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Trophic levels colonize sequentially but effects of habitat size and quality are transient

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ABSTRACT

Ecologists study assembling communities to understand mechanisms responsible for community-level patterns such as trophic structure. As communities assemble the incidence of each trophic level is conditional upon available resources such as prey, habitat area and productivity. Larger, more productive habitats may have more resources, increasing the potential to attract and to support greater species diversity, abundance, and more trophic levels. Predator trophic breadth and prey incidence may influence colonization order because obligate specialists have stricter prey dependencies than generalists do. In a system of stacked specialists, colonization may occur sequentially by trophic level because prey must be present before the next higher trophic level can colonize. Sequential colonization ordered by trophic level and by trophic breadth were tested with a field experiment and a Monte Carlo simulation. Community assembly was observed for an aphid food-web module composed of nine specialist and generalist predators colonizing plots seeded with California native annuals. To test the importance of habitat quality and resources, plots were manipulated for size (1 m² and 10 m²) and productivity (+/0 fertilizer), and then sampled for colonists many times during the growing season of 2003. Specialists from higher trophic levels were observed to colonize after their prey had arrived in the field experiment only, providing field support for the hypothesis of sequential colonization ordered by trophic level during community assembly. Intriguingly, generalist predators colonized later than specialists, despite the high and early availability of aphid prey. This finding contradicts the assumption that a narrow trophic breadth may disadvantage specialist colonizers. Initially, predator and prey densities increased on fertilized plots, but later this pattern was observed only on small plots. Patterns of sequential colonization order by trophic level and trophic breadth were demonstrated during community assembly, but the transient responses of colonizers to habitat size and productivity suggests that habitat resource effects deserve further study to determine their effects on trophic structure during community assembly.

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1. Introduction

Ecologists observe assembling communities to understand the mechanisms responsible for complex community structure and dynamics (Weiher and Keddy, 1995; Holt et al., 1999; Fukami, 2004). Observing community assembly and the order that species arrive can inform us of processes essential to structuring communities. This approach is used to examine impacts on community structure after natural and anthropogenic disturbances (Smith, 2006), community restoration (Summerville et al., 2006),

biological control (Schoenly and Cohen, 1991), and exotic species invasions (Fridley et al., 2007). Further examination of the interplay between community-based traits, such as trophic level or trophic breadth, will increase our understanding of factors that influence arrival order, species coexistence, colonization success, and overall community structure.

Community-based traits provide insight into mechanisms that produce trophic structure during community assembly (Fox and McGrady-Steed, 2002; Piechnik et al., 2008). As ecologists we have limited ability to predict probable arrival times of colonizing species due in part to local stochastic processes (Hassel et al., 1991) and to regional-based gradients (Klemola et al., 2002). However, observational and experimental evidence demonstrate community assembly to yield more than just random collections of species. Some interesting non-random patterns and explanations for

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trophic structure have emerged; trophic structure equilibrium formation by trophic groups or guilds (Heatwole and Levins, 1972), facilitation of predator colonization by prey (Glasser, 1982), and the colonization order of trophic breadths explaining constant connectance for food-webs of different sizes (Piechnik et al., 2008). Identifying dominant factors that produce these and other emergent patterns of trophic structure, such as effects of habitat quality or colonization order by trophic level, will further our understanding of the community assembly process, leading to better predictions about factors influencing community membership.

The trophic-rank species–area relationship (Holt et al., 1999) combines island biogeography theory (MacArthur and Wilson, 1967) with a species incidence function (Gilpin and Diamond, 1981) to explain higher trophic level spatial and temporal incidence (fully described in Holt et al., 1999). Described as a “conditional incidence function”, trophic level incidence is conditional upon the presence of the next lowest or prey trophic level, resulting in combined incidence probabilities of the predator and its prey (Gilpin and Diamond, 1981; Hanski, 1992). This conditional incidence of prey applies in particular to specialist predators that have limited prey choices and thus depend on their prey to colonize first. Generalists do not have such prey constraints and subsequently may have different temporal and spatial incidence patterns. Trophic level spatial incidence is based on patch size and maintained by colonization and extinction dynamics (MacArthur and Wilson, 1967). Higher trophic levels need larger areas to meet their greater per capita energy needs (Elton, 1927; Hutchinson, 1959; McNab, 1963; Cagnolo et al., 2009) and to make up for diminished energy transfer between trophic levels (Lindeman, 1942). Large areas may support more species at higher trophic levels compared to smaller areas (Holt et al., 1999; Holt and Hoops, 2005, but see Srivastava et al., 2008) and potentially have greater abundances of higher trophic levels. Thus, the trophic-rank species–area relationship describes higher trophic level presence as dependent upon the prior colonization of prey, combined with the need for more habitat area (Pimm, 1982; Slobodkin, 1961) as more trophic levels are added.

Support for the trophic-rank species–area model as an explanation of community assembly and patterns of trophic structure is mixed (Holt et al., 1999). An area-dependent response by trophic generalist and specialist colonists of mangrove islands was not observed by Piechnik et al. (2008), but Glasser (1982) did observe some positive area relationships for re-colonizing predators using the same mangrove island arthropod censuses. Because predators are thought to be sensitive to habitat size and disturbance factors (Tscharrntke et al., 2002), it is reasonable to expect sensitivity to other kinds of habitat quality besides area, such as local productivity effects (Oksanen et al., 1981; Anderson and Wait, 2001, but see Srivastava et al., 2008). Fertilizing can increase primary productivity, improve plant quality and biomass (Siemann et al., 1998), and can increase overall herbivore and predator abundances and species richness (Siemann, 1998). Increased productivity might affect the arrival of trophic levels during community assembly, where larger and more productive habitats have greater herbivore densities, subsequently supporting greater abundances of higher trophic ranks (Schoener, 1989).

Manipulating habitat size and productivity during community assembly may produce empirical insights into how species respond to habitat quality traits during assembly at the local scale. Up until now there are few if any direct experimental tests of sequential colonization by trophic rank (Holt et al., 1999) that also include effects of habitat quality using a food-web module, as presented here.

I used an aphid food-web module with specialist and generalist predators to examine the colonization patterns by trophic levels,

and population responses by each species to habitat size and enrichment. The concepts of trophic breadth and trophic rank (Holt et al., 1999) were applied to the arrival time of aphids and their predators to experimental field plots, and to a post-hoc simulation. Structured as a natural arthropod colonization experiment, I examined how habitat quality (e.g. enriched plots) and size might influence colonization order and the abundance of different trophic levels. Colonizing insects were sampled for one growing season to address the following questions concerning colonization order and predator–prey density responses to habitat area and quality: First, is there sequential colonization by trophic levels from low to high? Do generalists colonize before specialists? Second, are the density of prey and the presence of (specialist) predators linked? And lastly, how do habitat size and productivity affect colonization and densities of species and trophic levels?

2. Methods

Aphids and their predators were sampled while colonizing plots of California native annuals that were manipulated for size and productivity (fertilizer). These plots were established in a central California field and maintained as “terrestrial islands”. Aphids and their specialist and generalist predators were sampled multiple times throughout a field season, while plants were sampled only at the end of the season and tested for a productivity response. Species and trophic levels were tested for area and productivity effects, while trophic levels and trophic breadths were tested for ordered sequential colonization.

2.1. Experimental design

This experiment was a 2×2 completely randomized block design with 6 blocks; factors were plot size (1 m^2 and 10 m^2) and fertilizer (Osmacote™ (14-14-14) time release at 90.7 kg/ha) or none. Near the end of January 2003, plots were established in a bare agricultural field of 5.7 A on the University of California, Davis campus. Blocks were 9 m from each other, and there were 4 m between each plot within a block. Both 1 m^2 and 10 m^2 plots were planted with a seed mixture of four California native annual plants that have overlapping distributions, and that were known to attract insects. Seeds from these three co-occurring native species, *Lasthenia glabrata* (goldfields (0.228 g/m^2)), *Layia platyglossa* (tidy tips (1.721 g/m^2)), and *Nemophila menziesii* (baby blue eyes (0.803 g/m^2)), were sown in each plot along with the western native cover crop species *Phacelia tanacetifolia* (scorpion weed (0.459 g/m^2)). Oat bran (500 mL/m^2) was mixed with these small seeds to improve coverage and evenness while seeding plots.

To equalize effort across plot sizes, I sampled 1 m^2 areas of small and large plots on each collection date. The vigorous insect sampling methods used were known to damage plants, therefore each block had six additional small plots, three treatment and three control, to accommodate four sampling dates. Sampling knocked down 1 m^2 areas of the large plots (10 m^2) on each sample date, but the plants remained alive after sampling, therefore maintaining the majority of the 10 m^2 vegetated area. Thus, each of the six blocks contained four small plots (1 m^2) and one large plot (10 m^2) of the treatment and control. Weeds were hand-removed within plots on a weekly basis. Between most sample dates, I rototilled around every plot and all remaining unplanted ground in the study area to maintain each plot as a “terrestrial island”.

2.2. Food-chain module

Natural colonization order was observed for three aphid species and their known predators, which represent roughly 35% of the

total abundance of all insects collected (Table 1). Colonists were defined as both larvae and adult insects sampled during the study, and though eggs were commonly observed on plots, only larvae were identified and counted as colonists. Larval movement between plots was deterred by maintaining tilled ground between all plots to discourage movement by increasing the desiccation/predation risk when moving to a nearby plot. Arrival time and densities were monitored for these polyphagous aphid species (primary consumers): *Myzus persicae* (Sulzer), *Schizaphis graminum* (Rondani), and *Aulacarthum solani* (Kaltenbach). Aphids were classified and analyzed by size on each date. Small aphids were of early instar apterae (no wings), while large aphids were late instar apterae and alates (with wings).

2.3. Sampling

Insects were sampled during the weeks of March 19 (date 1 – week 0), April 5 (date 2 – week 3), May 5 (date 3 – week 7), and May 31, 2003 (date 4 – week 11) by: 1) pitfall trapping, 2) sweep-netting, and 3) suction-sampling with a Burkard Vortis (Arnold, 1994). All insects were stored in 90–95% ethanol. The sample size was 1 m² for all plots. First, pitfall traps were made from 266.2 mL (9 oz.) plastic drinking cups and sunk into the ground until the top was flush with ground level. Dilute soapy water was added before sunset and left out for approximately 38 h (i.e., two nights and one day). After collecting the pitfall traps, insects were collected from plots by sweeping a 45 cm diameter heavy sweep-net four times through the top 10 cm of the vegetation canopy. Lastly, a Burkard Vortis was used to suction-sample insects from the entire plant stem and flowers, including the ground beneath the plant (Arnold, 1994). A random number generator was used to determine the plot sampling order within a block on a given date, and to decide which 1 m² portion of the 10 m² plots would be sampled. Insect samples were sorted and identified to genus and enumerated (Wharton et al., 1997; Blackman, 2000; Heiss, 1938; American Insects Projects, Inc., 2002; Tauber and Tauber, 1974; C. Tauber personal communication; S. Heydon personal communication).

To determine above ground plant biomass, plant material was collected from a 108.5 cm × 24 cm quadrat from each plot at the end of the growing season (June 15, 2003). These samples were taken from small plots and sections of large plots that were previously unsampled. Plant stems were sheared at soil level, collected, bagged and frozen for 24 h (maximum temperature: –50 °C), and then dried for 21 days (temperature variation: maximum 45 °C/minimum 20 °C) in an outdoor

subterranean drying room. Once dried, the plant material was manually cleaned of dirt and weighed. Total carbon (TC%) and nitrogen (TN%) content were determined from samples of the plant with the most biomass, *P. tanacetifolia*, from fertilized and unfertilized plots. Once ground to a particle size of <0.47 mm, these samples were tested for amounts of TC% and TN% as a percentage of total dry weight using the Carlo-Erba combustion method (UC-ANR Lab, Davis CA).

2.4. Analyses

2.4.1. Sequential dependency – field data

Tests for sequential dependency, or sequential colonization by trophic levels from lowest to highest, were performed using a mixed model ANOVA-PROC MIXED (SAS 9.1.3, SAS Institute Inc., 2000–2004) least squares mean (LSM) approach on trophic level abundance, with fixed effects as trophic level, sample date, trophic level × sample date, and the random effect of block. First, each trophic level on each sample date was tested for positive abundance using the trophic level × date least squares mean (LSM) (one-tailed). Predator and prey trophic levels were then tested against each other within each sample date by using the difference between their trophic level × date LSMs (DLSM = LSM_{predator} – LSM_{prey}), and then analyzed (*t*-value). Trophic breadth, or sequential colonization by generalists and specialists, was similarly tested using the same ANOVA-PROC MIXED model (LSM) on abundance of trophic breadth group, with fixed effects of specialist/generalist (*s/g*) designation, sample date, *s/g* designation × sample date, and the random effect as block. Colonization order of generalists and specialists was compared as a group within a sample date using a *t*-test on the difference in the LSM for the trophic breadth × date effect (DLSM = LSM_{generalist} – LSM_{specialist}). All abundances were square root +0.05 transformed (Zar, 1984), with all *P*-values Tukey-adjusted for multiple comparisons and the significance levels were set at $\alpha = 0.05$.

2.4.2. Sequential dependency – permutation analysis

Commonness of the sequential colonization by trophic-rank pattern was tested by randomly assembling communities of specialists. The null hypothesis was that sequential dependency is not a pattern found in assembling aphid food-web modules. All individuals were weighted equally with respect to their trophic level or arrival time. This permutation test was restricted by date across four sample dates and done in R with the package sample (R 2.13.1, R Development Core Team, 2011, 2012). The colonist pool

Table 1

List of species in the food-web module sampled in 2003. Species number corresponds to taxa and taxonomic aggregations whose trophic interactions are described by Table 2.

Species ID	Genus	Species	Family	Order	Trophic level	Generalist/Specialist
1	<i>Lasthenia</i>	<i>glabrata</i>	Asteraceae	–	1	N/A
	<i>Layia</i>	<i>platyglossa</i>	Asteraceae	–	1	N/A
	<i>Nemophila</i>	<i>menziesii</i>	Hydrophyllaceae	–	1	N/A
	<i>Phacelia</i>	<i>tanacetifolia</i>	Hydrophyllaceae	–	1	N/A
2	<i>Aulacarthum</i>	<i>solani</i>	Aphidae	Homoptera	2	S
	<i>Myzus</i>	<i>persicae</i>	Aphidae	Homoptera	2	S
	<i>Schizaphis</i>	<i>graminum</i>	Aphidae	Homoptera	2	S
3	<i>Aphidius</i>	sp.	Broconidae	Hymenoptera	3	OS
4	<i>Hippodamia</i>	<i>convergens</i>	Coccinellidae	Coleoptera	3	FS
5	<i>Allograpta</i>	sp.	Syrphidae	Diptera	3	FS
	<i>Eupeodes</i>	sp.	Syrphidae	Diptera	3	FS
6	<i>Chrysoperla</i>	<i>carnea</i>	Chrysopidae	Neuroptera	3	FS
	<i>Hemerobius</i>	<i>pacifica</i>	Hemerobiidae	Neuroptera	3	G
7	<i>Orius</i>	sp.	Anthicoridae	Homoptera	3	G
8	<i>Asaphes</i>	<i>suspensus</i>	Pteromalidae	Hymenoptera	4	S
	<i>Asaphes</i>	<i>californicus</i>	Pteromalidae	Hymenoptera	4	S
	<i>Pachyneuron</i>	<i>californicus</i>	Pteromalidae	Hymenoptera	4	S

had 69,385 individuals from four sample dates and were distributed unevenly across 4 trophic levels: 67,870 trophic level 2 (aphids), 1419 trophic level 3 (primary parasitoids), and 96 trophic level 4 (hyperparasitoids). Each random sample was drawn from the entire colonist pool, and a random sample had the exact same numbers of individuals as taken from the field on a given sample date (date 1 = 17,189; date 2 = 47,956; date 3 = 3681; date 4 = 559). Trophic level data were counted and recorded, and after replacement the random sampling process was repeated for the next sample date. A colonization series consisted of four draws, representing each field sample date and containing the same number of individuals observed on each date. Each of these 10,000 colonization series was tested in R for sequential colonization by trophic level: date 1 having no individuals from trophic levels 4 and 3, and date 2 having no individuals from trophic level 4. Trophic level 2 (aphids) was assumed to be present on all sample dates. Each colonization series was also tested using the less strict sequential dependency criterion of the field counts for trophic levels 3 and 4 on dates 1 and 2. Colonization series with sequential dependency were summed under each criterion. The significance level was set at $\alpha = 0.05$, and P -values were calculated by dividing the number of series with sequential colonization by 10,000.

2.4.3. Predator–prey associations

A logistic regression was used to test for associations between predators and their prey without considering effects of experimental treatments (Hosmer and Lemeshow, 2000; SAS Institute Inc., 2000–2004). The log-likelihood of a predator’s presence was defined by the probability of colonizing success ($p(x)$), divided by the probability of failing to colonize ($1 - p(x)$). The logistic regression model used maximum likelihood methods to estimate regression coefficients as odds ratios using prey density (x_1) for β_1 , sample date (x_2) for β_2 , and when applicable host density (x_3) for β_3 (eq. (1)).

$$\text{logit}(P) = \ln \frac{p(x)}{1 - p(x)} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \quad (1)$$

Prey density (x_1) and host density (x_3) were continuous variables, while sample date (x_2) and predator presence/absence were categorical variables. The log of a predator’s odds is a multiplier for change in the probability of predator presence when prey abundance increases by one unit. Positive associations have odds ratios greater than one and negative associations are less than one. Significance of odds ratios was tested using a log-likelihood ratio test, and 95% confidence intervals were calculated. Each predator life stage was tested for an aphid association in the case of those predators that prey on aphids as larvae and adults. Because some taxa may not depend upon their prey to colonize, I tested for prey associations with sample date, and a prey \times date interaction, but I did not estimate odds for when prey are absent (β_0). Only adult prey densities were used because determining the trophic level of an aphid parasitoid is difficult even upon dissection.

2.4.4. Habitat quality – size and productivity

Fertilizer effects on above ground biomass, as TC%, and TN%, were determined with a paired t -test. A Cohen’s (1988) d -analysis measured the effect size of fertilizer on plant biomass.

A repeated measures ANOVA (RM-ANOVA – type III) was used to detect density responses by all taxa and trophic levels to size and fertilizer treatments, and treatment combinations across four sampling dates (SYSTAT, 2004). Because the two lacewing taxa, *Orius* sp., and the syrphid flies colonized after date 1 and at times had low densities, when possible I analyzed their responses using an RM-ANOVA including the last three sample dates, or by an ANOVA on each date when appropriate. To determine fertilizer, plot

size, and fertilizer \times plot size effects across life-history stages of each taxon, I analyzed responses of both the adult and larval stages for each date separately using ANOVAs. Density data were transformed using a square root +0.5 transformation (Zar, 1984). All graphs were done in R (2.15.1) with packages grid (R Development Core Team, 2011, 2012), plotrix (Lemon, 2006), psych (Revelle, 2012) and Unicode (Hornik, 2012). These analyses were used to explore which species might contribute most strongly to patterns of colonization to generate future research. No adjustments were made for multiple comparisons. Therefore, a type I error inflation is possible within this particular set of analyses.

3. Results

3.1. Predator colonists

Aphid generalist predators and primary parasitoids made up trophic level 3, while trophic level 4 consisted of the hyperparasitoids that use aphids as a host (Table 2). Trophic level 3 generalists included adults and larvae of: *Hippodamia convergens* (Coleoptera: Coccinellidae), *Chrysoperla carnea* (species complex) (Chrysopidae), *Hemerobius pacificus* (Neuroptera: Hemerobiidae), larvae only of *Eupeodes* sp., *Allograpta* sp. (Diptera: Syrphidae), and *Orius* sp. (Heteroptera: Anthocoridae). The “Syrphidae” group included individuals of *Eupeodes* sp. and *Allograpta* sp., pooled and analyzed as a single species because their densities were low for most sample dates and their trophic habits are presumed to be the same (Heiss, 1938). *Aphidius* sp., was the obligate specialist in trophic level 3, and consumed aphids by parasitizing or stinging adult and immature aphids, depositing an egg internally, and then chewing an exit hole in the aphid’s body upon completing its lifecycle (Minks and Harrewijg, 1988). Taxa that could be generalists or facultative specialists depending on prey densities, such as *H. convergens*, *Eupeodes* sp. and *Allograpta* sp., were generalists in this study due to the lack of observational data demonstrating otherwise. Hyperparasitoids were obligate specialists at trophic level 4, and included *Asaphes suspensus*, *Asaphes californicus*, (hereafter *Asaphes* sp.), and *Pachyneuron californicus* (Hymenoptera: Pteromalidae). Hyperparasitoids prey on aphids by parasitism; searching and locating an already parasitized aphid, stinging and depositing their egg in the parasitized host. Hyperparasitoid larva develop within the aphid by consuming the developing larva of the endoparasitic braconid (*Aphidius* sp.) (Minks and Harrewijg, 1988).

Table 2
Trophic connections for all taxa listed in Table 1 (Species ID). No trophic interaction is represented by a “0”, while a “1” represents a trophic interaction.

		Prey							
		1	2	3	4	5	6	7	8
P r e d a t o r	1	0	0	0	0	0	0	0	0
	2	1	0	0	0	0	0	0	0
	3	0	1	0	0	0	0	0	0
	4	0	1	1	0	0	0	0	1
	5	0	1	1	0	0	0	0	1
	6	0	1	1	0	0	0	0	1
	7	0	1	1	0	0	0	0	1
	8	0	1	1	0	0	0	0	0

3.2. Colonization order: sequential dependency of trophic level and trophic breadth

Specialists colonized sequentially from the lowest to the highest trophic level (Figs. 1 and 2). Aphids (trophic level 2) had positive densities on date 1 followed by specialist predator (*Aphidius* sp.) (trophic level 3) on date 2 (Fig. 1). On each date colonist densities were typically greater than the density of their predators, except in the case of trophic level 4 (hyperparasitoids: *A. suspensus*, *A. californicus* (hereafter *Asaphes* spp.), and *P. californicus*). Densities of individuals in trophic level 4 increased between sample dates, but did not support the sequential dependency expectation of trophic level 4 colonizing on date 3 (Figs. 1 and 2). Randomly assembled communities did not produce colonization series that demonstrated patterns of sequential colonization by trophic level. In all cases, higher trophic levels were present on dates 1 and 2, and not at all on dates 3 and 4. This pattern was observed under the strictest criteria of sequential colonization of trophic levels by date ($P < 0.0000$), and under the relaxed criteria of field-based densities ($P < 0.0000$).

Specialists colonized before generalists. Specialists alone had significant positive plot densities on date 1 (Specialist LSM trophic breadth \times date effect = 1.448, $t = 5.72$, $P = 0.001$, Generalist LSM trophic breadth \times date effect = 0.169, $t = 0.67$, $P = 0.504$). Specialists' trophic breadth \times date effects were greater than generalists' until sample date 3 (date 3 DLSM specialist/generalist trophic breadth \times date effect = -0.6774 , $t = -2.11$, $P = 0.4133$).

3.3. Predator–prey abundance associations

Most specialist predators were positively associated with their prey or host taxa abundances, or with date \times prey abundance effects (Table 3). Hyperparasitoids were more likely to be present when prey (*Aphidius* sp.) or their hosts (aphids) had higher abundances. When analyzed separately, the two hyperparasitoid genera had positive but different associations to lower trophic levels;

Pachyneuron sp. presence was associated with increasing prey abundances (*Aphidius* sp.), while *Asaphes* spp. was associated with both host abundance (aphids) and sample date (Table 3). Primary parasitoid (*Aphidius* sp.) presence was weakly associated with the date \times aphid effect, and negatively associated with date. Generalist predators mostly had weak and negative associations with prey abundance and date (i.e., odds less than 1.0). Syrphid flies (*Allograptia* sp., *Eupeodes* sp.) and brown lacewings (*Hemerobius* sp.) had decreasing abundances in later sample dates, and negative associations with prey abundance (Fig. 2, Table 3). However all generalist predators showed positive associations with date \times aphid effects, except for *Orius* sp. which showed no associations.

3.4. Habitat quality: size and productivity effects

Trophic level 1 percent cover was equal across treatments and sample dates. Always the greatest percent cover, *P. tanacetifolia* dominated plots ($\geq 50\%$), while plot edges had at most 20% cover by *L. glabrata*, and 5% cover by *L. platyglossa* and *N. menziesii* combined. *Phacelia tanacetifolia* dominated and increased in total above ground dry biomass by 18% on fertilized plots ($t = -3.788$, $df = 8$, $P = 0.005$). Fertilized plots had more TC%, but not more TN% (total carbon (TC%): $t = 2.8119$, $P < 0.05$, Cohen's $d = 1.77$; total nitrogen (TN%): $t = 0$, $P > 0.50$).

Size and fertilizer treatments affected aphids and predators differently with each date (Fig. 2, Table 4: online supplement). Fertilizer effects were most prominent on sample date 1 with 27.6% more aphid instars ($F = 10.442$, $df = 1$, $P = 0.006$), and 75.5% more trophic level 3 predators ($F = 4.792$, $df = 1$, $P = 0.041$). Trophic level 4 also showed a trend of higher densities on fertilized plots on date 2.

Plot size effects were detected mostly after date 1. Small plots had a concomitant increase of aphids and most predators (and parasitoids) (Fig. 2, Table 4: online supplement). Small plots also had more aphids on dates 2 (+46%) and 3 (+34.2%), but the higher trophic levels had different responses to small plots on each date. On date 2, *Pachyneuron* sp. (trophic level 4) showed a trend of

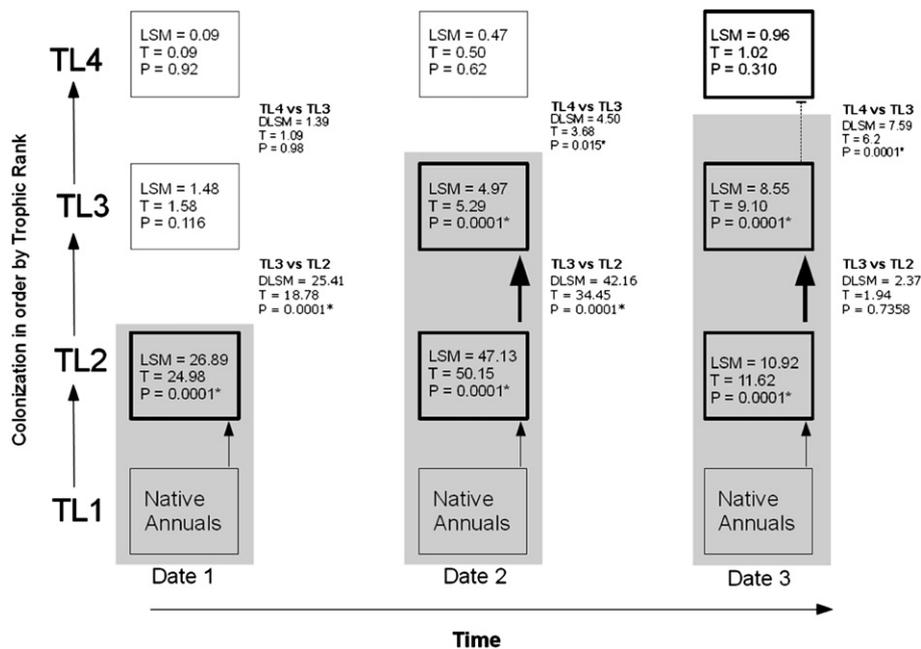
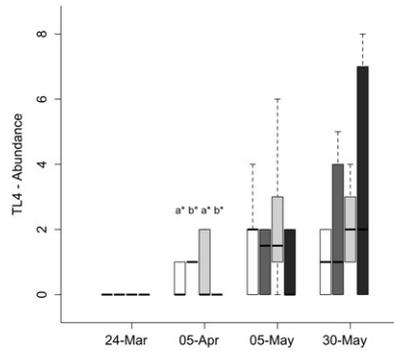
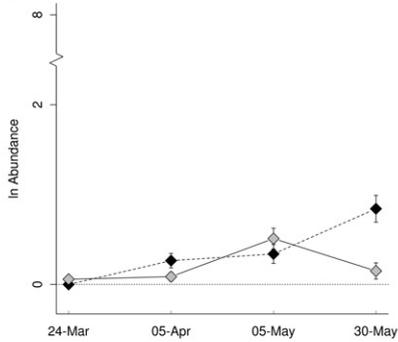
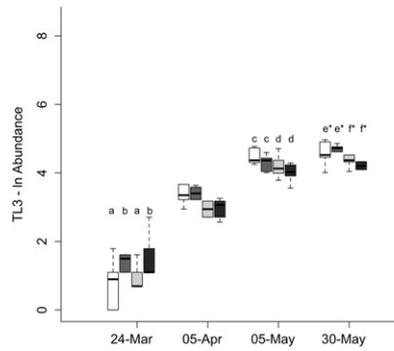
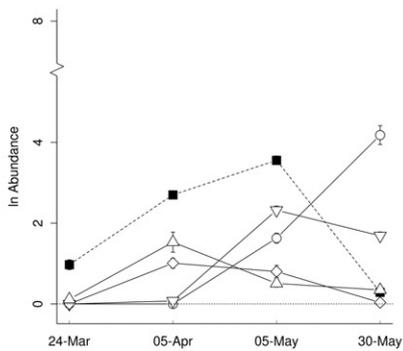


Fig. 1. Sequential colonization of trophic levels (TL) by aphids (TL2) and their specialist predators/parasitoids (TL3 & TL4). Trophic level presence was established for each sample date, and trophic level \times date comparisons were made between trophic levels by a method that compares the differences in the least squares mean estimates (DLSM) between sample dates. DLSM P -values are adjusted for multiple comparisons using a Tukey-adjustment. * indicates statistical significance ($\alpha = 0.05$). Both LSM and DLSM $df = 202$.

Trophic Level 4



Trophic Level 3



Trophic Level 2

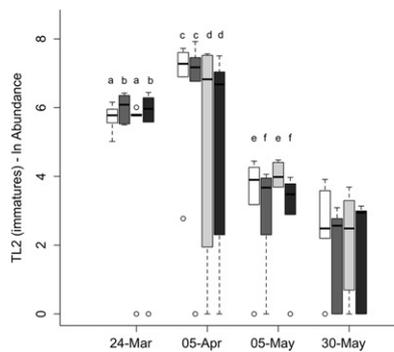
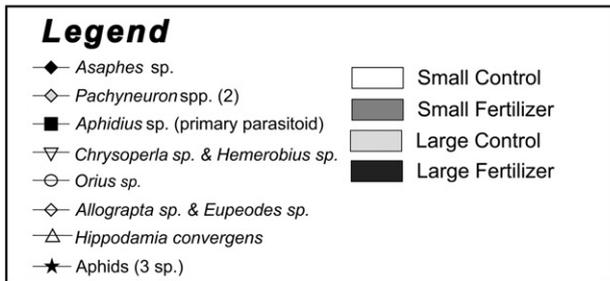
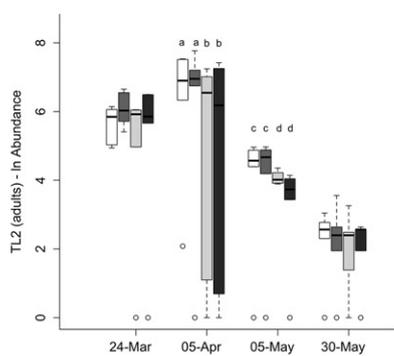
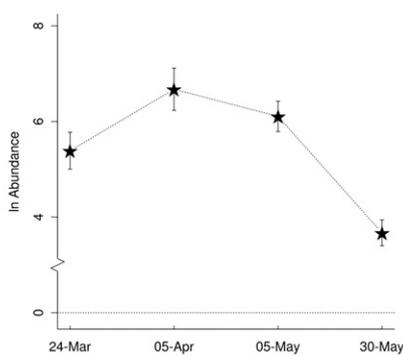


Fig. 2. Trophic level mean abundance by taxa (left column) and by treatment (right column) over one season in 2003. Abundance plots show specialists as filled symbols and generalists as unfilled symbols. Letters in box plots denote significant differences ($P < 0.05$), while * denotes a trend ($0.055 < P < 0.09$).

Table 3

Logistic regression analysis associating predator presence with prey abundance and host abundance. Trophic Level (TL) and Trophic Breadth (TB) are described in the first column, and consists of S = Obligate Specialists, Fac = Facultative Specialists, G(en) = Generalist. See Tables 1 and 2 for trophic associations and details on trophic levels. Species number are in “()” after names, and the life stages of predators are abbreviated as A = Adult and L = Larvae. The odds represent the multiplier for change in predator presence when prey abundance increases by one unit (see eq. (1) in text). Predator–prey or predator–date associations with bold *P*-values are statistically significant ($\alpha = 0.05$).

TL:TB	Predator (genus)	Stage	Prey	Association	Odds	95% CI upper	95% CI lower	<i>P</i> -value
4:S	<i>Pachyneuron</i> sp. (8)	A	<i>Aphidius</i> (3)	<i>Aphidius</i>	2.534	6.162	1.036	0.042
4:S	<i>Asaphes</i> sp. (8)	A	<i>Aphidius</i> (3)	Aphid	21.93	158.386	3.036	0.002
				Date	12.23	72.517	2.062	0.006
				<i>Aphidius</i>	2.567	7.453	0.884	0.083
3:S	<i>Aphidius</i> sp. (3)	A	Aphid (2)	Date	0.293	0.749	0.115	0.010
				Date × Aphid	1.315	1.58	1.095	0.003
3:G	<i>Allograpta</i> sp. & <i>Eupeodes</i> sp. (5)	L	Aphid/Fac (2)	Aphid	0.185	0.502	0.068	0.001
				Date	0.312	0.664	0.146	0.003
				Date × Aphid	1.396	1.638	1.19	0.001
3:G	<i>Hippodamia</i> sp. (4)	L	Aphid/Fac (2)	Date × Aphid	1.165	1.392	0.975	0.092
		A	Aphid/Fac (2)	Date × Aphid	2.877	8.695	0.952	0.061
3:G	<i>Hemerobius</i> sp. (6)	A	Aphid/Gen (2)	Aphid	0.07	0.365	0.015	0.002
				Date	0.074	0.563	0.01	0.012
				Date × Aphid	2.001	3.177	1.24	0.003
		L	Aphid/Gen (2)	Aphid	0.062	0.72	0.005	0.026
				Date	0.199	0.803	0.049	0.023
				Date × Aphid	1.743	2.591	1.172	0.006
3:G	<i>Chrysoperla</i> sp. (6)	A	Aphid/Gen (2)	Date × Aphid	1.326	1.845	0.953	0.094
3:G	<i>Orius</i> sp. (7)	A&L	Aphid/Gen (2)	None				

increased density (Table 4: online supplement). Trophic level 3 had greater densities on small plots on date 3 (+27.3%), as did the constituent species *Orius* sp. (+45.1%) and *Hemerobius* sp. (+44.4%) (Table 4: online supplement). Only syrphid flies favored large plots (+200%) (date 2, Table 4: online supplement). Most taxa responded inconsistently to treatments throughout the season.

4. Discussion

4.1. Colonization order: sequential dependency of trophic level and trophic breadth

Trophic levels colonized in sequential order (Figs. 1 and 2) (Holt et al., 1999) in this aphid food-web module. Specialist predators demonstrated close temporal dependence on their prey, but spatial constraints may also apply when prey are absent upon arrival, increasing the need to expand their search. Specialist predators have lifecycles closely linked to their prey's lifecycle (Godfray, 1994). Therefore, predators track prey population fluctuations and dispersal (Snyder and Ives, 2001) to more narrowly defined suitable habitat that is constrained in time and across space, thus specialist predators are quite efficient and effective (Godfray, 1994). However, sequential colonization by trophic rank may not happen in all systems with specialists, and may even skip a trophic level. Some predators race their prey to the host plant and arrive before their prey (Reddy et al., 2004; Zhu et al., 2005). Patterns from this field and permutation study of the aphid food-web module lend strong support for specialist colonization that was not entirely random; the arrival order was more than a random cross-section of a regional species pool, but colonization with ecological limitations applied in time, and potentially across habitat space. Broadly speaking, these temporal and spatial limitations could impact the dynamics of colonization and extinction, overall trophic structure, and species richness.

Trophic generalists arriving after specialists contrasts predicted plausible (Holt et al., 1999) and observed (Piechnik et al., 2008) colonization sequence pattern of diet-limited specialists following the arrival of generalists that eat many prey. This result is rather surprising because there is trophic support for these generalist taxa to be early colonizers. As a group, most have voracious appetites for aphids and other prey (Canard et al., 1984; Letourneau, 1990;

Rosenheim et al., 1993). Omnivorous biological control agents like *Orius* sp. can be early colonists that subsist on host plants until pests reach outbreak levels. Others, like the green lacewing (*Chrysoperla* sp.), have a long and active season as adults during the local winter months (Canard, 1997). Prey preferences can also produce strong predator responses. For example, *H. convergens* prefers aphids, uses aphid cues to find local populations (Evans and Dixon, 1986), and has strong population-level aggregations when aphid densities are high (Ives et al., 1993).

In other cases though, high aphid densities produce variable predator population responses as in the case of syrphid flies (*Allograpta* sp., and *Eupeodes* sp.) (Ambrosino et al., 2007). Late colonizing generalists may be inefficient at selecting suitable habitat and prey (Bernays and Funk, 1999), or perhaps these generalists are not strongly linked to prey, or even aphid densities as a consequence of local adaptive life-history strategies. For instance, *H. convergens* may have been delayed by its annual migration from the Sierra Nevada Mountain Range to the Central Valley of California (+250 km) (Rankin and Rankin, 1980). Limiting abiotic factors like temperature or humidity might also cause low initial local densities and negatively impact dispersal or egg-laying (Natskova, 1985; Tuda and Shima, 2002). Some generalists are also known to delay colonization until more food resources, such as pollen, are available (Eubanks and Denno, 1999). More investigation into landscape, community, and population-level mechanisms might isolate other factors contributing to the late arrival by these generalist predators.

4.2. Predator–prey associations

Some cases of specialist predator associations with their prey and hosts were particularly strong, indicating a tight link between predator incidence and density of lower trophic levels, for example *Pachyneuron* sp. was associated with its prey and *Asaphes* sp. with its host. These strong associations are likely due to arrival time and other hyperparasitoid population-level processes. Hyperparasitoid associations with their prey were strong in some cases, despite the fact that the association was with adult prey densities and not larval densities, the stage targeted by these predators. Adult prey abundance may or may not be important during the host locating process. An asynchronous parasitoid–hyperparasitoid emergence

may also produce this pattern. Surprisingly, aphid specialists *H. convergens* (facultative) and *Aphidius* sp. (obligate) did not show a strong association with their prey. Both use aphid semiochemicals to track prey, and in this case the lack of an association may have more to do with asynchronous population dynamics and predator arrival time, and less to do with delays from prey-choice decisions and prey-locating abilities. Underwhelming associations of generalist predators with prey densities suggests alternative processes aside from trophic effects were acting. Spatial processes such as dispersal may have delayed generalist predator arrival, including adult travel from more distant emergence sites or residing in marginal habitats until finding this site with high local aphid densities.

By arriving before generalists, specialists might increase their risk of intraguild predation, thereby decreasing local populations (Colfer and Rosenheim, 2001). Alternatively, if early arriving specialists reproduce fast enough, they may produce a generation before generalists and hyperparasitoids arrive. The colonization order of specialists before generalists observed in this field experiment, and demonstrated by patch coexistence models (Hassell and May, 1986) suggests prey specificity by different trophic breadths can influence trophic structure and community composition.

4.2.1. Habitat quality – productivity effects

Habitat size and productivity influenced densities of all colonists, but differently across sample dates. Nearly all trophic levels had an early season response to increased productivity by fertilizer. Larval aphids increased on enriched plots suggesting quality and quantity of primary production enhanced reproductive performance by consumers (Awmack and Leather, 2002). Trophic level 3 also increased as a result because of this increase in prey, a response that seemed largely driven by the trend of more parasitoids (*Aphidius* sp.). The trend of trophic level 4 increasing on fertilized plots on sample date 2 suggests a potential immediate response upon arrival by higher trophic levels to increased productivity and high host and prey densities (Cebrian et al., 2009). Plants may have had greater nitrogen content early in the season to support these higher trophic level responses, but this effect was not measured.

4.2.2. Habitat quality – size effects

All trophic levels had negative responses to habitat size after date 1, suggesting that small plots were more suitable habitat later in the season. Higher trophic levels may have pursued aphids across space and time, their response mirroring the greater abundances of aphids first on fertilized plots, and later on small plots. Taxa in all trophic levels had varied responses to habitat size on a given sample date, possibly to escape predation, or in response to some other disturbance in large plots including sampling. But a lack of overall habitat quality effects throughout the season suggests that habitat quality was ephemeral and intermittent, and that at least some of the factors behind these responses are likely outside the scope of this study.

There are several studies indicating that insect densities should decrease with decreasing patch size for herbivores (Karieva, 1985; Collinge, 2000; Cronin, 2004, but see Bukovinszky et al., 2005). Larger patches are assumed to have more resources and thus can support more species and/or greater densities of species (Collinge, 2000), particularly specialist herbivores (Karieva, 1985), and predators (Siemann, 1998; Tscharrntke et al., 2002). However, Braschler et al. (2003) found a similar result of smaller plots having higher aphid densities, which contradicts the common assumption of the species–area relationship that larger areas are likely to have more resources, commonly due to more heterogeneity (MacArthur and Wilson, 1967). Small plots supported higher densities of aphids from date 2 onward, and at times greater densities of both specialist

and generalist predators. Some aphid species, however, appear to select their hosts by combining habitat selection factors like area- and perimeter-dependent immigration, which can result in a negative density–area relationship (Bowman et al., 2002). Here, predators appear to be more tightly associated with prey responses and less with overall habitat size. There are many possible explanations for the observed negative density–area relationship. Density–area relationships may be species dependent, hinging on the contingency of primary patch establishment, host searching modes (Hambäck and Englund, 2005), increased apparency of resources like sunlight (Burgess et al., 2006), nectar or pollen (Aizen and Feinsinger, 1994). Some insects may also show a preference for higher quality plants on small plot edges over the lower quality interior plants on large plots which do not typically benefit from a nutrient release, which can occur after tilling (Kleijn, 1996).

4.3. Assessment of the model and the study system

It has been suggested that an appropriate model to test the trophic-rank species–area concept would be a parasitoid food-web module (Holt et al., 1999; Holt, 2002). However, the body size of parasitoids is generally the same size or smaller than their prey (Thies et al., 2003). Therefore, energy requirements for insects, and diminished energy transfer between trophic levels necessitating larger spaces (Holt et al., 1999), might not apply so strictly, particularly within this type of food-web module. This form of the trophic-rank species–area model might be more aptly tested on vertebrate grazers and their predators that require foraging range sizes to differ by an order of magnitude.

Although, having a strict specialist and generalist did make this a good system to test for patterns of trophic dependency during colonization, additional factors likely contributed to the arrival order of species. Others have demonstrated that priority effects, environmental factors, and dispersal distances may contribute significantly to species' arrival times (Tscharrntke et al., 2002). Furthermore, regional population dynamics and the surrounding landscape matrix also influences species' arrival time (Corbett and Rosenheim, 1996; Ricketts, 2001). Habitat selection behavior, such as female oviposition site selection, may also play an important role in arrival time and prey location. Site selection cues that influence the prey-locating process may include prey and plant chemical cues (volatile olfactory stimuli, Buitenhuis et al., 2005), avoiding copious amounts of honeydew (Seagraves, 2009), host densities and increased habitat complexity (Bezemer et al., 2010). Adding oviposition site selection to this model could enhance the meaning of “colonization”. Here, colonization was examined according to specific trophic relationships only. The hypothesis of sequential colonization might also benefit from a modification of the obligate and “stacked specialist” assumption that spans multiple trophic levels. An example of one modification would be to include other factors known to affect trophic structure such as behavior and the effect of interspecific interactions (Resitarits, 2001), and intraspecific trophic variation (Bolnick et al., 2011).

This experimental test of sequential colonization by trophic rank demonstrated a use of species' traits that revealed factors that influence trophic structure during community assembly, including colonization order by trophic breadth and sequential colonization by trophic level. Habitat size and quality were additional determinants of trophic structure by influencing prey, host, and higher trophic level spatial and temporal incidence. Further investigation of effects utilizing species trait combinations may improve our understanding of community structure during assembly and how it influences community membership. Refining the sequential dependency model of colonization (Holt et al., 1999) could increase the application of this model to enhance our understanding and

predictability of natural and anthropogenic disturbances (Smith, 2006), community restoration (Summerville et al., 2006), biological control (Schoenly and Cohen, 1991), and exotic species invasions (Fridley et al., 2007).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2012.11.002>.

References

- Aizen, M.A., Feinsinger, P., 1994. Habitat fragmentation, native insect pollinators and feral honey-bees in Argentine Chaco Serranoa. *Ecol. Appl.* 4, 378–392.
- Ambrosino, M.D., Jepson, P.C., Luna, J.M., 2007. Hoverfly oviposition response to aphids in broccoli fields. *Entomol. Exp. Appl.* 122, 99–107.
- American Insects Projects, Inc., 2002. American beetles. In: Arnett Jr., R.H., Thomas, M.C., Skelley, P.E., Frank, J.H. (Eds.), *Polyphaga, Scarabaeoidea Through Cuculionioidea*, vol. II. CRC Press, New York, NY.
- Anderson, W.B., Wait, A., 2001. Subsidized island biogeography hypothesis, another new twist on an old theory. *Ecol. Lett.* 4, 289–291.
- Arnold, A.J., 1994. Insect suction sampling without nets, bags or filers. *Crop. Prot.* 13, 73–76.
- Awmack, C.S., Leather, S.R., 2002. Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Entomol.* 47, 817–844.
- Bernays, E.A., Funk, D.J., 1999. Specialists make faster decisions than generalists, experiments with aphids. *Proc. Roy. Soc. Lond. B Biol.* 266, 1–6.
- Bezemer, T.M., Harvey, J.A., Kamp, A.F.D., Wagenaar, R., Gols, R., Kostenko, O., Fortuna, T., Engelkes, T., Vet, L.E.M., van der Putten, W.H., Soler, R., 2010. Behaviour of male and female parasitoids in the field: influence of patch size, host density, and habitat complexity. *Ecol. Entomol.* 35, 341–351.
- Blackman, R.L., 2000. *Aphids on the World's Crops: An Identification and Information Guide*, second ed. Wiley, New York.
- Bolnick, D.I., Amarasekare, P., Araujo, M.S., Burger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192.
- Bowman, J., Cappuccino, N., Fahrig, L., 2002. Patch size and population density: the effect of immigration behavior. *Conserv. Ecol.* 6, 9 [Online]. <http://www.ecologyandsociety.org/vol6/iss1/art9/print.pdf>.
- Braschler, B., Lampel, G., Baur, B., 2003. Experimental small-scale grassland fragmentation alters aphid population dynamics. *Oikos* 100, 581–591.
- Buitenhuis, R., Vet, L.E.M., Boivin, G., Brodeur, J., 2005. Foraging behavior at the fourth trophic level: a comparative study of host location in aphid hyperparasitoids. *Entomol. Exp. Appl.* 114, 107–117.
- Bukovinsky, T., Potting, R.P.J., Clough, Y., van Lenteren, J.C., Vet, L.E.M., 2005. The role of pre- and post-alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109, 435–446.
- Burgess, V.J., Kelly, D., Robertson, A.W., Ladley, J.L., 2006. Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of *Peraxilla tetrapetala* (Loranthaceae). *New Zeal. J. Ecol.* 30, 179–190.
- Cagnolo, L., Valladares, G., Salvo, A., Cabido, M., Zak, M., 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conserv. Biol.* 23, 1167–1175.
- Canard, M., 1997. Can lacewings feed on pests in winter? (Neur: Chrysopidae and Hemerobiidae). *Entomophaga* 42, 113–117.
- Canard, M., Séméria, Y., New, T.R. (Eds.), 1984. *Biology of Chrysopidae*. Dr W. Junk Publishers, The Hague, The Netherlands.
- Cebrian, J., Shurin, J.B., Borer, E.T., Cardinale, B.J., Ngai, J.T., Smith, M.D., Fagan, W.F., 2009. Producer nutritional quality controls ecosystem trophic structure. *PLoS ONE* 4, e4929. <http://dx.doi.org/10.1371/journal.pone.0004929>.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*, second ed. L. Erlbaum Associates, Hillsdale, NJ.
- Colfer, R.G., Rosenheim, J.A., 2001. Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* 126, 292–304.
- Collinge, S., 2000. Effects of grassland fragmentation on insect species loss, colonization and movement patterns. *Ecology* 81, 2211–2226.
- Corbett, A., Rosenheim, J.A., 1996. Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. *Ecol. Entomol.* 21, 155–164.
- Cronin, J.T., 2004. Host-parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia* 139, 155–164.
- Elton, C., 1927. *Animal Ecology*. Macmillan Co, New York, NY.
- Eubanks, M.D., Denno, R.F., 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* 80, 1253–1266.
- Evans, E.W., Dixon, A.F.G., 1986. Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *J. Anim. Ecol.* 55, 1027–1034.
- Fox, J.W., McGrady-Steed, J., 2002. Stability and complexity in microcosm communities. *J. Anim. Ecol.* 71, 749–756.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., Von Holle, B., 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88, 3–17.
- Fukami, T., 2004. Assembly history interacts with ecosystem size to influence species diversity. *Ecology* 85, 3234–3242.
- Gilpin, M.E., Diamond, J.M., 1981. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. *Proc. Natl. Acad. Sci. U.S.A.* 78, 392–396.
- Glasser, J.W., 1982. On the causes of temporal change in communities: modification of the biotic environment. *Am. Nat.* 119, 375–390.
- Godfray, H.C.J., 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, 473 pp.
- Hambäck, P.A., Englund, G., 2005. Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. *Ecol. Lett.* 8, 1057–1065.
- Hanski, I., 1992. Inferences from ecological incidence functions. *Am. Nat.* 119, 375–390.
- Hassell, M.P., May, R.M., 1986. Generalist and specialist natural enemies in insect predator-prey interactions. *J. Anim. Ecol.* 55, 923–940.
- Hassell, M.P., Comins, H.N., May, R.M., 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353, 255–258.
- Heatwole, H., Levins, R., 1972. Trophic structure stability and faunal change during recolonization. *Ecology* 53, 531–534.
- Heiss, E.M., 1938. A Classification of the Larvae and Puparia of the Syrphidae of Illinois Exclusive of Aquatic Forms. In: *Illinois Biol Monogr* 16(4). The University of Illinois Press, Urbana IL.
- Holt, R.D., Hoops, M.F., 2005. Food web dynamics in a metacommunity concept: modules and beyond. In: Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press, Chicago, pp. 68–93.
- Holt, R.D., 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecol. Res.* 17, 261–273.
- Holt, R.D., Lawton, J.H., Polis, G.A., Martinez, N.D., 1999. Trophic rank and the species-area relationship. *Ecology* 80, 1495–1504.
- Hornik, K., 2012. Unicode: Unicode Data and Utilities. In: R Package Version 0.1-3. <http://CRAN.R-project.org/package=Unicode>.
- Hosmer, D.W., Lemeshow, S., 2000. *Applied Logistic Regression*. Wiley, New York, NY.
- Hutchinson, G.E., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93, 145–159.
- Ives, A.R., Kareiva, P., Perry, R., 1993. Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74, 1929–1938.
- Karieva, P., 1985. Finding and losing host plants by *Phyllotreta* – patch size and surrounding habitat. *Ecology* 66, 1809–1816.
- Kleijn, D., 1996. The use of nutrient resources from arable fields by plants in field boundaries. *J. Appl. Ecol.* 33, 1433–1440.
- Klemola, T., Tanhuanpää, M., Korpimäki, E., Ruohomäki, K., 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99, 83–94.
- Lemon, J., 2006. Plotrix: a package in the red light district of R. *R News* 6, 8–12.
- Letourneau, D.K., 1990. Mechanisms of predator accumulation in a mixed crop system. *Ecol. Entomol.* 15, 63–69.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399–417.
- MacArthur, R., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

- McNab, B.K., 1963. Bioenergetics and the determination of home range size. *Am. Nat.* 97, 133–140.
- Minks, A.K., Harrewijg, P., 1988. *Aphids: Their Biology, Natural Enemies & Control*, vol. 2B. Elsevier, Amsterdam.
- Natskova, V., 1985. Influence of basic ecologic factors on the feeding capacity of some aphidophages in their larvae period. *Ekologia* 15, 35–42.
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118, 240–261.
- Piechnik, D.A., Lawler, S.P., Martinez, N.D., 2008. Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order. *Oikos* 117, 665–674.
- Pimm, S.L., 1982. *Food Webs*. Chapman and Hall, London.
- R Development Core Team, 2011, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. <http://www.R-project.org/>.
- Rankin, M.A., Rankin, S., 1980. Some factors affecting presumed migratory flight activity of the convergent ladybeetle, *Hippodamia convergens* (Coccinellidae: Coleoptera). *Biol. Bull.* 158, 356–369.
- Reddy, G.V.P., Tabone, E., Smith, M.T., 2004. Mediation of host selection and oviposition and behavior in the diamondback moth *Plutella xylostella* and its predator *Chrysoperla carnea* by chemical cues from cole crops. *Biol. Control* 29, 270–277.
- Resitarits Jr., W.J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). *Oecologia* 129, 155–160.
- Revelle, W., 2012. psych: Procedures for Personality and Psychological Research. Northwestern University, Evanston. <http://personality-project.org/r/psych.manual.pdf>. 1.2.1.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 20, 665–674.
- Rosenheim, J.A., Wilhoit, L.R., Armer, C.A., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96, 439–449.
- SAS Institute Inc., 2000. SAS 9.1.3 Help and Documentation. SAS Institute Inc., Cary, NC.
- Schoener, T.W., 1989. Food webs from the small to the large. *Ecology* 70, 1559–1589.
- Schoenly, K., Cohen, J.E., 1991. Temporal variation in food web structure: 16 empirical cases. *Ecol. Monogr.* 61, 267–298.
- Seagraves, M.P., 2009. Lady beetle oviposition behavior in response to the trophic environment. *Biol. Control* 51, 313–322.
- Siemann, E., 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79, 2057–2070.
- Siemann, E., Tilman, D., Haarstad, J., Ritchie, M., 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* 152, 738–750.
- Slobodkin, L.B., 1961. *Growth and Regulation of Animal Populations*. Holt, Rinehart, and Winston, New York.
- Smith, R.G., 2006. Timing of tillage is an important filter on the assembly of weed communities. *Weed Sci.* 54, 705–712.
- Snyder, W.E., Ives, A.R., 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82, 705–716.
- Srivastava, D.S., Trzcinski, M.K., Richardson, B.A., Gilbert, B., 2008. Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. *Am. Nat.* 172, 761–771.
- Summerville, K.S., Conoan, C.J., Steichen, R.M., 2006. Species traits as predictors of lepidopteran composition in restored and remnant tallgrass prairies. *Ecol. Appl.* 16, 891–900.
- SYSTAT, 2004. SYSTAT. Version 11.0. SYSTAT Software, Point Richmond, California, USA.
- Tauber, M.J., Tauber, C.A., 1974. Dietary influence on reproduction in both sexes of five predaceous species (Neuroptera). *Can. Entomol.* 106, 921–925.
- Thies, C., Steffan-Dewenter, I., Tschardt, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101, 18–25.
- Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecol. Res.* 17, 229–239.
- Tuda, M., Shima, K., 2002. Relative importance of weather and density dependence on the dispersal and on-plant activity of the predator *Orius minutus*. *Popul. Ecol.* 44, 251–257.
- Weiher, E., Keddy, P., 1995. The assembly of experimental wetland plant communities. *Oikos* 73, 323–335.
- Wharton, R.A., Marsh, P.M., Sharkey, M.J., 1997. Manual of the New World Genera of the Family Braconidae (Hymenoptera). In: Special Publication of the International Society of Hymenopterists No 1. The International Society of Hymenopterists, Washington, DC.
- Zar, J.H., 1984. *Biostatistical Analysis*, second ed. Prentice-Hall, Englewood Cliffs, NJ.
- Zhu, J., Obyrcki, J.J., Ochieng, S.A., Baker, T.C., Pickett, J.A., Smiley, D., 2005. Attraction of two lacewing species to volatiles produced by host plants and aphid prey. *Naturwissenschaften* 92, 277–281.