

Host plant quality, spatial heterogeneity, and the stability of mite predator–prey dynamics

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Abstract Population dynamics models suggest that both the over-all level of resource productivity and spatial variability in productivity can play important roles in community dynamics. Higher productivity environments are predicted to destabilize consumer–resource dynamics. Conversely, greater heterogeneity in resource productivity is expected to contribute to stability. Yet the importance of these two factors for the dynamics of arthropod communities has been largely overlooked. I manipulated nutrient availability for strawberry plants in a multi-patch experiment, and measured effects of overall plant quality and heterogeneity in plant quality on the stability of interactions between the phytophagous mite *Tetranychus urticae* and its predator *Phytoseiulus persimilis*. Plant size, leaf N content and *T. urticae* population growth increased monotonically with increasing soil nitrogen availability. This gradient in plant quality affected two correlates of mite population stability, population variability over time (i.e., coefficient of variation) and population persistence (i.e., proportion of plant patches colonized). However, the highest level of plant quality did not produce the least stable dynamics, which is inconsistent with the “paradox of enrichment”. Heterogeneity in plant productivity had modest effects on stability, with the only significant difference being less variable *T. urticae* densities in the heterogeneous compared to the corresponding homogeneous treatment. These results are generally congruent with metapopulation theory and other models for spatially segregated populations, which predict that stability should be governed largely by relative movement rates of predators and prey—rather than patch quality.

Keywords Paradox of enrichment · Productivity · Resource heterogeneity · Population stability · Persistence

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Introduction

In tritrophic systems the population dynamics of intermediate consumers are governed by both bottom-up (i.e., resource mediated) and top-down (i.e., predator mediated) processes (Price et al. 1980). For phytophagous arthropods plant nutrient quality or abundance can affect herbivore behavior and physiology, with ensuing impacts on overall population performance (Pfeiffer and Burts 1983). Such bottom-up effects on herbivore quality or abundance may ultimately manifest at the community level by mediating the stability of consumer–resource interactions (Fussmann et al. 2000) and, in a biological control context, natural enemy efficacy (Walde 1995).

Ecologists have long been concerned with why populations cycle and the stability of population dynamics (Elton 1924). Early population dynamics theory suggested that high system productivity (i.e., high resource or prey population growth in the absence of predation) should be destabilizing (Rosenzweig 1971). In other words, all else being equal, a resource enriched system should exhibit more extreme fluctuations or increased likelihood of extinction. Evidence for this prediction from experimental studies is equivocal, with both support for (Huffaker et al. 1963; Fussmann et al. 2000) and refutation of the destabilizing effect of enrichment (McCauley et al. 1988; McCauley and Murdoch 1990). More recent theory suggests that weaker than expected effects of enrichment on stability may stem from spatial segregation in populations (Jansen 1995), which has been supported empirically in model aquatic systems (Holyoak 2000). Nonetheless, the dynamic consequence of resource productivity for stability of terrestrial systems has been scarcely studied (Huffaker et al. 1963).

In addition to overall resource or prey productivity, spatial variability in productivity (i.e., heterogeneity) may play an important role in community dynamics. For phytophagous consumers, heterogeneity can stem from fine scale variation in nutrient availability (Daane and Williams 2003; Pfeiffer and Burts 1983) or edaphic conditions (Denyer et al. 2010), mixed plantings of different plant species (Banks 1998) or genotypes (Underwood 2009), or patchiness in prior herbivore damage (Utsumi et al. 2009). Such plant heterogeneity can impart unique dynamics to herbivore populations compared to homogeneous conditions (Helms and Hunter 2005; Underwood 2009). Population dynamics theory suggests that differences in demographic rates stemming from underlying resource heterogeneity may affect host–parasitoid or predator–prey interactions—by either directly increasing dynamic stability (McLaughlin and Roughgarden 1992) or by supplementing existing stabilizing sources of heterogeneity in consumer attack rate (Holt and Hassell 1993). Conversely, metapopulation models intended to describe predator–prey dynamics in inherently patchy environments suggest that spatial variability in patch quality has little effect on metapopulation stability (Sabelis et al. 2005). Yet, to date there have been few explicit experiments of the sort needed to reconcile these conflicting predictions regarding the role of resource heterogeneity on predator–prey stability (but see Mitsunaga and Fujii 1997).

Acarine predator–prey systems have long been used as model systems for testing population dynamics theory (Harmsen and Sabelis 1992). These systems are characterized frequently by overexploitation of prey at the local scale by highly efficient predators, which leads ultimately to local extinction (Pels and Sabelis 1999; Nachman and Zemek 2003) but with potential for persistence at the metapopulation scale (Sabelis et al. 1991). Thus, many studies have investigated factors that may affect the stability of these interactions, including spatial structure and patch number (Huffaker et al. 1963; van de Klashorst et al. 1992), dispersal abilities (Sabelis et al. 1991; Zemek and Nachman 1998), and habitat complexity (van de Klashorst et al. 1992; Janssen et al. 1997). Collectively

these studies indicate that complexity in spatial structure, by limiting predator efficiency, is important for regional persistence of mite populations (Ellner et al. 2001).

Phytophagous mites are common pests that cause significant damage to a wide range of plant species (Huffaker et al. 1969). As with other herbivores, the population growth rates of these mites depend on aspects of plant condition and nutrient quality, including: plant genotype (Underwood 2007), prior herbivory (Karban and English-Loeb 1990), and fertilizer (Walde 1995). In addition predatory mite movement is driven largely by the distribution and abundance of prey mite populations (Zemek and Nachman 1998). However, the extent to which bottom-up differences in phytophagous mite demographic rates or spatial variability in mite productivity may mediate the stability of mite predator–prey dynamics has not been evaluated.

I conducted a pair of experiments to test the hypothesis that plant nutrient quality affects the stability of acarine predator–prey interactions. First, I quantified spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), population growth on individual host plants over a gradient of nitrogen availability. Results from this first experiment were then used in a field experiment to define appropriate soil nutrient additions to produce a linear gradient in plant quality and heterogeneity in quality in a multi-patch design. These experiments were used to evaluate two predictions: (1) high plant quality destabilizes interactions, whereas (2) heterogeneity in quality promotes stability.

Materials and methods

Plant quality and prey population growth

I set up a greenhouse experiment to quantify *T. urticae* population performance over a gradient in plant nitrogen availability. The purpose of this experiment was to estimate prey population growth rates on single plants in the absence of predation, then use this to guide fertilizer addition levels for a later study of multi-patch mite predator–prey interactions.

Strawberry plants (*Fragaria ananassa* Duchesne cv. “Jewel”; Lassen Canyon Nurseries, Yuba City, CA, USA) were potted in 10 cm pots that were filled with a 5:1:1 mixture of vermiculite, coarse sand, and soil (UC Berkeley “Genetics” mix; approx. 6:1:1:1 top-soil:coarse sand:fine beach sand:peat moss by volume). These plants were then covered individually by a 60 × 60 × 60 cm mesh and plastic cage (Bugdorm 3, Megaview Sciences Inc., Taiwan) and were housed in a greenhouse at UC Berkeley’s Gill Tract field station (Albany, CA, USA). I watered the plants twice per week and once per week I made nutrient additions via 100 ml of a Hoagland’s solution (Ross 1974) with 0, 5, 10, 20, or 40 mM of nitrogen [$\text{Ca}(\text{NO}_3)_2$ and KNO_3 ; all other essential plant nutrients were the same]. There were 26 total cages with 6 replicates at 0, 5, and 40 mM N, and 4 replicates at 10 and 20 mM N. The pot soil mixture and nutrient additions were intended to allow explicit control of the amount and type of available nutrients to produce a gradient from high (e.g., 0 mM) to low (e.g., 40 mM) N stressed plants. After 3 weeks of fertilizing, all plants were infested with *T. urticae* by introducing a 1 cm² clipped section of lima bean (*Phaseolus lunatus* L.) leaf from a colony established from mites originally provided by Biotactics Inc. (Romoland, CA, USA). Mean (\pm SD) mite density on these clippings based on 10 counted samples was 27 ± 16 mites in the adult or deutonymph stages. After infestation, strawberry plants were censused weekly for 5 weeks. At each of these census dates, I collected a 1 cm² clipping from each leaf, and counted the number of spider mites of all stages on each clipping.

Data analysis

I compared the change in spider mite population density between the first and last censuses with ANOVA, with fertilizer level treated as a fixed factor (Crawley 2009). Spider mite density was calculated as the total number of all mite stages divided by the number of 1 cm² clippings counted for each plant at a given census. Population change was calculated by subtracting the density on a given plant at the first census from the density at the fifth census. Thus positive values represent an increase in population density over the study. This metric is intended to serve as a proxy for population growth rate. A significant effect of fertilizer level was followed-up with pair-wise *t* tests among fertilizer levels, while controlling for multiple tests.

Plant quality, heterogeneity, and predator–prey population stability

Next I conducted a field study with *T. urticae* and its predator, *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) to evaluate the effect of bottom-up enrichment on the stability of a multi-patch consumer–resource interaction. This experiment manipulated separately (1) overall quality of all plant patches, and (2) spatial variability in plant quality (i.e., heterogeneity) for *T. urticae*.

The experiment included 8 strawberry plants in each of 40 1.55 × 1.55 × 2 m tall lumite screen cages (21 × 21 threads/cm, Synthetic Industries Inc.). Plants were grown individually in 10 cm pots with the same soil and vermiculite mix as before, arranged in a circle with approximately 30 cm spacing between adjacent pots so that leaves of adjacent plants were not touching each other. This spacing was intended to act as a slight barrier to dispersal, which previous work suggests is necessary for persistence (McCauley et al. 2000). Cages were assigned randomly to one of four fertilizer treatments. Three treatments correspond to a gradient in soil N availability via weekly additions of 100 ml of Hoagland's solutions at 1, 5, or 15 mM N to all 8 plants per cage in the Low, Medium, or High fertilizer treatments (*n* = 10, 9, 10 cages), respectively. This range of fertilizer levels was chosen, based on results from the greenhouse experiment, to result in a linear gradient of prey mite population growth, with the Medium fertilizer level intermediate between the other two. The fourth treatment included heterogeneous application of 1 mM N solution to four plants (Het-Low) and 15 mM N to the remaining four plants (Het-High), with different N applications interspersed within a cage (*n* = 11 cages). This Heterogeneous treatment is intended to include approximately the same per cage average nutrient addition as the Medium treatment, but with greater spatial variability in plant quality.

After 4 weeks of fertilizing I placed a *T. urticae* infested bean clipping on each plant (mean ± SD of mobile stages only for 20 clippings = 37 ± 22). Three weeks later I placed a *P. persimilis* infested bean clipping onto each plant (mean ± SD of nymphs and adults for 20 clippings = 8 ± 6). Clippings were collected from a *P. persimilis* colony established from mites originally provided by Biotactics Inc. and raised on *T. urticae*. Beginning 2 weeks after predator introduction (to allow sufficient time for populations to establish) I censused all cages 5 times over the next 6 weeks. For the three homogeneous treatments I censused four plants per cage and in the Heterogeneous treatment I censused two high (15 mM N) and two low (1 mM N) fertilized plants per cage, with alternation of the plants being censused between adjacent weeks (i.e., each plant sampled every 2 weeks; 3 times over the duration of the study). At each census I counted the number of leaves on each plant, measured the size of every leaf (length of the mid-vein of the leaflet), and collected one leaflet from each leaf. This sampling scheme was meant to provide consistent

sampling effort at the individual plant and cage scales, while limiting the impact of the necessarily destructive nature of sampling for mites.

All collected leaflets were placed in bags and returned to the lab, where I counted the total number of eggs, larvae/nymphs, and adults of each mite species per leaflet. Spider mite and predator mite population densities at a given census were calculated for each plant by dividing the total number of mites of all stages by the mean leaflet length for the plant. Given the fairly consistent shape of leaflets, this measure of leaf size is not expected to unreasonably influence mite density estimates.

Leaflets from the final census were used to determine plant carbon and nitrogen content, as a measure of plant quality. Leaflets were oven dried for 3 days at 60°C, then I ground them to a fine powder using a Wigglebug mill for 1 min, then leaf nitrogen and carbon were measured using a CE Elantech NC2100 elemental analyzer.

Data analysis: plant response

To evaluate the effect of fertilizer addition on plant quality I compared leaf number and leaf size over the course of the experiment, and leaf nitrogen content at the last census. Leaf number and size were analyzed using separate linear mixed effects models with fertilizer treatment as a fixed effect and cage nested within census date as a random variable (Crawley 2009). This design accounts for variation associated with repeated measurement of plants within a given cage over census dates. Significant effects were followed-up with pair-wise linear mixed effects models among fertilizer treatments and between low or high fertilized plants in the homogenous versus heterogeneous treatments, while controlling for multiple tests. I tested for treatment effects on leaf carbon to nitrogen ratio (%C/%N) using a linear mixed effects model with individual plant nested within cage as a random variable. A significant effect was followed-up with pair-wise linear mixed effects models among fertilizer treatments and between low or high fertilized plants in the homogenous versus heterogeneous treatments, while controlling for multiple tests.

Data analysis: predator–prey dynamics

The hypotheses being tested concern the effects of plant quality on the stability of consumer–resource interactions, rather than offering predictions for specific consumer and resource densities. The relatively short duration of the field study precluded use of a press or pulse perturbation to evaluate stability (Glasby and Underwood 1996). Therefore, I estimated the effect of fertilizer treatments on what are assumed to be two correlates of stability (Connell and Sousa 1983) in the transient phase: (1) variability in population density (Holyoak 2000; Mueller and Joshi 2000), and (2) patch persistence (Dayton et al. 1984).

I compared variation in predator or spider mite densities using coefficient of variation (CV; Mueller and Joshi 2000). CV is a scaled measure of variability relative to the mean (SD/mean). Thus, less stable high amplitude fluctuations would result in relatively larger CV values than low amplitude fluctuations as long as the equilibrium is not also substantially higher for the high amplitude fluctuation. Spider mite and predator mite CVs were determined by calculating the standard deviation of mite density for individual plants over all censuses, then dividing by the mean mite density for each plant over those same censuses. This approach has been used to quantify stability in other spatially subdivided predator–prey model systems (Holyoak 2000). These values were compared among fertilizer treatments using separate linear mixed effects models with individual plant nested

within cage as a random variable (Crawley 2009). Significant treatment effects were followed up with pair-wise linear mixed effects models among treatments and between low or high fertilized plants in the homogenous versus heterogeneous treatments, while controlling for multiple tests.

As a second test of fertilizer effects on mite population stability I compared the proportion of plants within a cage at a given census that had persistent populations of *T. urticae* or *P. persimilis*. This analysis is intended to reflect the likelihood of patch apparent extinctions among fertilizer treatments. The proportions of colonized plants were compared among treatments with separate linear mixed effects models for each species, with cage census as a random variable.

Results

Plant quality and prey population growth

The change in *T. urticae* population density between the first and fifth censuses differed significantly among fertilizer levels ($F_{4,21} = 7.287$, $P = 0.0008$). Mite population density failed to increase at the lowest fertilizer level, but was increasingly positive at higher fertilizer levels (Fig. 1). *T. urticae* densities at the final census showed a similar pattern, with mean densities (\pm SE) of 1.17 (± 0.46), 7.44 (± 2.35), 13.61 (± 2.61), 13.32 (± 2.35), and 17.61 (± 2.86) mites/cm² at 0, 5, 10, 20, and 40 mM N, respectively. These results suggest that fertilizer levels of 0, 5, and 15 mM N would provide a near-linear gradient of plant quality on which to study *T. urticae*–*P. persimilis* interactions.

Plant quality, heterogeneity, and mite population stability

Plant response

Both leaf number ($F_{3,36} = 17.583$, $P < 0.0001$) and leaf C:N ($F_{3,36} = 24.834$, $P < 0.0001$) were significantly affected by fertilizer treatment, whereas leaf width was not ($F_{3,36} = 1.619$, $P = 0.20$). Leaf number was lower in the Low fertilized plants compared to the other treatments (Table 1). The Heterogeneous treatment did not differ from the Medium treatment, but high fertilized plants in the Heterogeneous treatment had a greater

Fig. 1 Mean (\pm SE) change in *Tetranychus urticae* density of all stages combined among fertilizer levels between the first and fifth censuses. Points with different letters denote significant differences

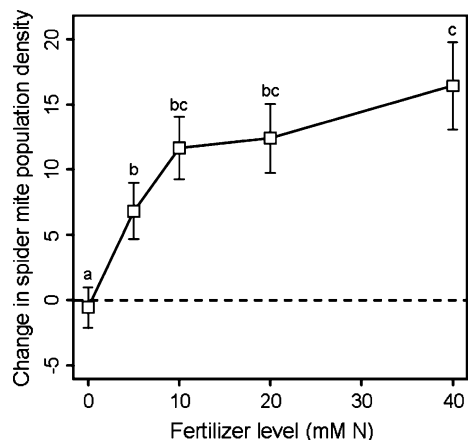
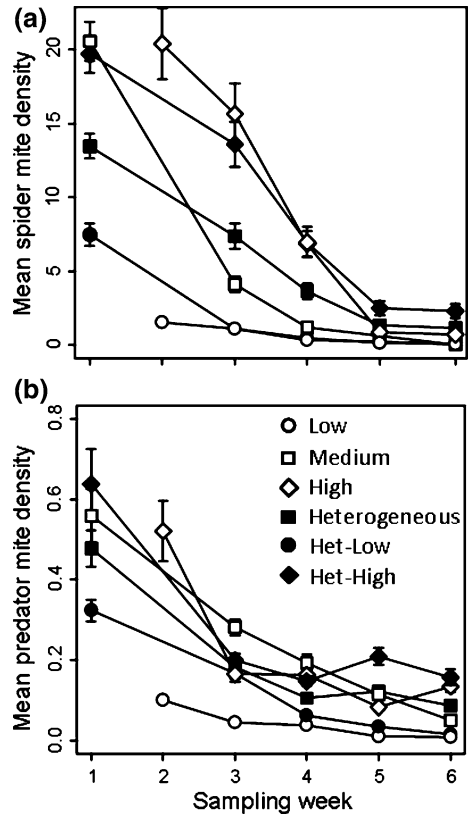


Table 1 Plant and mite responses to fertilizer levels, expressed as means (\pm SE) over all censuses

Response ¹ variable	Fertilizer treatment					
	Low ²	Medium	High	Heterogeneous	Het-Low ^{3,4}	Het-High
Number of leaves	8.177 \pm 0.293 ^a	12.070 \pm 0.433 ^b	12.421 \pm 0.335 ^b	12.458 \pm 0.404 ^b	9.053 \pm 0.348 ^A	15.893 \pm 0.574 ^{B,*}
Leaf C:N	34.072 \pm 1.518 ^a	23.441 \pm 0.728 ^b	20.761 \pm 0.703 ^c	25.294 \pm 1.054 ^b	29.922 \pm 1.283 ^A	20.424 \pm 0.812 ^B
Prey variability	1.1186 \pm 0.106 ^a	1.764 \pm 0.123 ^b	1.266 \pm 0.111 ^a	1.330 \pm 0.135 ^a	1.709 \pm 0.100 ^{A,*}	1.281 \pm 0.137 ^B
Predator persistence	0.427 \pm 0.055 ^a	0.792 \pm 0.055 ^b	0.757 \pm 0.055 ^b	0.738 \pm 0.055 ^b	0.658 \pm 0.055 ^{A,*}	0.836 \pm 0.055 ^B

¹ Leaf number, C:N, and prey CV calculated as means per cage averaged over all censuses. Persistence calculated as overall proportion per cage averaged over all censuses
² Different lower case letters denote significant differences among fertilizer treatments
³ Different upper case letters denote significant differences between Low and High fertilized plants within the Heterogeneous treatment (Het-Low vs. Het-High)
⁴ Significant differences between the Low or High fertilizer treatments versus Low or High fertilized plants in the Heterogeneous treatment are denoted by **#"

Fig. 2 *Tetranychus urticae* (a) and *Phytoseiulus persimilis* (b) density (total number of all stages/cm of leaf length per plant) within a cage among fertilizer levels over time



mean number of leaves than in the homogeneous treatment. Leaf C:N at the final census was lower at higher N addition levels, but did not differ between the Medium and Heterogeneous treatments (Table 1).

Mite population response

Although individual plants in each of the treatments showed dynamics that may represent predator–prey cycles, after averaging among plants and between replicates the treatments all show a strong monotonic decline (Fig. 2). Both predator mite and especially spider mite densities started higher at higher fertilizer levels but declined quickly—to very low densities by the last census. At the end of the study, across all treatments, 41% of plant patches showed local apparent extinction of *T. urticae* and 48% had no *P. persimilis*. Densities were consistently low in the Low treatment. For both species, the densities in the Heterogeneous treatment were qualitatively more similar to the Medium treatment than the other two fertilizer levels. The high and low fertilized plants in the Heterogeneous treatment most closely followed the trajectories of the High and Low fertilized treatments, respectively—especially for *T. urticae* dynamics (Fig. 2a).

Tetranychus urticae coefficient of variation across censuses was significantly affected by fertilizer treatment ($F_{3,36} = 5.645$, $P = 0.0028$), whereas *P. persimilis* CV was not ($F_{3,36} = 0.732$, $P = 0.54$). Variation in *T. urticae* density was higher in the Medium

treatment than in the other homogenous treatments and the Heterogeneous treatment (Table 1). Spider mite CV was also higher for the low fertilized plants in the Heterogeneous treatment compared to the Low homogeneous treatment.

Phytoseiulus persimilis patch persistence across censuses was significantly affected by fertilizer treatment ($F_{3,36} = 14.942$, $P = 0.022$), whereas *T. urticae* persistence was not ($F_{3,36} = 0.732$, $P = 0.54$). The Low fertilized treatment supported a lower proportion of colonized plants by predator mites than the other treatments (Table 1), and was significantly lower than the low fertilized plants in the Heterogeneous treatment.

Discussion

Several different terms exist in the ecological literature to describe the relative level of stability of a population or collection of interacting populations. Among the commonly used terms are: resistance, elasticity, resilience, and persistence—whose different meanings encapsulate unique aspects of stability and the evidence necessary to evaluate it (Connell and Sousa 1983). Given the monotonic decline in mite populations over a relatively compressed time scale it was not possible to conduct a perturbation experiment, which is necessary to evaluate the stability of a point equilibrium (Glasby and Underwood 1996). Therefore I estimated two alternative proxies for mite predator–prey stability, temporal population variability (i.e., coefficient of variation—Holyoak 2000; Mueller and Joshi 2000) and a lack of local population extinction (i.e., patch persistence—Dayton et al. 1984). Both of these stability metrics showed effects of plant quality associated with the different fertilizer treatments. However, the prediction for a destabilizing effect of overall plant quality was not supported and the prediction for a stabilizing effect heterogeneity was only modestly supported.

The “paradox of enrichment”, an outcome of simple predator–prey models that include saturation in the predator feeding rate at higher prey densities (Rosenzweig 1971), suggests that more productive environments should result in less stable dynamics for well mixed populations. Conversely, if populations are subdivided into distinct patches, productivity is not expected to affect stability (Jansen 1995). Huffaker et al. (1963) varied the number of orange patches available to phytophagous mites, which may be viewed as a manipulation of resource productivity, and found shorter duration of mite persistence at the higher resource level—supporting the paradox of enrichment. In the current study the nutrient additions I made to strawberry plants increased plant quality, both in terms of leaf number and plant N content, which led to greater *T. urticae* population growth on plants receiving more N. A gradient in plant quality affected both *T. urticae* population variability and *P. persimilis* persistence, which supports the general hypothesis that productivity affects stability (Fussmann et al. 2000). However, both metrics of mite stability showed non-linear patterns in which the highest N addition level was not the least stable. Thus, these results do not obviously support either of the two classes of model predictions.

In the case of *P. persimilis* persistence in the homogeneous treatments, which was lower at the low N level compared to higher fertilizer levels, it is plausible that the results are attributable to a threshold metabolic requirement for predators. Other studies have shown that low productivity habitats can lead to shortening of food chain length (Jenkins et al. 1992). Thus, very low productivity may destabilize predator–prey interactions by facilitating predator extinction. This mechanism, however, would not explain why population variability was highest at the intermediate N level.

Many studies have investigated how heterogeneity in consumer attack rate stemming from aggregation of consumers, differential resistance to attack, or the presence of refuges can affect population dynamics (e.g., Hassell 1978). More recent models suggest that heterogeneity in the demographic characteristics of hosts and parasitoids (Holt and Hassell 1993) or predators and prey (McLaughlin and Roughgarden 1992) may increase further population stability. In effect, these models predict that habitat heterogeneity increases stability because low productivity patches have low host densities, and therefore incur less intense attack, resulting in a partial refuge. Partial refuges supply a small number of individuals to more productive patches, which stabilizes regional dynamics. The heterogeneous fertilizer additions I made produced greater spatial variability in predator and prey mite abundance compared to the corresponding homogenous medium N treatment (MP Daugherty, unpublished data). However, the only evidence that heterogeneity in plant quality affected mite stability was lower *T. urticae* population variability in the heterogeneous compared to homogenous medium N treatments—there were no significant differences in *P. persimilis* population variability or the persistence of either species.

The only other experimental test of resource heterogeneity and stability involved a study of bean weevil and parasitoid dynamics, for which weevil development rate depends on bean type (Mitsunaga and Fujii 1997). This study found that host-parasitoid persistence was not facilitated by mixed bean assemblages—it was highest on just the poorer quality bean type. Their result is likely attributable to higher parasitism rates in the presence of high quality beans, which meant that a potentially important non-demographic stabilizing sources of heterogeneity, heterogeneous attack rates, was missing (Holt and Hassell 1993). In the current study the generally weak effect of heterogeneity in plant quality may have also occurred because of similar spillover predation. Predator mite persistence was higher in low N patches in the heterogeneous treatment compared to plants in the homogenous low N treatment, suggesting that spatial coupling of high and low quality patches occurred. Such predator spillover from high quality patches may limit the potential for low quality patches to act as partial refuges, thereby weakening the stabilizing effects of demographic heterogeneity.

Another explanation for the observed weak effects of heterogeneity in plant quality is that this acarine predator–prey system behaves as a true metapopulation. In this scenario stability is an ongoing balance between prey colonizing new patches and predators driving newly discovered patches extinct (Zemek and Nachman 1998; Pels and Sabelis 1999), rather than patches having distinct dynamics. Habitat structure, especially as it relates to differential dispersal rates by predators and prey (Sabelis et al. 1991), is important for that balance (McCauley et al. 2000; Ellner et al. 2001). But heterogeneity in patch quality is not expected to influence stability (Sabelis et al. 2005). Thus if *P. persimilis* were able to efficiently find and extirpate *T. urticae* on different strawberry plants, regardless of fertilizer level, any stabilizing effects of spatial variability in *T. urticae* demographic rates would be constrained.

In agricultural systems fertilizer addition can play an important role in pest dynamics (Pfeiffer and Burts 1983). The extent to which such resource enrichment leads to pest outbreaks depends on the ability of natural enemies to compensate rapidly for increasing pest populations (Walde 1995). The extent to which productivity will affect the stability of such interactions will depend on whether these systems behave as spatially variable but well mixed populations versus patchy metapopulations, an understanding of which requires refined measures of how plant spacing and prey abundance affect predator movement and attack rate.

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References

- Banks J (1998) The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. *Oecologia* 117:239–246
- Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. *Ecology* 121:789–824
- Crawley M (2009) *The R book*. Wiley, West Sussex
- Daane KM, Williams LE (2003) Manipulating vineyard irrigation amounts to reduce insect pest damage. *Ecol Appl* 13:1650–1666
- Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R, Ven Tresca D (1984) Patch dynamics and stability of some California kelp communities. *Ecol Monogr* 54:253–289
- Denyer JL, Hartley SE, John EA (2010) Both bottom-up and top-down processes contribute to plant diversity maintenance in an edaphically heterogeneous ecosystem. *J Ecol* 98:498–508
- Ellner SP, McCauley E, Kendall B, Briggs CJ, Hosseini PR, Wood SN, Janssen A, Sabelis MW, Turchin P, Nisbet RM, Murdoch WW (2001) Habitat structure and population persistence in an experimental community. *Nature* 412:538–543
- Elton CS (1924) Periodic fluctuations in the numbers of animals: their causes and effects. *Brit J Exp Biol* 2:119–163
- Fussmann GF, Ellner SP, Shertzer KW, Hairston NG (2000) Crossing the Hopf bifurcation in a live predator–prey system. *Science* 290:1358–1360
- Glasby TM, Underwood AJ (1996) Sampling to differentiate between pulse and press perturbations. *Environ Monit Assess* 42:241–252
- Harmsen R, Sabelis MW (1992) Of mites and models: an introduction to the symposium proceedings. *Exp Appl Acarol* 14:179–184
- Hassell MP (1978) *The dynamics of arthropod predator–prey systems*. Princeton University Press, Princeton
- Helms SE, Hunter MD (2005) Variation in plant quality and the population dynamics of Herbivores: there is nothing average about Aphids. *Oecologia* 145:197–204
- Holt RD, Hassell MP (1993) Environmental heterogeneity and the stability of host–parasitoid interactions. *J Anim Ecol* 62:89–100
- Holyoak M (2000) Effects of nutrient enrichment on predator–prey metapopulation dynamics. *J Anim Ecol* 69:985–997
- Huffaker CB, Shea KP, Herman SG (1963) Experimental studies on predation: complex dispersion and levels of food in an acarine predator–prey interaction. *Hilgardia* 34:305–330
- Huffaker CB, van de Vrie M, McMurry JA (1969) The ecology of Tetranychid mites and their natural control. *Annu Rev Entomol* 14:125–174
- Jansen VAA (1995) Regulation of predator–prey systems through spatial interactions: a possible solution to the paradox of enrichment. *Oikos* 74:384–390
- Janssen A, van Gool E, Lingeman R, Jacas J, van de Klashorst G (1997) Metapopulation dynamics of a persisting predator–prey system in the laboratory: time series analysis. *Exp Appl Acarol* 21:415–430
- Jenkins B, Kitching RL, Pimm SL (1992) Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. *Oikos* 65:249–255
- Karban R, English-Loeb GM (1990) A “vaccination” of Willamette spider mites (Acari: Tetranychidae) to prevent large populations of Pacific spider mites on grapevines. *J Econ Entomol* 83:2252–2257
- McCauley E, Murdoch WW (1990) Predator–prey dynamics in environments rich and poor in nutrients. *Nature* 343:455–457
- McCauley E, Murdoch WW, Watson S (1988) Simple models and the variation in plankton densities among lakes. *Am Nat* 132:383–403
- McCauley E, Kendall B, Janssen A, Wood S, Murdoch W, Hosseini P, Briggs C, Ellner S, Nisbet R, Sabelis M, Turchin P (2000) Inferring colonization processes from population dynamics in spatially-structured predator–prey systems. *Ecology* 81:3350–3361

- McLaughlin JF, Roughgarden J (1992) Pattern and stability in predator–prey communities: how diffusion in spatially variable environments affects the Lotka–Volterra model. *Theor Popul Biol* 40:148–172
- Mitsunaga T, Fujii K (1997) The effects of spatial and temporal environmental heterogeneities on persistence in a laboratory experimental community. *Res Popul Ecol* 39:249–260
- Mueller LD, Joshi A (2000) *Stability in model populations*. Princeton University Press, Princeton
- Nachman G, Zemek R (2003) Interactions in a tritrophic acarine predator–prey metapopulation system V: within-plant dynamics of *Phytoseiulus persimilis* and *Tetranychus urticae* (Acarina: Tetranychidae, Phytoseiidae). *Exp Appl Acarol* 29:35–68
- Pels B, Sabelis MW (1999) Local dynamics, overexploitation and predator dispersal in an acarine predator–prey system. *Oikos* 86:573–583
- Pfeiffer DG, Burts EC (1983) Effect of tree fertilization on numbers and development of pear psylla (Homoptera: Psyllidae) and on fruit damage. *Environ Entomol* 12:895–901
- Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Ann Rev Ecol Syst* 11:41–65
- Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387
- Ross CW (1974) *Plant physiology laboratory manual*. Wadsworth, Belmont
- Sabelis MW, Diekmann O, Jansen VAA (1991) Metapopulation persistence despite local extinction: predator–prey patch models of the Lotka–Volterra type. *Biol J Linn Soc* 42:267–283
- Sabelis MW, Janssen A, Diekmann O, Jansen VAA, van Gool E, van Baalen M (2005) Global persistence despite local extinction in acarine predator–prey systems: lessons from experimental and mathematical exercises. *Adv Ecol Res* 37:183–220
- Underwood N (2007) Variation in and correlation between intrinsic rate of increase and carrying capacity. *Am Nat* 169:136–141
- Underwood N (2009) Effect of genetic variance in plant quality on the population dynamics of a herbivorous insect. *J Anim Ecol* 78:839–847
- Utsumi S, Nakamura M, Ohgushi T (2009) Community consequences of herbivore-induced bottom-up trophic cascades: the importance of resource heterogeneity. *J Anim Ecol* 78:953–963
- van de Klashorst G, Readshaw JL, Sabelis MW, Lingeman R (1992) A demonstration of asynchronous local cycles in an acarine predator–prey system. *Exp Appl Acarol* 14:185–199
- Walde SJ (1995) How quality of host plant affects a predator–prey interaction in biological control. *Ecology* 76:1206–1219
- Zemek R, Nachman G (1998) Interactions in a tritrophic acarine predator–prey metapopulation system: effects of *Tetranychus urticae* on the dispersal rates of *Phytoseiulus persimilis* (Acarina: Tetranychidae, Phytoseiidae). *Exp Appl Acarol* 22:259–278