevents simple rules from providing more than general guidelines for predicting permeability. It is therefore necessary to study permeability for particular organisms and habitat couplings.

Considerations for ecology

Given the ubiquity of habitat linkages and their potential to alter or structure communities, populations, and environments, it is critical that we incorporate aquatic-terrestrial linkages into ecological thinking. A better understanding of habitat connectivity at the land-water interface will improve both empirical and theoretical ecology, and will inform conservation biology in theory and practice.

Habitat linkages are of importance to both terrestrial and aquatic ecological researchers, since they are often the driving force structuring ecosystems. This is true for linkages that are trophic, demographic, environmental, and behavioral. In many cases, attempting to fully understand the dynamics of a focal habitat will be doomed to failure if external forcing through habitat connectivity is ignored. In the previous example for islands in the Gulf of California, the effects of the extensive marine input leads to extraordinarily high densities of spiders on land, and an apparent trophic cascade, which could not be explained by evaluating *in situ* production alone. This has been appreciated for some time for terrestrial effects on aquatic systems, with studies outlining phenomena such as watershed connectivity (Likens and Bormann 1974) and the effects of terrestrial food resources in streams (Minshall 1967, Cummins et al. 1973, Wallace et al. 1997b). But only recently has the reciprocal case of aquatic effects on terrestrial systems begun to be vigorously pursued, with studies highlighting the role of emerging insects as prey for forest consumers (Jackson and Fisher 1986, Gray 1993, Sanzone et al. 2003) and the role of salmon carcasses in terrestrial ecosystems (Gende et al. 2002a).

The importance of linkages between habitats has been explored in great detail theoretically for movement of single species (metapopulation theory; e.g., Levins 1969, reviewed by Hanski and Gilpin 1997) and nutrients (reviewed by DeAngelis 1992). More recently, the influence of habitat linkages on communities has been explored (Polis et al. 1997a, Huxel and McCann 1998, McCann et al. 1998, Huxel et al. 2002). These studies have profoundly affected the way ecologists think about connectivity between habitats. For example, Huxel and McCann (1998) explored the influence of allochthonous inputs across habitat boundaries on food web stability. They found that low to moderate amounts of allochthonous inputs relative to autochthonous productivity (that originating in the focal habitat) could

stabilize various kinds of food web dynamics. Huxel et al. (2002) also examined whether food web structure influenced the degree of impact of allochthonous inputs on the stability of food webs. Specialization at the top trophic level (such as with scavengers) on either allochthonous or autochthonous resources tended to limit the indirect effects of allochthonous inputs. . In contrast, generalists that feed on allochthonous as well as autochthonous prey can exhibit increased densities due to the allochthonous resources, resulting in increased predation pressure on autochthonous prey and possible ramifying effects.

Both of these studies (Huxel and McCann 1998; Huxel et al. 2002) also found that differences among trophic levels in linkage among habitats significantly influenced food web stability. If allochthonous resources are utilized by the second trophic level in a three trophic level system, then generalists (herbivores for example) will impact the first trophic level and provide increased resources for the third trophic level. Specialists at the second trophic level (perhaps detritivores) will not directly impact the first trophic level, but will provide increased resources for the third trophic level (Huxel et al. 2002). Therefore understanding how allochthonous resources are being used by the recipient community, and in particular what trophic levels are involved in the linkage among habitats, is of considerable importance in discerning the response of the recipient community to these inputs.

Considerations for conservation

Integrating the study of habitat connectivity into our research will improve our understanding of ecological systems and theories, and this will provide various benefits to conservation, in both theory and practice. Two aspects of connectivity and conservation deserve particular attention: situations where habitat linkages at the land-water interface have been altered by humans, and ways in which information about linkages can be used to improve the practice of conservation.

Anthropogenic alterations

Despite a substantial number of studies of terrestrial impacts on aquatic systems, the systematic study of habitat connectivity at the land-water interface is a relatively young field. Thus, questions of alterations to historical connectivity between these two systems remain largely unanswered, at least explicitly. There are nonetheless some clear examples of anthropogenic alteration of connectivity at the land-water interface, such as coastal armoring (seawalls and rip-rap) affecting sand flow to beaches (Runyan and Griggs 2003), or the effects of levee construction on connectivity between riverine and riparian or floodplain habitats

(e.g., see Wiens 2002 and references therein).

Habitat linkages that have likely been lost or diminished due to anthropogenic influence are numerous, and include alterations to physical structure as well as human impacts on the biological elements that mediate connectivity. These changes can potentially reduce natural connectivity (“hypoconnectivity”). There are a number of instances where anthropogenic influence has led to hypoconnectivity at the land-water interface. Salmon, for example, represent a significant source of food for a number of terrestrial vertebrates, and significantly affect terrestrial communities and production, both directly and indirectly (see discussion above). However, salmon populations have decreased dramatically in recent decades due both to physical alterations of the landscape, such as damming of rivers and loss of habitat, and biological alterations through harvesting (e.g., Nehlsen et al. 1991; Neville et al. Chp. 13). This decline in trophic subsidy is affecting terrestrial ecosystems, through diminishing connectivity at the land-water interface (e.g., see Gende et al. 2002a and references therein). Similarly, the loss of boundary areas (marshes in particular) between terrestrial and aquatic environments limits the linkages between the land and the sea. Over 90% of Pacific saltwater and Great Lake freshwater marshes have been lost, largely due to direct human habitat alteration (Schoenherr 1992, Ohio Lake Erie Commission 2000), leading to both a loss of water quality and limitation of aquatic resources available to terrestrial consumers.

Channelization of river basins and conversion of lakes to reservoirs has also greatly influenced the connectivity between land and water. This occurs in three major ways (Ward 1998). First, canals and reservoirs tend to be deeper and have steeper banks than their natural counterparts, limiting productivity (Malanson 1993). This results in less resources for terrestrial consumers (e.g., raccoons, birds, foxes, bears; Daniels 1960). Second, since the canals tend to be deeper, they also do not warm as much as shallow streams, thus reducing evaporation (Karr and Schlosser 1978). Third, channelization reduces the amount of sediment deposited on the floodplain of the river system. The loss of terrestrial habitat in the Mississippi river basin is a prime example (Gagliano et al. 1981). The Kissimmee River in Florida also is a good example in that historically it had a floodplain 1.5-3.0 km wide and covered an area of 180 km² (Dahm et al. 1995, Toth 1995). Channelization for flood control transformed the natural shallow stream course of 166 km into a straight canal 90 km in length 9 m in depth, and 100 m in width. The floodplain was deprived of sediments, seasonal patterns of stream flow were reversed, 12,000-14,000 ha of wetlands were lost, and biological communities were disrupted (Koebel 1995).

Further, connectivity between coastal consumers (utilizing aquatic resources) and inland habitats have been dissected in many regions by roads and highways (Forman and Alexander 1998). This can potentially restrict access to these trophic resources for wide-ranging species such as coyotes or small mammals (Carlton and Hodder 2003). This lack of connectivity could have wide-ranging effects on

terrestrial communities both through lowering population densities of consumers that are subsidized by aquatic resources and by restricting the flow of aquatic nutrients to inland habitats (e.g., Rose and Polis 1998, Polis et al. 1997a).

It should be noted here that connectivity is not necessarily a virtue from a conservation standpoint. Anthropogenic changes have often *increased* connectivity between systems (“hyperconnectivity”; Crooks and Suarez Chp. 18), with deleterious effects. For example, land-use changes in many regions have led to increases in sedimentation above natural levels, destroying or converting intertidal and subtidal marine habitats (Norkko et al. 2002, Hewitt et al. 2003). Commercial fishing also creates hyperconnectivity between the land and the sea, moving over 75 million tons of marine biomass onto land worldwide, 27 million tons of discarded non-target animals (bycatch), as well as 126,500 tons (dry weight) of algae (Watson and Pauly 2001, McHugh 2003), with ramifications for the entire oceanic ecosystem (Dayton et al. 1995, Dayton et al. 2002). Other examples of hyperconnectivity include nutrients moving from land to water creating problems with eutrophication of lakes, rivers, and marine systems (Carpenter et al. 1999); the flow of contaminants and diseases between terrestrial and aquatic systems (Harvell et al. 1999, Neal et al. 2003); and salt-water intrusion leading to the loss of trees (Cyrus et al. 1997).

Conservation implications

Recognizing and understanding habitat linkages at the land-water interface is necessary for effective conservation. As most examples in this chapter illustrate, there are frequent, strong interactions between the aquatic and terrestrial ecosystems, with one habitat’s influence often dominating the dynamics of the other over vast temporal and spatial scales. Besides the conservation benefits inherent in the increased understanding of nature, there are some very specific areas in which connectivity at the aquatic-terrestrial interface will benefit conservation scientists.

Siting decisions for areas of protection for threatened species or habitats will be greatly improved by integrating aquatic-terrestrial connectivity into the decision-making process. For example, streams have traditionally been considered to be recipients, rather than sources, of resources in terrestrial systems (Power 2001). Yet a conservation biologist concerned about protecting temperate forest herpetofauna who ignored riverine inputs might miss a foraging resource that can increase growth rates of their target organism by as much as 700% (Sabo and Power 2002). Clearly habitat location relative to aquatic resources can be critically important. Similarly, our research in Baja California on the effects of boundary type on connectivity suggests that the location of a protected area relative to the coast will profoundly affect the type and degree of trophic subsidy from the marine ecosystem.

A better understanding of functional linkages would also assist in questions about buffer zones and spatial scale of protected areas. Studies of the effects of marine inputs on terrestrial ecosystems (e.g., Polis and Hurd 1995, Stapp et al. 1999) clearly demonstrate that it can be important to account for marine input to understand the dynamics of terrestrial systems. However, there is only inferential information regarding the distance offshore from which these resources originate. Fundamental questions are still unanswered about how far offshore one must protect a habitat to ensure adequate connectivity (in this example, flow of allochthonous input). It is also not clear how far inshore linkages penetrate to impact terrestrial communities. An understanding of the spatial properties of these linkages will provide conservation biologists with better tools to protect threatened habitats and organisms.

Conclusion

Even such seemingly distinct systems as land and water are deeply interconnected across a wide range of spatial and temporal scales. As ecologists and conservation biologists, we would benefit from broadening our traditional scope of study to include processes and habitats beyond our focal system, and to explicitly incorporate spatial interconnections at every opportunity.

This is not without its challenges. Terrestrial and aquatic ecosystems are often influenced by processes operating at vastly different spatial and temporal scales, and therefore interactions between the two should be expected to be particularly complex and non-linear (Steele et al. 1993, Carr et al. 2003, Talley et al. 2003). Further, there are differences in evolutionary history, dominant taxa, life-history strategies, and numerous other factors that add complexity to integrating connectivity between these two types of systems into our science. It is clear from the examples presented that the spatial and temporal scales of study can influence our perception, terminology and appreciation for the dynamical consequences of interhabitat connections in profound ways. There are also more prosaic difficulties—there are very real differences between many aquatic and terrestrial ecologists. They go to different schools, receive funding from different agencies, and attend different meetings, all of which will require greater interdisciplinary effort to integrate connectivity at the land-water interface into our science (Talley et al. 2003). Overcoming such difficulties requires collaboration to allow us to include a broad span of study methods and scales. We also need to embrace an integrative conceptual framework that promotes thinking both theoretically and empirically about the full scope of interhabitat connections.

Despite these challenges, there are some spectacular examples of success studying connectivity at the land water interface. The work of Gary Polis, Mary Power, Shigeru Nakano, and Mary Willson (e.g., Nakano and Murakami 2001, Power 2001, Polis et al. 2004, Willson et al. 2004 and references therein) has pushed this field of inquiry forward with elegant and insightful experiments and analyses. It is our opinion that the study of these connections at the terrestrial-

aquatic interface complement those better-studied connections relating to source-sink, metapopulation, and corridors being examined in other chapters in this volume. For example, source-sink dynamics emphasize only demographic linkages and assume no feedback between heterogeneous source and sink habitats. By contrast metapopulation studies emphasize connections among similar habitats and allow these to be bidirectional. Corridors may also be bidirectional and can either serve as sources of colonization or may enlarge habitats on much shorter time scales. These issues of directionality, feedback, and temporal variation/time scale are all topics that cover a small part of the framework considered here, but do so in more elaborate detail and often more quantitatively than our descriptive review. The incorporation of abiotic fluxes into concepts like source and sink dynamics will also help to achieve a more integrated and complete ecological framework for considering the importance of connectivity.

The habitats that comprise the land-water interface, such as coastal zones, riparian areas, lakes, and floodplains, are among the most productive and biologically diverse areas on earth (e.g., see Hansen and di Castri 1992, Mitsch and Gosselink 2000 and references therein). The habitats are also a nexus for human activity, vital for transportation, production of energy, water storage, and food resources. Over 50% of all humans live within 60 km of the coast, and that number is expected to grow to 75% by 2020 (DeMaster et al. 2001). That these critical biological and human resources overlap so strongly means that human alteration to natural connectivity at the land-water interface will become increasingly important in the years ahead. It behooves us both as ecologists and as conservationists to find further creative ways to understand these phenomena.

Acknowledgments

The authors would like to thank M. Sanjayan, K. Crooks and A.-L. Harrison for their hard work in organizing this volume, as well as the Society for Conservation Biology and The Nature Conservancy for their financial and organizational assistance. We also thank the National Science Foundation for support (D.T. and G.H. were supported by NSF DEB-0079426, G.H. by NSF CHE-0221834 - BE/CBC, and M.H. was supported by NSF DEB-0213026 to M.H. and Alan Hastings). D.T. was also supported in part by the National Sea Grant College Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under NOAA Grant #NA04OAR4170038, project #R/CZ-190A, through the California Sea Grant College Program; and in part by the California State Resources Agency. The views expressed herein do not necessarily reflect the views of any of those organizations. We would also like to thank the San Francisco Bay National Estuarine Research Reserve, the Romberg Tiburon Center for Environmental Studies, San Francisco State University, the University of South Florida and University of California, Davis. This manuscript was greatly improved thanks to the thoughtful comments of C. Baxter, K. Crooks, T. Talley, and an anonymous reviewer.

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	No Feedback	Feedback
Unidirectional	A	B
Bidirectional	C	D

Figure 1. Two axes of dynamical features: feedback and directionality. See text for description and examples.

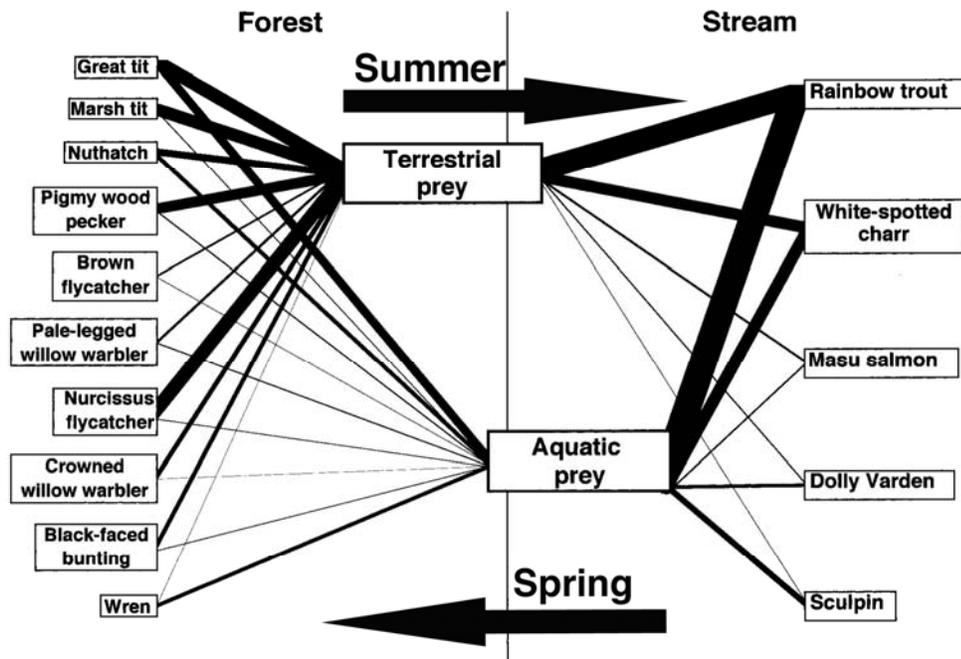


Figure 2. Food web linkage across a forest–stream interface representing predator subsidies by allochthonous, invertebrate prey flux. Relative contributions of terrestrial and aquatic prey to the annual total resource budget of each species are represented by line thickness. Note that the dominant direction of subsidy changes with season. Adapted from Nakano and Murakami 2001.

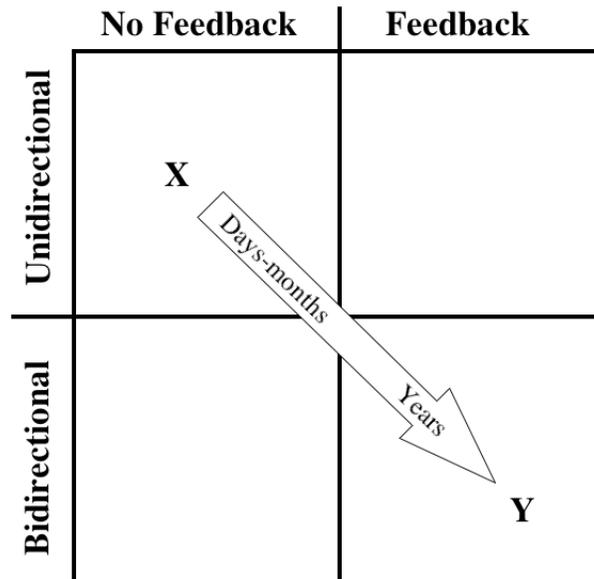


Figure 3. Scale dependence of habitat connectivity. The classification of connectivity between two habitats can depend on the scale over which the dynamics are viewed. Here, if the trophic connection between a riparian and adjacent aquatic habitat are viewed within season (“X”, Nakano et al. 1999), the relationship appears to be one of unidirectional connectivity without feedback. When viewed over longer time scales (“Y”, Nakano and Murakami 2001) the connection is seen as bidirectional with feedback.

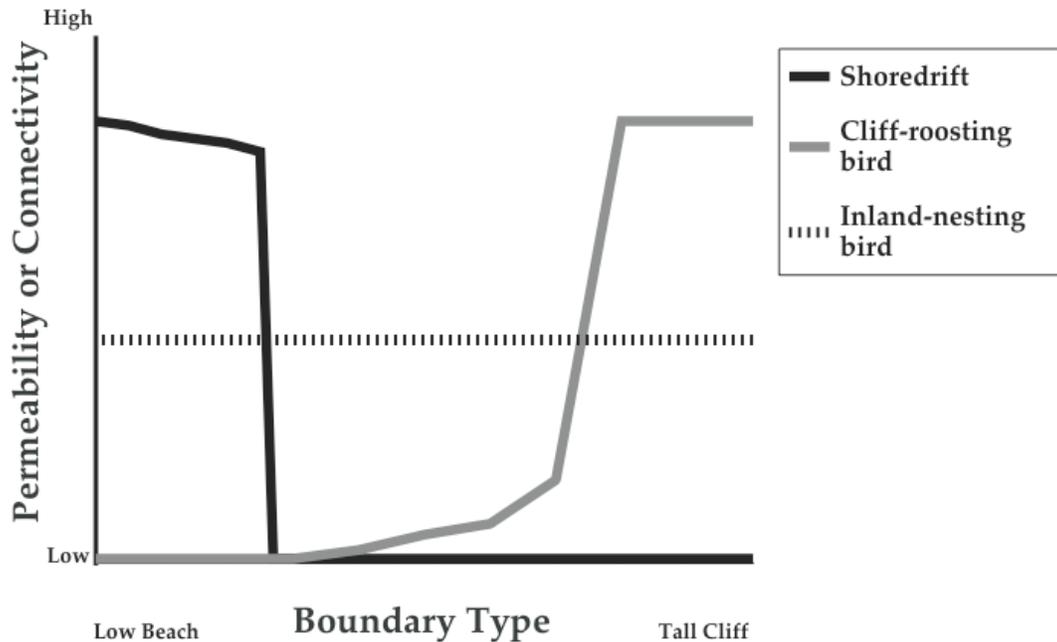


Figure 4. A conceptual model of the effect of boundary structure on connectivity. The Y-axis represents either permeability or connectivity, assuming a positive correlation between those factors. The X-axis is a measure of boundary structure, in this example steepness of the shore from low (beach) to steep and tall (cliffs). Shoredrift input will be high (high connectivity), and decrease slightly with increasing height until attaining some threshold, at which shoredrift will no longer penetrate across the boundary. Cliff-roosting birds, on the other hand, would only rarely use low shorelines, but at a threshold height would preferentially choose those habitats, increasing connectivity. For seabirds that nest inland, there would be some level of connectivity that is independent of the boundary type.