Impacts of temporal variation on apparent competition and coexistence in open ecosystems

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The natural world is variable both in space and in time, but little ecological theory has been explicitly devoted to analyzing the consequences of both kinds of variability operating simultaneously. This issue is examined relative to the indirect interaction of apparent competition, which can limit the membership of prey communities. One limiting case that provides a useful starting point is to imagine that a local community is influenced by coupling with an external source landscape, but has little reciprocal influence on that landscape. There usually will be some rate of input of a locally inferior species that suffices to 'swamp' a superior species and drive it to extinction. We use simple models of apparent competition to show that when one superimposes upon this scenario temporal fluctuations, mediated through shifts in parameter values, such variation can either magnify the importance of the external input, or reduce it, depending on which component of the system experiences variation. We examine this in the case of both slow variation (for which we suggest a protocol that may be useful in a wide range of ecological models), and fast variation. The theoretical studies presented here provide examples of the rich range of outcomes that may arise due to temporal variability in spatially heterogeneous landscapes.

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"*It is at the crossroads of space and time that population biologists will meet their greatest challenge.*" (p. 79, Cappuccino et al. 1995).

A major frontier in contemporary population and community ecology is linking the mechanistic drivers of local dynamics with processes acting at large spatial and temporal scales (Lawton 1995, Huston 1999, Naeem 2001). This statement applies across ecological systems and taxa, but it may apply with particular force to plant-herbivore interactions. Plants and their herbivores almost always experience the world at different spatial scales (Holt 1996, Ritchie and Olff 1999). After an initial seed or spore stage, individuals of non-clonal terrestrial plants are sedentary, and even clonal species grow and maneuver over limited spatial arenas. As measured at this scale, individual herbivores typically range widely in their foraging, coupling the dynamics of spatially separated plant populations. Even if herbivores are relatively sedentary, seed dispersal can couple the dynamics of distinct habitats, as can the movements of top predators (e.g. some vertebrate predators, such as jaguars, roam over huge areas, Koford 1983). In a landscape mosaic with habitats varying in local productivity, 'spillover' of predators and prey from productive into unproductive habitats can profoundly influence the likelihood and magnitude of unstable dynamics (Oksanen et al. 1999, 2001, Lidicker 2000, Oksanen and Oksanen 2000, Holt 2002).

It is a truism to state that the ecological world is variable in both space and time. Many ecologists have been impressed with the great spatial and temporal variability of plant-herbivore interactions (Thompson 1982, pp. 134–135). Insect herbivores often exhibit high levels of population variability (Inchausti and Halley

2001), which likely reflects at least in part their sensitivity to variation in the weather (Solbreck 1995, Azerefegne et al. 2001). Despite the manifest importance of environmental variation in both space and time, there have been surprisingly few attempts to examine the consequences of combining these forms of variation for population dynamics, community structure, and ecosystem functioning (Sears et al., in press). The reason for this neglect is surely that because ecological systems are quite complex, for the purposes of clear understanding it is useful (and indeed essential) to simplify systems in one dimension, while retaining complexity in others. However, one has to worry about whether or not something essential is missing, when one does not consider the joint impact of variation in space and time. In this paper, we will present some first steps towards understanding the consequences of combining temporal variability and spatial heterogeneity, focusing on the problem of the coexistence of interacting species in local communities (Chesson 2000).

To make any headway, we of course must also make simplifying assumptions. Rather than deal with entire communities, we consider a particular 'community module' – interactions among a small number of species linked in a specified structure of interactions (Holt 1997). Much of our thinking in community ecology has been shaped by analyses of simple community modules, which provide intellectual tools for a sharpened understanding of dynamics of more complex, multispecies webs. In landscape and metapopulation ecology, a conceptual simplification analogous to community modules is to examine flows in highly simplified landscapes, such as between a few discrete habitat patches (e.g. 'source' and 'sink' habitats in population dynamics; Holt 1985, Pulliam 1988, Polis et al. 1997). Analyses of simple landscapes can illuminate dynamics in much more complex landscapes (Hanski 1999). We consider the indirect interspecific interaction of apparent competition between alternative prey species sharing a predator species in a focal habitat, in which one prey species or the predator can receive immigrants from the surrounding landscape. For simplicity, we ignore reciprocal impacts of the focal habitat on the landscape. Fig. 1 shows three spatial scenarios that we consider.

To assess the impact of spatial flows in a variable environment, it is necessary to first have a clear sense of the consequences of such flows in a constant environment. In Scenario I (Fig. 1, top), the environment is constant in a focal habitat. We assume the local community settles down to a stable equilibrium. In a spatially open community, with a constant input of one (or more) community members, landscape 'forcing' can influence the persistence of other community members. Given competitive interactions within a trophic level (direct, exploitative or apparent), inferior competitors can be sustained by recurrent immigration. If competition is not completely asymmetric, locally superior species that are not themselves spatially subsidized can be harmed by external inputs of inferior competitors, and may even be excluded. Below, we examine the impact of external subsidies on apparent competition between a pair of species sharing a natural enemy. As a hypothetical example, imagine that in the focal habitat an oligophagous seed predator (e.g. a bruchid beetle) consumes the seeds of two plant species with different microsite requirements (so they do not directly compete). One species is better adapted to tolerating herbivory in that habitat, and can sustain the seed predator at densities sufficient to exclude the second species. However, the second plant species is sustained in a different, adjacent habitat, which provides a source for recurrent seed input. The first model we examine leads to a condition for persistence of the locally favored species, in the face of such inputs in a constant environment.

In Scenario II (Fig. 1, middle) there is again a constant input from external sources, but the focal species in the local community now experience fluctua-
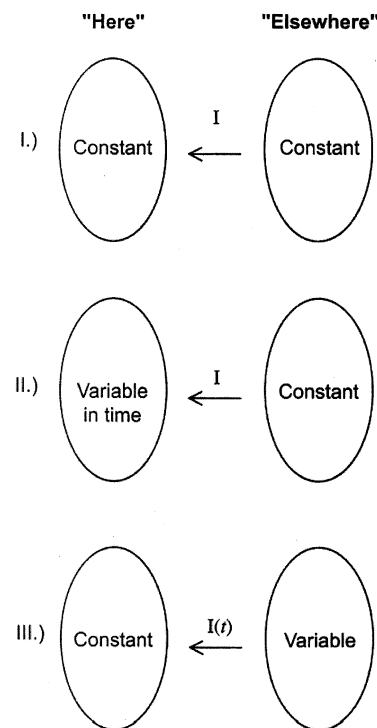

Fig. 1. Three simple spatial scenarios. In each case, a local community is connected via immigration to an external landscape. Reciprocal influences of that community on the landscape are ignored. Scenario I. Both the local environment and the external landscape are constant in time, and have stable interactions. The input (denoted by I) displaces the community from its local equilibrium. Scenario II. The external environment is constant, so inputs are constant, but the local environment is variable. Scenario III. The local environment is constant, but the external environment is not, leading to variable rates of input.

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tions in growth rates, for instance because of variation in the weather, or sporadic disturbance, or variation elsewhere in the community (e.g. in pollinator activity). Below we explore how such variation alters the impact of external inputs on local apparent competition, relative to an otherwise similar but constant environment. The basic, qualitative message is that temporal variation has a range of influences, sometimes magnifying the impact of external inputs upon coexistence, and sometimes diluting such impacts.

In Scenario III (Fig. 1, bottom), the environment of the focal community is constant, but the external world is not. Thus, the magnitude of inputs varies. A final plausible scenario (not pictured) would involve simultaneous variation in local growth and inputs.

Scenario I: spatial subsidies in constant environments

Consider a system where a generalist predator with a pronounced numerical response limits the abundance of either of two prey species in a habitat patch. In general, these qualitative assumptions imply the existence of the indirect interaction of apparent competition (Holt 1977, 1997, Holt and Lawton 1994), in which prey species indirectly depress each other's abundance via a shared predator. We assume the two prey species do not directly compete, so local coexistence rests entirely on the ability of each species to withstand predation. In simple models of apparent competition in closed communities, the dominant prey is the one sustaining the highest predator density (Holt et al. 1994). This dominance in apparent competition may reflect several aspects of local superiority: for instance, a given prey species may have a higher local growth rate, or it may enjoy a lower attack rate in the local environment (Holt and Lawton 1994).

In open communities, dominance may instead be governed by the strength of coupling between the habitat patch and the surrounding landscape: a locally inferior species may dominate due to spatial subsidies (Holt, in press). To illustrate this effect consider the following model:

Predator: $\quad dP/dt = P(a_1 b_1 R_1 + a_2 b_2 R_2 - m)$

Prey species 1: $\quad dR_1/dt = R_1(r_1 - d_1 R_1 - a_1 P)$

Prey species 2: $\quad dR_2/dt = R_2(r_2 - d_2 R_2 - a_2 P) + I$

$$(1)$$

Model (1) assumes the predator has linear functional and numerical responses to each prey species, and that each prey species has logistic growth in the local environment (d_i gauges strength of direct density depen-

dence in species i). Prey species 2 has a regular influx of immigrants drawn from external sources. (Passive back-flows from the focal habitat into the landscape, i.e. emigration, constant on a per capita basis, are absorbed into the realized intrinsic growth rate, r_i.) The model is a caricature of any real one-predator, two-prey system (e.g. predators will usually have saturating, nonlinear functional responses). However, it is a useful caricature, as it illustrates with a minimum of algebraic complexity phenomena that arise in more complex models, and provides a basis for exploring impacts of temporal variation.

If an equilibrium exists with all species, that equilibrium is locally stable. Prey species 2 enjoys regular input and so will persist. The problem of coexistence is borne entirely by prey species 1, which depends solely upon in situ recruitment. Let P^* and R_2^* respectively denote the abundance of the predator and prey 2, when prey 1 is very rare. If the predator is at equilibrium, for prey 1 to increase when rare requires $r_1/a_1 > P^*$. But in this limit of low numbers for prey 1, predator abundance is determined just by its interaction with prey 2. We assume the predator can be sustained by prey 2, even without the subsidy. The equilibrial abundance of predators supported by prey 2 alone is:

$$P^* = \frac{r_2 - d_2 R_2^*}{a_2} + \frac{I}{a_2 R_2^*} = \frac{r_2 - d_2 m/(a_2 b_2)}{a_2} + \frac{I b_2}{m} = P(q)$$
$$(2)$$

In (2) 'q' represents any one of the parameters in the model appearing in the algebraic solution on the left. The notation $P(q)$ simply denotes that equilibrial predator density is a function of one or more parameters (we use this expression below). The expression for P^* cleaves into two parts, matching the two sources of prey recruitment: the predators sustained by in situ recruitment of prey species 2, and those sustained by external subsidy.

Prey species 1 persists provided $r_1/a_1 > P^* = (r_2 - d_2 m/a_2 b_2)/a_2 + I b_2/m$. If density dependence in prey 2 is weak, or the predator effectively limits prey numbers, this simplifies to:

$$r_1/a_1 > r_2/a_2 + I b_2/m \qquad (3)$$

If prey 1 is locally superior at growth or predator escape, so that $r_1/a_1 > r_2/a_2$, it cannot be excluded by apparent competition in a closed environment. In simple models, this inequality defines local dominance among alternative prey sharing a predator (Holt 1977, 1997, Holt and Lawton 1994). However, a locally superior species can be excluded given sufficient inputs of the alternative prey. Such exclusion is likely if 1) the two prey do not differ greatly in r/a, 2) the subsidized prey is a high quality food for the predator, 3) the predator has low mortality, and 4) attack rates are

high. Exclusion by a spatial subsidy is more likely if input is large relative to local productivity (gauged by r_i). Subsidy-driven exclusion is most likely to occur in low-productivity habitat pockets, surrounded by a landscape higher in productivity. (Similar effects occur in open systems with exploitative competition, Holt, in press, Holt et al., in press.)

Scenarios II and III: spatial subsidies in temporally varying environments

The above model illustrates how spatial subsidies lead to 'spillover' effects, potentially altering the structure of local communities (Holt, in press). We now use this model to explore how different avenues of temporal variation influence the coexistence of alternative prey species. We permit different model parameters to vary deterministically, and use either numerical simulations or time-averaging (Levins 1979) to explore the impact of such variation.

If prey species 2 continually immigrates from the external landscape, it persists even in a variable environment. So we focus on prey species 1, which is not being rescued by immigration. If this species is rare at time t, its growth rate is $dR_1/dt = R_1[r_1(t) - a_1(t)P(t)]$. For simplicity, assume that prey species 1 when rare experiences a constant environment, except for fluctuations in predator abundance. Temporal variation in predator abundance can arise from environmental variation directly experienced by the predator, or more indirectly due to environmental variation imposed on the alternative prey. We use the notation '$\langle X \rangle$' to denote a time-average of some variable quantity, X. Formally, over a time T, the time-average of X is $\langle X \rangle = (\int_0^T X(t)\, dt)/T$. If X is periodic, T is the period; otherwise, one takes T indefinitely large (assuming variation of X is bounded). Because integration is a linear operation, if a is a constant, $\langle aX \rangle = a\langle X \rangle$, and $\langle X + Y \rangle = \langle X \rangle + \langle Y \rangle$. By Jensen's inequality (Hardy et al. 1952, Ruel and Ayres 1999), if X is non-negative but varying we know that $\langle 1/X \rangle > 1/\langle X \rangle$.

With this notation, the condition for persistence of prey species 1 is simply $r_1/a_1 > \langle P \rangle$, where average predator abundance is determined by the interaction between the predator and the alternative prey (Holt 1997). In the constant environment, the persistence condition (given above) is $r_1/a_1 > P^*$. The effect of temporal variation is thus assessed by comparing $\langle P \rangle$ in the variable environment, to P^* evaluated with all parameters constant (at their average values). If environmental variation depresses $\langle P \rangle$ below P^*, this facilitates persistence of prey species 1; if instead temporal variation increases $\langle P \rangle$, prey coexistence is hampered. In the next few paragraphs, we first examine an analytically tractable case (slow temporal variation), and then

numerically explore the impact of faster, periodic variation.

i. Slow variation

For sufficiently slow rates of environmental change, populations should 'track' a moving equilibrium, assuming that there is a stable equilibrium at each point in time. This observation permits a qualitative, first-order assessment of the effect of slow temporal variation on long-term species coexistence.

For model (1), the predator abundance sustained by prey species 2 in a constant environment is given by expression (2). Now let one parameter q vary slowly, whereas the others remain constant. We assume that to a good approximation, predator numbers track the (moving) equilibrium given by (2). (We assume that the magnitude of variation is such that the term $r_2 - d_2 R_2^*$ in (2) remains positive.) In the algebraic expression (2) for $P(q)$, we set $q = q(t)$, and take the time average of the resulting expression for $P(t)$. By rules noted above for the operation of time-averaging, if a given parameter q appears only as a simple multiplier in the numerator, then $\langle P(q) \rangle = P(\langle q \rangle)$, and average predator abundance is unchanged by temporal variation in this parameter. By inspection of expression (2), we note that three parameters appear as simple multipliers in the numerator: the intrinsic growth rate of prey species 2, r_2, its rate of input from external sources, I, and the strength of direct density dependence in the local environment, d_2. These parameters directly govern prey dynamics, in the absence of the predator. Hence, in this example, temporal variation in predation emerging indirectly from environmental variation imposed upon prey 2 does not alter average predator abundance. It follows that such variation (when sufficiently slow) does not affect the condition for persistence of an alternative, non-immigrant prey species.

However, this is not true for variation in other model parameters. Consider the rate of predator mortality, m. This parameter enters twice, once via the numerator of a term involving prey density dependence, and once via the denominator of the prey subsidy term. By the rules of time-averaging, variation via the former has no effect on average predator abundance, but variation in the latter inflates predator abundance (because $\langle 1/m \rangle$ exceeds $1/\langle m \rangle$ and therefore $\langle P \rangle$ exceeds P^*).

In short, temporal variation in predator mortality rates increases the average abundance of a predator sustained by a prey with external subsidies. This effect is larger, the greater the subsidy. This inflationary effect of variation upon predator abundance should hamper persistence of a resident, superior prey. Temporal variation can thus destroy prey species coexistence.

By contrast, temporal variation in prey quality for the immigrant species, measured by b_2, decreases average predator numbers (because the parameter appears in the denominator of a negative term), and so makes it harder for a locally superior prey species to be excluded by a subsidized prey species. However, this effect diminishes when prey density dependence is weak, or when the predator is sufficiently effective to ignore such density dependence.

Finally, variation in the rate of attack a_2 can either increase or decrease average predator abundance, depending on the overall effectiveness of the predator in limiting prey numbers. In the limit of weak prey density dependence (d_2 approximately zero), variation in attack rates increases average predator numbers, and thus makes it more difficult for the superior resident prey species to persist.

We can get an analytic expression for the impact of variation by taking a Taylor expansion of $P(q)$ around the average value of q, q_{av} ($= \langle q \rangle$), and then time averaging, leading to

$$\langle P(q) \rangle = P(q_{av}) + \langle (q - q_{av}) \rangle dP/dq$$
$$+ 0.5 \langle (q - q_{av})^2 \rangle d^2P/dq^2 + \cdots \qquad (4)$$

where the derivatives are evaluated at q_{av}. The first term is the equilibrial value for P, when q is at its mean value. The second term is zero, and in the third term $\langle (q - q_{av})^2 \rangle = \Phi_q^2$, the variance of q. If q is r_2, d_2 or I, the second and higher order derivatives are 0, so the average P is equal to its equilibrium. For small variation of other parameters, we can truncate the series after the third term, and the effect of temporal variation in q on average predator abundance depends upon the curvature of P as a function of q (at q_{av}); given a non-zero curvature, the magnitude of the effect scales with the magnitude of temporal variance in the parameter. For instance, if the algebraic form of $P(q)$ can be written as $z + y/q$ (e.g. for immigrant prey quality in (2) above) after substitution we find that

$$\langle P(q) \rangle = z + (y/q_{av})(1 + \Phi_q^2/q_{av}^2) = z + (y/q_{av})(1 + CV_q^2) \qquad (5)$$

where CV_q is the coefficient of variation in parameter q. If y is negative, temporal variation in q depresses average predator abundance; if y is positive, variation inflates predator abundance.

Thus, temporal variation in the environment can have a variety of disparate effects upon prey species coexistence, depending on which species in the system experiences such variation, and which specific parameter is a conduit for such variation. In the above model, local variation in the demographic parameters of an immigrant prey species has no effect upon average predator numbers, and thus no effect upon the deter-

ministic rules for persistence of a second, non-immigrant prey species. By contrast, variation in parameters influencing predator growth can alter average predator numbers (in either direction), and hence temporal variation can either facilitate or hamper prey species coexistence.

The above argument can be extended to simultaneous variation in multiple parameters of the resident species. In this case, a multi-variable form of Taylor's series must be used, which will include terms involving covariances. However, these terms will include the second partial derivatives with respect to the corresponding pair of parameters. In our expression for P^*, all second (and higher) partial derivatives not involving a_2, b_2 or m are zero. Therefore, slow variation in the immigrant parameters (r_2, d_2 or I) cause no change in mean predator numbers, even if more than one are varying simultaneously.

ii. Fast variation

Environments may often change too rapidly for systems to track local equilibria. It is in general difficult to solve analytically for average densities in nonlinear systems with time-varying parameters. Instead, one can explore the impact of temporal variation upon species coexistence numerically. Fig. 2–4 show representative examples of such studies for model (1). As before, we assume prey species 1 (the non-immigrant) experiences temporal variability solely through effects upon average predator abundance. Coexistence is more difficult if for a given parameter q, temporal variation increases time-averaged predator abundance.

In these examples, we permitted each model parameter q to vary sinusoidally according to $q(t) = q_{av} [1 + x \sin(2\pi ft)]$, where q_{av} is the average value of parameter q, x defines the maximal fractional deviation of the parameter from its average value, and f is the frequency of the sine-wave variation. This protocol permits us to compare constant environments with a range of variable environments, all of which have the same average parameter value but differ in their magnitude or frequency of variation. In the simulations, x was chosen so that parameters would remain biologically reasonable (e.g. all attack rates were positive). The examples demonstrate that the frequency as well as magnitude of environmental variation can have strong effects on average abundance and species coexistence (Gonzalez and Holt 2002, Holt et al., in press).

In the results shown in Fig. 2A, the subsidized prey does not experience direct density dependence ($d_2 = 0$), and $f = 0.06$ (corresponding to moderately slow variation). Fig. 3 shows a typical predator trajectory (solid line), compared with the moving equilibrium (dashed line). There is at best a very rough correspondence
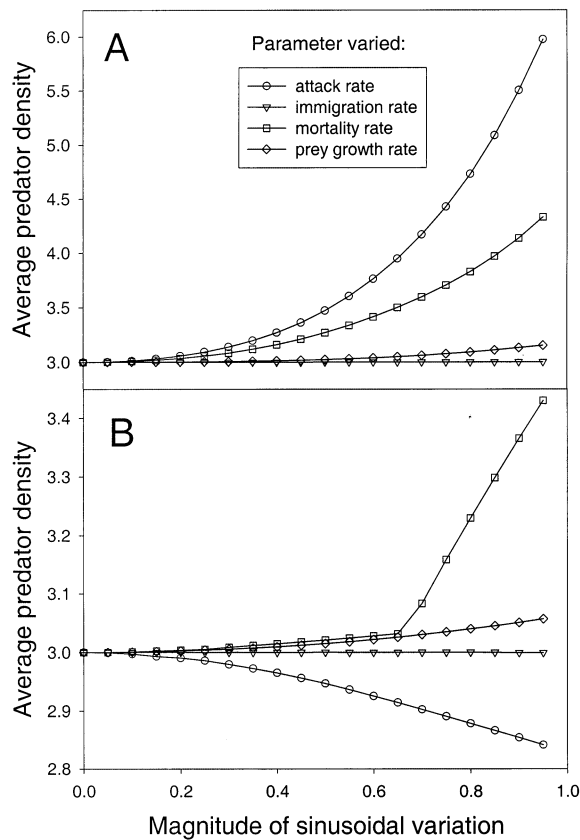
Fig. 3. Predator density through time, given sinusoidal variation in attack rates. For the example shown, $r_2 = 0.4$, $b_2 = m = I = 1$, $d_2 = 0$. Solid horizontal line: equilibrium P for constant $a_2 = 0.2$. Solid wavy line: $P(t)$ for sinusoidal $a_2(t) = 0.2(1 + 0.5 \sin 2\pi ft)$ where $f = 0.06$ (as in Fig. 2A). Dashed line: moving equilibrium P with sinusoidal a_2.

Fig. 2. Time-averaged predator density for model (1), with sinusoidal variation in one parameter at a time with very weak density dependence (d_2 set to 0). The magnitude of the variation (x in the text) is the abscissa. The mean values of the parameters are $a_2 = 0.2$, $r_2 = 0.4$, $b_2 = m = I = 1$. A. Slow variation (frequency $f = 0.06$). In all cases, average predator density either remains constant or increases with increasing magnitude of parametric variation. Note: the relative positions of the lines can be altered by changing the mean values of the parameters. B. Fast variation ($f = 0.24$).

between realized predator numbers and the moving equilibrium. Nonetheless, when time-averaged predator density is evaluated for different magnitudes of variation, the qualitative conclusions we reached by assuming a moving equilibrium in a slowly varying environment still hold. For instance, average predator density is independent of the magnitude of variation in prey immigration rate (Fig. 2A, line with triangles). Increasing the magnitude of variation in attack rates or predator mortality increases average predator abundance, and does so substantially if the amplitude of variation is large. However, there is now a small increase in average predator density with increasing variation in prey intrinsic growth, an effect not predicted by assuming a tightly-tracked, moving equilibrium.

In the results reported in Fig. 2B, we again examine the system with no direct density dependence for the subsidized prey, but now with faster variation ($f =$
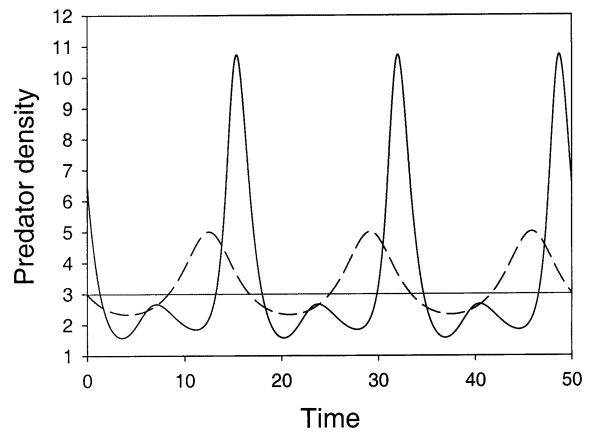
0.24). Again, variation in prey immigration has no effect, and variation in prey growth rate has only a small effect, on average predator abundance. Variation in predator mortality increases average predator numbers, particularly when such variation is large in magnitude. But variation in attack rates depresses predator numbers.

In the examples shown in Fig. 2, the magnitudes of the effects with fast variation are all reduced, compared to systems with slower variation (compare the ordinates of Fig. 2A and B). However, this need not always be the case, given resonance effects and nonlinear dynamics. Fig. 4A shows how average predator abundance varies as a function of the frequency of variation for each parameter. The effect of temporal variation depends upon the frequency of variation, as well as its magnitude, in a parameter-specific manner.

At low frequency (the leftmost points in Fig. 4), species' densities tend to follow their (moving) equilibria. At high frequencies (the rightmost points in Fig. 4), variations in densities are small and approximately sinusoidal, so the mean is close to the equilibrium values with each parameter at its mean. At intermediate frequencies, more complex patterns of variation may emerge. With the parameters used in Fig. 4A, the system has a natural frequency of about 0.12 (with constant parameters, it oscillates at this frequency as it settles to its equilibrium). As a parameter is varied at some frequency, it will tend to make the species' densities vary at the same frequency, except near multiples or sub-multiples of the natural frequency. For example, with a parameter varying at half (0.06) or twice (0.24) the natural frequency, species' densities can consist of alternating large and small peaks, due to the interaction of the two frequencies (see Fig. 3). These changes in the
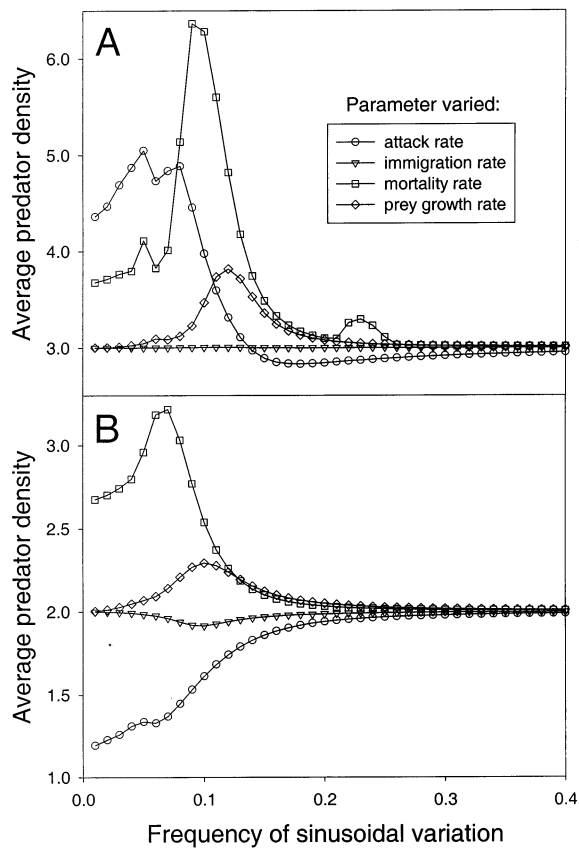
Fig. 4. Time-averaged predator density as a function of the frequency of sinusoidal variation in parameters. The average parameter values are $a_2 = 0.2$, $r_2 = 0.4$, and $b_2 = m = I = 1$. The time-varying parameter changes in accord with $q(t) = q_{av}(1 + 0.8 \sin 2\pi ft)$, where q_{av} is the average parameter value. Note that at high frequencies the densities converge on the equilibrium provided by assuming parameters are fixed at their mean values. A. No density dependence ($d_2 = 0$). B. With density dependence ($d_2 = 0.04$).

pattern of the densities cause the complex response shown in Fig. 4A.

Finally, in Fig. 4B we introduce direct density dependence in the prey ($d_2 = 0.04$). Without variation, an increase in prey density dependence indirectly reduces predator abundance, and so facilitates prey coexistence. The effect of variation is generally smaller in magnitude but in the same direction as without density dependence. The major exception is variation in attack rate, which depresses average predator density with density dependence. With very fast variation, average density again converges on the equilibrial density (Fig. 4B, right side).

In general, these numerical studies support the qualitative conclusions reached earlier, based on the assumption that a system tracks a moving equilibrium. In an open system with external inputs of one prey species, there is no general, universal effect of temporal variation upon the likelihood of prey species coexistence (as

assessed by the impact of such variation upon predator abundance). Temporal variation can at times depress predator abundance, for instance if prey experience strong direct density dependence. Temporal variation in some system attributes (e.g. prey immigration rates) may have little or no effect on deterministic conditions for species coexistence. Finally, temporal variation in some parameters may greatly exacerbate the problem of prey coexistence (e.g. if such variation is mainly experienced by a predator via its own mortality).

In the models explored above, one prey species was assumed to enjoy a spatial subsidy, but not the predator. In many open systems, it may be more likely that subsidies will be observed in consumers than in their resources. A specialist herbivore can in principle greatly suppress the plant species it requires, even to the point of local extirpation, if its numbers can be sustained by immigration. Consider the following simple model illustrating this effect: $dP/dt = P(abR - m) + I$, and $dR/dt = R(r - dR) - aPR$. Because the immigrant predators must be born elsewhere, and their parents must have consumed prey to reproduce, predator subsidies implicitly involve indirect interactions between alternative prey populations occupying different habitats (Holt and Hochberg 2001). Following the same protocol sketched above, if we consider slow temporal variation in each parameter, taken separately, it is readily shown that the only parameter for which variation influences the long-term average growth rate of the prey, when rare, is the predator mortality rate. Variation in predator mortality increases average predator numbers, and so makes it harder for the prey species to persist in the local environment. This particular result appears to be quite robust; a combination of spatial subsidies (to either the prey, or the predator) and temporal variation in predator mortality makes persistence of locally specialized prey more difficult.

Conclusions

The most important insight provided by the above models may be that there is no generic effect of temporal variation upon species coexistence in open communities, but rather that a variety of outcomes are possible, depending upon which facet of the system provides an avenue for the expression of temporal variation. In some circumstances temporal variation in open systems can weaken the impact of external subsidies on coexistence, but in others temporal variation can greatly aggravate the problem of coexistence between species. Abrams (1999) has likewise emphasized the range of effects on coexistence that are possible when considering the impacts of exogenously or endogenously driven temporal variation.

The analysis of temporal variation sketched above suggests a general protocol that may be broadly useful for assessing the impact of slow variation upon local community structure. The central paradigm of community ecology is that to understand community structure, one focuses on conditions for a species to increase when rare (Law and Morton 1996, Loreau and Mouquet 1999). If interspecific interactions are important, the per capita growth rate of an invading species will be a function of the densities of the resident community members. If the local environment varies slowly, and the dynamics of the resident community tend towards a moving equilibrium, the functional form of this equilibrium may permit a first-order assessment of the impact of temporal variation upon species coexistence.

Consider for instance the classical Lotka-Volterra model for direct competition between two species: $(dN_i/dt)/N_i = r_i - d_i N_i - d_{ij} N_j$, $i, j = 1, 2$, and $i \neq j$. Here, N_i is the density of competitor i, r_i is its intrinsic growth rate, d_i is the strength of direct density dependence in species i, and d_{ij} is the strength of density dependence exerted by species j upon species i. If species i is rare, and species j is at its carrying capacity ($K_j = r_j/d_j$), species i increases if $r_i > d_{ij} N_j^* = d_{ij} r_j/d_j$.

Now assume slow variation of one parameter, so that species j stays near its (changing) carrying capacity. The effect of variation upon species coexistence is parameter-dependent. If temporal variation influences intrinsic growth rates or the strength of interspecific density dependence (d_{ij}), one can just replace r_i with $\langle r_i \rangle$ and d_{ij} with $\langle d_{ij} \rangle$ in the invasion condition; slow variation has no effect upon coexistence. By contrast, variation in the strength of density dependence for the resident species (d_j) increases the average density of the resident, and makes exclusion of the invading species more likely. Thus, slow variation in intraspecific density dependence makes coexistence more difficult, whereas variation in intrinsic growth rates or interspecific interaction strengths has no effect.

A number of caveats are in order.

First, we have considered variation that affects the resident species, but not the growth parameters of the species whose persistence is of concern. More broadly, one might expect that species might experience complex patterns of covariation among parameters, both directly and indirectly (via shifts in other species' abundances, etc.). Consider again our expression for persistence of a non-immigrating prey species, facing mortality from a predator maintained by an immigrating prey species. Applying time-averaging, the expression for persistence is $\langle r_1 \rangle > \langle a_1 P \rangle$, which simply states that the average intrinsic rate of increase should exceed the average rate of mortality inflicted by the predator. This in turn can be written as $\langle r_1 \rangle > \langle a_1 \rangle \langle P \rangle + \text{Cov}(a_1, P)$, where $\text{Cov}(a_1, P)$ is the covariance between the attack rate a_1, and predator density, P. With a constant attack rate all the points made

above still hold; e.g. variation in the non-immigrant prey's intrinsic growth rate does not, in a deterministic model, affect conditions for its persistence.

However, if the attack rate upon the non-immigrating prey itself varies, then one must consider the pattern of covariation between attacks and predator abundance, as well as effects of variation upon average predator numbers. In our example, assume predator abundance varies because of variation in the attack rates. If predator attacks on the two prey species change in lock-step, so that $a_1(t) = k a_2(t)$, where k is a positive constant, and the environment changes slowly, so that predator numbers are approximately at equilibrium, the rate of mortality upon prey species 1 when it is rare is $a_1(t)P(t) = (r_2 - d_2 m/(a_2(t) b_2)) k + a_1(t) I b_2/m$. Variation in attack rates increases the time-averaged magnitude of the term stemming from prey density dependence, and thus lowers the average rate of predation upon the non-immigrant prey when it is rare. Hence, correlated variation in attack rates among prey tends to facilitate their coexistence.

Second, we have largely focused on one simple model, dealing with one particular question of species coexistence (apparent competition via a shared predator). Changing the model form will surely influence a number of our particular conclusions. For instance, preliminary studies (Holt and Barfield, unpubl.) of models with saturating functional and numerical responses suggest that these traits make it more likely that temporal variation depresses predator numbers. If this proves to hold across a wide range of models, it may be the case that temporal variation will often prove to facilitate prey species coexistence, via the relaxation of apparent competition. By contrast, in models of keystone predation, unstable dynamics often makes coexistence harder (Abrams 1999).

Third, we have examined variation that can be mimicked by deterministic fluctuations in the parameters of standard ecological models, and examined the consequences of this for the long-term average rate of increase for a species when it is rare. This neglects the important problem of persistence posed by demographic stochasticity even in constant, favorable environments. A population may have a positive expected long-term growth rate, yet still go extinct if forced to very low densities episodically. Species which cannot replenish their numbers from an external pool are likely to go extinct if forced to low densities with sufficient frequency. This suggests that large-amplitude temporal variation may quite generally disfavor any species which are not part of a broader regional pool, permitting recurrent immigration to rescue populations (Brown and Kodric-Brown 1977) from transient periods of low numbers, in effect tilting the balance between regional and local processes (Partel et al. 1996, 2000), in favor of the former. This observation should pertain broadly to any community in which a set of

resident, locally superior species contend with an influx of immigrant species, regardless of the details of the mechanisms of the interactions amongst residents and immigrants.

Finally, a significant challenge is to relate these rather abstract models more directly to empirical plant-herbivore and other natural enemy-victim systems. Many plants have seed banks or structurally unavailable tissues, which makes it more difficult for herbivores to directly cause extinction, at least over short time-scales. Moreover, herbivores often seem to matter mainly in modulating competition for resources (Holt et al. 1994), a factor which is ignored in the above models. Many plant-herbivore interactions involve species with significant age or stage structure in seasonal environments, and the differential equation models and conclusions explored above are likely to be inadequate descriptors, except as possibly inspirational metaphors for the rich variety of disparate impacts of temporal variation one might expect to observe in natural systems. Finally, it is important to address the issue of temporal variation in more complex food webs, in which predation and resource limitation can both constrain species coexistence (as in trophic cascades, Carpenter and Kitchell 1993, Pace et al. 1999, Polis 1999, Power 2000).

In conclusion, a significant task for future theoretical and empirical studies is to understand the combined effects of temporal and spatial heterogeneity in determining the realized structure of ecological communities. In some cases, it appears that environmental variability facilitates species coexistence (Chesson 2000), but in others variation may destroy coexistence (this paper, Abrams 1999). Given the massive anthropogenic changes in landscapes and temporal patterns of environmental conditions the world is now experiencing, there is an urgency now more than ever in understanding more deeply the implications of temporal variability in a spatially heterogeneous world.

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