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Using plant volatile traps to estimate the diversity of natural enemy communities in orchard ecosystems

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Abstract

In this study we used sticky traps baited with plant volatile lures to monitor the biodiversity of natural enemies in orchard ecosystems in the western U.S. We compared the diversity of predator genera from season total trap catches in 37 different orchards (apple, cherry, pear and walnut) over a two-year period (2010-2011) using standardized Hill number biodiversity indices and community similarity profiles. For a subset of 23 of these orchards we were also able to monitor the change in biodiversity of predator genera over the full growing season in the different orchard crops. A total of 37,854 individuals from 31 different genera of foliage-active generalist predators were collected from all orchards combined. Mean sample coverage was high (0.98) and richness, diversity and evenness differed between crops in 2010, but not in 2011. There was more than 90% similarity in the richness of predator genera among crops and among orchards within crops, but a greater level of differentiation was observed among orchards when variation in their relative abundance and dominance in the communities was taken into account. There was a consistent rise in predator generic richness and diversity through the season in both years for apple, cherry and pear orchards, but in walnut orchards, a steep rise from March to May was followed by a decline through the rest of the season. In an additional component of the study, the species level similarity of predator and parasitoid communities was analyzed for total season trap catch data from six walnut orchards. The rarefied species richness of parasitoids was much greater than that for predators, although the diversity, evenness and dominance of the parasitoid species varied considerably among orchards. The results from this study highlight the fact that natural enemy communities in orchard ecosystems can be effectively monitored using plant volatile traps, and that these communities are surprisingly diverse despite frequent disturbance from pest management intervention.

Keywords: apple, evenness, parasitoid, pear, predator, richness, walnut

1. Introduction

For agriculture to become more sustainable in the future, it will need to meet the challenge of maintaining or enhancing production, improving its resilience, and reducing negative effects on the environment (Foley et al., 2011). To address these issues, greater attention is being paid to enhancing the benefits from natural enemies that provide pest control services in agricultural crops (Jones et al., 2009; Crowder and Harwood, 2014). In general, natural enemies colonize agricultural crops from the surrounding landscape and there is growing evidence that biological control services are reduced to a greater extent in simple versus complex landscapes (Chaplin-Kramer et al., 2011; Letourneau et al., 2011; Veres et al., 2013). In addition, increased use of insecticides in agricultural crops has been shown to result in consistent negative effects on local biodiversity and biological control services (Geiger et al., 2010). To moderate these effects of agricultural intensification, conservation biological control seeks to enhance the activity of natural enemies through habitat manipulation to favor natural enemies over arthropod pests and to protect natural enemies from the harmful effects of pesticides (Jonsson et al., 2008; Crowder and Harwood, 2014; Mills, 2014).

In general, evidence supports a strong linkage between biodiversity and ecosystem function (Cardinale et al., 2006, 2012; Balvanera et al., 2014). Biological control, as a specific ecosystem service, is also considered to be influenced by the biodiversity of local natural enemy communities. From a meta-analysis of the available literature, Letourneau et al. (2009) found a positive effect overall of natural enemy richness on the suppression of herbivore abundance in agricultural habitats. However, the effect of natural enemy richness is not always positive, and some studies have shown either no effect or a negative effect depending on the extent of either functional complementarity or antagonistic interactions among species (Letourneau et al., 2009; Snyder and Tylianakis, 2012; Crowder and Jabbour, 2014). A number of other factors, such as host diversity, complex host life cycles, and host abundance,

may also influence the linkage between herbivore abundance and natural enemy richness (Tylianakis and Romo, 2010). More recently, the supposition that species richness is the best measure for estimating the effectiveness of biological control services in agroecosystems has been questioned, with some studies showing that the functional complementarity of enemy species may be better represented by species evenness (Crowder et al., 2010; Crowder and Jabbour, 2014).

Although conservation biological control as an approach to enhancing biological control services in agriculture has received increasing attention in the literature, it has yet to be more widely adopted and implemented by agricultural managers (Cullen et al., 2008; Goldberger and Lehrer, 2016, this issue). The lack of adoption can be affected by a wide variety of factors, but a key factor is undoubtedly a lack of progress in developing quantitative measures of the impact of resident natural enemies that are accessible to managers (Macfadyen et al., 2015) and economic evaluations of the contribution of conservation biological control to integrated pest management (Naranjo et al., 2015). In addition, there is a continuing need for the development of monitoring tools that managers can easily use for evaluating the local biodiversity of natural enemy communities in agricultural crops.

While pheromones have been widely implemented for monitoring the abundance and seasonal activity of a variety of crop pests since the mid 1980s (Witzgall et al., 2010), developing new tools for monitoring the activity of natural enemies has lagged far behind. Monitoring for natural enemies remains based on labor intensive approaches, such as host rearing to estimate parasitism and either sweep nets or beating trays to estimate predator abundance (Mills, 2005), methods that are of limited use for making pest management decisions. Fortunately, more recently there has been increasing interest in the potential for using plant- or host-associated volatiles for monitoring and even manipulating natural enemies in agricultural crops (Khan et al., 2008; Jones et al., 2009, 2011; Hare, 2011; Meiners and Peri, 2013). As part of a large, multi-state, project we investigated the use of plant volatile traps for monitoring the biodiversity of natural enemies in orchard crops in the western U.S. and

here we present a comparative study of spatial variation among orchard crops and temporal variation through the growing season. In the absence of previous research on this topic, our hypotheses were: 1) that natural enemy biodiversity would be comparable between different orchard crops within the western region, and 2) that natural enemy biodiversity would increase to a maximum mid-season and subsequently decline through the rest of the season.

2. Materials and methods

2.1. Traps and trap deployment

The diversity of the predator and parasitoid communities present in apple, cherry, pear and walnut orchards in the western U.S. was examined using trap catch data that were collected in 2010 and 2011 as part of a natural enemy phenology study described in Jones et al. (2016a, this issue). Apple, cherry and pear orchards were monitored in the Wenatchee region and apple and pear orchards in the Yakima region of Washington (WA), cherry and pear orchards in the Hood River region of Oregon (OR), and walnut orchards in the Sacramento valley of California (CA). For the purpose of this study, the data were restricted to the years 2010 and 2011 when traps were deployed in all three western states for the full season. Four apple and three cherry orchards in the Wenatchee region, WA and three cherry orchards in the Hood River region, OR were excluded from the 2011 data set as the combination of plant volatile lures used in these orchards differed from those used in other orchards that year. In addition, the three cherry orchards monitored in the Hood River region, OR in 2010 were excluded as they were not monitored for the full season. Consequently, there were 19 orchard locations in 2010 and 15 in 2011 (Table 2) for which predators and parasitoids were monitored through the season from March through September using traps baited with plant volatile lures. In 2010, large white plastic delta traps

with sticky liners (Suterra LTD, Bend, OR) were used and these were replaced with one-sided white or yellow sticky panel traps (Alpha Scents, Inc., West Linn, OR) in 2011. Details of the construction and composition of the plant volatile lures are provided by Jones et al. (2016b, this issue).

The traps were baited with one of four lure combinations: acetophenone (Acros Organics, 3 ml per lure, release rate 58.7 mg/d), phenylacetaldehyde (SAFC Supply Solutions, 0.5 ml per lure, release rate 4.9 mg/d), geraniol (SAFC Supply Solutions, 1 ml per lure, release rate 9.9 mg/d) plus methyl salicylate (SAFC Supply Solutions, 3.5 ml per lure, release rate 78.6 mg/d) plus 2-phenylethanol (Sigma-Aldrich, 3 ml per lure, release rate 12.8 mg/d), and an unbaited delta trap in 2010; and geraniol plus 2-phenylethanol (yellow panel trap), methyl salicylate plus 2-phenylethanol (white panel trap), geraniol plus methyl salicylate plus 2-phenylethanol (white panel trap), and an unbaited yellow panel trap in 2011. Four replicate blocks of traps, with all four lure combinations represented in a block, were deployed at each orchard location in each of the two years. The traps were monitored weekly to count the numbers of natural enemies present. Sticky liners or panels were covered with clear Saran™ wrap (S. C. Johnson & Son, Inc. Racine, WI), and frozen at -20°C until natural enemy taxa could be identified.

The plant volatiles used as lures in this study are all known to be floral scents (Knudsen et al., 1993). Floral volatiles were selected for this study rather than green leaf volatiles or herbivore-induced plant volatiles as they are generalized attractants for a broader range of natural enemy taxa (Jones et al. 2016b, this issue). Although the specific lure combinations differed between years, there was considerable overlap among the individual floral volatiles used each year, and these changes were made in an attempt to further broaden the range of natural enemy taxa attracted to the traps. Further details of the responses of different natural enemy taxa to these floral volatiles can be found in Jones et al. (2016b, this issue).

Very few of the insect parasitoids could be identified to species and there was considerable variation between locations with regard to the consistency in identifying the parasitoids to either genus

or family. Consequently the main focus of this study was on the insect predators trapped through the season at each orchard location. The insect predators collected from the traps could not be identified to the species level for all locations and therefore the analysis of the diversity of predator communities was based on predator genera. For the six orchard locations in California, however, all predators were identified to species and all parasitoids were assigned to morphospecies, allowing for a separate species-level analysis of the biodiversity of natural enemy communities in walnuts. The three most abundant taxa were considered to be the dominant members of the natural enemy communities at each orchard location.

2.2. Data analysis

Three separate sets of analyses of the natural enemies communities were carried out; 1) an analysis of spatial variation in the diversity of predator genera based on season total trap catch for all orchard locations, 2) an analysis of the temporal variation in diversity of predator genera from a subset of orchards with sufficient monthly trap catches throughout the season, and 3) an analysis of the diversity of predator and parasitoid species based on season total trap catch in walnut orchards only.

For the first analysis of spatial variation in the diversity of predator genera from season total trap catches for 37 orchard locations over the two-year period (see Table 3 below), trap catches from April through September were used to standardize the sampling effort at each location. The samples from each natural enemy community were based on combined counts for all four lures in each of the four blocks of traps and these counts were summed over the entire season. For the second analysis of the temporal variation in diversity of predator genera through the season, counts from all four lures in each of the four blocks were summed for the four weeks of each month. As Gotelli and Chao (2013) recommend a minimum sample size of 20-50 individuals for meaningful comparisons between samples,

a minimum sample size of 30 individuals was used. In some orchard locations the number of predators trapped in a particular month fell below 30 individuals. When this occurred for more than one month through the season, the orchard locations were excluded, leaving a subset of 23 from the larger data set of 37 orchard locations for the analysis of seasonal variation in the diversity of predator genera; 11 apple orchards in the Wenatchee and Yakima regions of WA, six pear orchards in the Hood River region of OR and the Yakima region of WA, four walnut orchards in the Sacramento valley of California, and two cherry orchards in the Wenatchee region of WA. Using this subset of orchard locations allowed us to extend the months of the season from March through September for all crops, with the exception of apples in 2011 which were limited to April through September. For the third analysis of predator and parasitoid species diversity from season total trap catches in walnut orchards in the Sacramento valley of CA over the two-year period, the six orchard locations were analyzed by combining counts from all four lures in each of the four blocks of traps for the complete season from March through September.

It is well known that diversity increases consistently with sampling effort and that to avoid substantial bias in the estimation of biotic diversity it is necessary to use rarefaction to standardize for sample size before comparison of biodiversity indices among different communities (Colwell et al., 2012; Chao et al., 2014). We used *EstimateS* version 9.1.0 (Colwell, 2013) for individual-based rarefaction without replacement, repeating the randomizations 1000 times to generate rarefied estimates of expected taxon richness (R), exponential Shannon entropy (1D), and the number of rare taxa represented as singletons (f_1) and doubletons (f_2). Standardized sample sizes (based on the smallest actual sample sizes) were 123 individuals for the analysis of the diversity of predator genera for the 37 orchard locations, 30 individuals for the analysis of seasonal variation in the diversity of predator genera for the subset of 23 orchard locations, and 208 individuals for the analysis of the diversity of predator and parasitoid species for the six walnut orchard locations.

A series of diversity indices were used to analyze the natural enemy communities in this study (Table 1). Taxon richness represents the number of predator genera, or predator and parasitoid species, present in the natural enemy communities sampled in an orchard. Taxon richness can be measured in different ways; the observed number of taxa actually sampled from an orchard (R_{obs}), a nonparametric estimate (R_{Chao1}) of the asymptotic number of taxa present in an orchard had the sampling effort been extended beyond that actually used (Chao, 1984; Gotelli and Chao, 2013), and a comparative estimate (R) of the number of taxa present for sampling data that have been rarefied to a standardized sample size (Colwell et al., 2012). Rarefied taxon richness ($R, q = 0$) and exponential Shannon entropy (${}^1D, q = 1$) are the first two components of a unified family of diversity indices known as Hill numbers that are defined by their order q and that satisfy the replication principle required for comparison among multiple communities (Hill, 1973; Jost, 2006; Chao et al., 2014). When $q = 0$, the relative abundance of the component taxa is ignored and both rare and common taxa are treated equally, but when $q = 1$, the component taxa are weighted by their proportional abundance to represent the effective number of taxa in the community. Based on multiplicative partitioning, these two diversity indices can be used to estimate the corresponding taxon evenness (1E) for a community (Jost, 2010; Tuomisto, 2012), which describes the equitability on a scale from 0 (low) to 1 (high) of the relative abundances of the component taxa. Based on multiplicative partitioning of the alpha (within community) and beta (between communities) components of diversity (Jost, 2007; Chao et al., 2012), the compositional similarity (or level of differentiation) between communities can be compared using a multiple-community, abundance-based overlap index (C_{qN}) (Chao et al., 2008, 2012). This overlap index scales from 0 when all communities are distinct to 1 when all communities are identical, and represents the mean proportion of taxa shared by the N communities. As with Hill numbers for diversity indices, the order q determines the sensitivity of the overlap index to the relative abundance of the component taxa in each of the N communities (representing all taxa when $q = 0$, effective taxa when $q = 1$, and only the

common taxa when $q = 2$), and can be used to construct similarity profiles (Gotelli and Chao, 2013). A flat similarity profile of overlap index with respect to order q indicates that both dominant and rare taxa are shared between communities, whereas a negative profile suggests that there is greater differentiation between communities for the dominant taxa than for the rare taxa.

The diversity metrics were analyzed in R (version 3.0.3) using either generalized linear models (glm) for season total trap catch or linear mixed effects models (lmer) in the lme4 package (Bates et al., 2015) for monthly total trap catch. As different sets of lures were used for the plant volatile traps in 2010 and 2011, the trap catches from each year were analyzed separately. Orchard crop (apple, cherry, pear, walnut), natural enemy group (predator, parasitoid) and month were included as fixed factors, and orchard location was used as a random factor to take into account the lack of independence of the monthly samples within each orchard location. The significance of the fixed effects in the models was tested by deletion (Crawley, 2013). When significant effects of fixed factors were detected, the levels within each factor were tested using the general linear hypothesis test function (glht) of the multcomp package (Hothorn et al., 2008) incorporating the least-squares means function (lsmeans) from the lsmeans package (Lenth, 2015).

3. Results

A total of 37,854 predators were caught on the plant volatile traps over the two-year period, with seasonal totals in an orchard varying from 123 individuals in a pear orchard in Hood River (OR) in 2010 to 4,338 individuals in an apple orchard in Wenatchee (WA) in 2010 (Table 2). The predators were from 31 genera and all represented species that are active in the foliage of the orchard trees. The range of abundance varied from a mean (\pm SE) season total trap catch of 796.33 ± 165.15 for *Chrysoperla* in the Yakima region (WA) in 2011, to 0.20 ± 0.20 for *Coccinella*, *Hippodamia* and *Orius* in the Hood River

region (OR) in 2010 (Table 3). Twelve of the predator genera were dominant members of the natural enemy communities at one or more of the orchard locations over the two year period (Table 2), and included six syrphid genera (*Allograpta*, *Eupeodes*, *Heringia*, *Platycheirus*, *Syrphus*, *Toxomerus*), three neuropteran genera (*Chrysopa*, *Chrysoperla*, *Hemerobius*), two heteropteran genera (*Campylomma*, *Deraeocoris*) and one coccinellid genus (*Stethorus*). The proportional abundance of the three most common genera combined varied from 0.52 to 0.94 between orchard locations (Table 2). Two of the predator genera were dominant in all four orchard crops in most of the regions sampled, including *Chrysoperla*, which was dominant in 87% or more of the orchard locations in both years, and *Eupeodes*, which was dominant in 100% of the orchard locations in 2010, but only 27% of the orchard locations in 2011. Other predator genera were dominant only in particular orchard crops and regions (Table 2), such as *Platycheirus* in pear orchards in the Hood River region (OR) and *Allograpta* in walnut orchards in the Sacramento valley (CA). In addition, the dominance of *Heringia* in apple orchards in the Wenatchee region (WA) and of *Hemerobius* in pear orchards in the Hood River region (OR), was primarily limited to the year 2011. Among the rare predator genera (Table 3), six were restricted to one region in one year (*Hyperaspis*, *Microwisea*, *Olla*, *Phytocoris*, *Pipiza*, and *Symphorobius*), while another six were more broadly represented in most orchard locations in both years (e.g., *Coccinella*, *Harmonia*, *Hippodamia*, *Orius*, *Scaeva*, and *Sphaerophoria*).

A total of 15,120 predator and parasitoid individuals were caught on the plant volatile traps at walnut orchard locations in the Sacramento valley (CA), and seasonal totals for either natural enemy group varied from 208 individuals in 2010 to 3168 individuals in 2011 for (Table 4). There were 18 predator species and 99 parasitoid species in 2010, and 23 predator species and 93 parasitoid species in 2011. The range of abundance of predator species varied from a mean (\pm SE) seasonal total of 1167.67 ± 237.31 individuals of *Chrysoperla carnea* (Stephens) trapped in 2011, to 0.33 ± 0.33 individuals of *Geocoris uliginosus* (Say) and *Sphaerophoria sulphuripes* (Thoms.) in 2010. There were five dominant

predator species in the walnut orchards which included the syrphids *Allograpta obliqua* (Say), *Eupeodes fummipennis* (Thoms.), and *Toxomerus marginatus* (Say), and the neuropterans *C. carnea* and *Hemerobius pacificus* Banks. Parasitoid species abundance in the walnut orchards ranged from 475.66 ± 237.31 individuals of a *Brachyserphus* sp. (Hym.: Proctotrupidae) in 2011 to 0.33 ± 0.33 individuals for 25 different unidentified species in 2010. There were 11 dominant parasitoid species in the walnut orchards that included the *Brachyserphus* sp., *Leptopilina* sp. (Hym.: Eucoilidae), three braconid species (*Trioxys pallidus* (Hal.), *Aphidius* sp., *Meteorus* sp.), three ichneumonid species (*Aclastus* sp., *Glypta* sp., *Lysibia* sp.), a *Conostigmus* sp. (Hym.: Megaspilidae), an *Epyris* sp. (Hym.: Bethyridae) and an unidentified pteromalid species. The proportional abundance of the three most common predator species combined or three most common parasitoid species combined varied from 0.23 to 0.91, and the predator species showed greater levels of dominance than the parasitoid species (Table 4).

3.1. Season totals for predator genera

From the analysis of season totals for predator genera, the mean sample coverage (C_n) was high for both the 19 orchards sampled in 2010 (0.980 ± 0.002 SE) and for the 15 orchards sampled in 2011 (0.980 ± 0.001 SE). This indicates that on average the probability of finding an additional predator genus was 0.02 for each additional individual trapped at an orchard location. Consequently, the estimated asymptotic generic richness was either the same as the observed generic richness or only slightly higher, with the exception of six orchards locations (representing all four crops) where it was 25% higher or more (Table 2). For further analysis of the predator communities, the rarefied data were used to standardize for variation in sample size between orchard locations. Generic richness was generally greater in 2011 than in 2010 (Fig. 1a), and was greater in apple and pear orchards than in walnut orchards in 2010 ($F_{3,15} = 2.91$, $P = 0.06$), although there was no effect of crop in 2011 ($F_{2,12} = 0.24$, $P =$

0.79). Similarly, for the diversity of predator genera (Fig. 1b) there was a significant effect of crop in 2010 ($F_{3,15} = 3.81, P = 0.03$), with pear orchards showing greater diversity than cherry orchards, but no effect of crop in 2011 ($F_{2,12} = 1.59, P = 0.24$). For predator generic evenness (Fig. 1c) there was again a significant effect of crop in 2010 ($F_{3,15} = 3.43, P = 0.04$), with generic evenness being greater in pear than in cherry orchards, but no effect of crop in 2011 ($F_{2,12} = 3.21, P = 0.08$).

The mean (\pm SD) asymptotic richness of predator genera for the communities from all locations combined was 27.25 ± 0.74 for the 19 orchards sampled in 2010, and 28.00 ± 0.49 for the 15 orchards sampled in 2011. For comparison of the similarity in composition of predator genera between orchard locations each year, similarity profiles were constructed (Fig. 2). The zero order multiple-community overlap indices, which ignore relative abundance, suggested a greater than 90% overlap ($C_{0N} > 0.9$) of predator genera both between orchard crops within years (Fig. 2a) and between orchard locations within crops (Fig. 2b,c). However, the similarity profiles for higher order indices generally declined, indicating a greater level of differentiation between orchards and crops for effective predator genera ($q = 1$) and common predator genera ($q = 2$). The decline was particularly steep for walnuts in 2010, indicating that the common predator genera differed considerably between walnut orchard locations that year. This was due to dominance by *Eupeodes* in one orchard, but by *Toxomerus* in a second orchard, and by *Chrysoperla* in a third orchard (Table 2). In contrast, pears had a much flatter profile for 2010, indicating that the same predator genera (*Chrysoperla* and *Eupeodes*) dominated the communities in all pear orchards sampled that year (Table 2). The similarity profiles for apple orchards were consistent in both years, but this does not mean that the same genera dominated the predator communities in both years as *Eupeodes* was the dominant genus in 2010 whereas *Heringia* was dominant in 2011 (Table 2). It is notable also that the similarity profiles for pears and walnuts changed between years with pear orchards showing the least differentiation in common predator genera in 2010, but walnut orchards showing the least in 2011.

3.2. Monthly totals for predator genera

A subset of 23 orchard locations had sufficient sample sizes to monitor changes in predator generic diversity through the season, and among crops. The generic richness of the predator communities showed a significant crop by month interaction in both years (2010, $F_{17,70.3} = 4.33$, $P < 0.001$; 2011, $F_{11,53.7} = 3.54$, $P = 0.001$), and a significant main effect of month (2010, $F_{6,70.4} = 8.33$, $P < 0.001$; 2011, $F_{6,53.9} = 4.60$, $P < 0.001$). For apple, cherry and pear orchards, predator generic richness increased more gradually and consistently throughout the growing season in both years, whereas for walnut orchards predator generic richness rose more steeply from March to May and subsequently declined through the rest of the season (Fig. 3 a,b). Predator generic diversity also showed a significant crop by month interaction in both years (2010, $F_{17,70.3} = 3.08$, $P < 0.001$; 2011, $F_{11,53.9} = 2.12$, $P = 0.03$), and a significant main effect of month (2010, $F_{6,70.5} = 5.61$, $P < 0.001$; 2011, $F_{6,54.1} = 3.14$, $P = 0.01$). The interaction between crop and month was similarly driven by the difference in pattern of increase in predator generic diversity over the season between apple, cherry and pear orchards versus walnut orchards (Fig. 3 c,d). In contrast to predator generic richness and diversity, the generic evenness of the predator communities showed no crop by month interaction, and significant independent effects of both crop (2010, $F_{3,13.3} = 9.52$, $P < 0.001$; 2011, $F_{2,10.6} = 13.78$, $P < 0.001$) and month (2010, $F_{6,70.6} = 7.89$, $P < 0.001$; 2011, $F_{6,54.9} = 6.05$, $P < 0.001$). The effect of crop resulted from evenness being greater in walnut versus cherry orchards in 2010 and in apple versus pear orchards in 2011 (Fig. 3 e,f). The month effect appears to have resulted from a greater evenness of the predator genera both early and late in the season compared to mid-season.

3.3. Season totals for natural enemy species in walnuts

The mean sample coverage was higher for predator species (0.992 ± 0.002 SE in 2010; 0.981 ± 0.001 in 2011) than for parasitoid species (0.907 ± 0.012 in 2010; 0.922 ± 0.008 in 2011) for the three walnut locations sampled each year. The mean (\pm SD) asymptotic richness was estimated to be 18.5 ± 1.3 in 2010 and 23.0 ± 0.48 in 2011 for predator species, and 124.1 ± 13.7 in 2010 and 92.4 ± 0.9 in 2011 for parasitoid species. Further analysis of the natural enemy communities in walnut orchards was again based on rarefied data to take into account the variation in sample sizes between orchard locations. The species richness of the natural enemy communities was significantly greater for parasitoids than predators in both years (2010, $F_{1,4} = 17.43$, $P = 0.01$; 2011, $F_{1,4} = 15.79$, $P = 0.02$; Fig. 4a). In contrast, there was no effect of natural enemy group in either year for species diversity (2010, $F_{1,4} = 3.75$, $P = 0.13$; 2011, $F_{1,4} = 3.82$, $P = 0.12$; Fig. 4b) or species evenness (2010, $F_{1,4} = 0.09$, $P = 0.78$; 2011, $F_{1,4} = 0.96$, $P = 0.38$; Fig. 4c). This was due to a much greater level of variation in these two metrics between orchard locations for parasitoids than for predators.

The mean (\pm SD) asymptotic species richness for the communities sampled from the three orchards combined was 18.5 ± 1.30 for predators and 124.08 ± 1.30 for parasitoids in 2010, and 23.00 ± 0.48 for predators and 92.43 ± 0.91 for parasitoids in 2011. The multiple-community similarity profiles again showed greater than 90% of the predator and parasitoid species were shared between orchards in each of the two years (Fig. 4d). The strongly negative profile for predator species in 2010, also seen from the analysis of predator genera (Fig. 2b), was due to a switch in dominance between orchards from *E. fumipennis* and *H. pacificus*, to either *T. marginatus* or to *C. carnea*. The similarity profiles for predator species in 2011 and for parasitoid species in both years showed a similar pattern, indicating that while there was little differentiation in the representation of species between orchard locations, there was 40-65% differentiation in which species were the most common. In addition, while both *T.*

pallidus and *Brachyserphus* sp. were dominant members of the parasitoid community in both years, the other dominant parasitoid species were totally distinct between years (Table 4).

4. Discussion

In this study we used plant volatile traps to monitor the biodiversity of natural enemies in four orchard crops in the western U.S. As natural enemy taxa can differ in their response to particular plant volatile lures (Jones et al., 2016b, this issue), we focused on traps baited with a range of generalist rather than specialist lures to monitor the broader natural enemy community over the growing season of two successive years. The asymptotic regional richness of predator genera among orchard crops was estimated to be 27 in 2010 and 28 in 2011. Similarly, for walnut orchards in California, the estimated asymptotic richness was 19 in 2010 and 23 in 2011 for predator species, and 124 in 2010 and 92 in 2011 for parasitoid species. Few other studies have estimated the biodiversity of natural enemies in orchard crops, but in apple orchards in New Zealand, Shannon entropy indices (H') for natural enemy species collected from beating trays reached a maximum of $H' = 0.76$ (Wearing et al., 2011) which corresponds to a diversity of ${}^1D = 2.14$. In our study, the corresponding diversities of predator genera varied from ${}^1D = 2.93$ in cherry to ${}^1D = 5.46$ in pear in 2010 and from ${}^1D = 5.78$ in pear to ${}^1D = 7.56$ in apples in 2011. Thus the predator communities in orchards in the western U.S. were at least 2 - 3 times more diverse than those found in apple orchards in New Zealand, which probably reflects the lower biodiversity of invertebrates in New Zealand as an island nation versus the much larger continental land mass of the western region of the U.S. (Goldson et al., 2014).

Many of the predator genera and species identified from the plant volatile traps are known predators of primary or secondary pests in the orchard trees (Horton et al., 2012). However, some of the heteropteran (e.g., *Geocoris*, *Nabis*) and syrphid (e.g., *Platycheirus*, *Sphaerophoria*) genera may have

been more associated with prey feeding in resident vegetation or planted cover crops on the orchard floor (Rotheray, 1989; Braman, 2000). For the parasitoids monitored in walnut orchards, their true identity and host associations remain unknown for most species. The more dominant parasitoid species included some that are associated with secondary pests of walnuts, such as *T. pallidus* a specialist parasitoid of walnut aphids, and *Glypta* sp. a likely parasitoid of leafrollers. Others, however, such as *Brachyserphus* sp. a probable parasitoid of nitidulid beetles and *Leptopilina* sp. a probable parasitoid of drosophilid flies, parasitize insects that are associated with the husks of nuts previously damaged by walnut husk fly, walnut blight or sunburn (Michelbacher and Ortega, 1958). Irrespective of the true host associations of the natural enemies trapped, this monitoring program has highlighted the very diverse nature of the natural enemy communities present in orchard crops in the western U.S., despite the intensive approach used for orchard crop production in this region (Jones et al., 2009).

The natural enemy communities that we monitored in this study were restricted to those species that have active flight in the adult stage, and so excluded several natural enemy taxa of importance such as epigeal predators, wingless parasitoids and spiders that can be of importance in orchard crops (Allen and Hagley, 1990; Riddick and Mills, 1994; Monzó et al., 2011; Unruh et al., 2016, this issue). Other sampling methods that have been used to monitor natural enemies in orchard crops include beat trays (Benhadi-Marin et al., 2011; Wearing et al., 2011; Horton et al., 2012), pitfall traps (Riddick and Mills, 1995; Wearing et al., 2011), yellow pan traps or sticky cards (Wearing et al., 2011; Schuber et al., 2012), and corrugated cardboard bands (Marliac et al., 2015). Among these alternatives some are more selective in the range of natural enemy taxa sampled, such as pitfall traps (epigeal predators), beat trays (juvenile foliage predators) and cardboard bands (overwintering and cryptic predators and parasitoids), while others such as yellow pan traps or stick cards are equally broad, but are also restricted to actively flying species. Through use of plant volatile traps that combine both chemical and visual cues for natural enemies we believe that our monitoring program is the first to have

conducted a more extensive quantification of the biodiversity of actively flying predators and parasitoids in orchard crops.

Our analysis from 34 orchards over the two-year sampling period showed a surprisingly high level of similarity in the predator communities between orchard crops and locations, matching our initial hypothesis, with most predator genera shared among all the communities sampled. While apple, pear and walnut share codling moth as a key pest, and aphids and spider mites as secondary pests, the pest management programs typically practiced in these crops differ substantially (Gallardo et al., 2016, this issue). The notable difference in genera and species of natural enemies trapped between the two years is likely due in part to the change from white delta traps in 2010 to white and yellow sticky panels in 2011. For example, with the exception of *Stethorus* (Maeda et al., 2015), coccinellid genera tend to be less responsive to plant volatiles, but are readily attracted to yellow sticky traps (Schmidt et al., 2008), and thus were monitored more effectively in 2011 when yellow sticky panels were used. In contrast, Horton et al. (2012) observed little year to year variation in the relative abundance of predator taxa using beat tray sampling in apple orchards in Washington. While many factors can influence temporal and spatial patterns in the dominance of natural enemy taxa, there is growing evidence that one of the most important, especially for predators, is agricultural intensification (Philpott, 2013). Both the frequency of pesticide use and the toxicity rating of the pesticides used are known to influence the diversity of natural enemies in many perennial crops (Suckling et al., 1999; Thompson and Hoffmann, 2006; Wearing et al., 2011; Mates et al., 2012; Marliac et al., 2015).

Our observations from monitoring the seasonal variation in biodiversity of natural enemies showed that the richness and diversity of predator genera tended to increase through the growing season from March to September in both years, while evenness either remained more constant through the season or showed a slight increase at the start and end of the season. With the exception of walnut orchards (see below) these patterns did not match our initial hypothesis that all metrics would increase

to a maximum mid-season. Few other studies have monitored the diversity of natural enemies through the season, but Wearing et al. (2011) also found a similar pattern of increase in the diversity of natural enemies collected through the growing season from beating tray samples in apple orchards in New Zealand. The seasonal pattern found in walnut orchards differed from that observed in the other orchard crops in that the richness and diversity of both predator genera and predator species increased more strongly early in the season from March to May, but subsequently either remained more or less constant or even declined through the rest of the season and consequently matched our initial hypothesis. It is generally believed that natural enemies have their greatest impact on crop pests at the start of the season when low pest populations are more vulnerable and natural enemy/pest ratios can be more favorable for reducing or delaying pest population growth (Welch and Harwood, 2014). Consequently, the lower richness and diversity of predator genera in all four orchard crops early in the season may be indicative of less effective biological control services at this critical time of the season. Whether this results from natural variation in patterns of phenology among predator species or from the use of delayed dormant pesticides in these orchard crops deserves further attention in the future.

For agricultural production to become more sustainable in the future there will be a greater need for inclusion and management of the natural ecosystem services that have been diminished by the recent trend toward agricultural intensification (Crowder and Harwood, 2014). While the value of natural enemies in controlling crop pests has been known for some time (Jonsson et al., 2008), the importance of pest suppression as a regulating ecosystem service has only more recently been appreciated (Cardinale et al., 2012; Holland et al., 2012). Successful enhancement of ecosystem services such as biological control requires not only a good understanding of the service providers and their functional traits (Luck et al., 2009), but also the tools to efficiently monitor the effects of management practices on natural enemy communities. In this study, we have shown that plant volatile traps can be used as an effective tool for monitoring the biodiversity of natural enemy communities in western

orchard crops. However, for plant volatile traps to be used more broadly in monitoring natural enemy communities in agricultural crops, it will be necessary to establish a causal linkage between biodiversity and biological control services and to clarify the potential for complementarity versus redundancy among the functional traits of natural enemy species (Balvanera et al., 2014; Crowder and Jabbour, 2014).

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Figure legends

Fig. 1. Biodiversity indices a) richness R , b) diversity 1D , and c) evenness 1E , for predator genera based on rarefied season totals from plant volatile traps placed in 34 orchards in the western U.S. in 2010 and 2011 for different orchard crops.

Fig. 2. Similarity profiles for a) all orchards combined in 2010 and 2011, b) all orchards for each crop in 2010, and c) all orchards for each crop in 2011, based on the effective mean proportional overlap of predator genera per community C_{qn} for season total catch from plant volatile traps for 34 orchards in the western U.S.

Fig. 3. Seasonal pattern of biodiversity indices a,b) richness R , c,d) diversity 1D , and e,f) evenness 1E , for predator genera based on rarefied monthly totals from plant volatile traps for 23 orchards in the western U.S. in 2010 (first column) and 2011 (second column) for different orchard crops.

Fig. 4. Biodiversity indices a) richness R , b) diversity 1D , and c) evenness 1E , and d) similarity profiles for predator and parasitoid species based on rarefied season totals from plant volatile traps for 6 walnut orchards in the western U.S. in 2010 and 2011.

Table 1

Index	Explanation	Estimator
R_{obs}	Observed taxon richness	The actual number of different taxa sampled
$R_{Chao\ 1}$	Nonparametric asymptotic taxon richness estimator	$R_{obs} + f_1^2/(2f_2)$ if $f_2 > 0$ $R_{obs} + f_1(f_1 - 1)$ if $f_2 = 0$
1D	Exponential Shannon entropy for Hill number of order 1	$exp\left(-\sum_1^R p_i \ln p_i\right)$
1E	Absolute evenness for Hill number of order 1	${}^1D/R$
C_n	Coverage/ taxon sampling completeness	$1 - f_1/n \left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right]$
C_{qN}	Family of community overlap indices for Hill numbers of order q	$\frac{[1/{}^1D_\beta]^{q-1} - (1/N)^{q-1}}{1 - (1/N)^{q-1}}$

Table 2

Year	Crop	Region	Orchard location	<i>n</i>	<i>R_{obs}</i>	<i>R_{Chao1} ± SD</i>	Proportional abundance of dominant genera	Genera in order of dominance
2010	Apple	WA - Yakima	1	1199	17	17.0 ± 0.1	0.78	<i>Eupeodes, Chrysoperla, Deraeocoris</i>
			2	537	15	15.0 ± 0.8	0.87	<i>Chrysoperla, Campylomma, Eupeodes</i>
			3	483	9	9.0 ± 0.6	0.94	<i>Chrysoperla, Eupeodes, Stethorus</i>
			4	519	15	20.0 ± 5.5	0.87	<i>Chrysoperla, Campylomma, Eupeodes</i>
		WA - Wenatchee	1	1070	18	18.5 ± 1.3	0.79	<i>Campylomma, Eupeodes, Deraeocoris</i>
			2	4338	20	23.0 ± 4.2	0.89	<i>Chrysoperla, Eupeodes, Deraeocoris</i>
			3	2191	14	14.0 ± 0.2	0.80	<i>Eupeodes, Chrysoperla, Syrphus</i>
			4	1333	17	17.0 ± 0.6	0.81	<i>Eupeodes, Chrysoperla, Campylomma</i>
	Cherry	WA - Wenatchee	1	1188	18	23.0 ± 5.5	0.94	<i>Chrysoperla, Eupeodes, Chrysopa</i>
			2	321	16	31.0 ± 13.6	0.87	<i>Chrysoperla, Eupeodes, Syrphus</i>
			3	2382	15	15.3 ± 0.9	0.89	<i>Eupeodes, Chrysoperla, Chrysopa</i>
	Pear	OR - Hood River	1	312	12	12.3 ± 0.9	0.80	<i>Chrysoperla, Eupeodes, Platycheirus</i>
			2	269	12	15.0 ± 4.5	0.80	<i>Chrysoperla, Eupeodes, Toxomerus</i>
			3	123	10	11.0 ± 2.3	0.66	<i>Eupeodes, Platycheirus, Chrysoperla</i>
			4	483	15	16.5 ± 2.6	0.76	<i>Chrysoperla, Eupeodes, Syrphus</i>
			5	350	11	11.0 ± 0.2	0.75	<i>Chrysoperla, Eupeodes, Heringia</i>
Walnut	CA - Sacramento valley	1	1913	12	12.0 ± 0.6	0.63	<i>Eupeodes, Hemerobius, Allograpta</i>	
		2	1362	9	9.0 ± 0.1	0.85	<i>Toxomerus, Eupeodes, Chrysoperla</i>	
		3	436	9	9.0 ± 0.2	0.91	<i>Chrysoperla, Allograpta, Eupeodes</i>	
2011	Apple	WA - Wenatchee	1	1065	18	18.0 ± 0.3	0.60	<i>Heringia, Eupeodes, Chrysoperla</i>
			2	2054	18	24.0 ± 7.2	0.62	<i>Chrysopa, Heringia, Chrysoperla</i>
			3	1177	18	18.3 ± 0.9	0.66	<i>Heringia, Deraeocoris, Eupeodes</i>
			4	1610	18	18.0 ± 0.3	0.60	<i>Chrysoperla, Heringia, Campylomma</i>

Pear	OR - Hood River	1	685	12	12.0 ± 0.6	0.85	<i>Platycheirus, Hemerobius, Chrysoperla</i>
		2	259	12	12.0 ± 0.6	0.77	<i>Platycheirus, Chrysoperla, Hemerobius</i>
		3	226	15	15.0 ± 0.6	0.52	<i>Hemerobius, Platycheirus, Chrysoperla</i>
		4	491	14	14.0 ± 0.6	0.67	<i>Platycheirus, Chrysoperla, Hemerobius</i>
		5	328	14	14.0 ± 0.3	0.63	<i>Chrysoperla, Platycheirus, Hemerobius</i>
	WA - Yakima	1	1226	21	22.0 ± 1.8	0.81	<i>Chrysoperla, Chrysopa, Campylomma</i>
		2	2173	18	18.0 ± 0.2	0.71	<i>Chrysoperla, Chrysopa, Deraeocoris</i>
		3	1834	20	21.0 ± 2.3	0.76	<i>Chrysoperla, Chrysopa, Stethorus</i>
Walnut	CA - Sacramento valley	1	2512	18	19.0 ± 2.3	0.78	<i>Eupeodes, Toxomerus, Allograpta</i>
		2	1020	17	17.0 ± 0.3	0.67	<i>Toxomerus, Chrysoperla, Allograpta</i>
		3	385	15	20.0 ± 6.0	0.69	<i>Chrysoperla, Allograpta, Eupeodes</i>

Table 3

Region	CA – Sacramento Valley		OR – Hood River		WA – Wenatchee			WA – Yakima	
Crop	Walnut		Pear		Apple		Cherry	Apple	Pear
Year	2010	2011	2010	2011	2010	2011	2010	2010	2011
No. orchards	3	3	5	5	4	4	3	4	3
Coccinellidae									
<i>Adalia</i>		1.00 ± 0.00				21.50 ± 17.97			6.00 ± 2.52
<i>Coccinella</i>		8.33 ± 3.33	0.20 ± 0.20		9.75 ± 3.64	2.00 ± 1.08	2.33 ± 0.88	1.25 ± 1.25	3.00 ± 1.15
<i>Cycloneda</i>			0.40 ± 0.24	2.00 ± 0.89					2.67 ± 1.33
<i>Harmonia</i>		6.00 ± 3.06	0.40 ± 0.24	1.80 ± 0.92	4.25 ± 3.07	12.00 ± 11.67		0.25 ± 0.25	39.33 ± 25.83
<i>Hippodamia</i>	1.00 ± 0.58	6.67 ± 3.18	0.20 ± 0.20	2.20 ± 1.02		14.00 ± 7.13		8.25 ± 7.26	14.33 ± 9.94
<i>Hyperaspis</i>								0.50 ± 0.50	
<i>Microweisea</i>									2.00 ± 2.00
<i>Olla</i>		6.00 ± 5.51							
<i>Stethorus</i>				15.80 ± 7.05	1.25 ± 0.95	41.75 ± 25.81	1.00 ± 0.58	10.75 ± 5.25	50.33 ± 26.83
Hemiptera									
<i>Anthocoris</i>							0.33 ± 0.33		9.33 ± 4.26
<i>Campylomma</i>			3.80 ± 3.32	1.80 ± 1.11	168.75 ± 99.64	125.75 ± 60.87	0.67 ± 0.67	75.00 ± 40.86	115.00 ± 52.58
<i>Deraeocoris</i>			7.80 ± 3.56	23.40 ± 11.92	98.75 ± 48.34	167.75 ± 41.92	9.00 ± 1.53	29.25 ± 25.92	94.00 ± 69.01
<i>Geocoris</i>	0.33 ± 0.33					0.50 ± 0.50	0.67 ± 0.33	0.75 ± 0.48	
<i>Nabis</i>					1.00 ± 0.58	2.25 ± 0.48	1.00 ± 0.33		
<i>Orius</i>		3.67 ± 1.76	0.20 ± 0.20	0.80 ± 0.80	20.50 ± 8.31	2.50 ± 0.87	5.00 ± 1.00	7.25 ± 3.92	21.67 ± 4.70
<i>Phytocoris</i>		3.67 ± 1.76							
Neuroptera									
<i>Chrysopa</i>	11.33 ± 0.33	46.33 ± 17.98	1.40 ± 0.75	0.80 ± 0.58	56.75 ± 22.50	188.25 ± 133.04	79.67 ± 70.24	11.75 ± 5.59	358.67 ± 107.22
<i>Chrysoperla</i>	268.33 ± 45.24	171.67 ± 25.83	117.20 ± 28.63	61.60 ± 9.33	729.75 ± 506.92	214.50 ± 83.12	593.33 ± 243.93	257.00 ± 25.20	796.33 ± 165.15

<i>Eremochrysa</i>					1.25 ± 0.48	0.50 ± 0.29	0.33 ± 0.33	13.50 ± 12.18	
<i>Hemerobius</i>	144.67 ± 130.19	55.67 ± 16.68	12.80 ± 3.10	53.40 ± 15.46	7.50 ± 0.87	58.25 ± 6.34	5.00 ± 0.58	6.50 ± 1.55	42.00 ± 2.65
<i>Symphorobius</i>					0.50 ± 0.29				
Syrphidae									
<i>Allograpta</i>	153.00 ± 85.85	181.00 ± 71.33			0.25 ± 0.25				0.33 ± 0.33
<i>Eupeodes</i>	238.67 ± 133.48	444.33 ± 378.83	90.80 ± 17.48	23.00 ± 4.87	938.75 ± 259.28	134.50 ± 27.12	500.67 ± 401.67	215.50 ± 135.94	82.00 ± 33.50
<i>Heringia</i>			18.60 ± 6.35	7.40 ± 1.57	19.25 ± 5.99	387.25 ± 4.25	12.67 ± 5.17		29.67 ± 11.86
<i>Paragus</i>	1.00 ± 1.00	5.33 ± 5.33							
<i>Pipiza</i>					0.25 ± 0.25				
<i>Platycheirus</i>	22.00 ± 13.61	48.33 ± 6.12	16.80 ± 3.29	173.40 ± 70.04	15.25 ± 4.87	39.00 ± 8.53	5.67 ± 4.67	1.50 ± 0.65	28.00 ± 20.13
<i>Scaeva</i>	3.33 ± 1.76	26.33 ± 23.36	6.40 ± 1.29	2.80 ± 1.07	29.25 ± 9.62	3.50 ± 1.55	10.00 ± 4.73	20.50 ± 18.51	2.00 ± 1.15
<i>Sphaerophoria</i>	1.33 ± 1.33	13.33 ± 6.36	1.00 ± 0.45	4.40 ± 1.33	11.50 ± 4.17	13.50 ± 8.51	2.67 ± 1.20		7.33 ± 3.48
<i>Syrphus</i>	35.33 ± 26.84	27.33 ± 24.34	15.40 ± 4.34	14.00 ± 1.95	82.25 ± 26.33	33.50 ± 7.60	49.33 ± 39.84	9.25 ± 6.01	9.67 ± 2.91
<i>Toxomerus</i>	356.67 ± 220.91	250.67 ± 122.51	14.00 ± 3.33	9.20 ± 2.56	36.25 ± 15.63	13.75 ± 9.50	17.67 ± 16.67	15.75 ± 3.97	30.67 ± 5.33

Table 4

Year	Enemy group	Orchard location	<i>n</i>	<i>R_{obs}</i>	<i>R_{Chao1} ± SD</i>	Proportional abundance of dominant species	Species in order of dominance
2010	Predator	1	1913	17	20.0 ± 4.6	0.63	<i>E. fumipennis</i> , <i>H. pacificus</i> , <i>A. obliqua</i>
		2	1362	15	16.5 ± 2.6	0.85	<i>T. marginatus</i> , <i>E. fumipennis</i> , <i>C. carnea</i>
		3	436	9	9.0 ± 0.3	0.91	<i>C. carnea</i> , <i>A. obliqua</i> , <i>E. fumipennis</i>
	Parasitoid	1	803	54	77.1 ± 13.1	0.78	<i>Leptopilina</i> sp., <i>Brachyserphus</i> sp., pteromalid sp.
		2	857	79	92.1 ± 7.6	0.27	<i>Leptopilina</i> sp., <i>Glypta</i> sp., <i>Conostigma</i> sp.
		3	208	54	79.0 ± 13.6	0.41	<i>Trioxys pallidus</i> , <i>Brachyserphus</i> sp., <i>Meteorus</i> sp.
2011	Predator	1	2512	22	22.0 ± 0.5	0.78	<i>E. fumipennis</i> , <i>T. marginatus</i> , <i>A. obliqua</i>
		2	1020	21	21.0 ± 0.4	0.67	<i>T. marginatus</i> , <i>C. carnea</i> , <i>A. obliqua</i>
		3	385	19	21.0 ± 2.9	0.69	<i>C. carnea</i> , <i>A. obliqua</i> , <i>E. fumipennis</i>
	Parasitoid	1	3168	69	72.5 ± 3.7	0.45	<i>Brachyserphus</i> sp., <i>Aphidius</i> sp., <i>T. pallidus</i>
		2	1112	80	85.0 ± 4.3	0.23	<i>T. pallidus</i> , <i>Epyris</i> sp., <i>Aclastus</i> sp.
		3	1344	58	61.1 ± 3.1	0.70	<i>Brachyserphus</i> sp., <i>T. pallidus</i> , <i>Lysibia</i> sp.

Table 1

The indices of diversity used to analyze the natural enemy communities, where p_i is the relative abundance of the counts for taxon i , n is number of individuals sampled, N is the number of communities sampled, and f_1 and f_2 are the number of taxa represented by a single and two individuals respectively.

Table 2

Number of individuals (n), observed (R_{obs}) and estimated (R_{Chao1}) generic richness, and the combined proportional abundance and identity of the three most common genera from the season total trap catch for predator genera at each of the orchard locations.

Table 3

The mean (\pm SE) season total per orchard for each genus of predators collected on plant volatile traps in apple, pear and walnut orchards in the western U.S. in 2010 and 2011.

Table 4

Number of individuals (n), observed (R_{obs}) and estimated (R_{Chao1}) species richness, and the combined proportional abundance of the three dominant (most common) species from the season total trap catch for predator and parasitoid species at each of the walnut orchard locations.

Fig. 1

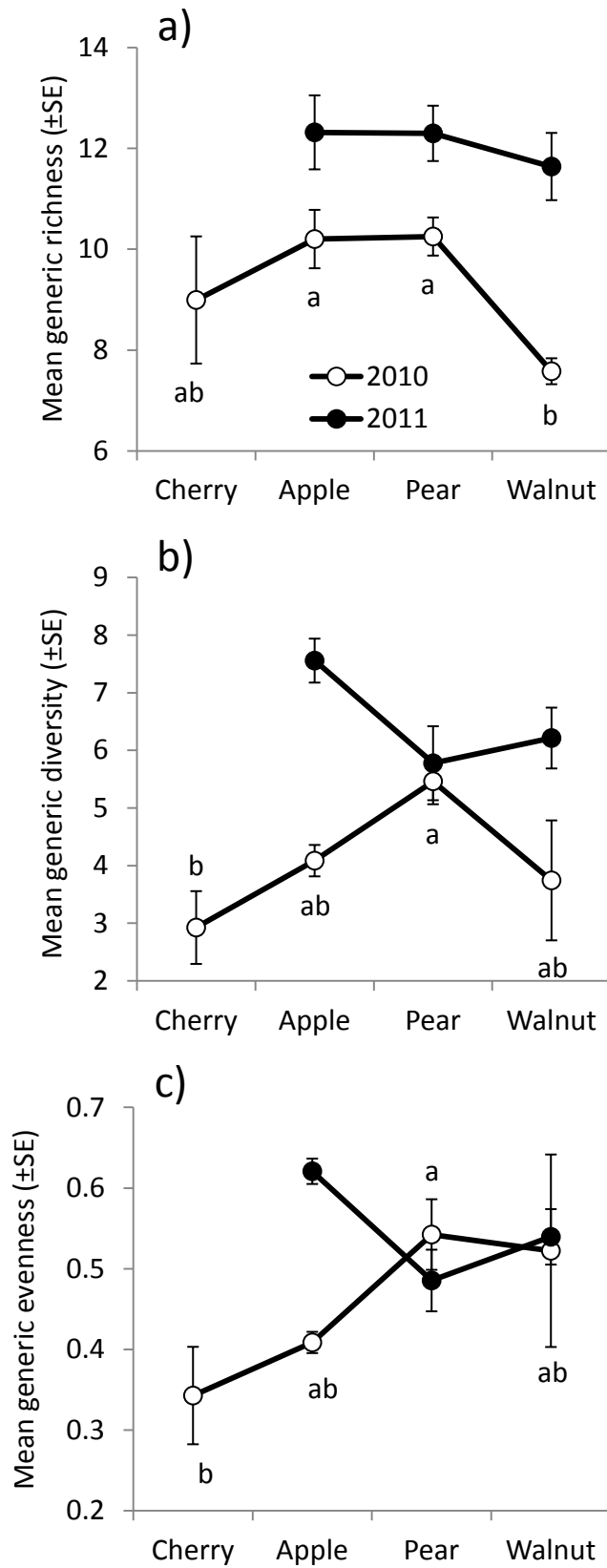


Fig. 2

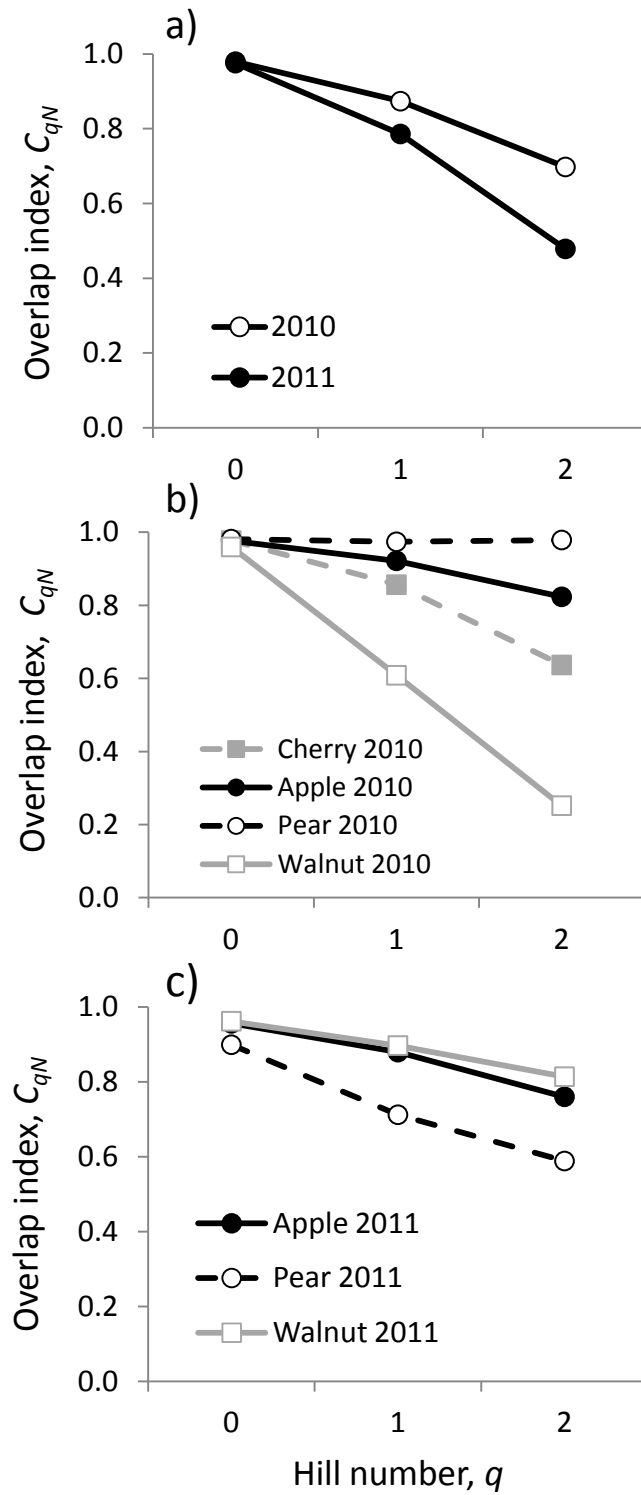


Fig. 3

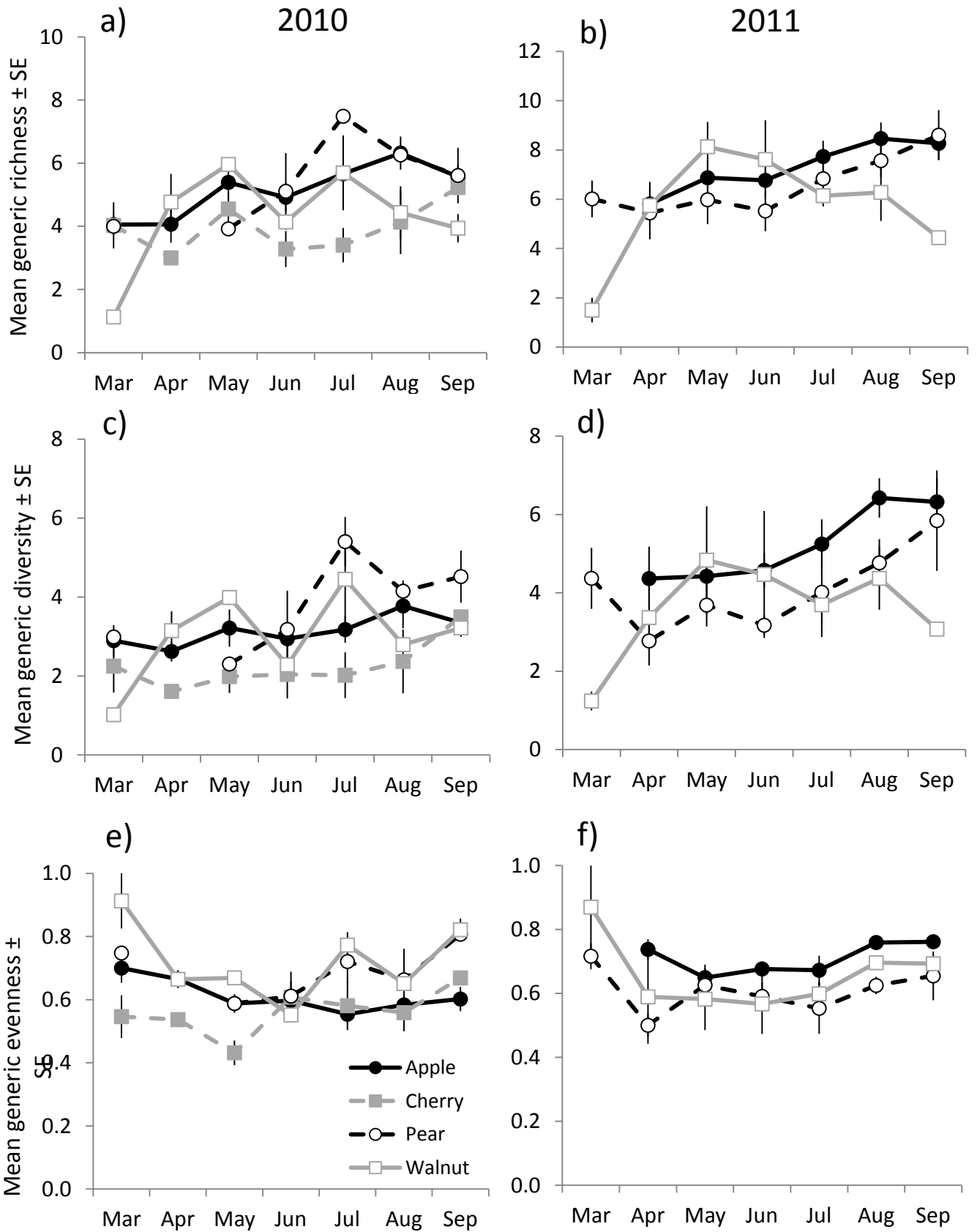


Fig. 4

