



Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems

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Ecological coupling by material exchanges or dispersal between spatially distinct communities has important impacts on ecological processes, such as diversity–stability relationships, ecosystem function, and food web dynamics. One important mode of coupling between ecosystems occurs via organisms with complex life histories, which often switch between distinct ecosystems during their life cycle, and so can be channels of material exchanges between these ecosystems. Some organisms with complex life histories (e.g. frogs, dragonflies) can be abundant and effective predators during one or more life stages, and so provide conduits for strong direct and indirect interactions across ecosystem boundaries, linking the dynamics of discrete and often quite dissimilar community types. We present simple models and a case study (tailored to pond ecosystems), to explore how interactions within larval habitats can indirectly impact ecological interactions in adult habitats. Using our case study as a springboard, we propose that cohorts of predators emerging from natal habitats (e.g. ponds) cast ‘predation shadows’ on the surrounding adult (e.g. terrestrial) landscape. Trophic interactions within ponds, and the distribution of ponds on the landscape, can thus affect the spatial pattern in the strength of these predation shadows, creating strong spatial patterning in terrestrial trophic cascades. Our findings emphasize the importance of organisms with complex life histories as generators of strong links across ecosystem boundaries, and as potential sources of spatial variation in the strength and indirect impacts of interspecific interactions.

Ecologists have long recognized that ecological coupling by exchanges of materials or energy among spatially distinct communities can have important impacts on a variety of ecological processes, such as diversity–stability relationships, ecosystem function, and food web dynamics (Polis et al. 1997, 2004, Loreau et al. 2003, Loreau and Holt 2004, Holyoak et al. 2005, Schreiber and Rudolf 2008). Even Charles Elton noted that “no habitat component with its animal community is a closed system. . . they are constantly passed by population movement. . . every community unit is partly interlocked with others, not necessarily its nearest neighbors” (Elton 1966, chapter 19). Most studies on spatial coupling among ecosystems have to date largely focused on flows of energy or nutrients into the base of food webs, or supplementing the diets of consumers (Heatwole 1971, Hasler 1975, Polis and Hurd 1996, Polis et al. 1997, McClelland and Valiela 1998) (Fig. 1A). Well-documented examples include studies of the effects of allochthonous input of organic matter onto oceanic islands (Anderson and Wait 2001, Barrett et al. 2003), and of terrestrial arthropods on the community dynamics of headwater streams (Nakano et al. 1999). There has also been considerable attention given to the spatial coupling of consumers and resources via recurrent migration (Holdo et al. 2006), by movement of individual animals across multiple habitats within a home range (Holt 1996)

(Fig. 1B), and via dispersal of organisms between habitat patches (Hanski and Gilpin 1997, Holyoak et al. 2005) (Fig. 1C). Predators moving between habitat patches can have particularly strong impacts upon local community and ecosystem dynamics. Polis et al. (1997, 2004) touch on a number of examples of consumer movement generating strong impacts on community structure. But relative to analyses of resource subsidies, few attempts have been made to quantify the expected magnitude of the impacts of such consumer fluxes. One widespread scenario where such consumer fluxes are conspicuous and potentially important is for predators that have complex life histories, with different life history stages exploiting distinct habitats.

Consumers with complex life histories in effect create an obligate coupling between discrete ecosystems (Schreiber and Rudolf 2008). For instance, amphibians, dragonflies, and damselflies have complex life histories (henceforth, CLHs), are predators during one or more life stages, and switch habitats at metamorphosis. Consumers with ontogenetic habitat shifts such as these taxa can be conduits for direct and indirect interactions across ecosystem boundaries and provide both obligate, annually recurrent links between the species interaction webs of otherwise discrete, often highly dissimilar community types, and material exchanges between these spatially distinct ecosystems (e.g. water to land; Nakano et al. 1999, Sabo and Power 2002, Baxter

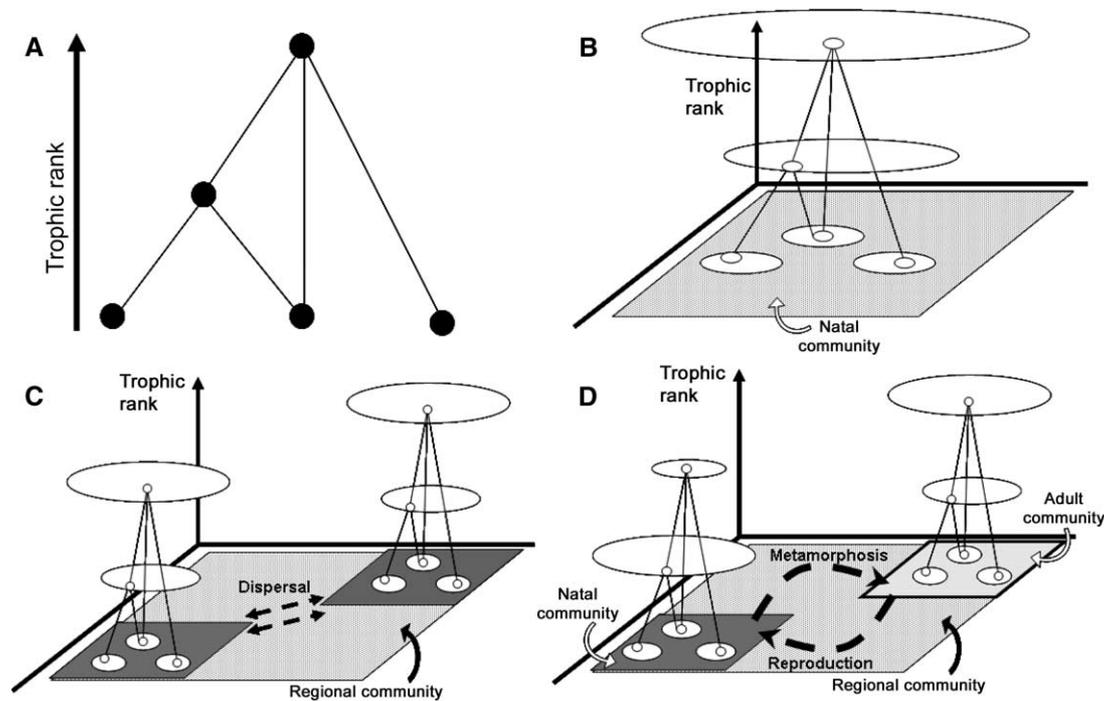


Figure 1. Schematic of food webs in space. (A) Classic food web showing links between trophic levels with the highest trophic level located at the top. (B) Classic food web placed in space (after Holt 1996), where top predators link multiple local communities via movements within their home range. (C) Exchanges of materials and organisms in a metacommunity, where organisms disperse between habitats. (D) Community linkages via organisms with complex life histories and ontogenetic habitat shifts, where the organisms as they move through their life cycle create obligate links (dashed arrows) between two very distinct communities (e.g. ponds and the surrounding terrestrial landscape for frogs).

et al. 2004; below- to above-ground, Strong 1999) (Fig. 1D).

Metamorphosing consumers, if sufficiently abundant, should lead to trophic cascades in the recipient interaction webs. Because metamorphosis from the larval to adult stage typically occurs in spatially circumscribed habitats (e.g. ponds and lake margins for dragonflies and frogs), from which individuals move away after they emerge, predator impacts should vary greatly across space. We refer to this phenomenon as a predation shadow, because populations of predators with complex life histories emerging from natal habitats in effect cast ‘shadows’ of consumption as they move across the recipient habitats where they spend their adult lives. Predation shadows could generate strong spatial patterning in the magnitude of trophic cascades. Such consumer linkages across ecosystems should be pronounced when organisms with ontogenetic habitat shifts are abundant. For example, dragonflies are often conspicuously common in both freshwater bodies (as juveniles) and nearby terrestrial habitats (as adults). A recent study found adult dragonflies both to be abundant near fish-free ponds (where larval dragonflies enjoyed low mortality rates), and to indirectly decrease terrestrial plant pollination rates. The reason was that predation by dragonflies sharply reduced the abundance of pollinating insects, relative to littoral zones near ponds with fish where dragonfly abundance was much lower due to fish predation upon larval dragonflies (Knight et al. 2005).

So, trophic cascades can transcend ecosystem boundaries. If consumers are resource-limited, the availability and

productivity of prey in one habitat, used by one life stage for the predator, can indirectly influence the intensity of predation in another habitat exploited by the predator at another life stage. Predators with CLHs can thus act as avenues of an indirect interaction – apparent competition – between prey species in physically separated habitats (Holt and Lawton 1994, Polis et al. 1997, Schreiber and Rudolf 2008).

Investigating the linkages between ecosystems created by predatory organisms with CLHs poses many challenges for both empiricists and theorists. Most empirical research on the ecological impact of such organisms has focused on single demographic stages or habitats. For example, we know much about the ecological interactions and dynamics of larval amphibians and odonates in temporary ponds (Wissinger 1988, Wilbur 1997), but considerably less about the factors controlling their fecundity and survival as adults, and their ecological interactions at that life stage. But the necessary coupling between larval and adult habitats (Fig. 1D) creates an avenue through which organisms residing in different ecosystems can interact indirectly, and at times strongly (Knight et al. 2005).

The objectives of this study were to: 1) develop a framework using models to explore how predators with ontogenetic habitat shifts might drive indirect species interactions across ecosystem boundaries, for two distinct habitats (one used by the juvenile stage of the predator, and the other used by adults); and 2) to develop a case study of ponds where we can calculate the potential magnitude of and spatial pattern in predation shadows, and associated

trophic cascades, generated by amphibian predators that switch habitats at metamorphosis. We use reasonable estimates of amphibian abundance, per capita consumption rates, and movement distances to model, first, the predation shadow for a single pond, and then the compound predation shadow for a realistic Florida landscape with multiple ponds. When ponds are closely juxtaposed the intervening strips of terrestrial habitat will receive influxes of emergent predators from multiple ponds, so the predation shadows cast by each pond overlap. Idiosyncrasies in pond placement should create a highly heterogeneous landscape of spatially varying predation pressure, with comparable patterning in the strength of trophic cascades. This modeling exercise leads to a plausible scenario for the spatial pattern of the predation pressure exerted by ponds on a terrestrial landscape, and provides a hypothesis for future experimental and observational field studies.

Predator shadows due to complex life histories: a model for apparent competition between prey in distinct adult and larval habitats

We suggest that ontogenetic habitat shifts by predators is a widespread mechanism leading to predator shadows in landscapes. We will use a simple model to illustrate some general points about landscape-scale indirect interactions in systems where habitats are coupled by predators with complex life cycles. Our approach complements that of Schreiber and Rudolf (2008), by considering qualitative properties of a model that includes a broad range of density-dependent processes that emerge from resource exploitation. Imagine that there are two discrete habitats (Fig. 1D). A predator is born in one habitat, matures, moves to the other habitat, and then reproduces, completing the life cycle (Fig. 2). We assume that there is a single resource (prey) population in each habitat. In the natal habitat, juveniles at

density J occur, supported by resources with an abundance of R . Juvenile mortality m is assumed to decrease, and the development or growth rate g to increase, with increasing R (g is the rate at which juveniles mature to adults). In the other habitat, there are adults at density A , feeding on a prey species at density R' . Adult fecundity f is assumed to increase and adult mortality m' to decrease, with increasing R' . We assume that the predator populations are food-limited, so they do not experience direct density dependence, but instead are regulated indirectly via their impact upon prey abundance, and that births, deaths, and maturation from juveniles to adults can all be represented by continuous-time formulations. We use F and F' respectively to describe juvenile and adult prey recruitment, and c and c' for per capita consumption rates by the juvenile and adult predator; all of these quantities in general should depend upon local prey abundance. The model for the predator and its juvenile and adult prey is then:

$$\begin{aligned} \frac{dR}{dt} &= F(R) - c(R)J \\ \frac{dR'}{dt} &= F'(R') - c'(R')A \\ \frac{dJ}{dt} &= f(R')A - m(R)J - g(R)J \\ \frac{dA}{dt} &= g(R)J - m'(R')A \end{aligned} \tag{1}$$

Note that space is not explicitly included in the above model, so that it could also apply to a system with juveniles and adults in the same habitat, as long as they have different prey and interact only through fecundity and growth. We can use the above general formulation to infer a necessary relationship between the abundance of prey in the two habitats. Assume the system settles to equilibrium. Setting

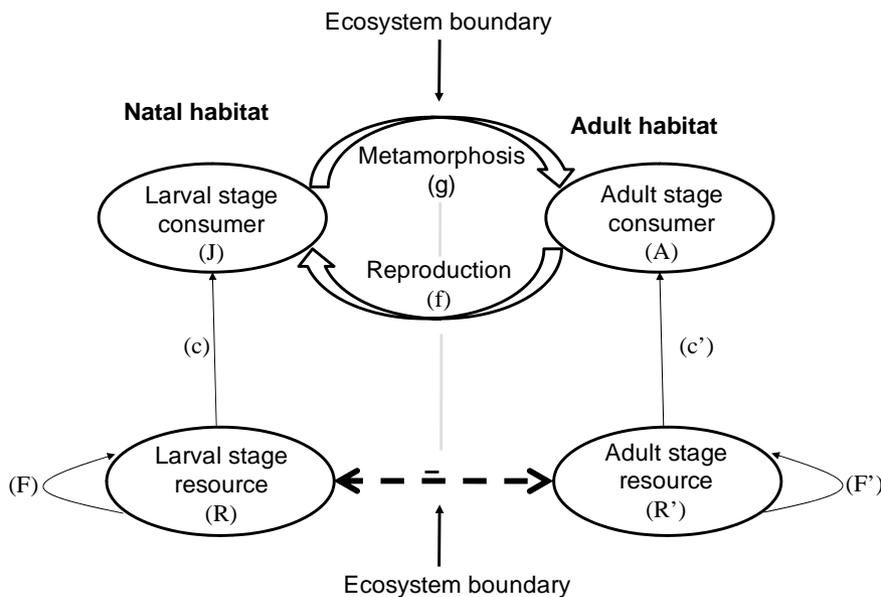


Figure 2. A model for apparent competition between prey in distinct adult and larval habitats. A predator is born into the natal habitat, then matures and moves to the adult habitat and reproduces, adding offspring back into the natal habitat. Letters in parenthesis correspond to the parameters in Eq. 1–3 and Appendix 1.

dA/dt to 0 gives $A = gJ/m'$; substituting this into the dJ/dt equation and then setting the resulting expression equal to zero leads to a necessary relationship between R and R' at equilibrium:

$$\frac{f(R'^*)}{m'(R'^*)} - \frac{m(R^*)}{g(R^*)} = 1 \quad (2)$$

where the asterisk denotes equilibrium. If an equilibrium with all species exists, at that equilibrium the ratio of the adult predator per capita fecundity rate to the adult mortality rate, minus the ratio of juvenile predator per capita mortality rate to the maturation rate, must equal unity.

We can interpret Eq. 2 as follows. The quantity $1/m'$ is the expected time an individual is an adult before it dies. The first term of the left side of Eq. 2 is thus the expected production of offspring, over the lifetime of an individual, given that it becomes an adult. The quantity $1/g$ is the expected time an individual stays a juvenile before maturation. The quantity m is a measure of the number of deaths expected in the juvenile class, per unit time. So, m/g is the expected number of deaths that will occur during the period of juvenile maturation. For the population to persist, each breeding adult must have an expected production of offspring over its lifetime that exceeds this expected loss during the juvenile maturation period by unity (so that each adult will replace itself).

Equation 2 implies a necessary relationship between equilibrium resource levels in the two habitats. Any change in a parameter of the system that leads to an increase in the equilibrium abundance of the resource in the adult habitat (R'^*) increases fecundity and lowers adult mortality. For equilibrium to be realized, this must be offset by an increase in mortality or decrease in growth rate in the juvenile stage, which in turn requires that R^* be lower. The same is true in the other direction; any change that increases juvenile resources at equilibrium, R^* , decreases juvenile mortality and increases the growth rate. So for the predator population to be at equilibrium there must be a corresponding reduction in adult fecundity, and/or increase in adult mortality, which in turn requires that R'^* be reduced. Thus, there is an emergent $(-, -)$ interaction between larval and adult resource abundances, evaluated at equilibrium (this result can be formally shown using the chain rule).

In a phase plane with axes of prey densities, Eq. 2 defines a predator zero-growth isocline, which has a negative slope. One of us (Holt 1977) used a somewhat simpler argument to show that apparent competition between alternative prey species encountered within a given habitat was expected for any food-limited predator that could settle to demographic equilibrium with its food resources. The argument just presented shows that the same is true when the resources are encountered sequentially during a life history. Assuming that resources must be consumed for adults to reproduce (i.e. $f(0)=0$), the isocline defined by Eq. 2 cannot intercept the R -axis, so in this case the adult resource cannot be driven extinct because of apparent competition – the depth of the shadow of predation cast by the juvenile habitat on the adult habitat is constrained by predator demography. However, the predator zero-growth isocline can in principle intercept

the R' -axis, if there is a maximal rate of mortality that juveniles can be expected to suffer, even in the absence of juvenile resources (e.g. because eggs are provisioned with resources). So the juvenile resource might be at risk of extinction due to apparent competition. If instead juveniles must consume some resources to survive and grow to the adult stage, then again the predator isocline cannot intersect the R' -axis, and so the juvenile resource cannot be driven to extinction by shared predation.

The above argument rests upon the assumption that the system can in fact reach and stay at an equilibrium. Furthermore, the conclusion about apparent competition between prey in distinct habitats because of predator shadows is qualitative, and it would be useful to develop a stronger quantitative sense of the magnitude of the effect. Towards the latter end, we consider a special case of model 1 (Eq. 1), and present some results regarding stability of the overall equilibria of model 1 in Appendix 1.

For our illustrative example, in each habitat we assume that each individual has a linear functional response to its resources, so each juvenile consumes its resource at rate cR , and each adult at rate $c'R'$. We further assume that juvenile mortality and adult fecundity both depend upon resource consumption, but with different functional dependencies. The more juveniles have to eat, the lower their mortality should be. A simple mathematical form that leads to this pattern is

$$m = \frac{q}{cR}$$

so that mortality declines hyperbolically with increasing consumption; if there are no juvenile resources, death is instantaneous. For adult fecundity, we simply assume that $f = ec'R'$ where e converts resources consumed into offspring born (i.e. the predator numerical response is proportional to its functional response). Finally, we assume that the rates of maturation from juvenile to adult and adult mortality are fixed. (Schreiber and Rudolf 2008 by comparison in their specific model put indirect density dependence via linear resource consumption rates into juvenile maturation and adult fecundity.)

To complete the model, we need to include expressions for resource dynamics in each habitat. This can be done in a variety of ways, but in the interest of simplicity, as an example we assume that in the juvenile habitat, resources are supplied allochthonously at rate I , wash out or decay at rate μ , and are also consumed. In the adult habitat, we assume that the resource is a living prey population that grows logistically, with intrinsic growth rate r' and carrying capacity K' . There are many systems where these might be reasonable assumptions. For example, juvenile frogs can live in ponds that receive allochthonous inputs from a stream, whereas adult frogs can feed on terrestrial insects that are self-recruiting. With these assumptions, Eq. 1 become:

$$\frac{dR}{dt} = I - \mu R - cRJ,$$

$$\frac{dR'}{dt} = r'R' \left(1 - \frac{R'}{K'} \right) - c'R'A$$

$$\frac{dJ}{dt} = ec'R'A - \frac{qJ}{cR} - gJ \quad (3)$$

$$\frac{dA}{dt} = gJ - m'A$$

For resources to be at equilibrium in each habitat, we must have

$$R^* = \frac{I}{\mu + cJ} \text{ and } R'^* = K' \left(1 - \frac{c'}{r'} A \right)$$

Substituting leads to an expression for juvenile mortality that increases linearly with juvenile density, and an expression for adult fecundity that declines linearly with adult density. Substituting in turn into the basic demographic equations for the predator, we end up with explicit closed-form solutions for equilibrium juvenile and adult predator densities:

$$J^* = \Phi/\Psi \text{ and } A^* = \frac{g}{m'} J^*,$$

where

$$\Phi = \frac{g}{m'} ec'K' - \frac{q\mu}{cI} - g \text{ and } \Psi = \frac{g}{m'} ec'K' \frac{c'}{r'} \frac{g}{m'} + \frac{q}{I}$$

All these equilibrium values are positive if and only if $gec'K'/m' > q\mu/cI + g$. For the predator, i.e. J and A , to increase when rare, the equilibrium with $J^* = A^* = 0$ (for which $R^* = I/\mu$ and $R'^* = K'$) must be unstable. At this equilibrium, the Jacobian is

$$\begin{bmatrix} -\mu & 0 & -cI/\mu & 0 \\ 0 & -r' & 0 & -c'K' \\ 0 & 0 & -(q\mu/cI + g) & ec'K' \\ 0 & 0 & g & -m' \end{bmatrix}$$

Because there are four 0s in the lower left quadrant, the eigenvalues are those of the upper left and lower right 2×2 submatrices. The former are $-\mu'$ and $-r'$, so the latter eigenvalues determine the stability. The system is unstable if the determinant of the lower right submatrix is negative, which is true if $(q\mu/cI + g)m' < gec'K'$. This is equivalent to the condition above for all equilibrium values, including predator densities in each habitat, to be positive. So there are no alternative equilibria, with and without the predator, for this particular realization of model 1 (also, there is only one equilibrium with the predator present, in contrast to the results in Schreiber and Rudolf 2008; Appendix 1).

With this specific version of model 1, the predator zero-growth isocline is a hyperbola with negative slope [$R'^* = m'(1 + q/gcR^*)/ec'$; Fig. 3A], as expected from our analysis above of the form of the general isocline equation given by Eq. 2. Hence, there can be apparent competition between the different prey sustaining the predator in the different habitats, and ambient resource levels in one habitat will indirectly depend upon the resource supply rate (among other factors) in the other habitat. Fig. 3B provides a numerical example for this specific model showing how equilibrium abundance of the living prey population found in the adult habitat is depressed by the supply of the allochthonous resources sustaining juveniles in their habitat. For a small rate of allochthonous input, few predators are

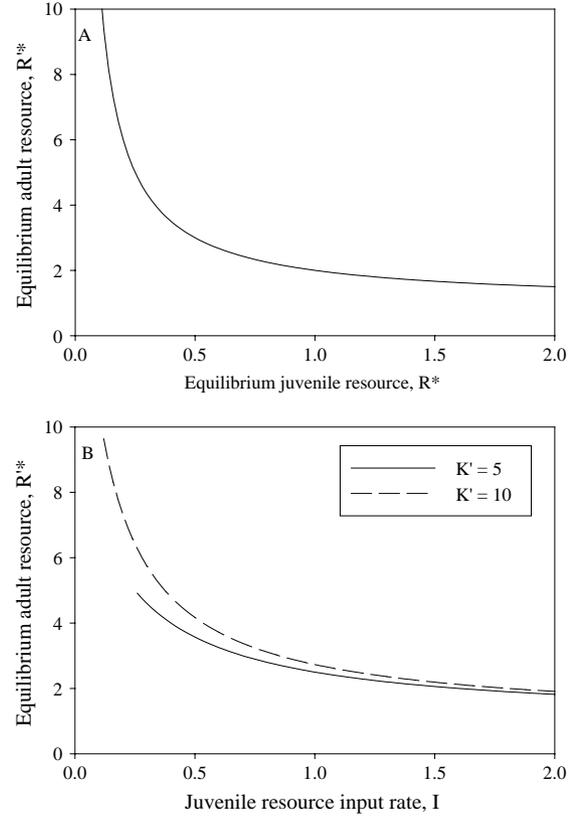


Figure 3. Examples of apparent competition between two prey populations, one in a juvenile habitat, the other in an adult habitat. (A) Isocline showing the necessary relationship between prey abundances in natal and adult habitats at equilibrium (predator zero-growth isocline) using the model in Eq. 3. All relevant parameters set to unity (the plot does not depend on parameters only in the resource equations). (B) As described in detail in the text, we assume allochthonous recruitment at rate I for the juvenile habitat, and logistic growth for the prey attacked in the adult habitat. Increasing resource input rate to the juvenile habitat depresses prey abundance in the adult habitat. For a small rate of input, few predators are sustained (due to high juvenile mortality), and so the prey in the adult habitat experiences little predation and will be near carrying capacity. Conversely, when the allochthonous resource has a high input rate, a large predator population is sustained, which as adults suppress resources in the adult habitat to low numbers. This apparent competition will not lead to extinction. The model parameters are all set to unity, except for prey carrying capacity and juvenile resource input rate (noted in the figure). The curves in B are plotted for parameters for which the predator persists; at lower values of I , and K , the predator itself goes extinct.

sustained (due to high juvenile mortality), and so the prey population in the adult habitat experiences little predation and will be near its carrying capacity. Conversely, when the resource in the juvenile habitat has a high input rate, a large predator population is sustained, which as adults then suppress resources in the adult habitat to low numbers. This provides a concrete example of the qualitative result presented above, that apparent competition between prey in distinct habitats emerges via the predator's complex life history (see Schreiber and Rudolf 2008 for another example using a model with quite different assumptions). The strength of the predation shadow observed in the adult

habitat thus depends upon the magnitude of resource supply rates in the larval habitat. Although the system is sometimes unstable (Appendix 1), for the parameter sets in Fig. 3B, the equilibria are stable, as they were for most parameter sets we tried.

This simple model can be modified in a variety of ways, but to explore these elaborations in any detail would go beyond the main purpose of this paper. Broadly similar results regarding the negative indirect interaction between the equilibrium abundances of alternate prey used at different life history stages can arise in systems with quite different assumptions about the predator life history, such as discrete-time dynamics or fixed maturation periods (Holt unpubl.). Saturating functional and numerical responses by the consumer to its resource in one habitat will of course constrain the indirect impact of that resource on the resource population consumed in the other habitat, as will direct density dependence in the predator (e.g. due to cannibalism or interference behavior), which would weaken apparent competition, and might even lead to indirect positive interactions among alternative prey (Holt 1977). We caution that unstable dynamics can arise, even without these complications (Appendix 1), and including saturating functional responses only makes such dynamical instability more likely. It is well-known that the response of systems at equilibrium to parameter changes can be a poor indicator of how average properties of the same system change in response to shifts in parameter values (Abrams 1992, 1999, Abrams et al. 1998), and so our conclusions about indirect interactions due to shared predation between resources in distinct habitats may need to be substantially modified when dynamics are strongly unstable. (See Appendix 1 for a discussion of stability in the above model.)

An empirically grounded scenario for predation shadows

To develop a plausible, empirically-grounded scenario for ecosystem linkages via predators with CLHs, we characterized the likely pattern of predation shadows at the water-to-land interface using a heuristic model based on published data from pond ecosystems in the southeastern United States. Pond ecosystems are an ideal system for exploring predation shadows because they are replete with species that have CLHs, and many are important consumers during one or more life stages (e.g. frogs and dragonflies). Moreover, the larval ecology of these organisms has been well-studied (Wissinger 1988, Wilbur 1997), and broadly corresponds to the dynamics modeled above. Specifically, we explore how changes that decrease juvenile mortality (m) and increase juvenile growth rate (g) (e.g. as a result of increases in juvenile resources, R , or decreases in mortality factors), should affect the magnitude of the predation shadow cast by predators emerging from natal habitat onto adult habitat. For example, we know that larval habitat quality can influence both the number and condition of animals that successfully metamorphose, and so abundant larval resources should lead to strong predation shadows and trophic cascades on the terrestrial ecosystem.

As a concrete illustration of the potential magnitude of predation shadows, consider published estimates of

amphibian density from a recent mark-capture-recapture study of a temporary pond in South Carolina (Gibbons et al. 2006). Gibbons et al. (2006) surrounded a large (about 10 ha) seasonal wetland (Ellenton Bay) at the Savannah River Site (SRS) with a drift fence, and over a single year (2003–2004) documented the cumulative emergence of over 360 000 frogs, representing 24 species and encompassing more than 1450 kg of biomass. We use these data, along with allometric relationships and plausible assumptions about individual movements, post-metamorphosis, to estimate the predation shadow and associated trophic cascades expected for this ecosystem. We then scale up the shadow effect by estimating the magnitude of predator shadows in a complex of ponds in a spatially realistic landscape, to examine how the predation shadows cast by these ponds overlap, generating a complex spatial pattern in the likely strength of trophic cascades. Finally, we simulate the impacts of adding a mortality agent to the natal habitats to explore how food web interactions and mortality in the natal habitat might affect both the magnitude and spatial variation of these predation shadows and trophic cascades.

Estimating consumption of arthropods by emerging predators

To estimate rates of consumption of terrestrial arthropods by these metamorphosing amphibians, we use known allometric relationships relating prey consumption to predator biomass. Each predator of species i is assumed to consume prey at a rate determined by its body size P_i (in kg). We estimate attack rate by an individual of consumer species i (a_i), expressed in terms of kg prey biomass ingested per day, using an ingestion rate–body size scaling relationship for poikilotherms (Peters 1983):

$$a_i = 0.0096 P_i^{0.82} \quad (4)$$

We estimated individual predator biomass, P_i , for those species reported in Gibbons et al. (2006) by using known length-to-weight scaling equations for amphibians (Pough 1980). Few spatially explicit data are available for post-metamorphic densities of amphibians as a function of distance from their natal habitats; therefore, we assume that the density of predators declines exponentially from the pond's edge, so that $A_{i,d} = A_{i,0}e^{-d/\beta}$ where $A_{i,d}$ is the density of species i at distance d from the pond's edge and β is a scale parameter (200 m). From Gibbons et al. (2006), we have total numbers A_i , from which we can determine $A_{i,0}$ by integrating $A_{i,d}$ over the entire area surrounding the pond:

$$A_i = \int_r^\infty 2\pi\rho A_{i,d} dp = \int_r^\infty 2\pi\rho A_{i,0} e^{-(p-r)/\beta} dp = 2\pi A_{i,0} \beta (r + \beta)$$

where r is the radius of the pond (since density is a function only of distance to the center of the pond, for the differential of area, we used $2\pi\rho dp$, the area of a ring of width dp at a distance p from the center). This equation gives $A_{i,0} = A_i/[2\pi\beta(r + \beta)]$, and so the total consumption density at the pond edge across all species n is $C = \sum_{i=1}^n a_i A_{i,0}$ and the predation shadow for each pond is $S = Ce^{-d/\beta}$.

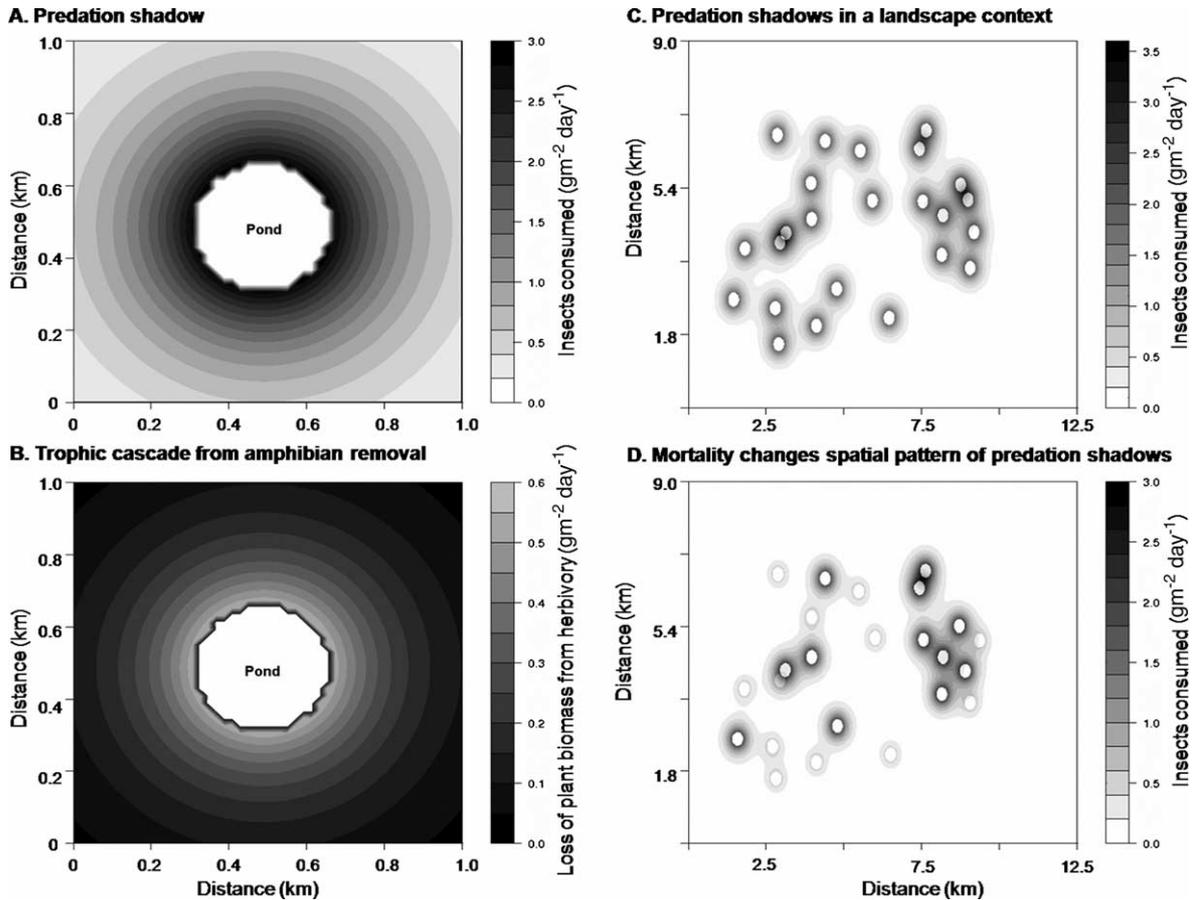


Figure 4. Effects of emerging amphibians on the surrounding landscape. (A) The amount of insect biomass removed by predators emerging from a single pond. (B) Trophic cascade that would result from absence of emerging predators. Lighter colors represent absence of plant biomass due to consumption by herbivorous insects not consumed by amphibians. (C) Predation shadow in panel (A) in a landscape context. (D) Increased larval mortality in half of the ponds affects the spatial patterning of the predation shadow effect.

Using this approach we are likely to overestimate the actual influence of the amphibians in the Gibbons et al. (2006) study, because we are not accounting for the (likely) temporally staggered emergence of amphibians that occurred over the season, and post-emergent mortality. However, the momentous biomass documented in the Gibbons et al. (2006) study is not a unique occurrence. For example, Turner (1962) discusses an estimated 175 million *Rana pipiens* metamorphosing from wetlands around Oconto, Minnesota. Many freshwater ecosystems are highly productive, veritable hotbeds of life, and potential sources for substantial predator populations that can strongly impact the surrounding terrestrial landscape. Thus, we think the analysis we present provides a heuristically plausible view of the likely importance and spatial expression of predation shadows in landscapes comprised of mixes of aquatic and terrestrial habitats, and we hope this exercise provides stimulation for direct experimental and comparative analyses.

To examine how predation shadows might scale up when multiple ponds occur within the surrounding matrix, and to make steps towards gauging potential spatial variation in the strength of trophic cascades, we modeled cumulative predation shadows based on the spatial positions of 20 ponds within the Ordway-Swisher Biological

Station (OSBS, Putnam County, Florida). To identify pond locations we imported satellite images from Google Earth, overlaid a grid, and identified the coordinates for the center of each pond. These ponds are biologically quite similar to the one studied by Gibbons et al. (2006), with qualitatively similar amphibian consumers by species composition and abundance (McCoy unpubl.). For simplicity, we assume all ponds modeled to be 356 m in diameter (approx. size of Ellenton Bay; ca 10 ha), and we calculated predation shadows using estimates of frog biomass derived from Gibbons et al. (2006). Because some ponds are closely juxtaposed, and others are at some distance, the predation shadows cast by some ponds should overlap to create a highly spatially heterogeneous landscape of predation pressure.

Next, we estimated the effects of increasing larval mortality on the strength and spatial pattern of the predation shadow and trophic cascade. Specifically, we reduce the biomass of emerging amphibians in half of the ponds by 50 percent. This scenario approximates conditions that may be associated with reduced allochthonous inputs into these ponds, leading to lower juvenile resources (i.e. lower R in Eq. 1) and causing increased juvenile mortality (m) and decreased juvenile growth rate (g).

Estimating the cascading effects of emerging predators on terrestrial food webs

To examine the potential cascading food web effects of these amphibian predators on surrounding recipient habitats, we quantified the plant biomass consumed by herbivorous arthropods in the absence of predation. This required that we first calculate the predation pressure that would occur when amphibians were present, and then use that number to represent the total arthropod biomass removed. For this analysis we assume that prey preference by amphibians is proportional to prey abundance. Thus, the herbivorous insect biomass consumed by the predators equals the fraction of total insect biomass comprised of herbivores in the community. Plant biomass consumed by herbivorous insects was then quantified using the ingestion rate–body size scaling relationship for poikilotherms (Eq. 4). Note that this allometric relationship was derived for carnivorous poikilotherms; we are unaware of published scaling relationships for ingestion rates in poikilothermic herbivores. Because the relationship between ingestion rate and body size does not differ between herbivorous and carnivorous homeotherms (Farlow 1976, Peters 1983), we assume that this relationship also does not differ between herbivorous and carnivorous poikilotherms.

To determine the fraction of arthropods that are herbivorous, we conducted field surveys at six ponds on the Ordway-Swisher Biological Station during summer 2006. At each pond we performed standardized sweep net samples along three 50-m transects. All arthropods sampled were identified to family and categorized into four size classes based on length (<5 mm, 5–10 mm, 10–20 mm, 20–30 mm). The average biomass of an individual of each size class was then calculated using published length–weight scaling equations for terrestrial insects (Sabo et al. 2002), using the average length of insects in the size class. The total herbivore biomass was then found by multiplying each of these by the abundance of herbivores in the corresponding size class per meter square.

Results

Field surveys

From field surveys at six ponds on the Ordway-Swisher Biological Station, we found, on average, 91.3 (SE 18.75) insects per 50-m transect. Most of the arthropods captured were intermediate in size with the vast majority falling within size class 2 (size class 1 = 12%, size class 2 = 63%, size class 3 = 18%, size class 4 = 7%), and approximately 40 percent were herbivorous species. Using length–weight scaling equations (Sabo et al. 2002) we estimated from these data that the overall average individual mass of the insects was approximately 0.15 g.

Predation shadow at a single pond

Using data from Gibbons et al. (2006), we estimated the total arthropod biomass consumed in the predation shadow around a 356-m diameter pond to be 837 kg per day. The predation shadow expected from this single

pond embedded in a 1.0 km² landscape is shown in Fig. 4A. This amount of consumption is equivalent to an average of 0.93 g m⁻² day⁻¹ (over the approximately 0.9 km² terrestrial habitat modeled in Fig. 4A). Assuming the average mass of insects calculated from our field survey (0.15 g), we estimated that amphibians emerging from this single pond could consume approximately 5 580 000 insects per day.

Trophic cascade from a predation shadow

In our field surveys 40% of the arthropods were herbivores. We estimated that an average sized herbivorous insect could consume 0.07 g plant biomass per day (using Eq. 4, coupled with the average size of the insects in our sample). By multiplying the fraction that were herbivores by our estimate of consumption, we estimated that, in the absence of these emergent amphibian predators, there would be an additional 82.6 kg per day (average = 0.09 g m⁻² day⁻¹ over the approximately 0.9 km² terrestrial habitat modeled in Fig. 4B) increase in plant biomass consumed by insects (Fig. 4B).

On a landscape scale, the scenario we have developed suggests that the cumulative predation shadow can be quite strong in areas where the shadows of multiple ponds overlap (Fig. 4C–D). The biological context of the pond neighborhood can have important implications for the relative magnitudes and impacts of predation shadows. For example, in our heuristic simulation we found that amphibian predators would consume approximately 21 300 kg of insect biomass per day; however, increasing larval mortality rates by 50% in half of the ponds reduced the total insect biomass removed by 38% (8000 kg) and changed the spatial patterning of trophic cascades (Fig. 4D). Thus, in this scenario, reducing total amphibian predator biomass by 25% generates a trophic cascade increasing the plant biomass consumed by herbivorous arthropods per day by approximately 1500 kg (over the approximately 114 km² depicted in Fig. 4C–D).

Discussion

In this study, we have argued that predators with CLHs create obligate links between distinct ecosystems via their consumptive effects in both larval and adult life history stages. We then developed a plausible set of calculations to demonstrate that these consumptive effects of predators with CLHs emerging from ponds (i.e. anuran amphibians) can cast substantial ‘predation shadows’ on the terrestrial landscape surrounding their natal habitat, and that these shadows of consumption in landscapes containing multiple ponds can lead to complex spatial patterns in the expected magnitude of trophic cascades.

Apparent competition between prey populations in distinct adult and larval habitats

The scenario portrayed in our simple model for two habitats coupled by a predator with a CLH falls broadly under the rubrics of shared predation and apparent

competition (Holt and Lawton 1994). The resource populations in the two habitats indirectly interact via a numerical response by their shared predator. Most previous theoretical and empirical studies of apparent competition between prey in spatially extended systems have considered habitats, in each of which a prey species – if sufficiently abundant and productive – could sustain on its own a predator population (Holt 1984, Bonsall and Hassell 1998). In this case, it is possible for one prey species to indirectly exclude another via ‘spillover’ predation, even though the two species never come into contact directly. By contrast, if a predator has a complex life history and must consume different resources at each stage, such prey exclusion is less likely. If the resource base in each habitat is comprised of a single prey species, then if that prey species goes extinct, so will the predator (in our two-habitat scenario). In an open system, the excluded prey species can then invade. This in turn implies that neither prey species can stably exclude the other species locally, mediated through the predator.

There are however two circumstances where predators with CLHs can lead to prey species exclusion in a particular habitat. First, there may be multiple prey species in each habitat; whichever prey species have relatively low reproductive potentials or high exposure to predation in a given habitat compared to other prey species in the same habitat are vulnerable to elimination. Second, instead of two coupled habitat patches, there could be an array of patches used at each stage of the predator’s life history. In this case, predator population persistence will depend upon the entire array of coupled patches, and so predation could be sufficiently intense within a given patch to exclude the prey found there.

Schreiber and Rudolf (2008) recently considered apparent competition between prey in different habitats, using a specific model in which larval predator development is predicated upon resource availability in the larval habitat, and fecundity depends on resources in the adult habitat. Our theoretical results complement theirs in several ways. First, our qualitative analysis of model 1, leading to the isocline expression given by Eq. 2, demonstrates that apparent competition between prey species utilized in different stages of a predator’s life history should be present across a wide range of models differing in the detailed assumptions they make about the relationship between prey consumption and predator demography and developmental rates. Both Schreiber and Rudolf (2008) and ourselves used specific models to draw out more detailed conclusions, but this qualitative result transcends differences between our models.

There are of course important differences that emerge among different systems, depending on the details of predator demography, development, and prey recruitment. Schreiber and Rudolf (2008) for instance show that in a specific model where maturation rates and fecundity depend linearly on prey availability, that alternative states are possible, as well as limit cycle dynamics. We show in Appendix 1 that for our specific model 3 (Eq. 3), where predator maturation rates are fixed, only a unique equilibrium exists, but again unstable dynamics may emerge. We also present some analyses of stability in important limiting cases of the general model, as well as of the specific model,

and these analyses suggest two broad causes of unstable dynamics. First, developmental rates may be density-dependent and this can be destabilizing even if resource dynamics do not promote instability (this was shown for instance in the limiting case of the general model that arises when both resources equilibrate rapidly, Appendix 1). Second, if resources do not equilibrate fast, and one of them is a biotic resource (e.g. with logistic growth), the system can also be unstable, even if predator developmental rates are fixed. An important task for future theoretical work will be to map out how the details of predator resource dependency, as such dependency plays out through the predator’s life history, are reflected in the dynamical stability and potential alternative states of the prey communities coupled by predators with complex life histories.

Empirical scenario

Our empirically-based model suggests that metamorphosing predators cast ‘predation shadows’ on the recipient landscape surrounding their natal habitat. Importantly, however, the strength of the trophic cascade that results from these shadows may change dramatically as a function of distance from the natal (source) habitat. Cascading effects may be quite strong locally, near the pond margin, or in land strips between nearby ponds, then weaken with distance from the natal habitats. Consistent with findings from other experimental studies of trophic cascades in terrestrial food webs (Shurin et al. 2002), the predicted strength of trophic cascades from the predation shadows in our analysis of amphibians is rather weak: ranging from approximately 1% ($\sim 0.04 \text{ g m}^{-2} \text{ day}^{-1}$ across the landscape depicted in Fig. 4C) to more than 5% ($\sim 0.17 \text{ g m}^{-2} \text{ day}^{-1}$ across the landscape depicted in Fig. 4A–B) of the average daily plant production for temperate forests (average NPP = $3.3\text{--}4.2 \text{ g m}^{-2} \text{ day}^{-1}$; Whittaker 1970). However, near the edge of ponds, or when the predation shadows of multiple ponds overlapped, the local strength of the trophic cascade can be expected to be quite strong. In our example on the order of 10 percent or more of average plant productivity near pond margins can be released by top-down predation (Fig. 4B). Thus, the predation shadows cast by the emergence of predators with CLHs can potentially generate significant spatial heterogeneity in the strength of trophic cascades across the landscape. However, more spatially explicit empirical data on predator densities is necessary to confirm the realism of the strong spatial trends identified in this study.

In the trophic cascade literature, there has been relatively little attention given to spatial variability in the strength of the cascade (Polis et al. 1997, Huxel and McCann 1998, Howeth and Leibold 2008). Spatial variation in predator abundance, prey availability and vulnerability, among other factors, should lead to substantial variation in the magnitude of cascades, even at local scales. For instance, in Yellowstone National Park, deer and elk avoid small copses of aspen and cottonwoods, because of the higher risk of mortality from predators, which in turn permits substantial recruitment of these woody species within these copses, but not outside (W. Ripple, pers. comm.). Even cascades that as a whole seem weak across a landscape could be locally quite

strong, and thus contribute significantly to heterogeneity in community patterns and ecosystem function at a landscape scale.

Our analysis highlights a gap in knowledge about demographic parameters critical for understanding the breadth and magnitude of the effects of organisms with CLHs for linking natal and adult habitats. We can not estimate parameters for our model for apparent competition between prey in distinct adult and larval habitats because organisms with CLHs are typically only well studied during one life history stage (typically the natal stage). Our empirical model also has made many simplifying assumptions because of a lack of data on post-metamorphic amphibians. For instance, we know little about post-emergence mortality of the metamorphosing predators and thus do not account for it in our calculations. High rates of mortality would shrink our estimates of the magnitude of the predation shadows and resultant trophic cascades. Moreover, a better understanding of the detailed nature of adult amphibian movement patterns is needed to calculate spatial density profiles, and one should ideally account for how this changes over the season after emergence pulses. The dynamics of insect prey populations are also not well understood, and could influence the magnitude of expected cascades. If insect prey populations replenish slowly after consumption by amphibian predators, there will be a lingering depression in abundance long after the initial emergence of the predators from the pond. Alternatively, there could be rapid compensation, leading to a weak and transient trophic cascade effect. The dynamics of prey recruitment will thus strongly influence temporal variation in the strength of the trophic cascade. We note that our empirical scenario considered only amphibian predators. But in these same ponds, dragonflies, damselflies and other consumers with CLHs can be abundant, and so also can contribute to the generation of strong spatial shadows. Our calculations might thus strongly underestimate the quantitative magnitude of the actual predation shadows produced from ponds with diverse mixes of predators with CLHs. Finally, it will be important in future studies to carry out experimental manipulations at appropriate spatial scales to confirm these back-of-the-envelope calculations. It should be noted that for the particular systems and environments modeled in this example, such manipulative experiments would be quite challenging to set up and execute, and calculations of the sort provided here are necessary to determine if the predicted effects are sufficiently large in magnitude to warrant such a massive and laborious effort.

Implications

We have here focused on how predators with CLHs might affect terrestrial community dynamics via consumption of herbivores. There are numerous direct and indirect pathways involving these predators. For example, Knight et al. (2005) showed that dragonflies emerging from ponds reduced both pollinator visitation rates and pollination success for a terrestrial and emergent plant species. These effects seemed to reflect both mortality inflicted by dragonflies on insect pollinators and the non-consumptive

effects of dragonfly presence on pollinator foraging decisions. Thus, predator emergence from ponds could significantly alter both the primary productivity and genetic structure of the surrounding plant communities. For example, plants near ponds with dense populations of frogs and dragonflies may rely more on vegetative reproduction in response to reduced pollinator abundance. Another likely and interesting complication is that emerging predators with CLHs might consume arthropod predators that also limit and regulate insect herbivores, and this indirect effect could influence the direct effect of these emerging predators upon insect herbivore abundance.

Although in this paper we have focused on predator shadows that emerge (almost necessarily) when the predator has a complex life history, the concept of predator shadows is much broader than this. Whenever predators are mobile, a productive habitat can cast a shadow of predation upon nearby unproductive habitats. Holt (1984) for instance developed simple models for this effect for two habitats with different prey species, coupled by density-independent predator movement, and he derived conditions for prey species coexistence in terms of prey intrinsic growth rates, attack rates, and predator movement rates. Prey in unproductive habitats should often have low intrinsic growth rates there, and be vulnerable to exclusion due to predator spillover from more productive habitats. Rand et al. (2006) found that generalist predators could be sustained in productive agricultural habitats, and then move into and inflict substantial mortality in natural habitats.

Mobile higher order consumers that link food webs in space can also stabilize communities by coupling systems with different strengths of interactions and asymmetrical abundances (McCann et al. 2005, Rooney et al. 2006). One important task for future work will be to revisit linkages among food webs in space for systems where the coupling exists because of ontogenetic habitat shifts by top predators. The models presented here (Appendix 1) suggest that coupling via ontogenetic habitat shifts by predators can be either stabilizing or destabilizing, depending on the nature of prey recruitment and the demographic influence of prey consumption on predator demographic parameters.

Gauging the indirect effects of CLH predators between disparate habitat types has important implications and applications for ecosystem management. In addition to being important avenues for the exchange of materials and modulating local interactions, organisms with CLHs provide conduits for the exchange of contaminants between ecosystems (Johnson and Ringler 1979, Currie et al. 1997, Reinhold et al. 1999, Cristol et al. 2008). This role may be especially important for animals that are top predators in either or both the natal and adult habitat, because toxins bio-accumulate, and so top predators tend to have high contaminant loads, relative to their body size.

Conclusions

Although we have here focused on interactions at the land-water interface, cross-ecosystem connections emerging from ontogenetic habitat shifts are by no means restricted to aquatic-terrestrial boundaries. Organisms with CLHs are

common components of most natural systems and likely play an important role as connectors across many types of ecosystem boundaries and communities (Polis et al. 1997, 2004, Nakano et al. 1999, Strong 1999, Power 2001, Sabo and Power 2002, Baxter et al. 2004, Schreiber and Rudolf 2008). For example, many parasites with complex life cycles utilize hosts inhabiting very different habitats. Understanding the role of predators and parasites with CLHs as dynamical connectors among distinct environments is a ripe area for future empirical and theoretical research. Attaining a better appreciation of interactions among ecosystems via CLH organisms will undoubtedly enhance our understanding about the manifold consequences of connectivity among habitat types, and the mechanisms driving local and regional patterns of diversity.

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Appendix 1. Stability of two-habitat model for a predation shadow

The general model (Eq. 1) in the main text is a four-dimensional system, and we have not been able to find transparent necessary and sufficient conditions for its stability. Even for the simpler model, given by Eq. 3, assessing stability conditions is challenging, but it can be shown numerically that sometimes the system is unstable. The Jacobian of this system of equations is

$$\begin{bmatrix} -I/R^* & 0 & -cR^* & 0 \\ 0 & -r'R^*/K' & 0 & -c'R'^* \\ qJ^*/cR'^2 & ec'A^* & -ec'gR'^*/m' & ec'R'^* \\ 0 & 0 & g & -m' \end{bmatrix}$$

where the equilibrium values are those for which the predators are present. The characteristic equation of this matrix has coefficients $a_4 = 1$,

$$\begin{aligned} a_3 &= m' + I/R^* + r'R^*/K' + ec'gR'^*/m', \\ a_2 &= m'I/R^* + m'r'R^*/K' + Ir'R^*/K'R^* \\ &\quad + Igec'R'^*/m'R^* + qJ/R^* + r'gec'R'^2/K'm', \\ a_1 &= m'Ir'R^*/K'R^* + r'Igec'R'^2/K'm'R^* \\ &\quad + qJ(m' + r'R^*/K')/R^* + gec'^2A^*R'^* \quad \text{and} \\ a_0 &= m'qJr'R^*/R^*K' + Igec'^2A^*R'^2/R^*. \end{aligned}$$

All the coefficients are obviously positive, which is a necessary condition for local stability, but stability also requires that $a_2a_3 > a_1$ and $a_1(a_2a_3 - a_1) > a_0a_3^2$. These conditions are often met, but are sometimes violated, for example when $I = 1$, $\mu = 0.1$, $c = 10$, $r' = 1$, $K' = 1$, $c' = 300$, $e = 1$, $m' = 5$, $g = 1$, $q = 2$ (the variables in the system

can be normalized to eliminate r' , K' , e and I , which were therefore set to unity). The determination of the exact conditions for stability requires substituting the equilibria into the coefficients and then using the two inequalities above. The result is far too cumbersome to be useful (except when solving numerically). Since we have not been able to characterize in a simple fashion the necessary and sufficient conditions for stability, we instead here provide some illuminating special cases.

In the general model provided by Eq. 1, if we assume that both resources equilibrate much faster than J and A , we can assume that resources track J and A according to the solution of $dR/dt = 0$ (solving for R as a function of J) and $dR'/dt = 0$ (solving for R' as a function of A). We then substitute both resulting terms into the dJ/dt equation, and end up with a two-dimensional dynamical system (the parameters in the dA/dt equation are unaffected by resources, so it is used as is). This protocol assumes that there is a unique non-trivial solution, which is true for the specific model (Eq. 3), but is not true in general (Schreiber and Rudolf 2008). Alternative equilibria can arise for instance if there are sufficiently strong nonlinearities, e.g. saturating functional responses, or Allee effects.

This procedure can be generalized as follows. Assume that because of resource dependencies and rapid resource equilibration, adult resource levels can be given as a function of adult abundance, and juvenile resource levels can be written as a function of juvenile abundance. Then, fecundity f and adult mortality m' can be written as functions of adult density, and juvenile mortality m and growth rate g in like manner as functions of juvenile density. [For example, for Eq. 3 in the main text, $R^* = I/(\mu + cJ^*)$ and $R'^* = K'(1 - c'A^*/r')$, so $m = q/cR^* = q(\mu + cJ^*)/cI$ and $f = ec'R'^* = ec'K'(1 - c'A^*/r')$, and g and m' are constant.]

These assumptions lead to the system

$$\frac{dJ}{dt} = f(A)A - m(J)J - g(J)J$$

$$\frac{dA}{dt} = g(J)J - m'(A)A.$$

The zero-growth isocline for Eq. 3 for the juvenile is $ec'K'(1 - c'A^*/r')A^* = [q(\mu + cJ^*)/cI + g]J^*$, while that for the adult is $gJ^* = m'A^*$. The second of these is a straight line, and the first is an ellipse. Therefore, there can be a maximum of two crossings, and one of these is at the origin. Therefore, there can be only one equilibrium with the predator present. In contrast to this, in the model of Schreiber and Rudolf (2008), both zero-growth isoclines are parabolic, so there can be multiple equilibria with the predator present [they assume both resources are logistic (we assume this for only the adult resource) and linearly affect reproduction (as we do) and maturation (constant in our model), while predator mortalities are fixed (juvenile mortality is hyperbolic in our model)].

The Jacobian of this system is

$$\begin{bmatrix} -m - g - \frac{dm}{dJ}J - \frac{dg}{dJ} & f + \frac{df}{dA}A \\ g + \frac{dg}{dJ}J & -m' - \frac{dm'}{dA}A \end{bmatrix}$$

evaluated at the equilibrium. One possible equilibrium has the predator absent, in which the Jacobian is

$$\begin{bmatrix} -m(0) - g(0) & f(0) \\ g(0) & -m'(0) \end{bmatrix}$$

This equilibrium is stable, and the predator cannot increase when rare, if and only if $f(0)/m'(0) - m(0)/g(0) < 1$. The right side is the difference between average adult production and the average number of offspring that die before adulthood, all at very low predator density, which must exceed one (an average adult must more than reproduce itself) for the predator to increase when rare. It can easily be shown that one condition for an equilibrium with the predator present is $f(A^*)/m'(A^*) - m(J^*)/g(J^*) = 1$ (setting both derivatives above to 0). This can in general not be satisfied with $f(0)/m'(0) - m(0)/g(0) < 1$ unless the relation of one of the parameters to its argument is the opposite of the expected one (increases in mortality and decreases in fecundity and growth with increasing predators). This is because any of these expected changes will either cause the first term, $f(A^*)/m'(A^*)$, to drop, or the second term, $m(J^*)/g(J^*)$, to increase. Either will cause the right side of the inequality above to drop with positive J^* and A^* substituted for the zeroes. If the right side is less than one with no predators, it will be even lower and therefore still less than one with predators. Therefore the condition for an equilibrium with the predator cannot be satisfied if the predator cannot increase when rare, unless at least one parameter departs from expected dependence on J or A . [For Eq. 3, $m(0) = q\mu/cI$ and $f(0) = ec'K'$, so the condition for increase of the predator when rare is $ec'K'/m' - q\mu/clg > 1$. This is the same condition derived in the main text.]

If the predator is present, this system is stable if and only if

$$m + g + \frac{dm}{dJ}J + \frac{dg}{dJ}J + m' + \frac{dm'}{dA}A > 0$$

and

$$\begin{aligned} & \left(m + g + \frac{dm}{dJ}J + \frac{dg}{dJ}J \right) \left(m' + \frac{dm'}{dA}A \right) \\ & > \left(f + \frac{df}{dA} \right) \left(g + \frac{dg}{dJ} \right) \end{aligned}$$

If the growth rate is fixed, $dg/dJ = 0$, and the two conditions become

$$m + g + \frac{dm}{dJ}J + m' + \frac{dm'}{dA}A > 0$$

and

$$\left(m + g + \frac{dm}{dJ}J \right) \left(m' + \frac{dm'}{dA}A \right) > \left(f + \frac{df}{dA} \right) g$$

The first condition is always satisfied if each mortality rate is a non-decreasing function of the corresponding density (so neither derivative is negative), as would normally be expected. The second condition can be rewritten

$$(m + g)m' - fg > \frac{df}{dA}g - m' \frac{dm}{dJ}J - (m + g) \frac{dm'}{dA}A$$

At equilibrium, the left side is 0. Stability therefore only requires that the right side is negative, as it will surely be if fecundity is a decreasing function of adult density, or if either mortality term is an increasing function of its density (and none of these goes in the opposite direction). Again, this is exactly the form of density dependence that would be expected to arise from competition for a limiting resource.

In short, the bottom line is that if maturation rates are fixed, but fecundity or juvenile or adult mortality (or all of these) depends upon a resource, and resources equilibrate fast so that this dependence can be expressed as direct density dependence in these demographic rates, then the equilibrium is stable.

By contrast, if the maturation rate depends on juvenile density (indirectly reflecting resource limitation), it is possible for the system to be unstable. For example, suppose that the mortalities and fecundity are all fixed. Then, stability requires $m + g + Jdg/dJ + m' > 0$, which is not necessarily satisfied if $dg/dJ < 0$. Instability is likely if overall mortality rates are low, there are high juvenile numbers, and increases in juvenile density greatly depress juvenile maturation rates.

The above remarks apply to a broad range of models. For greater specificity, it is useful to focus again on the specific model of the main text (Eq. 3). This system has a single equilibrium (given in the text), which is often stable, but is sometimes unstable. We here present some limiting approximations, which are illuminating.

If both resource populations equilibrate quickly, then we have a two-dimensional system. Because we have assumed that growth rates are fixed, the general result above ensures that the overall system is stable.

To reduce the system from four dimensions to three, we will assume that each of the resources in turn equilibrates rapidly, while the other resource does not. Assuming that the rapidly equilibrating resource is the adult resource R' , we can set $dR'/dt = 0$ and solve for $R' = K'(1 - c'A/r')$, and substitute this into the dJ/dt equation, leading to

$$\frac{dR}{dt} = I - \mu R - cRJ$$

$$\frac{dJ}{dt} = ec'K' \left(1 - \frac{c'A}{r'} \right) A - \frac{qJ}{cR} - gJ$$

$$\frac{dA}{dt} = gJ - m'A$$

The Jacobian of this system is

$$\begin{bmatrix} -I/R & -cR & 0 \\ qJ/cR^2 & -g - q/cR & ec'K'(1 - 2c'A/r') \\ 0 & g & -m' \end{bmatrix}$$

evaluated at the equilibrium with predator present. The characteristic equation for this Jacobian is a cubic equation,

with coefficients $a_3 = 1$, $a_2 = I/R + q/cR + g + m'$, $a_1 = I/R(g + q/cR) + m'I/R + qJ/R + gec^2K'A/r'$ and $a_0 = m'qJ/R + Igec^2K'A/r'R$ [the substitution $ec'K'(1 - 2c'A/r') = m'(g + q/cR)/g - ec^2K'A/r'$ was used to get these results]. The system is stable if and only if $a_2 > 0$, $a_0 > 0$ and $a_1a_2 - a_0 > 0$. The first two conditions are clearly satisfied, because all terms of a_2 and a_0 are positive, and the last is satisfied because the two terms of a_0 both result from multiplying a_1 and a_2 , leaving only positive terms. Therefore, the equilibrium of this system with the predator present (which is the same as that of the original system) is always locally stable. So we can conclude that if the adult resource tracks the adult density, and the juvenile resource freely varies, the full system is locally stable, given that an equilibrium exists.

A different result is obtained if we instead assume that the juvenile resource R tracks the juvenile density. Its value will be $R = I/(\mu + cJ)$, which can be substituted into the dJ/dt equation, leading to

$$\frac{dR'}{dt} = rR' \left(1 - \frac{R'}{K'} \right) - c'R'A$$

$$\frac{dJ}{dt} = ec'R'A - \frac{qJ}{cI}(\mu + cJ) - gJ$$

$$\frac{dA}{dt} = gJ - m'A$$

The Jacobian of this system is

$$\begin{bmatrix} -r'R'/K' & 0 & -c'R' \\ ec'A & -g - q(\mu + 2cJ)/cI & ec'R' \\ 0 & g & -m' \end{bmatrix}$$

evaluated at the equilibrium with predator present. All the coefficients of the characteristic equation can be shown to be positive [the substitution $g + q(\mu + 2cJ)/cI = qJ/I + ec'gR'/m'$, at equilibrium, is used to show this and for the result below]. However, the remaining condition is that $a_1a_2 > a_0$, which is

$$\begin{aligned} & \left(\frac{r'R'}{K'} + \frac{qJ}{I} + \frac{ec'gR'}{m'} + m' \right) \left[\frac{r'R'}{K'} \left(\frac{qJ}{I} + \frac{ec'gR'}{m'} \right) + \frac{m'qJ}{I} \right] \\ & > ec'^2gAR' + \frac{m'r'R'}{K'} \frac{qJ}{I} \end{aligned}$$

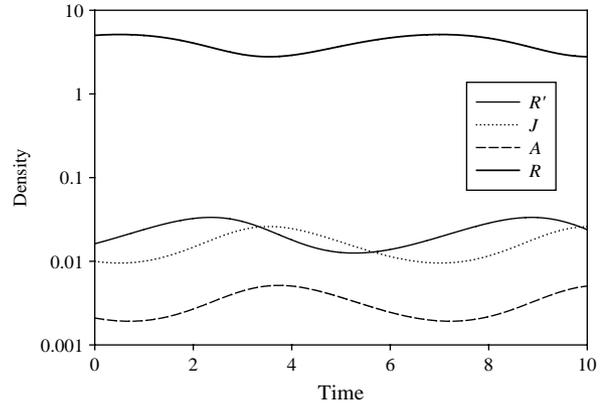


Figure A1. An example of limit cycles in species densities for an unstable equilibrium for a system in which juvenile resource density R is assumed to equilibrate instantaneously. The top curve is R' . $I = 1$, $\mu = 0.1$, $c = 10$, $r' = 1$, $K' = 1$, $c' = 300$, $e = 1$, $m' = 5$, $g = 1$, $q = 10$.

The second term on the right is equal to one of the product terms on the left, but the first term on the right is not, and it can be shown that this inequality can be violated for some choices of parameters (such as the parameters of Fig. A1).

Given that the equilibrium is locally unstable, the next question is the asymptotic behavior of the system. Our numerical explorations have shown only limit cycle behavior (Fig. A1 shows an example), but it is impossible to preclude more complex dynamics.

The analyses presented here suggest that in the general model (Eq. 1) there are two broad classes of processes that can lead to instability. First, developmental rates may be density-dependent (this was shown in the limiting case of the general model that arises when both resources equilibrate rapidly). Second, if resources do not equilibrate fast, and one of them is a biotic resource with logistic growth, one can observe instability (this was shown for the specific model).