Toward More Integrated Ecosystem Research in Aquatic and Terrestrial Environments

JANNE SOININEN, PIA BARTELS, JANI HEINO, Miska LUOTO, AND HELMUT HILLEBRAND

Aquatic and terrestrial ecosystems are tightly linked through the fluxes of organisms and matter. However, aquatic and terrestrial ecologists have mainly studied these ecosystems separately, a "splendid isolation" historically fostered by disciplinary boundaries between institutes and funding schemes. Here, we synthesize the progress made in joint aquatic and terrestrial research and suggest new approaches to meeting future research challenges in changing environments. Aquatic and terrestrial organisms use cross-system subsidies to a comparable extent and addressing reciprocal subsidies is therefore necessary in order to understand biodiversity and functioning of both aquatic and terrestrial ecosystems. We suggest that the metacoeosystem framework could be expanded to explicitly consider cross-system fluxes of matter differing in magnitude and quality. We further advocate the inclusion of cross-system analyses at broader spatial extents, for which remote-sensing applications would be a useful tool in environmental research at the land–water interface. A cross-ecosystem approach would therefore be valuable for a more thorough understanding of ecosystem responses to various stressors in the face of rapid environmental change.

Keywords: catchment, cross-ecosystem, metacoeosystems, remote sensing, subsidies

Although aquatic and terrestrial ecosystems share many fundamental characteristics of structure and function (Hairston et al. 1960), there has been a broad gap between aquatic and terrestrial ecologists in studying these ecosystem realms. Consequently, despite working on the same fundamental ecological issues, ecologists focusing on a given ecosystem still seem to mostly ignore studies conducted in other ecosystems (Menge et al. 2009). However, we argue that an even more severe shortcoming is that aquatic and terrestrial ecologists still typically conduct their research separately, focusing on either wet or dry ecosystems in the landscape, which actually comprises both. Bartels and colleagues (2012) included 71 studies of reciprocal subsidies between terrestrial and freshwater ecosystems in a meta-analysis (most of the studies included had been published after 2000). Compared with the number of studies conducted separately for terrestrial or aquatic ecosystems, the number of studies on reciprocal subsidies is still small. Menge and colleagues (2009) also stated that 60% of all research papers (N = 5824) published in a collection of leading ecological journals between 2002 and 2006 were terrestrial, whereas only 9% were freshwater, and 8% were marine studies. Therefore, the high number of papers focused on either terrestrial or aquatic environments in isolation clearly outnumbers the number of joint studies directly combining dry and wet ecosystems.

Studies in which the cross-system fluxes of material and energy between water and land were considered all highlighted the importance of such reciprocal subsidies to ecosystem function (Bartels et al. 2012). Moreover, studies on cross-system food web interactions have shown that aquatic and terrestrial food webs are often tightly linked and that landscape-level processes are highly important for our understanding of local interactions (Knight et al. 2005). Therefore, incorporating aquatic and terrestrial processes in collaborative research efforts is more than an incremental add-on to existing research; it is a necessity for ecologists in facing new research challenges to predict ecosystem- and landscape-level responses to environmental changes at broad spatial scales. We argue that such an integrative approach should be incorporated not only in research campaigns but also in major funding schemes and review processes that typically still separate aquatic and terrestrial research.

Objectives

Here, we synthesize the progress that has been made in joint aquatic and terrestrial research and suggest new avenues for such research. We emphasize that the structure and function of these two ecosystem types cannot be understood without...
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Box 1. Reciprocal subsidies between streams and their contiguous ecosystems.

Streams constitute only a minimal areal extent of the globe, but they are highly important in terms of overall length and consequent effects on other ecosystems (Allan and Castillo 2007). Interactions between stream and riparian ecosystems are prime examples of reciprocal subsidies, where organic material and terrestrial organisms enter the stream and emerging aquatic insects enter the riparian zone (Fisher and Likens 1974). The importance of riparian tree leaves entering stream has been examined in many studies (Allan and Castillo 2007). This allochthonous leaf material is an important driver of stream ecosystem structure and function, because it is key food resource for various invertebrate consumers (e.g., shredding stonefly and caddisfly larvae). These invertebrate consumers rely on this material for subsistence and have further effects on the breakdown of leaves in streams (Zhang and Richardson 2011).

Coarse particulate organic matter is broken down into fine particulate organic material that is further used by various invertebrate consumers (e.g., filtering blackfly and gathering midge larvae). The effects of riparian leaf material on stream ecosystems is therefore considerable, although its importance does not remain only in streams but feeds back to the riparian zone through emerging stream insects (Baxter et al. 2005, Allan and Castillo 2007). Emerging insects form an important but seasonally variable food source for terrestrial predators (e.g., birds, lizards, spiders, ground beetles; Nakano and Murakami 2001, Baxter et al. 2005). Often, the productivity of streams is transferred to these terrestrial predators, the densities of which may be higher near streams than further away from them. Furthermore, there are some riparian specialist species that rely on stream-based insect prey, sometimes even more than on terrestrial prey. Reciprocal subsidies are also manifested in the fact that both adults of aquatic and terrestrial insects fall into streams, thereby providing a food resource for stream fish (Nakano and Murakami 2001, Baxter et al. 2005). A considerable proportion of the diet of insectivorous fish is often accounted for by terrestrial prey, and this subsidy may effectively maintain fish populations even in streams where autochthonous production of prey is limited. The degree to which terrestrial insect prey determine the production of the young of fish in streams also has importance to migrations of diadromous fish to the sea. Finally, after spending a period in the sea, diadromous fish return to a stream for spawning or feeding. In the case of anadromous semelparous fish, which typically die after spawning (e.g., Pacific salmon), the corpses of dead fish may provide food and nutrients for various consumers (e.g., bears, birds) and drive ecosystem function especially in streams at high latitudes (Nakano and Murakami 2001). This is an excellent example of nutrients, material, and organisms produced in the sea to have effects on freshwater ecosystem functions and food web structure across ecosystem boundaries.

Cross-ecosystem subsidies

Aquatic and terrestrial ecosystems are inevitably linked through the movement of energy, nutrients, and material (box 2; Polis et al. 1997). Particularly, the fluxes of particulate organic matter (i.e., resource subsidies) play an essential role because of their potential to change community and food web dynamics in recipient ecosystems. Although these fluxes are reciprocal and ubiquitous, aquatic ecosystems generally receive larger amounts of organic subsidies than terrestrial ecosystems (Bartels et al. 2012). A multitude of empirical studies has clearly demonstrated the importance of organic subsidies to ecological communities (Richardson et al. 2010), albeit the majority of studies were focused solely on subsidies as nutritional supplements to the recipient consumer’s diet. Despite larger input to aquatic ecosystems, terrestrial and aquatic consumers use subsidies to a comparable extent (Bartels et al. 2012), likely because of differences in subsidy quality between ecosystems (Marcarelli et al. 2011). Synthesizing information from 71 studies, Bartels and colleagues (2012) found a median contribution of almost 40% of subsidized food to consumer diets in both aquatic and terrestrial systems. Consumption of subsidies can result in higher consumer numbers through spatial accumulation and/or enhanced reproduction by increasing individual growth rates (Wright et al. 2013).

Notably, the influence of subsidies can extend beyond the consumer level (McCann et al. 1998), substantially affecting food web dynamics within recipient ecosystems (Leroux and Loreau 2008). For instance, bottom-up and top-down effects following the input of subsidies have been repeatedly illustrated in aquatic and terrestrial ecosystems (Wallace et al. 1997, Murakami and Nakano 2002). Theoretical studies indicate that the impact of subsidies on food webs is largely determined by the amount of input that enters into the food web, the preference of the consumers, the trophic level that receives the input, and the relative duration of subsidy input compared with the consumers’ numerical response (Leroux and Loreau 2008, Takimoto et al. 2009). However, empirical studies in which these theories have been explicitly tested are scarce. In one of these studies, Klemmer and Richardson (2013) illustrated that trophic cascades were strong at low subsidy inputs. However, at intermediate to high subsidy levels, trophic cascades were absent because of complex community dynamics. Sato and Watanabe (2014) suggested that
size structure within a consumer population determined the effects of subsidies on trophic cascade. Moreover, the reception of multiple subsidies at multiple trophic levels may shift food web dynamics in nonlinear and unpredictable ways (Huxel et al. 2002).

All the above-mentioned examples highlight that nutrient, detritus, or prey subsidies can influence the food web structure and dynamics in the recipient ecosystems. However, evidence for systematic differences in responses to subsidies between ecosystems is currently lacking. Bartels and colleagues (2012) illustrated that aquatic ecosystems generally received larger amounts of matter produced outside of the focal ecosystem than terrestrial ecosystems, which suggests that aquatic ecosystems might be more susceptible to alterations in food web dynamics following the input of subsidies than are terrestrial ecosystems. Furthermore, aquatic ecosystems received subsidies at all trophic levels, although this was likely biased by the lack of studies in terrestrial ecosystems (Bartels et al. 2012). Aquatic ecosystems show a tendency to higher secondary production and stronger trophic cascades (Shurin et al. 2002, 2006), and potentially different responses in food web dynamics to subsidies might lead to these distinctions between aquatic and terrestrial ecosystems. We therefore encourage future research to investigate systematic differences in food web responses to subsidies between ecosystems.

Although subsidies are often limited in their spatial intrusion into the landscape, the effects on food webs and ecosystems might expand from their source. Mobile consumers adapt their behavior to track resource availability (the bird feeder effect; Eveleigh et al. 2007) if the landscape varies in resource quantity. The dispersal of subsidized consumers might affect communities at large scales, resulting in community-level responses far beyond the subsidies’ origin. Migratory birds, such as lesser snow geese (Chen caerulescens caerulescens) are strongly subsidized by agricultural crops in the southern and mid-continental regions of the United States, and the numbers of geese have grown because of the expansion of farm land and increased crop fertilization (Jeffries et al. 2004). The abundance of heavily subsidized geese has resulted in a sharp decrease of in situ productivity, in altered terrestrial arthropod populations, and in local declines in the breeding populations of other bird species in the geese’s breeding grounds in the Arctic (Srivastava and Jeffries 1996, Kotanen and Jeffries 1997). Furthermore, mobile consumers can provide a novel source of nutrients by excreting subsidy-derived nutrients (nutrient translocation; Vanni 2002), occasionally in very distant locations (Hilderbrand et al. 1999). In New Mexico, the daily foraging of geese moves substantial amounts of nutrients from farm fields to their roosting locations in wetlands (Post et al. 1998), supplying 40% of the nitrogen and 75% of the phosphorus in the wetlands’ annual nutrient input. Subsidies couple spatial matter and energy fluxes to the dispersal and spatial movements of the recipient organisms across ecosystem realms and are therefore ideally suited to examine the links between (meta-)community and (meta-) ecosystem ecology.

The input of nutrients derived from subsidies might be especially important for recipient ecosystems that have low productivity (Naiman et al. 2002), which then respond to alterations in more productive donor habitats. Such cascading effects between asymmetrically coupled adjacent ecosystems (Knight et al. 2005) have been illustrated: the occurrence of certain predators or differences in biodiversity and community composition can modify fluxes between aquatic and terrestrial ecosystems with substantial consequences for recipient community and ecosystem functioning (Knight et al. 2005, Epanchin et al. 2010), emphasizing the necessity of studying both ecosystems simultaneously. For example, Knight and colleagues (2005) documented that fish indirectly facilitated terrestrial plant reproduction through cascading trophic interactions beyond pond boundaries. In their study, fish reduced larval dragonfly abundances, resulting in fewer adult dragonflies. As adult dragonflies consume insect pollinators, plants near ponds with fish received more pollinators than do plants near ponds that lacked fish.
Particularly, human influences do not stop at ecosystem boundaries. Eutrophication is a prominent example, in which elevated nutrient inputs from the catchment due to changes in land use have been demonstrated to result in the reduction of whole lake productivity (Vadeboncœur et al. 2003). Although pelagic productivity generally increased in Danish lakes, elevated nutrient supplies resulted in the loss of important benthic pathways (Vadeboncœur et al. 2003). Similar effects have been illustrated for increased inputs of colored dissolved organic matter (i.e., brownification) from terrestrial ecosystems entering freshwater ecosystems (Karlsson et al. 2009).

The introduction of nonnative species can also affect cross-boundary fluxes in complex ways. For instance, the introduction of nonnative trout substantially reduced insect emergence, which lead to the reduced numbers of resident finches feeding on insects around ponds with trout (Epanchin et al. 2010). Therefore, we emphasize that ecosystem fluxes are not always beneficial but may result, for example, in eutrophication of water bodies, the introduction of invasive species, and associated negative influences on ecosystem structure and function.

**Metaecosystems and cross-system flows**

The relative scarcity of empirical studies on the interplay between aquatic and terrestrial ecosystems does not reflect recent theoretical advances. The theoretical foundations for cross-system comparisons have been laid out in the form of metacoeosystem theory, which extends metapopulation and metacommunity theory to ecosystems connected by the spatial flows of energy, materials, and organisms across ecosystem boundaries (Loreau et al. 2003, Massol et al. 2011). Whereas subsidies have initially been studied as unidirectional transfer, mostly from the perspective of the recipient ecosystem, metacoeosystem theory explicitly considers reciprocal fluxes between coupled systems and their compartments (nutrients, detritus, producers and consumers; figure 1). By including direct (physical) and indirect (organismal) fluxes of elements, single ecosystems can represent both sources and sinks in metacoeosystems for different agents (organisms and matter), depending on the balance of direct and indirect flows (Gravel et al. 2010a). Moreover, these dynamics can then feed back into coexistence and food web structure in the connected ecosystems (Gravel et al. 2010b).

Metaecosystem theory does not exclusively address cross-system flows but can be used to describe patches within one realm, compartments of a single ecosystem, or fluxes among ecosystem types. In this context, the theory is flexible with regard to the frequency of subsidies, spanning from systems with a single pulse or recurrent pulses to continuous flows between systems (Leroux and Loreau 2012). Recent years have seen the first empirical analyses with reference to this theory, but most examples involve subsystems within an ecosystem realm. Casini and colleagues (2012) analyzed 30 years of spatiotemporal data on food web dynamics in the Baltic Sea, whereas Menge and Menge (2013) used a metaecosystem approach to understand the consequences of upwelling in a rocky intertidal ecosystem. We strongly advocate adding cross-ecosystem tests of this theory, especially with regard to the reciprocal fluxes of different agents (detritus versus organisms, inorganic versus organic). One of the major advancement to be made is an explicit consideration of different currencies of exchange: a stoichiometric perspective on metaecosystem dynamics would allow an understanding of the different qualities of exchange. For example, nutrient-rich material in the form of organisms is transferred from aquatic to terrestrial systems, whereas nutrient-poor material (detritus) dominates the reciprocal flow (Bartels et al. 2012). Massol and colleagues (2011) additionally considered the explicit formulation of space in metaecosystem models as another major developmental step, because space is only implicitly addressed in current models. Such an explicit consideration of space in metaecosystem studies could use (and further develop) the large toolbox of spatial statistics developed within landscape ecology and spatial ecology in general.
Using remote sensing to quantify broad-scale patterns in land–water interactions

At larger spatial extents, experimental approaches for examining the cross-system food web interactions or material flows are often not feasible. To obtain a broader view over the patterns and processes linking aquatic and terrestrial systems, researchers may sample the same geographical region for aquatic and terrestrial organisms and examine, for example, how lake communities and terrestrial vegetation surrounding the same lakes respond to climatic gradients covered by the study region. Such joint broad-scale sampling campaigns for aquatic and terrestrial organisms are, however, surprisingly rare to date (but see Gurgel et al. 2014). A more feasible method for examining large-scale patterns is the use of remote sensing. The remote-sensing approach and the data derived with it are useful in obtaining environmental information for large regions in a consistent manner (Kerr and Ostrovsky 2003). They have been used by terrestrial ecologists for modeling variation in species richness (Nagendra 2001), in assessing ecological responses to environmental change (Pettorelli et al. 2005) and in studies of land cover patterns (Friedl et al. 2002). Recently, remote sensing has also been found to be a promising tool for aquatic ecologists; it has been used to infer lake temperatures, algal dynamics, and changes in water levels (Hampton 2013).

The normalized difference vegetation index (NDVI) is one of the most widely used remote-sensing-based metric to quantify terrestrial plant biomass as an estimate of primary production (Nagendra 2001, Pettorelli et al. 2005). It correlates strongly with the leaf area index, net primary production, percent leaf area greenness and is related to the amount of absorbed photosynthetically active radiation (Tucker 1979). We suggest, therefore, that remotely sensed metrics such as NDVI are highly useful not only for estimating terrestrial productivity at broad spatial scales but also for providing proxies for the amount of organic carbon, nitrogen, and phosphorus eventually entering aquatic ecosystems from the catchments (Finstad and Hein 2012, Soininen and Luoto 2012). The influence of catchment variables operating at intermediate scales between local (i.e., water chemistry and local biotic interactions) and regional (i.e., large-scale climatic variables) on aquatic biota has been, however, understudied. The terrestrial buffer zone near a water body is, nonetheless, potentially important for aquatic biota because of mediating the catchment effects on water chemistry (Maberly et al. 2003), as well as because of various processes in food webs operating at the land–water interface (Knight et al. 2005, Allan and Castillo 2007).

Because of such important catchment effects, remotely sensed catchment productivity may also be used to identify aquatic diversity hotspots even in remote regions in a cost-effective manner. Vinson and Hawkins (2003) showed that stream insect genera richness increased with mean NDVI at the global scale, even though at large productivity values, genus richness values tended to show large among-site variation. Finstad and Hein (2012) revealed that catchment NDVI predicted well Arctic char distribution possibly because of serving as a proxy for food availability in Norwegian lakes.

In a recent study, Soininen and Luoto (2012) documented that maximum NDVI was related to the richness of planktonic organisms independent of lake variables or geographical position of boreal lakes. In total, seven out of nine catchment predictors that were considered had a significant unique effect on phytoplankton richness. This unique effect of catchment on plankton richness possibly stemmed from catchment variables being more robust in time than snapshot measures of water chemistry, therefore reflecting the long-term environmental conditions. Moreover, catchment variables may have reflected the effects of some latent variables not measured in the freshwater ecosystem. Soininen and Luoto (2012) further showed that the catchment effect was, overall, comparable with the effect of local within-lake variables (i.e., water chemistry) and larger than the effect of geographical variables in these lakes. This highlights that disregarding catchment variables from freshwater studies may lead to biased conclusions of the importance of drivers and proxies of aquatic biodiversity. Overall, we encourage researchers to examine terrestrial–aquatic links further in light of ecological theory in order to detect potential mismatches between the theory and the empirical data collected during field surveys. For example, it would be important to reveal whether combining the data on aquatic and terrestrial ecosystems results in patterns that are opposite of those predicted by current ecological theory.

Collectively, the use of such remote-sensing-derived measures may decrease the need for extensive field sampling in terrestrial systems and can be useful for many conservation and management applications related to aquatic–terrestrial links (Kerr and Ostrovsky 2003). We further emphasize that factors operating at local, landscape, and broad scales are all important to be considered, especially in biodiversity studies, as the variation in species richness is known to be scale dependent (Chase and Leibold 2002) and related to variables acting at different scales (Heino and Peckarsky 2014). For example, Hessen and colleagues (2007) revealed that zooplankton richness was related to both local and large-scale geographical variables in Norwegian lakes.

Not only is the productivity of the catchment influential for the aquatic environment, but the heterogeneity of the terrestrial environment is also expected to be related to aquatic biodiversity because of the greater number of available abiotic and biotic conditions. Temporal and spatial patterns in aquatic physicochemistry, particularly the inputs of detritus and nutrients, are affected by the composition and structure of the surrounding terrestrial landscape (figure 2; Ward et al. 2002). Moreover, terrestrial environmental heterogeneity may dampen the effects of environmental impacts by decreasing the synchrony of population fluctuations. For example, in homogeneous catchments, aquatic species can be more strongly affected by climate change than in
that quantifying productivity and size of the source pools at larger spatial scales covering catchments may be more appropriate and more feasible for predicting aquatic biodiversity than measuring snapshot productivity based on water samples.

Conclusions

Aquatic and terrestrial ecosystems have been traditionally studied in isolation. In this article, we argue that such a gap between aquatic and terrestrial ecologists is largely artificial, given that there is plenty of evidence that these ecosystems are often tightly linked through the fluxes of organisms, material, and energy. We suggest three research avenues for a better integration of aquatic and terrestrial research:

First empirical analyses related to metaecosystem theory have just emerged, but most of these studies involve subsystems within only one ecosystem. We think that this is a major shortcoming, because the theory is flexible enough to be expanded so that the fluxes between coupled ecosystems can be considered, too. We therefore strongly advocate expanding the metaecosystem theory and also its empirical tests to cross-ecosystem studies.

Second, we suggest the explicit consideration of the nutritional quality of matter flowing between ecosystem compartments using a stoichiometric perspective on metaecosystem dynamics. This is because nutrient-rich material in the form of organisms is transferred from aquatic to
terrestrial systems, whereas nutrient-poor material typically dominates the reciprocal flow.

Third, when considering aquatic–terrestrial links at broad spatial scales, advances in remote sensing have provided metrics useful as proxies for estimating the extent of cross-system flows of matter from land to water. We therefore argue that catchment level productivity (e.g., NDVI values reflecting terrestrial productivity) should be considered more extensively as a potential predictor of the richness and composition of aquatic communities, because it may reflect the long-term environmental conditions in aquatic ecosystems better than the snapshot measures of water chemistry. Remote-sensing-based metrics may also be helpful in theoretical studies considering regional species pools and regional productivity instead of focusing solely on local communities and local productivity. We think that following these approaches would facilitate the shift from purely aquatic or purely terrestrial research toward a more holistic view on how biological communities and ecosystems function.

References cited


Figure 3. A comparison of diversity in lakes in unproductive and productive catchment. The blue circles are lakes, the arrows represent the passive dispersal of algae among lakes, and dark green color represents a productive catchment, whereas the light green color indicates a less productive catchment. The top row represents landscapes with a higher number of lakes, whereas the bottom row represents landscapes with fewer lakes. In the panels on the right, the lake with the dotted boundary represents a single productive lake (due to the point source of nutrients), whereas the solid boundary line indicates that all the other lakes in the same landscape are unproductive. Different symbols depict different algal species. Despite the high local nutrient supply, species richness may be low in lakes in an unproductive catchment because of a small regional species pool and associated low influx of colonists into the lake. In contrast, lakes in a productive catchment may have overall higher species richness because of a larger species pool, resulting in a steady flux of colonists into the lake. The species richness levels in lakes are also influenced by the number and size of the lakes in the catchment acting as source pools to individual lakes. In general, beta diversity should also be higher in a catchment with higher overall productivity (Chase and Leibold 2002, Bini et al. 2014).


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Janne Soininen (janne.soininen@helsinki.fi) and Miska Luoto are affiliated with the Department of Geosciences and Geography at the University of Helsinki, Finland. Pia Bartels is affiliated with the Department of Ecology and Environmental Science at Umeå University, in Umeå, Sweden. Jani Heino is affiliated with the Finnish Environment Institute, Natural Environment Centre, Biodiversity, in Oulu, Finland. Helmut Hillebrand is affiliated with the Institute for Chemistry and Biology of the Marine Environment, at Carl-von-Ossietzky University Oldenburg, in Wilhelmshaven, Germany.