Cross-ecosystem differences in stability and the principle of energy flux

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Abstract
Here, we review consumer-resource (C-R) theory to show that the paradox of enrichment is a special case of a more general theoretical result. That is, we show that increased energy flux, relative to the consumer loss rate, makes C-R interactions top heavy (i.e., greater C : R biomass ratio) and less stable. We then review the literature on the attributes of aquatic and terrestrial ecosystems to argue that empirical estimates of parameters governing energy flux find that aquatic ecosystems have higher rates of relative energy flux than terrestrial ecosystems. Consistent with theory, we then review empirical work that shows aquatic ecosystems have greater herbivore : plant biomass ratios while we produce novel data to show that aquatic ecosystems have greater variability in population dynamics than their terrestrial counterparts. We end by arguing that theory, allometric relationships and a significant, negative correlation between body size and population variability suggest that these results may be driven by the smaller average body sizes of aquatic organisms relative to terrestrial organisms.

Keywords
Aquatic, body size, consumer-resource theory, ecosystem, principle of energy flux, stability, terrestrial.

INTRODUCTION
Cross-ecosystem comparative studies have played a major role in uncovering the underlying patterns and processes that structure ecosystems (Elton 1927; Odum 1971; Hairston & Hairston 1993; Chase 2000; Shurin et al. 2006). In particular, research has demonstrated differences in the attributes of aquatic and terrestrial ecosystems. Compared with terrestrial ecosystems, aquatic ecosystems possess primary producers with higher growth rates, higher body size ratios of herbivores to primary producers and greater herbivory (Cyr & Pace 1993; Hairston & Hairston 1993; Cebrian 1999). Interestingly, many of these ecosystem attributes govern energy flow into and through a food web. Therefore, it is not surprising that these differences in attributes likely have profound consequences for processes occurring within ecosystems. Comparative experimental studies, for example, have shown that in general aquatic ecosystems show more evidence of trophic cascades (Shurin et al. 2002; Borer et al. 2005), and greater flux of carbon into living pathways compared with detrital pathways (Cebrian 1999, 2004; Cebrian & Lartigue 2004).

Stability has long been studied as a fundamental ecosystem process (May 1976, Pimm 1984; McCann 2000; Loreau et al. 2002). Stability can be defined in many ways. For example, the coefficient of variation (CV), a common empirical metric, is used to quantify stability by arguing that more variable systems are less stable. Greater variance in population dynamics, all else equal, means populations tend to spend more time at dangerously low densities, where environmental stochasticity can perturb these populations to local extinction. The stability of aggregate population and community dynamics may be a useful surrogate measure of stable ecosystem functioning since a dynamically stable system ought to deliver reliable ecosystem services (Naeem & Li 1997; Naeem 1998; Armsworth & Roughgarden 2003).

Given its importance, it is surprising that empirical understanding of stability has remained elusive. Microcosm studies have started to attack this problem (McGrady-Steed et al. 1997; Naeem & Li 1997) and field studies of multi-trophic community stability exist but are far less common (Shurin et al. 2007). Despite a lot of cross-ecosystem comparisons researchers have yet to assess how stability changes across whole ecosystem types. Theoretical research using allometry and energetics suggests that stability may indeed vary across ecosystems (Shurin & Seabloom 2005). Some support for these predictions has come from studies where predator removals caused a greater reduction in plant and herbivore stability in benthic and pelagic lake systems compared with marine and terrestrial systems (Halpern et al. 2005). Despite these results, remarkably no direct comparison of the stability differences between ecosystem types exists.

In what follows, we first rephrase consumer-resource (C-R) theory in terms of the structural and dynamical implications of energy flux. To this end, we briefly review C-R theory to show that the well-known paradox of enrichment is really a subset of a more general, less understood, result of C-R theory we refer to as the principle of energy flux. The principle of energy flux states that any biological trait that increases the energy flux to the consumer, relative to its loss term (hereafter relative energy flux), tends to make the C-R biomass ratio top heavy (i.e. increases consumer : resource biomass ratio) and less stable (e.g., population dynamics more variable). We then examine allometric relationships and existing data on key biological parameters to argue that aquatic ecosystems tend to have higher relative energy flux from plant to herbivore. Thus, we predict that aquatic ecosystems should have a higher herbivore : plant ratio and more variable population dynamics than terrestrial ecosystems. Finally, we perform two quantitative tests of this prediction: (1) We reanalyse previously published data (Cebrian et al. 2009) and show that aquatic ecosystems indeed have more inverted biomass pyramids, a characteristic of higher energy flow and (2) Using a large data set of herbivore time series obtained from the Global Population Dynamics Database (NERC Centre for Population Biology 1999), we show that aquatic
ecosystems are less stable (i.e., more variable) than terrestrial ecosystems, and that these stability differences arise largely from the smaller size of organisms in aquatic ecosystems.

**C-R THEORY: THE PRINCIPLE OF ENERGY FLUX**

To understand the dynamics of complex systems, ecologists frequently simplify food webs by grouping species into trophic levels or fundamental modules comprised of key species interactions (Holt 1997; Milo et al. 2002; Melian et al. 2005; Stouffer et al. 2007). The simple two-species module, the C-R interaction, forms the basis of much ecological theory (Murdoch et al. 2003) and is one of the fundamental building blocks behind whole ecosystems. From this theory predictions can be generated concerning the stability of ecosystems are less stable (i.e., more variable) than terrestrial ecosystems, and that these stability differences arise largely from the smaller size of organisms in aquatic ecosystems.

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While the results from C-R theory are well known, here we rephrase them in a manner that facilitates cross-ecosystem comparison. Specifically, we seek to understand a general statement of how all key biological parameters of the C-R interaction influence the structure and stability of ecosystems. Perhaps one of the most famous results from C-R theory is the paradox of enrichment (Rosenzweig 1971), whereby increases in carrying capacity of the resource, inspire wildly unstable oscillations in many C-R models.

While an interesting result, there is a far more general and powerful result that encapsulates the paradox of enrichment and yet is seldom, if ever discussed to our knowledge.

In what follows we will show that any increase in flux between a consumer and a resource, relative to the consumer loss rate (relative energy flux), increases the consumer : resource biomass ratio and destabilises the interaction (i.e., increases population variability or makes the eigenvalue more positive). Here, we argue that this is a very general property of C-R models and so we will refer to this as the principle of energy flux. Importantly, this principle contains the paradox of enrichment and suggests that this famous result may not be much of a paradox, but rather a consistent response to over-fuelling consumer growth.

To show this more general result, let us examine a C-R model that does not oscillate (the Lotka–Volterra model):

\[
\frac{dR}{dt} = rR \left(1 - \frac{R}{k}\right) - aCR
\]

\[
\frac{dC}{dt} = eCR - mC
\]

as well as the Rosenzweig–MacArthur model which is well known to produce deterministic oscillations:

\[
\frac{dR}{dt} = rR \left(1 - \frac{R}{k}\right) - \frac{a_{\text{Max}}CR}{R + R_c}
\]

\[
\frac{dC}{dt} = e \frac{a_{\text{Max}}CR}{R + R_c} - mC
\]

here, \( r \) is the growth rate of the resource population \((R)\), \( k \) the carrying capacity of the resource, \( a \) the maximum consumption rate of the consumer population \((C)\) on the resource in the L–V model, \( a_{\text{Max}} \) is the maximum consumption rate in the R–M model, \( e \) the conversion efficiency of consumed biomass into new consumers, \( R_c \) is the half-saturation rate in the R–M model and \( m \) is the mortality rate or loss rate of the consumers. We choose both the L–V model and R–M model to emphasise that the result holds for models with stable equilibrium in a variable world as well as those models that readily produce cycles in a deterministic world. For clarity, let us assume that we are following biomass density in the above two models which means all per capita parameters (i.e., \( r, a, a_{\text{Max}} \) and \( m \) are in units biomass area\(^{-1}\) per time unit) while parameters (\( k \) and \( R_c \)) are in units (biomass area\(^{-1}\)) and \( e \) is dimensionless. See Yodzis & Innes (1992) for an explicit example of employing biomass in a Rosenzweig–MacArthur C-R model using allometric reasoning.

The Lotka–Volterra model yields a resource isocline \((C = r(1 - R/k)/a)\) and consumer isocline \((R = m/(ea))\) that generate the familiar phase space diagrams depicted in Fig. 1a–d. Similarly, the Rosenzweig–MacArthur model yields a resource isocline \((C = r(1 - R/k)/(R + R_c)/a)\) and a consumer isocline \((R = mR/(ea - m))\)

![Lotka-Volterra](image)

![Rosenzweig-MacArthur](image)

Figure 1 Depicts influence of changing biological parameters on the isoclines of the Lotka–Volterra model (a–d) and Rosenzweig-MacArthur (a’–d’) model. Increasing flux to the consumer (e.g., increased \(a, e, K\)) relative to consumer mortality (a–d) shifts the consumer isocline relative to the resource isocline from right to left. This has strong implications for community structure (\(C^* : R^*\) increases) and stability as discussed in text. Equilibria are denoted on axes. Solid circles are stable equilibria. A similar series of figures depicts the Rosenzweig–MacArthur model (a’–d’). Note, however, that left-shifted isoclines produce unstable equilibria starting at the geometry depicted in (c’).
and the phase space diagrams are depicted in Fig. 1a–d. In Fig. 1a–d, we display a generic set of isocline arrangements that occur when we increase the parameters $k$, $a$ or $e$. As we increase any of these parameters we tend to move the position of the consumer isocline relative to the resource isocline such that the consumer isocline shifts from right to left (Fig. 1a–d). Note that carrying capacity, $k$, produces this sequence of isoclines by moving the resource isocline alone, varying consumer efficiency, $e$, does this by moving just the consumer isocline (resource isocline remains constant) and varying maximum consumption rate, $a$, moves both isoclines but the changing consumer isocline dominates and drives the sequence in Fig. 1a–d. Increases in any of these parameters therefore produce a series of isocline sketches that qualitatively match the sequence detailed in Fig. 1a–d. 

A similar sequence of changing isocline geometry occurs for the Rosenzweig–MacArthur model when we increase the related parameters $a_{\text{Max}}$, $e$ and $k$ (Fig. 1a’–d’). Biologically speaking, all the above cases (increasing maximum consumption rate, efficiency or carrying capacity) produce increases in energy flux to the consumer relative to the constant loss term, $m$. Note, reducing the half saturation, $R_o$, also increases maximum consumption rates and so, not surprisingly, produces the same sequence of geometrical changes (Fig. 1a’–d’).

There is one other way to change the relative energy flux to the consumer. If we decrease the loss parameter, $m$, and hold the other parameters constant then we find that we drive the same changing arrangement of isoclines for both the Lotka–Volterra (Fig. 1a–d) and the Rosenzweig–MacArthur (Fig. 1a’–d’). That is, decreasing $m$ shifts the consumer isocline from right to left again in both cases. The absolute flux to the consumer has clearly not changed; however, the flux to the consumer relative to the loss term ($m$) has increased. Thus, we can combine the above results generally and say that increases in the energy flux to the consumer, relative to the loss rate, tend to move the relative position of the isoclines (Fig. 1). This pattern holds for a broad set of C-R models. Now, given that the changing biology produces a consistent change in isocline geometry, it remains to ask what this means for the structure and dynamics of the C-R interaction.

Figure 2 shows the biologically interesting responses of the C-R model to changing the relative isocline position identified above. In both model cases, we change the relative isocline position by modifying the mortality parameter, $m$. We did this, because changing $m$ does not influence the resource isocline and thus the consumer isocline effectively monitors the relative position of the isoclines. Nonetheless, we could have also used any of the other parameters and

![Figure 2](image-url)

**Figure 2** Shifting the consumer isocline (dotted line) from right to left increases energy flow, increases C : R (a), increases maximum eigenvalue (b) and increases consumer CV after a perturbation from equilibrium (c) for the Lotka–Volterra model. Similarly, the result holds for the Rosenzweig–MacArthur model (a’–c’), where CV is measured on the attractor. Parameter values are: $r = 1.0$, $k = 1.0$, $a = 1.50$, $e = 0.50$ (L–V), $r = 1.0$, $a_{\text{Max}} = 1.50$, $k = 1.0$, $R_o = 0.40$, $e = 0.50$. In both cases, $m$ varies between 0.30 and 0.70 to generate the variation in isocline position.
produced qualitatively similar results to what are shown below. As we increase the relative flux of energy to the consumer, we also tend to simultaneously increase the amount of $C^*$ relative to $R^*$. This is evident from examination of the changing equilibria in Fig. 1a–d (L–V) and Fig. 1a′–d′ (R–M). Fig. 2a,b′, indeed, show for this specific example that the consumer : resource biomass ratio increases as the consumer isocline shifts to the left. Thus, as the relative energy flux increases we increase the $C : R$ biomass ratio.

We simultaneously find that there is a tendency for the C-R interaction to be destabilised as the consumer isocline shifts left (Fig. 2b,b′ and Fig. 2c,c′). Fig. 2b,b′ gives an example of this stability result in terms of the changing eigenvalue relationship for the L–V and R–M model, respectively. Recall that a more negative eigenvalue implies a more stable C-R interaction. Note, that for a very small region in consumer isocline value (at the extreme right of Fig. 2b,b′), stability increases as the isocline shifts left in both cases. After this brief stabilisation phase, all left shifts in the consumer isocline drive a decrease in stability. It turns out this stabilisation phase result occurs when the eigenvalue is real (i.e., no complex part). As soon as the model gives complex eigenvalues the stability decreases dramatically as the consumer isocline shifts left relative to the resource isocline. This destabilising region dominates ecological models thus suggesting that increased relative energy fluxes tend to destabilise interactions.

While eigenvalues are an interesting theoretical construct, it is easier to phrase stability results in terms of population variability for empirical analysis. Time series of population dynamics are common empirically and CV, as discussed, is easily measured from time series. As such, it is convenient to also look at CV theoretically. We will see that the results, in terms of the destabilising effects of increased energy flux, are the same as the eigenvalue results allowing us to test this theory by calculating CV from empirical time series. To do this, we perturbed $C$ and $R$ densities of the L–V model system every time unit, and calculated the CV, after a transient of 2000 time units. $CV$ was estimated as the standard deviation divided by the mean ($\sigma/\mu$) of the consumer time series following random uniform perturbations of a maximum of 5% away from $R$ and $C$ equilibrium values. For each change in parameter value, the CV was calculated as the average of 100 random perturbations. Fig. 2c shows the resulting average level of population variability for the stochastic L–V model system (1) as the consumer isocline shifts relative to the resource isocline. Moreover, increased relative energy flux (i.e., isocline shifts left) coincides with decreased stability or increased $CV$. This result is also produced in deterministic models, like the Rosenzweig-MacArthur, where increases in relative flux eventually push the C-R model to oscillations (Fig. 2c′). Here, too, the oscillations tend to grow with increases in carrying capacity ($h$), maximum consumption rate ($a$) or consumer efficiency ($\epsilon$).

There is one small difference in the stability response between the CV and the eigenvalue metrics of stability in Fig. 2. At high mortality rates, the CV curve continues to show a steady increase in stability (Fig. 2c,c′), while the eigenvalue curve start to show a decrease in stability when the eigenvalues are real, as noted above (Fig. 2b,b′). This different response occurs because the eigenvalue curve, when real, is in a sense measuring proximity to zero consumer densities (i.e. the transcritical bifurcation) and so is no longer a surrogate for CV. Note, however, that the CV metric, does not give us a clear idea of how close the consumer density is to zero for high $m$, just that it has modest variance relative to its equilibrium. Taken together, both metrics are informative – for very low flux rates $C$ tends to be dynamically stable but close to zero densities. Nonetheless, both results show that after a brief period, when $C$ is low, increases in flux consistently decrease stability.

Otto et al. (2007) noted that predator-prey biomass ratios eventually drove dynamic outcomes akin to the paradox of enrichment. They called this enrichment-driven instability (Otto et al. 2007). While true, it could be more generally seen as energy-flux driven instability as changing biomass ratios modify the relative energy flux between predators and prey, and so ultimately destabilise the web. Similarly, in an interesting contribution, Brose et al. (2006) pointed out that natural biomass ratios tended to produce positive diversity stability outcomes. Arguably, these constrained ratios seldom made it to high relative energy fluxes that readily produce instability. This positive relationship is especially likely if all interaction strengths tend to produce real eigenvalues (note the directional switch of the stabilisation result in Fig. 2b,b′).

Although not shown here, consumer interference produces results akin to the Lotka–Volterra model. The equilibrium remains stable but undergoes similar changes in $C : R$ ratio, eigenvalue and displays similar increases in variance under stochastic perturbations. The Type III functional response, which assumes reduced consumption rates at low resource densities, also produces the same qualitative results with one understandable exception. Increasing energy flux drives a stabilisation phase, a destabilisation phase as predicted, and then another stabilisation phase. Under the assumption of a Type III functional response, at low $R$ densities consumers have trouble feeding or finding resources and so the resource is little influenced by consumers at low resource density – the added biology of the Type III implies that the energy flux is weakened at low $R$ densities. This means the system should be made more stable in this region and this is what we find: sustained oscillations are lost and the dynamics strongly attract locally. The results resonate with the results above. It does mean, however, that in systems where refugia is high, heavy consumer : resource ratios can be stable. This result also can also occur for a consumer inflated in density by a consistent subsidy (Huxel & McCann 1998).

In contrast to the previous parameters, growth rate ($r$) shifts the resource isocline vertically up and down along the consumer isocline axis. Increasing $r$ does not influence stability as dramatically as all other parameters discussed above, but still increases stability up to a point until further increases decrease stability. The continuous, always locally stable, model employed here, however, hides some of the destabilising potential of increases in $r$. Increasing growth rate tends to destabilise systems as soon as there is any sort of oscillation (e.g. stable-limit cycles) or when the system is discrete (May 1976; Murdoch et al. 2003; Pachepsky et al. 2008). In the case of discrete models, increases in $r$ interact with the inherent lags in these models to inspire instability. As evidence for oscillations are common (Kendall et al. 1998), and natural populations tend to have some form of biology that produces a lag it seems likely that increasing $r$, and increasing flux, has the same destabilising influence, on average, as the other parameters above. That is, increasing $r$ increases flux to the consumer and tends to decrease the stability of the interaction. The general destabilising effect of $r$ is supported by empirical data, which confirms that increasing growth rate destabilises populations of fish (Anderson et al. 2008) and mammals (Erh et al. 2001).

While we have concentrated on the C-R interaction to facilitate tests at the plant-herbivore level, other theory suggests that the above general results hold for more complex webs. de Bruyn et al. (2007), for
example, created an energetic framework for trophic control that effectively argued that increased vertical flux of energy (i.e., energy that goes straight up a focal food chain) tended to drive top-heavy webs which produced greater trophic cascades and greater instability. de Bruyn et al. (2007) pointed out that interactions that damp vertical energy flux (e.g., intraguild predation) make the biomass pyramid more Eltonian and tend to reduce the destabilising influence of strong energy flux up the food chain. Here, things like intraguild predation damp vertical energy flux from a food chain and, in effect, act like the increased loss rate of the C-R theory discussed above. In addition, Shurin & Seabloom (2005) employed allometric reasoning to show that food chain models predicted stronger trophic cascades in aquatic than terrestrial ecosystems. The reasoning of both Shurin & Seabloom (2005) and de Bruyn et al. (2007) are entirely consistent with the principle of energy flux. Although some have argued that terrestrial ecosystems are more speciose (Strong 1992), to our knowledge there is no evidence that aquatic and terrestrial food webs differ in any way that promotes more damping in either of the ecosystems and so here we assume that damping between systems can be ignored. Finally, levels of omnivory are similar in aquatic and terrestrial ecosystems (Thompson et al. 2007). This lends some support to the notion that food webs may not be structurally different in different ecosystems. Thus, all else equal, the simple rules of C-R theory ought to hold.

In summary, C-R theory makes two general predictions that come from the principle of energy flux:

1. Biological parameters that increase energy flux to the consumer relative to its loss rate tends to drive more top heavy, less Eltonian (or similarly, more inverted) pyramids, and;
2. Biological parameters that increase energy flux to the consumer relative to its loss rate tend to destabilise the population dynamics of the interacting species.

Below, we argue that aquatic ecosystems have parameters that drive a greater relative flux to the consumer compared with terrestrial ecosystems. As a result, C-R theory predicts that aquatic ecosystems should have more inverted biomass pyramids and greater variability in population dynamics. We end by gathering comparative ecosystem data to test these predictions.

### LINKING THEORY TO ECOSYSTEM TYPE THROUGH ORGANISMAL ATTRIBUTES

Aquatic and terrestrial ecosystems differ in a variety of key attributes. Many of these attributes relate to energy flow and can be grouped primarily into those governing energy flow into the base of the food web (i.e. primary production) and those governing energy flow between trophic levels (i.e. consumption rates or interaction strengths). Many of these attributes map to parameters used in C-R theory as discussed above. In this section, we look at our empirical understanding of these parameters in aquatic and terrestrial ecosystems and then we make clear predictions for how differences in ecosystem type should affect biomass pyramids and stability.

At the base of the food web attributes governing primary production may have important consequences for energy flow. In general, aquatic primary producers possess less structural material (Elser et al. 2000) and contain more photosynthetic tissue (Elser et al. 2000). These differences result in higher growth rates in aquatic primary producers (Cebrian 1999; Elser et al. 2000). Based on C-R theory, the higher growth rates ($r$) observed in aquatic ecosystems should result in more inverted biomass pyramids and decreased stability compared with terrestrial systems. Another attribute of primary production, carrying capacity ($k$), does not seem to vary across ecosystem type. For example, a number of studies have empirically shown that NPP does not appear to vary across ecosystem type (Cebrian 1999, 2004; Cebrian & Lartigue 2004). This suggests that the main differences between aquatic and terrestrial ecosystems resulting from energy flow into the base of the food web should come from the higher growth rates of primary producers in aquatic systems.

Many differences in consumption rates exist across ecosystem types. These differences arise from a number of attributes differing across ecosystems. In aquatic ecosystems, the body size ratios of herbivores to primary producers are larger (Hairston & Hairston 1993; Chase 2000) and primary producers are more nutritious to herbivores (Polis & Strong 1996; Cebrian 1999; Elser et al. 2000). This results in greater herbivory in aquatic ecosystems (Cyr & Pace 1993; Hairston & Hairston 1993; Cebrian 1999). The higher consumption rates in aquatic ecosystems should have a large impact on parameters used in C-R theory. Higher consumption rates may manifest in higher maximum consumption rates and higher conversion efficiencies (i.e. $a$ or $d_{\text{max}}$ and $e$). As seen above, an increase in either or both of these parameters would result in an increase in energy flow, more inverted biomass pyramids, and a decrease in stability. Therefore we predict that aquatic ecosystems should be less stable than terrestrial ecosystems.

In addition to the cross-ecosystem differences in energy flow, the parameters used in C-R equations show allometric relationships (Yodzis & Innes 1992). As aquatic ecosystems tend to be composed of smaller organisms than terrestrial ecosystems (Shurin et al. 2006), this suggests that understanding how allometric scaling influences a number of these parameters may allow us insight into energy flow and community stability. For parameters in the resource equation, maximum growth rates, $r_{\text{max}}$ scale to body mass, $M_e$ as $r_{\text{max}} \propto M^{-1/4}$ (Brown et al. 2004) and carrying capacity (biomass density) scales to body mass as $k \propto M^{1/4}$ (Enquist et al. 1998; Brown et al. 2004). As for the consumer equation, maximum consumption rates scale to body mass as $a \propto M^{1/4}$ (Peters 1983; Brown et al. 2004). Mortality rates also scale to body mass as $m \propto M^{-1/4}$ (Brown et al. 2004). Finally, in contrast to the other parameters, there is no theoretical or empirically documented allometric relationship for the half-saturation constant, $R_c$ or conversion efficiency, $e$ (Yodzis & Innes 1992). However, the amount of mass-specific structural material (e.g. skeletal material, woody tissue) does positively scale to body mass: scaling exponents vary between 0.4 and 0.12 suggesting that efficiency should scale across ecosystem types (Schmidt-Nielsen 1984). As conversion efficiency is dimensionless, these positive exponents become negative when we divide through by biomass to remove the dimensions (exponents become $-0.88$ to $-0.40$). Thus, as others have argued (Strong 1992, Polis et al. 2000), aquatic pathways ought to tend to have far less structural material and promote high conversion efficiencies.

The above empirical allometric relationships speak to the relative position of the isolines in terrestrial vs. aquatic ecosystems. First, the consumer isoline scales (recall: $m_w/(e_a)$ following for the L–V model and $m_{R_c}/(e_a-m)$ for the R–M model) and $m_w$ and $d_{\text{max}}$ cancel each other out and the remaining influence of the conversion efficiency, $e$, shifts the consumer isoline strongly to the left as body size decreases in both models. Similarly, we can consider the resource isoline in light of the allometric empirical relationships. Here, the increased $r$ ($1/4$)
with body size increases energy flux while the empirical argument for decreased $k$ (1/4) cancels out this production (although, recall that Cebrian (1999, 2004) found no evidence for different carrying capacities between terrestrial and aquatic ecosystems).

In summary, the relationships suggest that the isocline should shift left relative to the resource isocline with reduced body size. Moreover, these arguments resonate with previous arguments. Strong (1992) and Polis et al. (2000) argued cogently that aquatic systems were more homogenised reducing prey refugia, more edible and tended to experience higher turnover rates than terrestrial ecosystems. All these effectively argue for higher energy flux through aquatic pathways as our allometric reasoning also suggests. Thus, differences in the attributes of aquatic and terrestrial ecosystems relate to differences in energy flow within ecosystems. Comparing cross-ecosystem differences to parameters used in C-R theory, we predict aquatic ecosystems should have high growth rates of primary producers and higher numerical responses by consumers. All of these predictions taken together suggest that energy flow in aquatic ecosystems should be higher, biomass pyramids more inverted and stability decreased relative to terrestrial ecosystems.

CROSS-ECOSYSTEM PATTERNS IN STABILITY

Having established clear predictions for how aquatic and terrestrial ecosystems might differ in stability, we now show two tests of these predictions using previously published empirical data. First, we compared the biomass pyramids of aquatic and terrestrial ecosystems, an indicator of the energy flow within ecosystems. Second, we compared the stability of ecosystems using CV of the time series for herbivores.

Ratio of herbivore to primary producer biomass

Data on the ratio of herbivore to primary producer biomass was obtained from Cebrian et al. (2009). Ecosystems definitions were generally consistent with Cebrian et al. (2009) and included aquatic (pelagic systems, sediment flats, macroalgal beds, submerged grass and meadows) and terrestrial systems (grasses, tundra heathlands, shrublands and forest). We made one change isolating wetland systems, considered terrestrial in Cebrian et al. (2009), for comparison to our other analyses.

Analysis of the data showed that aquatic ecosystems had significantly larger $H : P$ than did terrestrial ecosystems (Fig. 3, $t$-test: df = 47, $t = 10.14$, $P < 0.001$). As there was insufficient data, wetlands were not included in this analysis, although wetland $H : P$ appears to be intermediate to aquatic and terrestrial ecosystems (Fig. 3). Consistent with our theoretical predictions, this result suggests that aquatic ecosystems are characterised by more inverted biomass pyramids, a signature of high energy flow in ecosystems.

Herbivore time series

We surveyed a number of time series from the global population dynamics database (GPDD, NERC Centre for Population Biology 1999) and selected ones according to the following criteria. Only those time series with high reliability (i.e. indexes of 4 or 5 of 5) and with at least 10 continuous data points were selected from the GPDD. In addition, given the lack of data within the GPDD for a variety of trophic levels, we limited our analysis to primary consumers (i.e. herbivores). Ecosystem type was determined based on the biotope associated with each time series in the GPDD. Terrestrial ecosystems included coniferous forest, montane mixed or unspecified forest, deciduous forest and grassland biotopes. Aquatic ecosystems included limnetic and marine biotopes. Finally wetland ecosystems included the wetland biotope. From each time series we calculated the CV. Where there were multiple time series for a single species, CV was averaged for that species. Finally, we obtained the average body size (mm) for each species from the literature. This resulted in data for three ecosystem types: aquatic ($n = 13$), terrestrial ($n = 63$) and wetland ($n = 11$).

Consistent with our theoretical predictions, aquatic ecosystems had significantly larger CVs than terrestrial or wetland ecosystems (Fig. 4, ANOVA: df = 2, 84, $F = 8.19$, $P < 0.001$). Herbivores in aquatic ecosystems were significantly smaller than those in wetlands and terrestrial ecosystems (Fig. 4, ANOVA: df = 2, 84, $F = 43.49$, $P < 0.001$). We performed an ANCOVA, testing for effects of body size, ecosystem type and the interaction between them. Only body size was significant in explaining variation in CV whereby CV increased as body size decreased [Fig. 5, ANCOVA: df = 1, 84, $F = 45.92$, $P < 0.001$, relationship: CV = 1.72 – 0.38 * log(body size)]. Strikingly then, this analysis suggests that influence of ecosystem type is removed when body-size is part of the analysis. This still suggests that aquatic ecosystems are less stable than wetland or terrestrial ecosystems, but that this difference in stability likely arises from the fact that aquatic ecosystems largely possess smaller herbivores.

Our analyses confirm our predictions concerning stability differences made from C-R theory. The biomass pyramids of aquatic systems are more inverted compared with terrestrial ecosystems. This suggests aquatic ecosystems have greater energy flow into the food web and through the food web. Also as predicted, aquatic ecosystems show more variable population dynamics than terrestrial ecosystems.

Interestingly, variation in stability between aquatic and terrestrial ecosystems was driven by a larger pattern of increasing stability with increasing organism body size. From our synthesis of allometry with
Wetland ecosystems provided an interesting avenue for exploration as they are made up of both a terrestrial and an aquatic component. Therefore, they share many features and organisms common to both ecosystems. Preliminary trends from our results, while not statistically significant, suggest that the stability of wetlands may also be intermediate to terrestrial and aquatic ecosystems. This suggests that the terrestrial component of wetlands may act to stabilise the aquatic component (Rip et al. 2010). This is similar to theory showing the importance of organisms capable of coupling across habitats and ecosystems (Rooney et al. 2006). The potential intermediate stability of wetland ecosystems may provide an interesting avenue for future research.

A major advantage to cross-ecosystem studies is that they can often elucidate the underlying patterns and processes that structure ecosystems (Elton 1927; Odum 1971; Hairston & Hairston 1993; Chase 2000; Shurin et al. 2006). Here we have shown that aquatic ecosystems are dominated by increased energy flow which reduces the stability of these ecosystems relative to terrestrial systems. This cross-ecosystem result can be generalised to understand how perturbations to ecosystems might impact their stability. Many of these perturbations appear to increase the energy flow within ecosystems (e.g. loss of top predators, eutrophication, see review in Rooney et al. 2006). Given our results, this suggests that these perturbations may also be decreasing the stability of ecosystems.

Finally, these results are consistent with some of the emerging results from food web theory. As noted, recent theory on food webs has employed body size to constrain the dynamics of complex model systems (Emmerson & Raffaelli 2004, Woodward et al. 2005). As C-R body-size ratios increase, the influence on energy flux tends to increase and destabilise whole webs (Otto et al. 2007). Intriguingly, early work has suggested that natural systems may be constrained to predator–prey (or consumer-resource) body-size arrangements that mediate the relative flux of energy between species and so also mediate food web stability (Brose et al. 2006; Weitz & Levin 2006).

CONCLUSIONS

Here, we review consumer–resource theory to show that the paradox of enrichment is a special case of a more general and unknown theoretical result – the principle of energy flux. The principle of energy flux finds that increased energy flux, relative to the consumer loss rate, makes C-R interactions top heavy (i.e., > C : R biomass ratio) and less stable. Consistent with this unexploited C-R result, we show that aquatic ecosystems on average have higher energy flux, greater herbivore : plant biomass ratios and are less stable than terrestrial ecosystems. This pattern appears to result from the smaller body sizes of aquatic organisms relative to terrestrial organisms. Historically, cross-ecosystem studies have played a vital role in developing our understanding of ecological communities. Here we add to this knowledge by showing that differences in the attributes of these ecosystems have fundamental consequences for their structure and stability.

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