Interactive effects of plants, decomposers, herbivores, and predators on nutrient cycling

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Context

The rates and pathways of nutrient cycling through ecosystems depend on interactions between both bottom-up forces, including the chemical characteristics of biomass that influence its decomposition and consumption by higher trophic levels, and top-down forces, such as the nutritional requirements and metabolic efficiencies of consumers and decomposers that influence their feeding and excretion. At the base of the food web, nutrient cycling is influenced by whether NPP becomes detritus, entering the so-called "brown" food web, or is consumed by herbivores before death or senescence. Here, we use "nutrient" to refer to essential elements other than carbon (C), such as nitrogen (N), phosphorus (P), and calcium (Ca). The fraction of NPP in ecosystems that is consumed by decomposers (primarily bacteria and fungi) versus herbivores is hugely variable among ecosystems, with a larger fraction being consumed by herbivores in aquatic than in terrestrial ecosystems on average (Cyr and Pace, 1993; Cebrian and Lartigue, 2004). This pattern arises because primary producers in aquatic environments have higher nutritional quality than terrestrial primary producers (Cebrian and Lartigue, 2004) and are largely unicellular, whereas those in terrestrial ecosystems are multicellular and structurally complex – requiring compounds, such as lignin, that are difficult to digest (Lindeman, 1942; Shurin et al., 2006).

In this chapter, we discuss bottom-up and top-down influences on nutrient cycling (Fig. 9.1), focusing first on decomposer food webs, and the characteristics of primary producers (bottom-up forces) and decomposers (top-down forces)
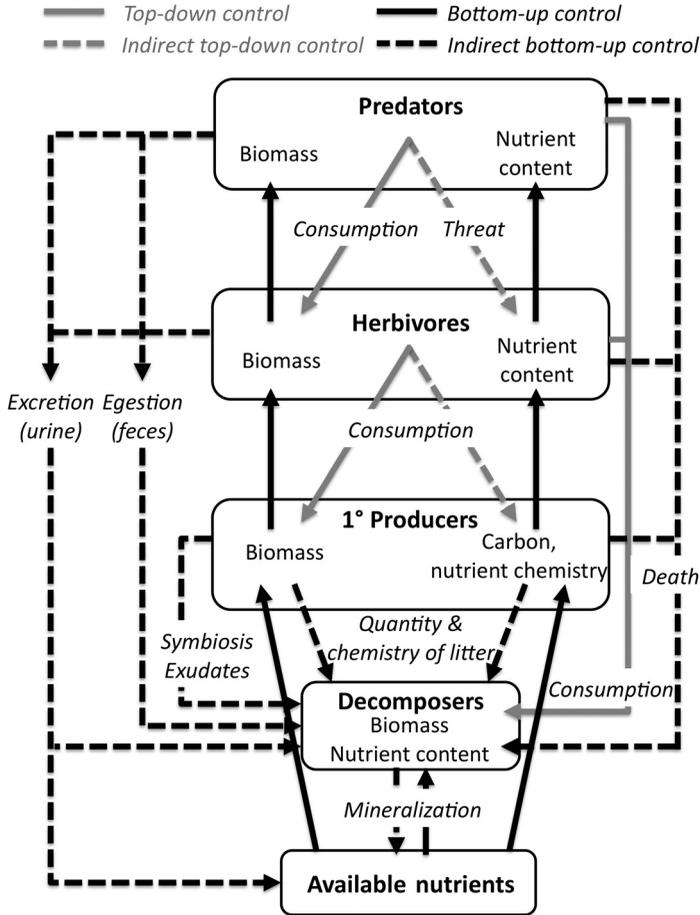
Figure 9.1 Conceptual diagram showing top-down and bottom-up effects on nutrient cycling. Solid black lines represent bottom-up control, whereby resources at one trophic level influence the biomass and nutrient content (and, for primary producers, carbon chemistry) of the next highest trophic level. Organisms can also exert indirect bottom-up control of decomposers and available nutrients (dashed black lines) through the production of excreta and through death (the production of cadavers and detritus). Primary producers also have indirect effects on nutrient cycling by supplying carbon to heterotrophic microbes, either by exuding soluble organic compounds into soil, sediment, or water that influence nutrient mineralization, or by supplying carbon to symbiotic organisms such as N-fixing microbes and mycorrhizae that influence nutrient availability. Solid gray lines represent top-down effects on nutrient cycling that occur through consumption effects on biomass or nutrient content of lower trophic levels (e.g., by changing nutrient content either within individuals or by changing species composition), or by inducing defenses. Higher trophic levels can also exert indirect top-down effects on nutrient cycling (dashed gray lines) by altering the feeding behavior (e.g., prey and location) of their prey.

that affect nutrient cycling. Next, we discuss herbivore-based food webs and highlight mechanisms by which herbivores can have top-down effects that either enhance or depress rates of nutrient cycling. Then, we extend that discussion to the influence of higher trophic levels on nutrient cycling. Finally, we discuss mechanisms by which trophic interactions mediate the transfer of nutrients among ecosystems.

Bottom-up and top-down influences on nutrient cycling in decomposer food webs

Bottom-up forces in decomposer food webs

Decomposers, primarily bacteria and fungi, but also detritivorous invertebrates and vertebrates, consume dead organic matter to obtain energy, and in the process of decomposition, break down macromolecules into smaller ones and excrete nutrients as waste products. The rate and stoichiometry of nutrients released during decomposition are influenced in part by interactions between bottom-up (i.e., primary producer detritus chemistry) and top-down (i.e., decomposer nutritional requirements and metabolic efficiency) factors, although bottom-up influences are better studied, at least in terrestrial ecosystems. For example, nutrient release from decomposing primary producer detritus is influenced by autotrophic tissue C:nutrient ratios. C:N and C:P ratios can vary among species in both aquatic and terrestrial systems by an order of magnitude (Reich and Oleksyn, 2004; Borer et al., 2013). Importantly, the C:nutrient ratios of detritus often far exceed those of decomposers (Sterner and Elser, 2002; Martinson et al., 2008), particularly for terrestrial leaf litter, which re-translocates *ca.* 50% of its nutrients prior to senescence (Kobe et al., 2005). Thus, during decomposition, nutrients limit use of C in detritus by decomposers, so detritus (along with its microbial decomposers) generally exhibits an initial period of nutrient uptake or "immobilization" during decomposition, followed by a period of nutrient release in proportion to mass loss (Staaf and Berg, 1981; Parton et al., 2007; Hobbie, 2008). The quantity of nutrients immobilized is influenced by the initial nutrient concentration: for litter with low initial nutrient concentrations, nutrients limit decomposition and litter exhibits more nutrient immobilization, whereas for litter with high initial nutrient concentrations, C limits decomposition, and litter exhibits nutrient release (Parton et al., 2007; Hobbie, 2008).

After the initial immobilization period, detritus generally releases nutrients in proportion to mass loss (Gessner et al., 1999; Hobbie, 2000; Parton et al., 2007; Hobbie, 2008). Thus, the rate of nutrient release from detritus is influenced by all of the various factors influencing decomposition rate, such as temperature and moisture, as well as bottom-up and top-down factors (i.e., the chemistry of primary producer biomass and decomposer characteristics, respectively). For instance, decomposition rates are slowed by high concentrations of complex,

low energy-yielding molecules such as lignin (Melillo et al., 1982; Cornwell et al., 2008). Similarly, decomposition is slowed by low concentrations of nutrients in detritus. Most work has focused on concentrations of N or P (Enriquez et al., 1993; Cornwell et al., 2008), but other elements are particularly important when the dominant decomposers have unique nutritional requirements (Kaspari and Yanoviak, 2009), such as Ca in the case of lumbricid earthworms (Hobbie et al., 2006), sodium (Na) in the case of termites (Kaspari et al., 2009), or manganese (Mn) in the case of lignin-degrading fungi (Berg et al., 2010). Primary producers may also influence decomposition by releasing labile organic substrates that can "prime" decomposition of more recalcitrant organic matter, stimulating microbial activity in both aquatic (Danger et al., 2013) and terrestrial (Phillips et al., 2011) ecosystems.

As a research community, we are far from being able to predict the nature of bottom-up control of decomposition; in particular, whether C quality (i.e., the complexity of C molecules) or nutrient concentration (and which nutrient) will limit decomposition in a particular ecosystem. Studies suggest that patterns of microbial decomposer nutrient limitation only partially follow those of nutrient limitation of NPP: when supplied as fertilizer, N does not always limit decomposition where N limits NPP, but P more consistently limits decomposition where P limits NPP, such as in tropical forests on highly weathered soils (Hobbie and Vitousek, 2000; Wieder et al., 2009). Further, the role of micronutrients, which are seldom measured, is becoming increasingly apparent in influencing decomposition rates (Kaspari et al., 2008; Berg et al., 2010).

Top-down forces in decomposer food webs

In decomposer food webs, top-down factors that influence rates and patterns of nutrient release from decomposing organic matter include the energy and nutritional requirements of decomposers. These requirements in turn are influenced by the nutrient stoichiometry of decomposer biomass and decomposer carbon use efficiency (i.e., the proportion of C consumed that contributes to growth as opposed to respiration). This has long been recognized and demonstrated in aquatic ecosystems (Redfield, 1958; Hall et al., 2011), where it is clear that the stoichiometry of bacteria can influence the stoichiometry of nutrients in the water column. In terrestrial ecosystems, direct demonstration of linkages between microbial characteristics and decomposing litter nutrient dynamics is hindered by the challenges associated with measuring and manipulating decomposer physiology and stoichiometry in soils. Nevertheless, theory suggests that variation in terrestrial decomposer stoichiometry and carbon use efficiency should affect patterns of nutrient immobilization and release from litter (Manzoni et al., 2010).

Indeed, there is strong evidence that microbial stoichiometry can vary in both aquatic and terrestrial ecosystems in ways that should affect nutrient dynamics during decomposition. Bacterial C:P ratios vary by an order of magnitude

in lakes (Hall et al., 2011) and marine ecosystems (Vrede et al., 2002). In soils, although average community microbial C:N and C:P ratios are fairly constrained across a wide variety of ecosystems, community microbial C:N ratios can vary by one and microbial C:P ratios by one to two orders of magnitude among different ecosystems (Cleveland and Liptzin, 2007; Manzoni et al., 2010). Such variation should have measurable effects on detrital nutrient dynamics: colonization of detritus by decomposers with narrower C:N or C:P ratios (i.e., with high nutrient requirements) should cause greater immobilization of N or P, respectively, delaying the point at which detritus switches from nutrient immobilization to release during decomposition (Manzoni et al., 2010).

Decomposer carbon use efficiency is another top-down factor that affects patterns of nutrient immobilization. Higher carbon use efficiency should drive greater immobilization: since more C is used for growth, more nutrients are needed to support that growth (Manzoni et al., 2010). Carbon use efficiency is sensitive to environmental conditions, decreasing with warming and increasing with increasing nutrient availability in both aquatic and terrestrial ecosystems (del Giorgio and Cole, 1998; Manzoni et al., 2012). These patterns imply that decomposers may release more nutrients during decomposition of similar substrates under warmer or under more nutrient-poor conditions.

Symbioses: a special case of interacting bottom-up and top-down forces

Nutrient cycling is also influenced by interactions between primary producers and symbionts, which can be conceptualized as interactions between bottom-up (primary producer) and top-down (symbiont) forces. An obvious example is the association of primary producers with bacteria that are able to acquire atmospheric N_2 through the process of N-fixation. In terrestrial ecosystems, these symbiotic associations occur primarily between plants in the pea family and bacteria called Rhizobia; between plants in other families and the bacterium *Frankia*; and between cyanobacteria or other N-fixing bacteria and a variety of hosts, including bryophytes, liverworts, hornworts, and cycads (Adams and Duggan, 2008). Examples in aquatic ecosystems include cyanobacteria that form symbiotic associations with various algae and the water fern *Azolla*, and other N-fixing bacteria that associate closely with roots of seagrasses (Welsh, 2000). These symbioses not only enhance the N nutrition of the primary producers involved in the symbioses, but also of neighboring organisms, as the N-rich tissues of N-fixing plants die, decompose, and release N into the environment (Lee et al., 2003). Indeed, this process underlies the use of "green manures" in both terrestrial ecosystems (e.g., use of plants in the pea family as cover crops) and aquatic ecosystems (e.g., use of *Azolla* in rice agriculture).

Terrestrial plants also influence nutrient cycling through their associations with mycorrhizal fungi; mycorrhizae generally increase the ability of plants to acquire nutrients from soils by increasing the volume of soil exploited.

In addition, different types of mycorrhizae are able to access (and influence the cycling of) different nutrients. For example, ectomycorrhizae and ericoid mycorrhizae – unlike arbuscular mycorrhizae or many non-mycorrhizal roots – have the ability to decompose organic matter and thus can access organic N pools, likely enhancing ecosystem N retention (Read, 1991; Lambers et al., 2008; Phillips et al., 2013).

Finally, some primary producers can enhance the supply and cycling of P through the production of specialized structures and enzymes. For example, some plants produce "cluster roots" that exude organic acids that increase the solubility of soil P (Lambers et al., 2008). These plants and others also secrete root phosphatase enzymes that cleave organically bound phosphate (Treseder and Vitousek, 2001; Lambers et al., 2008); these plants thus need not rely solely on decomposers to mineralize P for their uptake. Similarly, several phytoplankton taxa can excrete alkaline phosphatase and can thus enhance P-cycling in P-limited marine ecosystems (Hoppe, 2003).

Herbivores and nutrient cycling

A number of reviews have been published on the effects of herbivores on nutrient cycling that organize thinking around this issue in different ways (e.g., Hunter, 2001; Wardle, 2002; Bardgett and Wardle, 2003; Hartley and Jones, 2004; and many others). Although a review of this literature is beyond the scope of this chapter, we have chosen to highlight some of the mechanisms by which herbivores can both *accelerate* and *decelerate* rates of nutrient cycling in terrestrial and aquatic ecosystems.

Acceleration of nutrient cycling by herbivores

One of the most widely recognized effects of herbivores on nutrient cycling is the acceleration that can occur when herbivores excrete waste products that are more nutrient-rich than the primary producers that they consume, a process regulated by an interaction between bottom-up factors (the C:nutrient ratios of primary producers) and top-down factors (the production efficiencies and nutrient requirements of herbivores) (Hobbs, 1996; Bardgett and Wardle, 2003). If not consumed by herbivores, primary production enters the decomposer food web. In the case of leaf litter, this occurs after plants re-translocate some fraction of foliar nutrients, further reducing the nutritional content of plant litter. However, through their consumption of leaves prior to senescence, and their subsequent digestion, respiration, and excretion and egestion of wastes, some herbivores effectively partially break down organic material and reduce its C:nutrient ratio before it enters the decomposer pathway, thereby potentially accelerating microbial nutrient cycling (Hobbs, 1996; Lovett et al., 2002).

In aquatic ecosystems, various classes of herbivores increase nutrient cycling by releasing nutrients at a higher C:N but lower N:P stoichiometric ratio than in the ambient water (Vanni, 2002; Sereda and Hudson, 2011; but see

Atkinson et al., 2013). For instance, nutrient excretion by benthic invertebrates (e.g., insect larvae, annelids, mussels, and crustaceans) influences primary producer nutrient limitation and dynamics in freshwater and marine systems (Haertel-Borer et al., 2004; Conroy and Edwards, 2005; Alves et al., 2010; Atkinson et al., 2013). Similarly, nutrient recycling by zooplankton (e.g., copepods and cladocerans) can contribute significantly to the nutrient demand by phytoplankton (e.g., Attayde and Hansson, 1999; Pérez-Aragón et al., 2011). Vertebrate herbivores such as fish tend to excrete nutrients at lower rates than invertebrates but with similar N:P ratios (Attayde and Hansson, 1999; Sereda and Hudson 2011). They hence also significantly affect nutrient mineralization and primary productivity (Schaus and Vanni, 2000; Flecker et al., 2002; Burkepile et al., 2013).

In terrestrial ecosystems, N-rich frass (insect excreta) can stimulate N mineralization and leaching (Hunter, 2001; Frost and Hunter, 2007; but see Lovett et al., 2002). Furthermore, dead insects themselves may be more nutrient rich than the leaves they consume (and the litter that would otherwise fall to the forest floor), providing a nutrient-rich energy source for decomposers (Hunter, 2001). Accordingly, forest insect outbreaks have been linked in some instances to increased nitrate export in streams, although other systems strongly retain N transferred to the forest floor via frass and insect cadavers (Lovett et al., 2002; Hartley and Jones, 2004).

Herbivores also can accelerate decomposition processes and potentially nutrient cycling by concentrating, harboring, or cultivating decomposers in their guts, mounds, or gardens that are capable of breaking down compounds such as lignin or cellulose that the herbivores themselves cannot. Arguably the most well known terrestrial example of this is the ruminant ungulates, although termites also harbor intestinal protists and bacteria that can digest cellulose (Tokuda and Watanabe, 2007; Jouquet et al., 2011). Ruminant animals provide an example of the reduction in C:nutrient ratio that occurs with herbivory, described above. They are relatively inefficient at extracting N from their food, particularly from N-rich food, but are relatively efficient at extracting energy, because of their gut symbionts that aid in the digestion of cellulose and hemicellulose (Hobbs, 1996; Jarvis, 2000; Reece, 2013). Thus, the urine and dung produced by ruminants can be nutrient rich, particularly where herbivores are consuming relatively N-rich plant species (Ruess and McNaughton, 1988; Bardgett and Wardle, 2003). Consequently, grazing ungulates have been shown to increase rates of N cycling, with the best known examples in Serengeti National Park, Tanzania, Africa and Yellowstone National Park, Wyoming, USA. Ungulates increased N mineralization and gaseous N losses in both Serengeti (Ruess and McNaughton, 1988; McNaughton et al., 1997) and Yellowstone, where grazers also increased denitrification, but not N leaching (Frank and Groffman, 1998a; 1998b; Frank et al., 2000). In domesticated livestock systems, ruminants promote N losses via multiple pathways, including leaching, denitrification, and ammonia volatilization,

and P losses via erosion (Jarvis, 2000). Many aquatic herbivorous vertebrates (e.g., fish, turtles, and dugongs) also have specialized gut morphologies (e.g., hindgut) and microbiota (e.g., cellulose-decomposing bacteria) that help them to process aquatic plants and likely influence nutrient cycling (Stevens and Hume, 1998; Mountfort et al., 2002; Wu et al., 2012).

Other examples of enhanced nutrient cycling associated with herbivore–symbiont systems can be found among insects that cultivate fungi (Mueller et al., 2005). For example, fungus-growing termites (Macrotermitinae) collect plant detritus in their mounds and tunnels, and use it to cultivate white-rot fungi in a microclimate that is highly conducive to decomposition compared to the surrounding arid landscapes where they occur (Jouquet et al., 2011; Schuurman, 2012). The fungi specialize in lignin degradation and produce fungal nodules that are eaten by the termites. This greatly increases the digestibility of the nutrients contained in the litter gathered by the termites, improving its C quality and reducing its C:N ratio, sometimes by orders of magnitude (Mueller et al., 2005; Schuurman, 2012). Termite–fungal mutualisms can substantially increase overall decomposition rates in arid ecosystems, particularly for wood (Cornwell et al., 2009), with termites mediating 10–20% of the C mineralization in these ecosystems (Schuurman, 2012). The nutrients that flow via litter into macrotermitine mounds ultimately may be transferred to higher trophic levels, as termites constitute a significant source of nutrition for a variety of predators that are able to capture foraging termites or dispersing alates (winged termites), or break open termite mounds (Schuurman, 2012). Similarly, leaf-cutting ants in the Neotropics carry leaves (and other plant biomass) into their subterranean nests, where they are degraded by symbiotic fungi that the ants subsequently eat. Thus, fungus-growing termites and leaf-cutting ants similarly concentrate nutrients in their nests, while denuding the surrounding area (Meyer et al., 2013). As with the termites, leaf-cutting ants likely support higher trophic levels (Terborgh et al., 2001).

Physiological responses by primary producers to herbivory may also accelerate nutrient cycling. For example, there is ample evidence that herbivores can alter the chemistry of leaf litter, including its nutrient content, in ways that may accelerate decomposition. An increase in foliar (and litter) nutrient concentration is a common response to herbivory (Hunter, 2001; Bardgett and Wardle, 2003). This occurs because herbivores remove sinks for nutrients, and also because they can disrupt re-translocation and increase the fraction of leaves that fall when they are green, prior to senescence (Lovett et al., 2002; Chapman et al., 2003). Herbivores may also influence nutrient cycling by altering plant allocation of C. For example, in response to removal of aboveground tissues by herbivores, plants may allocate to replace lost tissues, reducing allocation to belowground production, as happens with seagrasses (Vergés et al., 2008). Decreased C availability to microbes in the soil or sediment may reduce nutrient

immobilization and increase nutrient availability (Holland and Detling, 1990). On the other hand, herbivory may stimulate exudation of C into the rhizosphere, stimulating microbial activity, which also may promote nutrient cycling (Bardgett and Wardle, 2003).

Although the mechanisms summarized above may increase nutrient cycling rates, whether increased rates of nutrient cycling in turn enhance primary productivity likely depends on several factors. For example, the direct negative impacts of consumption by herbivores on productivity (Milchunas and Lauenroth, 1993) may negate any positive effects of increased nutrient supply. Further, herbivores such as termites and leaf-cutter ants may concentrate nutrient availability spatially and temporally in ways that plants are unable to exploit. Finally, herbivores may promote nutrient losses from the ecosystem via migration, leaching, erosion, or gaseous N losses, leading to long-term decreases in nutrient supply despite short-term increases in nutrient cycling rates (Pastor et al., 2006; Doughty et al., 2013).

Deceleration of nutrient cycling by herbivores

In contrast to the examples cited above, herbivory may reduce rates of nutrient cycling if herbivores sequester nutrients into inaccessible pools, induce defenses, or preferentially feed on palatable species that also have relatively rapidly decomposing tissues, allowing unpalatable species with tissues that are poor quality for decomposers and herbivores alike to increase in abundance. An often-cited example of this mechanism at work is the boreal moose browsing system, for example, on Isle Royale, Michigan, USA (Pastor et al., 1988; 1993; 2006). There, moose prefer the more palatable deciduous species and fir (*Abies*), and avoid the less palatable spruce (*Picea*). Areas with long-term exclusion of moose exhibit reduced spruce abundance and higher rates of N cycling. But even without species turnover, herbivores may induce chemical changes in plants that reduce the decomposition rates of their tissues and slow rates of nutrient cycling. For example, terrestrial and aquatic primary producers can respond to herbivory by producing chemical defenses (Cronin and Hay, 1996; Karban and Baldwin, 2007; also, see Chapter 8). Given the close correspondence between traits of primary producers that deter herbivores and those that slow rates of decomposition (Grime et al., 1996), these induced defenses might be expected to decrease decomposition and nutrient cycling rates as well (Choudhury, 1988), although comparisons of decomposition rates among plants or algae with and without induced defenses are scarce.

An extreme example of selective feeding that depresses nutrient cycling occurs when herbivores preferentially feed on N-fixers and reduce their abundance in ways that measurably reduce N-fixation rates and, ultimately, soil and plant N pools (Ritchie and Tilman, 1995; Knops et al., 2000). However, chronic herbivory does not always lead to shifts in plant community composition toward

dominance by less palatable species, for reasons that are not entirely clear (reviewed in Hunter, 2001). For example, in a prairie ecosystem, grasshoppers preferentially fed on species with lower tissue N concentrations, thereby increasing abundance of species with high N tissue and accelerating N cycling (Belovsky and Slade, 2000).

Herbivores may also sequester nutrients in their bodies, potentially decreasing the amount of nutrients available for primary producers. This nutrient sequestration is especially significant for long-lived organisms and for vertebrates that have a P-rich skeleton (Vanni et al., 2013). For instance, in an oligotrophic, tropical stream, armored catfish (fam. Loricariidae) had a high body P content (because of their bony plates made of calcium phosphate) but fed on P-poor periphyton, which limited their growth (Hood et al., 2005). In turn, because of these biological constraints, armored catfish had very low P excretion rates and thus they immobilized in their bodies the limited P present in the system.

Top-down and bottom-up effects of predators on nutrient cycling

Predators, from consumers of herbivores and detritivores to top predators, are present in all ecosystems and are represented by a large diversity of organisms (e.g., protozoa, invertebrates, and vertebrates) having diverse functional attributes (e.g., size, anatomy, diet, and hunting strategy). Predation, through its consumptive and non-consumptive effects on lower trophic levels, directly and indirectly controls nutrient cycling (Schmitz et al., 2010). First, we present how predators can have direct top-down effects on nutrient cycling through a trophic cascade along the food chain. Then we show how predators can indirectly control nutrient cycling through top-down, non-consumptive effects. Finally, we explain how predators have a bottom-up effect on nutrient cycling through their release of nutrients.

Top-down control through consumptive effects

Food webs are often simplified as a trophic chain with primary producers, primary consumers, secondary consumers, and top predators (e.g., kelp, herbivorous invertebrates and fishes, carnivorous fishes, and sea otters; Halpern et al., 2006). Predators regulate the density of their prey by consuming individuals, which has cascading effects on the density of the prey of their prey, and ultimately on the density of primary producers and on the amount of nutrients they take up (Leroux and Loreau, 2010). Although most studies have focused on top-down interactions among predators, herbivores, and plants, predators can also have top-down effects on nutrient mineralization through cascading trophic effects on detritivores and bacteria (Dunham, 2008; Schmitz, 2010; Crotty et al., 2012).

Real food webs are often more complex than the classic trophic chain because many species are omnivorous, some carnivores feed on both herbivores

and secondary consumers, and because interaction strengths vary across predator–prey pairs (DeRuiter et al., 2005; Thompson et al., 2012). Therefore, the effect of a predator species on primary productivity depends on its trophic position and on the structure of the food web (Bruno and O'Connor, 2005; Dunham, 2008; Moksnes et al., 2008). Consequently, the overall top-down control of predation on nutrient cycling is determined by both the vertical and horizontal structure of the food web (Schindler et al., 1997; Duffy et al., 2007).

Top-down control through non-consumptive effects

Predators exert a density-mediated effect on their prey by killing individuals, but at the same time they can also have non-consumptive effects (i.e., trait-mediated effects; Schmitz and Suttle, 2001; Schmitz et al., 2004). Indeed, many organisms are able to detect predation cues and then change their physiology, behavior, and/or diet when facing a high predation risk. Changes in foraging activity and food selectivity under high predation risk have been reported for various herbivores: aquatic and terrestrial invertebrates (Schmitz and Suttle, 2001; Byrnes et al., 2006), ungulates (Frank, 2008), and marine vertebrates (Burkholder et al., 2013); also, see Chapters 4 and 5 for detailed examples in terrestrial ecosystems. Such changes in prey biology could be explained by a shift from N-limitation to C-limitation of metabolism and growth with increasing predation risk (Hawlena and Schmitz, 2010; Leroux et al., 2012). These changes in herbivore diet and activity can modify plant community composition (Schmitz, 2006), and thus primary productivity and nutrient cycling (Schmitz, 2008; Reynolds and Sotka, 2011). In addition, trait-mediated effects of predation on the nutrient content of prey can impact nutrient cycling by changing soil composition, which ultimately decreases litter decomposition (Hawlena et al., 2012). The change in prey traits can also directly affect mineralization by changing the contribution of prey to biophysical processes. For instance, in the presence of predatory fish, some benthic invertebrates spend less time feeding at the sediment surface and burrow deeper in the sediment, thus enhancing bioturbation, which results in higher mineralization rates (Stief and Hölker, 2006). Ultimately, the trait-mediated effects of predation can drive evolutionary processes (see Chapter 13).

Top-down control on nutrient fluxes between ecosystems

Trophic cascades most often affect nutrient cycling locally as predators and prey generally occur in the same ecosystem. However, many prey move between habitats and contribute to the spatial flux of nutrients (see Chapters 1 and 6). Predators of these mobile prey can thus initiate trophic cascades across ecosystem boundaries (e.g., from fish to riparian plants through aquatic predatory insects and terrestrial pollinator insects; Knight et al., 2005) or alternatively reduce the flux of nutrients from other ecosystems by targeting the vectors

of allochthonous inputs (e.g., foxes preventing birds nesting on islands, Maron et al., 2006). The role of predators as vectors of nutrients across ecosystem boundaries is detailed in the next section of this chapter.

Bottom-up control through nutrient recycling

Predators, as all animals, release dissolved metabolic wastes, such as ammonium, urea and phosphates, which are directly available, and often limiting, for primary producer growth. Hence, predators participate in the bottom-up control of food webs (Clarholm, 1985; Vanni, 2002; Schmitz et al., 2010). Although the microbial loop has long been seen as the main driver of mineralization, evidence has been accumulating during the last decade that animals can contribute to a significant portion of nutrient cycling, in both aquatic (Vanni et al., 2006; Roman and McCarthy, 2010; Allgeier et al., 2013; Layman et al., 2013) and terrestrial ecosystems (Clarholm, 1985; Beard et al., 2002). For example, grazing of soil bacteria by protists increases rates of N mineralization and N acquisition by plants (Clarholm, 1985; Schimel and Bennett, 2004). Rates and stoichiometry of nutrient excretion by animals are highly variable both within and among species (Vanni et al., 2002; Pilati and Vanni, 2007; Villéger et al., 2012a; 2012b). Indeed, excretion is the result of the balance between the nutrients assimilated and the nutrient demand for growth and maintenance. Therefore, diet quality, ingestion rate, assimilation efficiency, growth rates, and body nutrient content interact to determine the nutrient budget of an animal. Body mass, through its effect on metabolic rate, is the main factor influencing mass-specific excretion rates (Vanni et al., 2002; Hall et al., 2007; Sereda et al., 2008a), but nutritional and physiological variables also have a significant effect (Anderson et al., 2005). For instance, excretion rates of N and P tend to be higher for carnivorous fishes than for herbivorous species because of the lower N and P content of primary producers (Sereda and Hudson, 2011; Burkepile et al., 2013). Nutrient recycling by predators has an important effect on primary productivity (Vanni et al., 2006; McIntyre et al., 2008; Burkepile et al., 2013), especially when animals aggregate in local patches where they can create biogeochemical hotspots (Meyer and Schultz, 1985; Boulêtreau et al., 2011; Capps and Flecker, 2013), or when they speed up the incorporation of allochthonous nutrients (e.g., fish-consuming terrestrial insects; Wurtsbaugh, 2007; Small et al., 2011).

In contrast to excretion of metabolic waste, egestion does not directly contribute to release of nutrients, as the organic matter contained in feces (i.e., the portion of food not assimilated in the gut) must still be mineralized by decomposers. Rates and stoichiometry generally differ between excretion and egestion products, with, for example, feces having lower N:P ratios than dissolved wastes in a carnivorous fish species (Meyer and Schultz, 1985).

Besides being a source of nutrients, predators can also be nutrient sinks because of the large amount of nutrients they store in their bodies (e.g., in

N-rich proteins and nucleic acids, and P-rich fat and bones) and that are thus not available for other organisms (Sereda et al., 2008b; Vanni et al., 2013). This is particularly true for the P trapped in the bony structures of predators that are not easily decomposed and can thus be buried in the sediment before being mineralized (Vanni et al., 2013). On the other hand, nutrient storage in the body can thwart the export of nutrients to other habitats. For example, in oligotrophic lakes, the addition of fish preying upon zooplankton and storing consumed nutrients during winter prevents the sedimentation of P to the bottom of the lake, and hence sustains the amount of nutrients available for primary production during summer (Schindler et al., 2001).

Organisms mediate spatial transfer of nutrients across habitats and ecosystem boundaries

Ecological systems are not isolated units, as they export and receive matter and/or organisms from adjacent and even remote ecosystems. The concept of meta-ecosystems, extending the concept of metacommunities proposed for community ecology to account for source–sink dynamics in local species abundances (Leibold et al., 2004), has been recently proposed to emphasize the importance of these reciprocal fluxes of nutrients and organisms for ecosystem structure and functioning (Gravel et al., 2010; Massol et al., 2011; also, see Chapter 1). Indeed, most of the boundaries between spatially distinct units are permeable to the flows of nutrients, detritus, and living organisms, provided that physical vectors or mobile species allow their transport across these boundaries (Polis et al., 1997). These exchanges are often bidirectional, but their ecological consequences are noticeable, and hence studied, only when the allochthonous inputs (those from outside the ecosystem) correspond to a significant proportion of the autochthonous pool of nutrients (those from within the ecosystem). Since the seminal paper by Polis et al. (1997), which called for an integration of landscape and food web ecology, many assessments of these "trophic subsidies" have been done on various systems, from local to global scales. These studies have demonstrated that allochthonous inputs of nutrients and organisms significantly affect bottom-up and top-down control of nutrient cycling within the recipient ecosystem (Nakano and Murakami, 2001; Leroux and Loreau, 2010; Bartels et al., 2012; also, see Chapter 6).

The fluxes between systems are diverse in terms of what is moving (i.e., nutrients, detritus, plants, or animals), how it is moving (i.e., passively or actively), and which types of source and sink ecosystems are involved (Fig. 9.2). Here, we first present how primary producers can incorporate allochthonous nutrients in primary production. Then we present how primary producers and animals can incorporate the allochthonous organic matter passively transported by abiotic vectors. Finally, we show the unique role of mobile animals that can actively translocate nutrients across ecosystem boundaries from small to large scales.
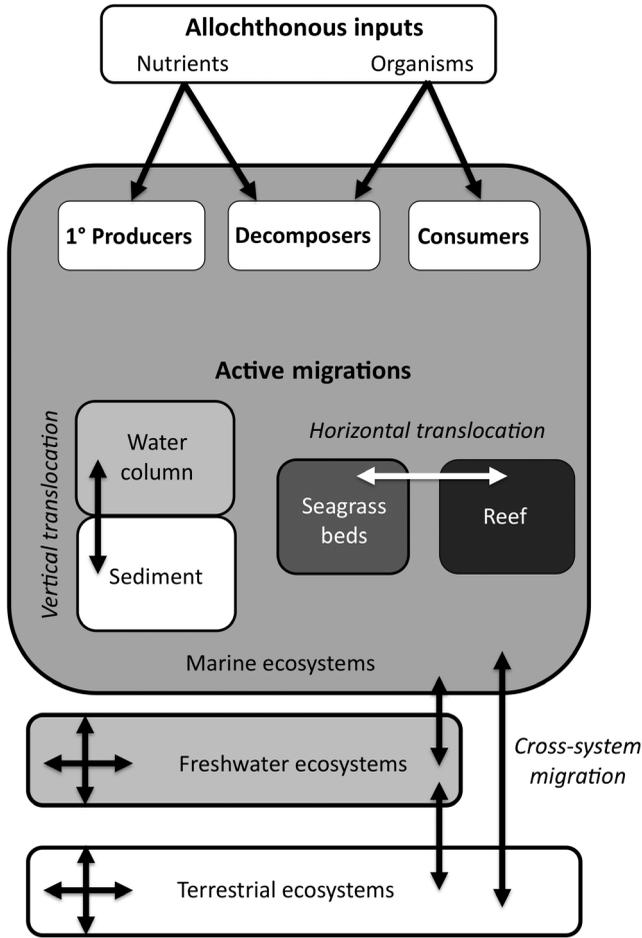
Figure 9.2 Movement of nutrients across ecosystem boundaries can occur among marine, freshwater, and terrestrial ecosystems because of allochthonous inputs of dead organisms and nutrients and because of migration. Similarly, within any of these broad ecosystem types, migration or movement of nutrients or dead organisms can occur between different habitat types (e.g., in marine ecosystems, migration can happen vertically between the water column and the sediment, or horizontally between reef and seagrass habitats).

Allochthonous flux of nutrients affects bottom-up control by primary producers

Global hydrological and atmospheric circulation strongly structures the flow of nutrients among ecosystems and can contribute to the bottom-up control of food webs. Atmospheric circulation continuously transports large amounts

of dust that can fertilize terrestrial and aquatic ecosystems from local to inter-continental scales. For example, dust from Australian deserts not only affects adjacent forests and lakes, but also contributes to sustaining the productivity of the western Pacific Ocean through iron input (McTainsh and Strong, 2007). This physical transfer of nutrients can even connect ecosystems on different continents. The most striking example is the flow of 10^6 metric tons of dust per year from the Sahara Desert to the Amazon basin. This dust, carried over the Atlantic Ocean, is estimated to bring more than $1\,kg$ of $P\,ha^{-1}\,y^{-1}$ and thus to support the high primary productivity of the Amazonian rainforest, which is growing on nutrient-poor soils (Swap et al., 1992).

Nutrients transported in precipitation can also subsidize ecosystems significantly (Kuhn, 2001; Chuyong et al., 2004). However, the main role of water as a vector of nutrients and organic matter is within and among aquatic ecosystems. Dissolved nutrients and particulate organic matter are transferred from soils to rivers, then to estuaries, and finally to marine ecosystems. Water flow hence subsidizes coastal marine ecosystems in nutrients and organic matter originating from freshwater ecosystems. For instance, some marine benthic food webs rely strongly on terrestrial particulate organic matter (Darnaude, 2005; Gillson, 2011). In marine ecosystems, large-scale currents also continuously transport nutrients horizontally and vertically (see Chapter 2). For instance, the powerful Humboldt Current along the west coast of South America creates an upwelling of nutrients that sustains high primary and secondary productivity in this region (Thiel et al., 2007).

Passive flux of plants and animals

Besides transporting nutrients and dissolved and particulate organic matter, air and water can also transport plants and animals across ecosystem boundaries. Organisms that are passively transported by these physical vectors are either dead (e.g., leaves in a forest, fragments of macroalgae in marine ecosystems, and animal carrion) or small animals that cannot escape the physical flow (e.g., insects and zooplankton). These organisms and their waste products are incorporated at different trophic levels in recipient food webs by detritivores, herbivores, and predators, and can represent a significant proportion of their resources. For instance, inputs of plant material (e.g., litterfall, fruit, seeds, and wood) and insects to freshwater ecosystems are an important source of organic matter for aquatic animals (Schindler and Scheuerell, 2002; Lamberti et al., 2010; also, see Chapter 6). Reciprocally, aquatic ecosystems can export organic matter to adjacent terrestrial ecosystems (Bastow et al., 2002; Crawley et al., 2009). For example, tides and waves leave large amounts of detached marine macrophytes on shores (Crawley et al., 2009), as well as animal carrion (e.g., fish and birds; Rose and Polis 1998). This aquatic organic matter significantly subsidizes terrestrial

herbivores (e.g., arthropods) and predators (e.g., lizards, birds, and coyotes) in habitats with low productivity, such as remote islands (Barrett et al., 2005) or desert coastal areas (Rose and Polis, 1998). Marine allochthonous resources thus have direct positive effects on terrestrial consumers (Dugan et al., 2003), as well as indirect effects on terrestrial plants through the nutrient recycling done by consumers (Spiller et al., 2010). Water flow can also carry subsidies among distant marine ecosystems, such as particulate organic matter from the open ocean to fringing coral reefs (Wyatt et al., 2010), or fragments of kelp from reefs to seagrass meadows (Hyndes et al., 2012). In the latter case, macroalgae fragments subsidize both grazers and decomposers living in seagrass habitats and subsequently contribute indirectly to the nutrients assimilated by seagrass.

Animal migrations between ecosystems

Besides passive fluxes of nutrients and organisms across ecosystem boundaries, active dispersion of organisms also contributes to the transfer of nutrients among ecosystems (Polis et al., 1997). Indeed, mobile animals have the unique ability to move nutrients across ecosystem boundaries through migrations on short (day/night) or long (season/year) temporal scales. More importantly, these active movements can be in the opposite direction to passive fluxes due to physical vectors (e.g., gravity and water flow). One of the most famous examples of an allochthonous subsidy supported by an animal migration is the anadromous salmon species (genus *Onchorhynchus*) in Western North America (Helfield and Naiman, 2001; Janetski et al., 2009). These species spawn in rivers in the USA and Canada, juvenile fish move to the Pacific Ocean, and after several years of growth in the marine ecosystem, mature adults migrate up their native river to reproduce and then die. Anadromous salmon thus transfer large amounts of marine-derived nutrients in their bodies, and their carcasses fertilize the recipient freshwater ecosystems (Moore et al., 2007). Indeed, carcasses are a resource for bacteria and aquatic macroinvertebrates (Wipfli et al., 1998; Winder et al., 2005), and they thus indirectly benefit invertivorous, juvenile anadromous salmonids and even non-migratory species (Wipfli et al., 2003). In addition, spawning salmonids are a prey for top predators (mainly bear), which transfer the marine nutrients contained in fish to riparian ecosystems through defecation. This allochthonous input of marine nutrients mediated by two animal species significantly influences the productivity and biodiversity of several components of riparian ecosystems, such as trees (Helfield and Naiman, 2001) and insects (Hocking and Reimchen, 2002; Hocking and Reynolds, 2011). Freshwater ecosystems also export nutrients to riparian ecosystems through the dispersion of flying insects; larvae grow on benthic subsidies before adults emerge and fly to surrounding habitat to reproduce and die. These allochthonous subsides can represent a large flux of nutrients around lakes and rivers (Nakano and Murakami, 2001; Gratton and Vander Zanden, 2009; also, see Chapter 6).

Animal migrations between habitats

Besides these massive and temporally limited animal migrations, animals also contribute to moving nutrients between neighboring habitats on a daily basis. Indeed, many species migrate between areas favorable for foraging and areas favorable for resting (e.g., that are less risky in term of predation). These daily movements, coupled with the inertia of the digestive process, contribute to subsidizing the resting habitats with nutrients coming from foraging areas that are often more productive. These allochthonous fluxes thus occur among habitats within aquatic or terrestrial ecosystems. For instance, herbivores such as roe deer graze in meadows, but rest in forest patches where they urinate and egest feces rich in N and P, thus subsidizing forests with nutrients derived from cultivated fields (Abbas et al., 2012). Birds can also contribute significantly to the allochthonous input of nutrients in forests (Fujita and Koike, 2009). In aquatic ecosystems, herbivorous and carnivorous vertebrates also transfer nutrients between habitats. For instance, haemulid fish feeding on invertebrates in seagrass patches during the night and resting near coral reefs during the day significantly increase coral growth through the excretion and egestion of nutrients coming from seagrass patches (Meyer and Schultz, 1985). Fish can also bring nutrients into enclosed habitats, such as small caves in rocky reefs, which are poorly connected with the water column (e.g., zooplanktivorous damselfish; Bray et al., 1981). Some fish species can even deliberately move far outside their feeding area for egesting their feces (Brown et al., 1996; Krone et al., 2008).

The potential of a species to transfer nutrients from its foraging habitat to its resting place is constrained by the lag between food ingestion and waste production. Therefore, most species transfer nutrients short distances (< 1 km) within aquatic or terrestrial ecosystems. However, some amphibious animals transfer nutrients across ecosystem boundaries. For example, oceanic birds feeding on marine prey (mainly fish) subsidize the terrestrial habitats where they rest or reproduce. The allochthonous nutrients released by birds (i.e., guano) shape the composition of plant communities and their productivity (Sanchez-Pinero and Polis, 2000; Fukami et al., 2006; Young et al., 2010). Large amphibious herbivores, such as *Hippopotamus*, also have the potential to move nutrients across the aquatic/terrestrial boundary (Naiman and Rogers, 1997).

Animal vertical migrations in stratified ecosystems

In addition to moving nutrients horizontally, animals also move nutrients between the vertical strata of ecosystems. For instance, in savanna, ground-dwelling predators feed on both ground and arboreal prey, and thus increase the coupling between the two food webs (Pringle and Fox-Dobbs, 2008). In freshwater and coastal marine ecosystems, many fish species feed on benthic prey and then swim in the water column (pelagic zone), where they release nutrients initially contained in their benthic prey. This vertical and horizontal

translocation of benthic nutrients can significantly increase planktonic productivity (Schaus and Vanni, 2000). In the ocean, whales foraging at depth move nutrients from deep habitats to the euphotic zone, which is often nutrient limited (Lavery et al., 2010; Roman and McCarthy, 2010). This "whale pump" thus counterbalances the sedimentation process of dead plants and animals that sink to the aphotic zone and helps sustain the productivity of the ocean.

The connection of nutrient cycles among and within ecosystems is mediated by primary producers and consumers through the transport and/or the incorporation of nutrients into food webs. Trophic subsidies vary in terms of the nature, intensity, and stability of the incoming flow of nutrients, the type of vector, and the characteristics of the local food web (Likens and Bormann, 1974; Polis et al., 1997; Lamberti et al., 2010). Comparisons among systems (e.g., aquatic versus terrestrial) are thus required for a global understanding of the interactive effects of species traits (e.g., diet, mobility, and metabolism) and food web characteristics (e.g., number of compartments and connectivity among them) on the impact of allochthonous fluxes on bottom-up control of food webs (Baxter et al., 2005; Gravel et al., 2010; Massol et al., 2011; Marcarelli et al., 2011).

Conclusion

Human activities are increasingly affecting nutrient cycles through the addition of anthropogenic N and P, as well as by modifying the composition and abundance of primary producer, decomposer, herbivore, and predator species in aquatic and terrestrial ecosystems. Therefore, future investigations are needed to quantify how these global changes affect the interactions between the bottom-up and top-down effects of organisms on nutrient cycles (see Chapter 14).

For instance, the diversity and abundance of predators are severely affected by human activities in many terrestrial and aquatic ecosystems, through exploitation but also through introduction of non-native species (Cucherousset and Olden, 2011; Estes et al., 2011). Developing an integrated approach that accounts for both their top-down and bottom-up effects on nutrient cycling, including indirect effects, is thus an urgent need. Toward this objective, functional traits (e.g., size, morphology, metabolic, and excretion rates) could offer an operational framework (Schmitz et al., 2010; Massol et al., 2011; also, see Chapter 8).

Human activities also impact allochthonous fluxes between ecosystems, directly by removing or adding organisms able to transport nutrients (e.g., through fishing and introduction of non-native species) and by changing ecosystem productivity (e.g., through pollution), and indirectly by altering the connectivity between ecosystems (e.g., through construction and removal of dams). Therefore, future developments of the meta-ecosystem concept (Gravel et al., 2010; Massol et al., 2011; also, see Chapter 1) should help to integrate spatial and functional ecology.

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