

# Are there real differences among aquatic and terrestrial food webs?

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Ecologists have long recognized the importance of predators in structuring both aquatic and terrestrial ecosystems<sup>1,2</sup>. However, since the inception of these hypotheses, there has also been considerable controversy surrounding the importance of predators relative to other limiting factors (e.g. resources and abiotic stresses). To disentangle these effects, modern ecologists rely on manipulative experiments<sup>3</sup>. Although experimental studies have facilitated insight into the detail and mechanisms that underlie the inner workings of a particular system, they have also meant that ecologists have inevitably specialized on studying a particular type of ecosystem (such as aquatic ecologists or grassland ecologists). Because small-scale experimental studies have perhaps been overemphasized relative to more synthetic comparative analyses, the degree to which we can generalize similarities and differences across ecosystems is limited.

In an insightful, but highly provocative, paper, Strong<sup>4</sup> asked 'Are trophic cascades all wet?' A trophic cascade is defined as a strong effect imposed by top predators on their prey biomass, which cascades down to plants in a food chain and plays an important role in determining the overall structure of the community<sup>5,6</sup>. By his question, Strong suggests that evidence for trophic cascades is common in aquatic ecosystems and rare in terrestrial ecosystems. Following Strong's comparison of terrestrial and aquatic ecosystems, there has been a recent surge of interest by ecologists to explore the general differences (as well as similarities) among these disparate types of ecosystems<sup>5-13</sup>. Here, I evaluate the available evidence, and several current hypotheses, concerning how these different types of ecosystems are structured.

## Patterns of food-web structure in aquatic and terrestrial ecosystems

In accordance with Strong's<sup>4</sup> hypothesis, several recent reviews<sup>5,6,9,12,14</sup> and meta-analyses<sup>15,16</sup> (Fig. 1a) suggest that the trophic cascade is typically strong in aquatic ecosystems. Although the evidence in these reviews is biased towards freshwater lake ecosystems, evidence from both stream<sup>17</sup> and marine<sup>18</sup> ecosystems show similar patterns. Furthermore, some evidence has accumulated to support Strong's hypothesis that trophic cascades involving components of the entire community ('community-level' trophic cascades) are rare in terrestrial ecosystems<sup>6,9,12</sup>. Indeed, the few studies documenting trophic cascades in terrestrial ecosystems are criticized because they only include a small subset of the interacting species within a community; thus, these are termed 'species-level' trophic cascades<sup>6,11,12</sup>.

**Recently, aquatic and terrestrial ecologists have put forward several hypotheses regarding similarities and differences in food-web structure and function among these ecosystem types. Although many of these hypotheses explore why strong top-down effects and trophic cascades might be less common in terrestrial than in aquatic ecosystems, there is little theoretical or empirical evidence available to support or refute these hypotheses. Many unanswered questions remain about potential differences across ecosystem types: progress will require empirical studies designed within a broader context that allows for more direct comparisons.**

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There are three main criticisms of the proposed generality that strong trophic cascades are common in aquatic ecosystems and rare in terrestrial ecosystems. First, the finding that most of the evidence supporting trophic cascades comes from aquatic ecosystems<sup>4,6,9,12</sup> could merely reflect the fact that aquatic ecologists have done many more studies on trophic cascades than have terrestrial ecologists<sup>11</sup>. Indeed, the deficiency of studies in terrestrial ecosystems probably results from the inherent difficulty in manipulating long-lived terrestrial plants and large vertebrate consumers on appropriate spatio-temporal scales (10–10 000 m<sup>2</sup> and months–decades), relative to rapidly growing aquatic algae and small invertebrate consumers (1–5 m<sup>2</sup> and days–months)<sup>11</sup>.

Second, recent reviews and meta-analyses<sup>14-16</sup> in freshwater lake trophic cascades combine experimental results and treat variation in the effect as noise (Fig. 1a). This has led to the suggestion that the strong trophic cascade in lakes represents one of the few generalities known in community ecology<sup>19</sup>. Alternatively, Leibold *et al.*<sup>10</sup> review many similar lake trophic cascade experiments and show explicitly that trophic cascades were not uniformly strong in lake experiments; instead, there was a considerable amount of variation in the magnitude of the effect (Fig. 1b).

Third, a variety of evidence has accumulated to suggest a strong role for consumer effects and trophic cascades in terrestrial ecosystems, including:

- A meta-analysis by Schmitz *et al.*<sup>13</sup> showing that the relative strengths of terrestrial trophic cascades are often as strong as those in aquatic ecosystems (Fig. 2). However, this analysis has been criticized because many of the reviewed experiments include only a subset of the species within the entire community – they more probably represent species-level trophic cascades<sup>6</sup>.
- Some of these species-level cascade experiments incorporate a large component of relatively simple communities<sup>13</sup>. For example, Strong *et al.*<sup>20</sup> provided evidence for a strong species-level trophic cascade that extended to an abundant nitrogen-fixing shrub in a simple dune ecosystem. Similarly, Spiller and Schoener<sup>21</sup> showed that the removal of top insectivorous predators (i.e. lizards and spiders) cascaded down to influence the most abundant shrub species in relatively simple island communities.
- Observational evidence gathered from forests in North America<sup>22,23</sup> suggested a strong role for predation by wolves in structuring populations of the dominant vertebrate herbivores (moose and deer), which cascade down

to indirectly influence plant abundance. Observational evidence from European tundra ecosystems suggests that predators play a similarly strong role in these communities<sup>24</sup>.

- Recent experiments have provided evidence for community-level effects of predators in terrestrial ecosystems. First, a large-scale, long-term experiment in the Canadian boreal forest<sup>25</sup> manipulated several factors, and showed strong direct effects of vertebrate predators on mammalian herbivores and of herbivores on plants, but weak indirect effects of predators on plants. Second, the large-scale removal of mammalian predators from a Chilean shrubland<sup>26</sup> allowed herbivores to increase in abundance and activity, and indirectly cascade to the plant community. Finally, the removal of insectivorous lizards in northern California meadows<sup>27</sup> showed a fourfold increase in herbivorous insect abundance, a nearly threefold decrease in total plant biomass and a shift in plant-species composition.

### Proposed hypotheses concerning aquatic–terrestrial differences

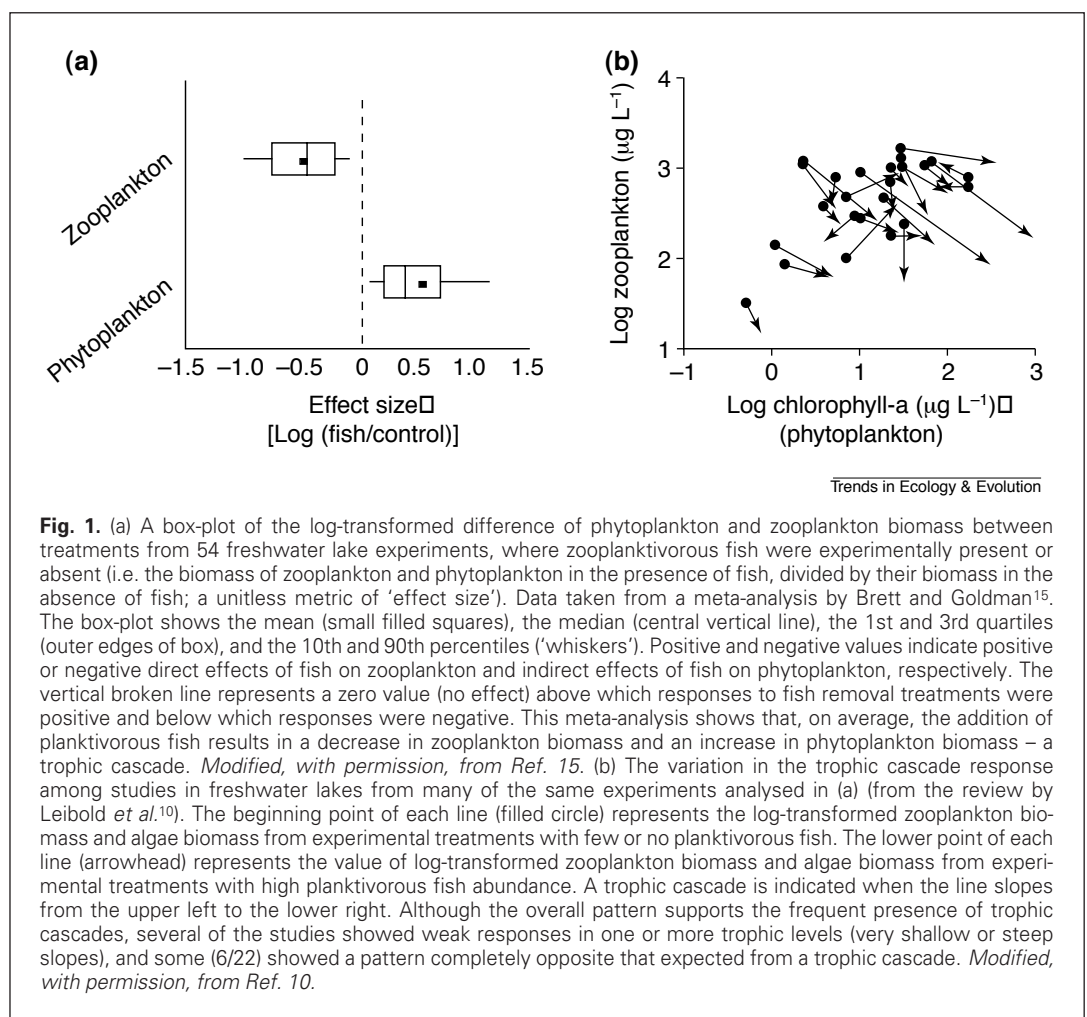
Although it remains unclear whether fundamental differences in the structure of aquatic and terrestrial food webs exist, several hypotheses have been put forward to explain the mechanisms behind this potential divergence; these are discussed in the next section.

#### *Terrestrial food webs are more complex than aquatic food webs*

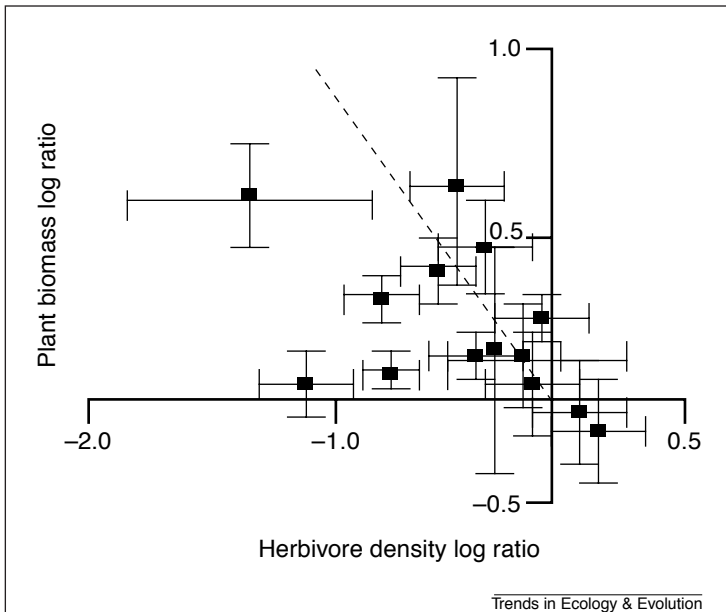
Hairston *et al.*'s<sup>1</sup> hypothesis that predators reduce the abundance of herbivores, which allows plants to flourish in terrestrial ecosystems (a trophic cascade), sometimes referred to as the 'green world hypothesis'<sup>12,24</sup>, was criticized early on by Murdoch<sup>28</sup>, and Erlich and Birch<sup>29</sup>. These criticisms emphasized the ability of several species of plants to defend (using spines and chemicals) against herbivores that might deter strong trophic cascades. Recent authors<sup>4,6,9,12</sup> expounded upon this view to suggest that terrestrial ecosystems are typically so complex, and plant defenses so prevalent, that strong food-web interactions and trophic cascades should be rare. These same authors suggest that a few key species and an overall less complex food web typically drive the trophic cascades observed in aquatic ecosystems. Two reasons have been suggested to explain why plant defenses and complexity might be more prevalent in terrestrial than aquatic ecosystems: (1) terrestrial ecosystems are more productive, and thus

have higher diversity and complexity<sup>4,9</sup>; and (2) aquatic ecosystems have rapid light attenuation, and thus favor species that are small and buoyant, rather than species that are chemically or structurally defended<sup>6,9,11,12</sup>.

I suggest that perceived differences between these ecosystem types might result because organisms within terrestrial ecosystems are typically classified at finer scales than organisms within aquatic ecosystems. Individual species of terrestrial plants and herbivores are relatively large, and are therefore easily identified and counted. Alternatively, the microscopic algae and zooplankton that dominate aquatic ecosystems are often lumped into broad categories (i.e. Chlorophyll-a for algae and lumping zooplankton species into higher taxonomic units). In reality, there can be hundreds of species of algae, vascular plants and animals even within a single lake or pond<sup>14,30</sup>, and thus these communities do not seem to be any less diverse than terrestrial ecosystems. Furthermore, defenses and compensation among prey species are not restricted to terrestrial habitats<sup>10</sup>. Many species of aquatic algae<sup>30–32</sup>, macrophytes<sup>33</sup>, zooplankton<sup>34,35</sup> and planktivorous fish<sup>36</sup> have chemical, structural and behavioral defenses that reduce their susceptibility to predators, and that mediate the strengths of trophic cascades among lake ecosystems. Importantly, some of the most well known examples of strong trophic cascades in lake ecosystems only included highly vulnerable planktivorous minnows<sup>14,37</sup>, and thus these studies did not consider the defended component of the planktivore community (e.g. spiny-rayed sunfishes)<sup>36,38</sup>, which could have severely diluted the effects of top predators.



**Fig. 1.** (a) A box-plot of the log-transformed difference of phytoplankton and zooplankton biomass between treatments from 54 freshwater lake experiments, where zooplanktivorous fish were experimentally present or absent (i.e. the biomass of zooplankton and phytoplankton in the presence of fish, divided by their biomass in the absence of fish; a unitless metric of 'effect size'). Data taken from a meta-analysis by Brett and Goldman<sup>15</sup>. The box-plot shows the mean (small filled squares), the median (central vertical line), the 1st and 3rd quartiles (outer edges of box), and the 10th and 90th percentiles ('whiskers'). Positive and negative values indicate positive or negative direct effects of fish on zooplankton and indirect effects of fish on phytoplankton, respectively. The vertical broken line represents a zero value (no effect) above which responses to fish removal treatments were positive and below which responses were negative. This meta-analysis shows that, on average, the addition of planktivorous fish results in a decrease in zooplankton biomass and an increase in phytoplankton biomass – a trophic cascade. *Modified, with permission, from Ref. 15.* (b) The variation in the trophic cascade response among studies in freshwater lakes from many of the same experiments analysed in (a) (from the review by Leibold *et al.*<sup>10</sup>). The beginning point of each line (filled circle) represents the log-transformed zooplankton biomass and algae biomass from experimental treatments with few or no planktivorous fish. The lower point of each line (arrowhead) represents the value of log-transformed zooplankton biomass and algae biomass from experimental treatments with high planktivorous fish abundance. A trophic cascade is indicated when the line slopes from the upper left to the lower right. Although the overall pattern supports the frequent presence of trophic cascades, several of the studies showed weak responses in one or more trophic levels (very shallow or steep slopes), and some (6/22) showed a pattern completely opposite that expected from a trophic cascade. *Modified, with permission, from Ref. 10.*



**Fig. 2.** A meta-analysis of trophic cascade experiments from terrestrial ecosystems showing the direct effects of carnivore removal on herbivore density and the indirect effect on total amount of plant biomass (a subset of the studies from Schmitz *et al.*<sup>13</sup>). Squares represent the mean response and bars represent the standard deviation. The broken line represents a 1:1 correspondence between the direct and indirect effects. Although many of these studies incorporated only a subset of the species within the entire ecosystem<sup>6</sup>, the relative magnitudes and variability of the effects are on the same order as those observed in aquatic trophic cascades (see Fig. 1). Modified, with permission, from Ref. 13.

*The number of trophic levels differs between aquatic and terrestrial ecosystems*

Hairston and Hairston<sup>8,39</sup> have suggested that in terrestrial ecosystems omnivory and intraguild predation truncate the food chain to three functional trophic levels, where predators reduce herbivore abundance and allow plants to flourish. Alternatively, they suggest that, in aquatic ecosystems, the physical constraints of water restrict omnivory and intraguild predation, thus four trophic level food chains are expected. Therefore, in aquatic ecosystems, top predators should reduce the abundance of intermediate predators, which allows herbivores to flourish and decimate plant production.

One of the primary predictions of Hairston and Hairston's<sup>8,39</sup> hypothesis, that herbivory should be higher in aquatic than in terrestrial ecosystems, is supported by empirical data<sup>7,8,12,39</sup>. For example, Cyr and Pace<sup>7</sup> showed that for a given level of primary productivity, aquatic herbivores consume, on average, nearly 300% more plant material than terrestrial herbivores (Fig. 3). However, these same data could be used to support a variety of other hypotheses, including Polis and Strong's hypothesis<sup>4,6,9,12</sup> that terrestrial ecosystems are more complex and have more defended plant species than aquatic ecosystems. In addition, there is little compelling evidence to support the underlying mechanisms of Hairston and Hairston's hypothesis. First, estimates of herbivore consumption rates do not necessarily correlate with their effects on plant biomass because many plants can regrow following herbivory<sup>40</sup>. Second, there is scant evidence available to suggest that the lengths of food chains are different in aquatic and terrestrial ecosystems<sup>9,24,41</sup>. Finally, there is considerable evidence that top predators frequently feed omnivorously in aquatic ecosystems<sup>14,41</sup>, and thus they might not be fundamentally different from terrestrial ecosystems in their structure.

*Timescale and turnover rates are faster in aquatic ecosystems*

The dynamics within aquatic planktonic communities can occur on the order of days, whereas dynamics within terrestrial communities occur on the order of years to decades<sup>11,12</sup>. However, the short timescale in aquatic ecosystems only applies to the planktonic community. When macrophytes, benthic invertebrates and fish are considered, the timescales become more similar to terrestrial ecosystems. Nevertheless, some have suggested that the differences in timescale might lead to fundamental differences in the structuring of these different ecosystems<sup>4,6,9,12</sup>, whereas others<sup>5,11,18,40</sup> suggest that this has simply made it easier to experimentally detect strong food-web interactions in aquatic ecosystems.

There might also be differences in the relative turnover rates between predators and prey in these different ecosystem types. In terrestrial ecosystems, the dynamics of producers (e.g. long lived grasses and trees) often occur on timescales much longer than the dynamics of their herbivores (e.g. insects and mammalian herbivores), whereas in aquatic ecosystems the dynamics of producers (e.g. algae) often occur at timescales shorter than their consumers (e.g. invertebrate grazers)<sup>6,11,12</sup>. This could perhaps explain why terrestrial ecosystems typically exhibit trophic pyramids (i.e. the standing biomass of plants is higher than that of herbivores), whereas sometimes this pyramid is inverted in aquatic ecosystems (i.e. more standing biomass of herbivores than plants)<sup>12</sup>.

*Other hypotheses concerning aquatic-terrestrial differences*  
Some other hypotheses have been put forward, but they have received much less attention and have little direct support, these include:

- Aquatic ecosystems are buffered more against variability and physical harshness than are terrestrial ecosystems; thus, food-web interactions should be stronger in aquatic ecosystems<sup>6,12</sup>.
- Aquatic ecosystems are more homogenous with distinct boundaries, but terrestrial ecosystems are heterogeneous with more fuzzy boundaries<sup>6,12</sup>.
- Algae in aquatic ecosystems are small and typically are wholly consumed by herbivores, whereas plants in terrestrial ecosystems can be larger and can achieve size-escapes from herbivores<sup>12,38</sup>.

**Some additional avenues for aquatic-terrestrial comparisons**

Several features of food webs are just beginning to be appreciated, but have not yet been directly contrasted between aquatic and terrestrial ecosystems. However, their recently stated importance, and their potential for divergence in media as different as air and water, makes them worth consideration.

*Nutrient recycling, ecosystem function and stoichiometry*

Recent studies in both aquatic<sup>42</sup> and terrestrial<sup>43</sup> ecosystems have emphasized the importance of nutrient recycling and ecosystem function to the dynamics and interactions among species within food webs. Nutrient recycling occurs through the incomplete assimilation of prey by predators, the excretion of waste products following protein metabolism and the decomposition of dead organisms. Although fundamental differences between ecosystem types are currently unknown, they are likely to be present and important. For example, waste products released in water probably diffuse more rapidly and might be much less patchy

than waste products released on land<sup>12</sup>. Furthermore, microbial processes that influence decomposition rates are likely to be water limited and should occur at more constant rates in water than on land. Such variability in the timing and spatial configuration of nutrient regeneration could have important effects on the structure and function of these different ecosystem types<sup>12</sup>.

Nutrient stoichiometry refers to the incorporation of a mass balance (i.e. neither a gain nor loss) of elemental nutrients [e.g. Carbon (C), Nitrogen (N) and Phosphorous (P)] into the dynamics of food webs, and has recently been recognized as an essential feature of understanding food-web processes<sup>44</sup>. Primary productivity in both freshwater and marine pelagic ecosystems is often thought to be P-limited, whereas primary productivity in terrestrial ecosystems is often thought to be N-limited<sup>44</sup>. In addition, aquatic studies typically consider C:N:P ratios, whereas terrestrial studies have typically focused on C:N ratios, thus ignoring their ratios with P, which seems to play an important role in growth rates and other physiological processes<sup>44</sup>. A stoichiometric perspective is likely to allow important comparisons among variable ecosystem types.

#### *The role of behavior and life history*

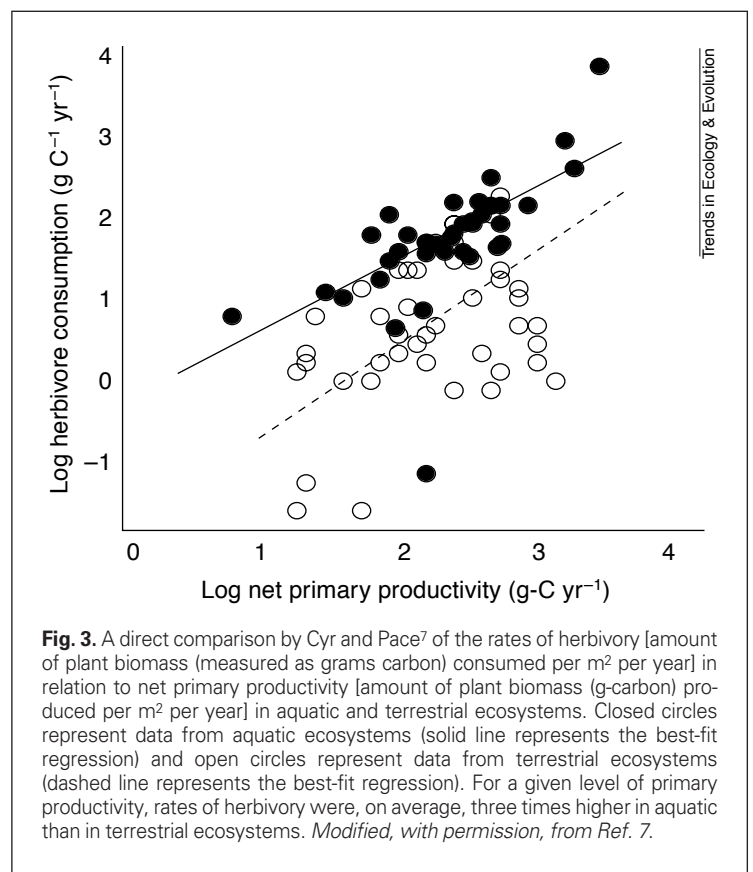
Prey species in both aquatic and terrestrial ecosystems can have plastic responses, in behavior (e.g. reduced activity) and/or in life history (e.g. morphological defense), to the presence of predators, which can then influence dynamics at the population and community levels<sup>45,46</sup>. Comparisons of these plastic responses in different ecosystem types have not been made directly, but several questions deserve attention. The use and reliability of chemical, visual and auditory cues might be fundamentally different in terrestrial and aquatic ecosystems, owing to the differences in the viscosity of air and water. Furthermore, differences in the reliability of these cues might lead to different sorts of plastic responses to predators among ecosystem types. For example, changes in prey behavior in response to predation risk represent reversible plastic responses, whereas changes in life history represent irreversible plastic responses. Variation in these plastic responses could have significant effects on the overall structure of the food web.

#### *Prey defense versus prey tolerance*

Prey tolerance (regrowth following consumption) to predators might structure the food web in a fundamentally different way than prey resistance (chemical or structural defenses) to predators<sup>47</sup>. Typically, terrestrial plants are partially consumed by herbivores and might have more opportunities to tolerate herbivory than aquatic algae that are wholly consumed. Thus, the relative roles of plant tolerance and resistance in food webs might be quite different between these ecosystem types.

#### **Comparisons at finer scales**

There are many finer scaled differences among ecosystem types than whether they occur in water or on land. Common segregations of terrestrial habitats include deserts, grasslands and forests. Similarly, common segregations of aquatic habitats include flowing streams, lakes and oceans. Just as there might be differences between aquatic and terrestrial ecosystems, there might also be differences within these types of habitat. For instance, the flowing water in streams and marine intertidal zones provides a different set of constraints to that of the more static water in lakes and open oceans.



**Fig. 3.** A direct comparison by Cyr and Pace<sup>7</sup> of the rates of herbivory [amount of plant biomass (measured as grams carbon) consumed per m<sup>2</sup> per year] in relation to net primary productivity [amount of plant biomass (g-carbon) produced per m<sup>2</sup> per year] in aquatic and terrestrial ecosystems. Closed circles represent data from aquatic ecosystems (solid line represents the best-fit regression) and open circles represent data from terrestrial ecosystems (dashed line represents the best-fit regression). For a given level of primary productivity, rates of herbivory were, on average, three times higher in aquatic than in terrestrial ecosystems. Modified, with permission, from Ref. 7.

To illustrate this point, consider the case of food-web interactions in freshwater lakes and streams. As discussed previously, a review of lake studies suggests that trophic cascades occur, but they are tempered by the compensatory responses of defended prey species<sup>10</sup>. However, in a well studied stream, disturbances imposed by periodic flooding eliminate the more defended species, thus enabling strong food-web interactions and trophic cascades<sup>48</sup>. An analogous distinction occurs between temperate grasslands and Arctic tundra. In temperate grasslands, there appears to be a similar role for defenses and compensation among plant species<sup>40</sup> to that observed in lakes. However, results from Arctic tundra<sup>24</sup> are more in accord with those from streams, where food webs seem to be simpler and interactions are much stronger. This suggests that food-web interactions in terrestrial grasslands might be more similar to aquatic lakes, whereas food-web interactions in aquatic streams might be more similar to terrestrial tundra.

Hypotheses attempting to explain variation in food-web structure among different ecosystems therefore need to consider a variety of factors – not only that some food webs are in water and others are on land. For example, the relative stability of grasslands and lakes might allow species to maintain tradeoffs among competitive efficiency versus defense against predators (i.e. keystone predation), and thus explain why these ecosystems have defended species in complex food webs. Alternatively, the stress (i.e. harsh winters) or disturbance (i.e. flooding) of tundra and streams might constrain the ability of species to exploit traits associated with defense, and thus explain why these ecosystems have less defended species in simpler food chains.

#### **Prospects**

Several ideas have been proposed to explain possible similarities and differences in the dynamics of food webs among different types of ecosystems. However, little

evidence is available to fully evaluate any of the observations or hypotheses. Here, I have highlighted a series of unanswered questions that I hope point the way to new syntheses. Currently, there are few empirical data available to make direct comparisons among ecosystem types (but see Refs 7,49). If ecologists who work in different ecosystem types begin to ask more synthetic questions, and collect their data and perform their experiments in ways that are analogous, we can begin to compare these ecosystems in a more comprehensive way than has previously been possible.

Unfortunately, ecologists who specialize in certain types of ecosystem tend to favor particular hypotheses and observations, and discount hypotheses and observations noted in other ecosystems. By embracing the observed variability within and among ecosystem types, we can begin to achieve the generalities and syntheses for which community ecologists often strive.

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