

Temporal dynamics of diversity in a tropical fruit fly (Tephritidae) ensemble and their implications on pest management and biodiversity conservation

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Received: 21 January 2013 / Accepted: 13 March 2013 / Published online: 5 April 2013
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Abstract The fact that pests are the most abundant species in agricultural settings has broadly precluded the attention to non-pest species and the study of temporal dynamics of diversity in agroecosystems. Because, agroecosystems hold increasingly important portions of biological diversity, understanding of non-pest species dynamics in such systems will contribute significantly to their conservation. In addition, deep understanding of both pest and non-pest population dynamics in a community context necessarily requires a long-term approach. By means of the analysis of weekly fruit fly sampling sessions across 12 years, in three tropical fruit orchards, we describe the temporal dynamics of species richness and turnover, structure and composition of *Anastrepha* fruit fly ensembles considering pest and non-pest species. Furthermore, we ask if time series of non-pest species covariate with time series of pest species, as a way to evaluate the best management scheme to minimize negative impacts of pest control on non-pest species. Among 18 *Anastrepha* fruit fly species detected over 12 years, five were considered as pest species. Fruit fly ensembles were characterized by strong seasonal dynamics composed of annual cycles. Sapodilla was the most diverse orchard. Overall, fruit fly ensembles appeared stable throughout time. The temporal dynamics of non-pest species covaried positively with temporal dynamics of pest abundance, with consequent management implications. Results suggest that in mango and grapefruit orchards, pest control could be focused during time periods with low potential impact on non-pest species; while in sapodilla orchards other approaches should be developed. The approach described here could be used in agroecosystems to minimize the impact of pest management on non-pest species particularly in

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highly anthropized landscapes and human-managed ecosystems were biodiversity conservation is a high priority.

Keywords Integrated pest management · Community dynamics · *Anastrepha* · Diversity · Time series analysis · Monitoring program

Introduction

Most pest management research generally focuses on the bionomics of individual species regardless of the community in which the pest species inhabits. This is because precisely pest species often are the most abundant in agroecosystems (Matson et al. 1997), and attention paid to other less abundant species may increase the costs to control the target pest species. However, such an approach potentially fails to recognize the impact of management actions for pest control on species diversity. Moreover, it forgoes looking at underlying community processes and interspecific coexistence mechanisms, whose understanding may help us to potentially minimize the impact of management actions on non-target species in the long term and to develop sustainable pest management practices. Nowadays, attention to non-pest species dynamics becomes relevant because of the importance of biodiversity conservation in the functioning of agroecosystems to improve integrated pest management programs and simultaneously maintain the viability of ecological processes in the system (e.g., Altieri 1999; Altieri and Nicholls 2004; Thomas 1999; Wilby and Thomas 2002; Zhang et al. 2007; Letourneau et al. 2009). Additionally, although the majority of conservation efforts have focused on protected remnants of pristine environments (Pimm et al. 2001; Vieira et al. 2012), protecting biological diversity existing in agricultural and forest ecosystems, and human settlements, which together account for 95 % of the terrestrial environment (Pimentel et al. 1992) is equally vital (Ascensao et al. 2012).

One interesting approach to disentangle the trade-off between control of pest species and maintenance of diversity of non-target species, might be to evaluate if temporal dynamics of abundance of pest species covary with temporal dynamics of species richness and abundance of non-target species. If abundance peaks of pest species covary significantly and positively with peaks of species richness, it would be expected that management actions will have the most negative impact on species diversity of non-target species. Indeed, more environmentally friendly actions would be expected when management actions on pest species are carried out when the diversity of remaining species is low.

Fruit fly species in the genus *Anastrepha* are the most important pests for fruit production in the American continent (Aluja 1994), causing huge economic losses and heavy investment in agrochemicals for control (McPherson and Steck 1996; Aluja and Mangan 2008). Among the 197 described species of *Anastrepha* (McPherson et al. 2000), only seven are considered pests due to damage impinged on fruit crops, and five of those species inhabit in Mexico (Aluja 1994). Fruit fly species ensembles in agricultural settings may be characterized by a few high-frequency and abundant species (those pest species related to particular host plants), and a subset of species with low abundance that cause negligible or no damage to fruit crops (Celedonio-Hurtado et al. 1995; Aluja et al. 1996). This suggests that any management action will have differential effects on non-pest species populations because pest species may build up to sum many times the abundance of non-pest ones. On the other hand, this may indicate that fruit fly ensembles in orchards are impoverished possibly due to previous management actions at orchard level and/or local extinction

processes at the landscape level in the recent past. However, regardless of its magnitude, the question if it is possible to minimize the negative impact of management actions on the remaining non-pest species gains relevance. Some fruit fly species from the subset of low abundance non-target species, may function as hosts of parasitoid species that also parasitize fruit fly pest species (Ovruski et al. 2000, 2004; Schliserman et al. 2004), as one of the main problems in agroecosystems has been identified as a lack of diversity in parasitoid hosts for alternation (Stary and Pike 1998). Additionally, reduction of herbivore diversity in agroecosystems may lead to changes in gene flow between parasitoid populations using different hosts and dominance of features of populations using the most abundant pest species (Stary and Pike 1998). Higher fruit fly parasitoid diversity and parasitism rates have been discovered in complex ecosystems with greater non-pest species diversity and abundance than in perturbed ecosystems (Aluja et al. 2003a, b). A greater diversity of herbivorous insects in agroecosystems has also been linked to greater diversity of predators (Altieri and Nicholls 1998; Wilby et al. 2005). In spite of the relative value of non-target fruit fly species, typically researchers and pest management agents investigate ecological phenomena of the most dominant fruit fly species associated to commercial host plants. Therefore, temporal dynamics of fruit fly diversity is often a neglected matter in pest management studies for fruit fly control, and to our knowledge, yet an untouched topic.

In this paper, we first examine the temporal dynamics of fruit fly diversity at a local scale across 12 years, and examine the composition and structure of *Anastrepha* fruit fly ensembles in mango, sapodilla and grapefruit orchards in Veracruz, Mexico. From a conservation standpoint, it has to be considered that given the current preponderance of anthropized landscapes (e.g., only 3 % of the original vegetation in the state of Veracruz remains undisturbed, Toledo-Aceves et al. 2011), actions taken to minimize negative impacts of human activity on biological diversity in agroecosystems may become increasingly important and certainly ethically called for.

In second place, we evaluate the degree of covariation between the temporal dynamics of the dominant fruit fly pest species of its corresponding orchard type, and the temporal dynamics of the subset of non-target fruit fly species in the same orchard. Specifically, we addressed the following questions: (1) What is the magnitude of the variation in fruit fly diversity among orchards over time? (2) What is the composition and structure of fruit fly ensembles and their temporal profile? (3) Do temporal dynamics of fruit fly pest species and non-target species covariate? Among other analyses, we used the goodness of time series analysis applied on 144 months of weekly fruit fly sampling sessions in each of the three orchards in an attempt to answer these questions.

Materials and methods

Study sites

Field data was collected between January 1994 and December 2005 in three commercial orchards, one in Martínez de la Torre (Lat 20° 04' N, Long 97° 04' W, 80 m) and two in Apazapan (Lat 19° 19' N, Long 96° 43' W, 293 m) in the State of Veracruz, Mexico. The grapefruit orchard in Martínez de la Torre is a 25 ha ruby red cultivar monocrop surrounded by groves of valencia orange, and marsh and ruby red grapefruit. Some of the adjacent groves have been unmanaged for some time and as a result, large *A. ludens* populations build up. This orchard is under intensive management practices considering local standards. Trees are fertilized on a yearly basis and pests and diseases controlled by

means of broad spectrum synthetic insecticide, acaricide and fungicide applications. In the case of fruit flies, calendar bait sprays (hydrolyzed protein mixed with an insecticide and water) are applied from July to September. The two orchards in Apazapan, which are grown next to each other, even though commercially viable, are poorly managed. The mango orchard (4 ha) is planted mainly with trees of the cultivar manila interspersed with local cultivars such as ‘papaya’, ‘manililla’, ‘tocotín’ and ‘petacón’. The orchard is bordered by trees of *Spondias purpurea* (Anacardiaceae). Management is restricted to occasional irrigation with water pumped from an adjacent river, and control of ants, which are a nuisance during harvest, by means of insecticides.

The sapodilla orchard (1.5 ha) contains trees from the cultivars ‘morena’ and ‘yoyo’, grafted on native *Manilkara sapota* (Sapotaceae). Fruit in this orchard are usually heavily infested with *A. serpentina* and management is also restricted to occasional irrigation during the peak of the dry season (April–June). As far as we know, nothing is done in these orchards to control fruit flies. Further details are given in Aluja et al. (2012).

Fruit fly sampling design

We choose to adopt a sampling scheme over extended time periods and across three types of orchards, rather than replicating in many similar orchards over shorter time periods. This decision was due to the fact that increasing spatial interspersed necessarily precludes temporal interspersed on a weekly sampling scheme because the cost of monitoring would be astronomical. With this decision, we also wanted to increase the probability of detecting rare species reported in the area 20 years ago (Aluja 1993) such as *Anastrepha robusta* or *Anastrepha chicleyae* and *Anastrepha bicolor* that may be in danger of local extinction.

Twelve McPhail traps (Steyskal 1977) were placed in the grapefruit orchard and sixteen McPhail traps in each of the two neighboring mango and sapodilla orchards. Each glass trap was baited with 10 ml of hydrolyzed protein (Captor Plus®, Agroquímica Tridente, Mexico City) and 5 g of borax (granular borax pentahydrate) mixed with 250 ml of water and hung on a tree (grapefruit, mango, sapodilla depending on orchard) at about 3–4 m from the ground. The spatial distribution of traps covered almost the entire surface of each orchard for the three orchard types. During each weekly trap service, fruit flies were collected and the traps were resupplied with a freshly prepared bait mixture. The fruit flies collected were transferred to vials with a 70 % alcohol and water solution transported to the laboratory, sexed, identified by one of us (LG), and kept in the entomological collection of the Red de Manejo Biorracional de Plagas y Vectores at the Instituto de Ecología, A.C. (Xalapa, Veracruz).

Data analysis

What is the magnitude of variation of fruit fly diversity among orchards over time?

To describe diversity variation throughout time, we built time series both for α and β diversity, considering the number of fruit fly species captured in all traps during the corresponding month for each orchard. This assumes that fruit fly captures are a good (unbiased) estimator of population fluctuations and temporal dynamics of diversity. Alpha (α) is the number of species present in each month. Beta (β) is the ratio between the number of species in 2 contiguous months and the average number of species of the 2 months (based in β of Whittaker 1960). Thus, $\beta > 1$ depicts a higher turnover of species between 2 months. To construct continuous series (due to absence of captures), the first

data of each series of β values (January 1994) was replaced by the mean of β values from January values of the remaining series (January 1995–2005). Thus, albeit these are not ‘real’ series, they represent the best possible approximation. Missing data (absence of captures) were interpolated from adjacent points in order to make continuous time series. Temporal trends in each series were determined by linear regression between the diversity series and the sampling date. Also, the trend and seasonality of time series were explored by autocorrelation functions (ACF), with which we built correlograms. The shape of the ACF in the correlogram is an indicator of periodicity in the series (Royama 1992).

What is the composition and structure of fruit fly ensembles and its temporal profile?

To explore temporal variability in composition of ensembles we also compared annually grouped data sets of species richness and their corresponding number of fruit flies captured for each species in each orchard. This analysis was carried out by means of two-way analysis of similarities (ANOSIM), considering the number of fruit flies captured monthly by species as a sampling unit, and year as an independent factor, with season nested in year. Similarity matrices for fruit fly species were built using the Bray–Curtis similarity index from the square root of $x + 1$, where x is the number of individuals of each fruit fly species. This analysis was performed with PRIMER v.5 software (Clarke and Warmick 1994).

Do temporal dynamics of fruit fly pest species and non-target species covariate?

We carried out cross-correlogram analyses between a pest species abundance time series (*A. fraterculus*, *A. ludens*, *A. obliqua*, *A. serpentina*, and *A. striata*) and an abundance and diversity (α) time series of non-pest species to establish the degree of covariance between time series. A significant cross-correlation (with Box–Ljung Q statistic) between two series at a particular lag means that the variation in the “response” series is due to or is coupled with the variation of the lagged series at the lag period indicated (Box and Jenkins 1976). We chose cross-correlations to lag 6 because the most important correlations would be within the same month and/or season, in order to suggest management actions related to the pest outbreak and fruit harvest period. Prior to cross-correlogram analyses, we built each pair of filtered time series to be evaluated, a prerequisite for cross time series, because filtered series represent the essential variability. First, we built time series of abundance of pest and non-pest species (both grouped). To do this we used monthly FTD (flies/trap/day index) values as detailed in Aluja et al. (2012). Second, we built the respective time series of α diversity but subtracting pest species. These time series were modeled by autoregressive integrated moving average (ARIMA) models, in order to make stationary series (Box and Jenkins 1976). The selection of the model was based on the significance of ARIMA parameters, the least mean square error and number of parameters, and by the absence of significance from autocorrelation and partial ACF at 24 lags. The following ARIMA models (approximate (McLeod and Sales) maximum likelihood procedure) were used in the cross analyses: α diversity series of sapodilla = (1,0,0) (0,1,1), mango (0,1,1) (0,1,1), and grapefruit (1,0,1) (0,1,1); α diversity series of non-pest species of sapodilla = (1,0,0) (0,1,1), mango = (0,1,1) (0,1,1), and grapefruit = (1,0,1) (0,1,1); abundance (FTD) series of pest species of sapodilla = (0,1,0) (2,1,0), mango = (1,1,1) (2,1,0), and grapefruit = (1,1,1) (1,1,2); abundance (FTD) series of non-pest species of sapodilla = (2,1,1) (2,1,0), mango = (2,1,1) (0,1,1), and grapefruit = (0,1,1) (2,1,0). All series as indicated by middle values within parenthesis in the ARIMA models were differentiated

with a non-seasonal lag of 1 (1 month) and a seasonal lag of 12 (1 year). The significance level of cross-correlations was established at $P < 0.0083$, after a Bonferroni correction for 6 lags (P level = 0.05/6). All analyses were carried out using Statistica 7.0 (StatSoft, Inc. 2004).

Results

What is the magnitude of variation in fruit fly diversity among orchards over time?

Overall, we captured eighteen *Anastrepha* fruit fly species. Thirteen species were detected in the grapefruit orchard, while 13 and 17 congeneric species were found in the mango and sapodilla orchards, respectively (Table 1), after the capture of 55,616 individuals corresponding to 27,592 single trap sessions. Species considered as pests in Mexico (*A. fraterculus*, *A. ludens*, *A. obliqua*, *A. serpentina*, *A. striata*) were the most common in the three orchards. In the grapefruit orchard, 99 % of individuals were represented by three species, while in both the mango and sapodilla orchards the same proportion was represented by five species (Table 1).

Both α and β diversity fluctuated throughout the 12 years of study in each one of the three orchards with an apparently stable pattern in the long term but with jumps between contiguous years (Fig. 1). However, no temporal trends were detected in the series of α and β diversity in the grapefruit (monthly mean \pm 1 SE, $\alpha = 1.8 \pm 0.1$, $N = 144$; β between months = 1.39 ± 0.03 , $N = 136$), mango ($\alpha = 2.99 \pm 0.19$, $N = 144$; $\beta = 1.42 \pm 0.03$, $N = 129$), or sapodilla ($\alpha = 3.11 \pm 0.2$, $N = 144$; $\beta = 1.44 \pm 0.03$, $N = 130$) orchards (adjusted $R^2 < 0.015$ in all cases). Thus, in the long term, both α and β diversity appeared as stable attributes of *Anastrepha* ensembles throughout the time of study.

Both α and β diversity exhibited seasonal fluctuations in the series. But the magnitude of seasonality effects was stronger in the mango and sapodilla orchards (Table 2; Fig. 2). In these orchards, the season with highest species richness was winter, while in the grapefruit orchard the seasonal dynamics appeared to be more stable for α and β diversity. In terms of seasonal abundance and species richness, pest species dominated spring and summer months in the three orchards (Table 2). This period was related to fruit availability mainly in the mango orchard, while in the sapodilla and grapefruit orchards the higher relative abundance was opposite to the fruit availability period. A similar decoupling between cropping season and pest outbreaks was observed in terms of monthly species richness. In the sapodilla orchard, higher species richness was found after the fruiting season, in the mango orchard before fruiting season, and in the grapefruit orchard there was a low species richness with two similar peaks in autumn and spring months (Table 2; Fig. 2). The ACF revealed for the three diversity series are characterized by seasonal processes (Fig. 3). However, in the grapefruit orchard this seasonal process is weakened, and it is mainly characterized by an autoregressive process of first order (Fig. 3). In turn, in the mango and sapodilla orchards, the seasonal process is evident, depicted by the seasonal wave just at lags 12 and 24 (each year; Fig. 3).

What is the composition and structure of fruit fly ensembles and their temporal profile?

The analysis of similarity tests showed that fruit fly ensemble structure and composition in the three orchards was driven mainly by seasonal effects (grapefruit = global $R = 0.295$; mango = global $R = 0.393$; sapodilla = global $R = 0.363$, $P = 0.001$ in all cases).

Table 1 Number of individuals of different *Anastrepha* fruit fly species captured in McPhail traps per orchard and year

Species	Orchard	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	Relative abundance ^a
<i>alveata</i>	Grapefruit		4	1						4	2			0.0015
	Mango	2	51	7		1	2	1	2	9	11	3	2	0.0091
	Sapodilla	1	22	29	6				4	9	14	5	8	0.0098
<i>bahiensis</i>	Grapefruit													
	Mango													
	Sapodilla					1		1						0.0002
<i>bicolor</i>	Grapefruit		1											0.0001
	Mango	2	3	1		1		3	3		3	2	7	0.0022
	Sapodilla	1	4	7				2	2	6	1	4	8	0.0033
<i>chiclayae</i>	Grapefruit		1	1	1									0.0004
	Mango	1		1								1	1	0.0004
	Sapodilla							1						0.0001
<i>cordata</i>	Grapefruit	1						2						0.0004
	Mango													
	Sapodilla													
<i>demata</i>	Grapefruit													
	Mango		2						1		3	2		0.0008
	Sapodilla		2		1					3	8	1	3	0.0018
<i>distincta</i>	Grapefruit		6		1			1						0.0011
	Mango	2											1	0.0003
	Sapodilla												2	0.0002
<i>fraterculus</i>	Grapefruit	3	6	73	160	3	3	13	18	6	19	1	3	0.0407
	Mango	88	40	237	1	3		13	9	11	25	76	143	0.0645
	Sapodilla	50	11	181	1	1		7	18	7	36	76	78	0.0465

Table 1 continued

Species	Orchard	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	Relative abundance ^a
<i>hamata</i>	Grapefruit													
	Mango													
	Sapodilla		1											0.0001
<i>ludens</i>	Grapefruit	329	1382	1026	902	292	206	2417	804	384	1818	800	229	1.4007
	Mango	129	69	49	15			15	17	29	20	37	249	0.0628
	Sapodilla	53	11	46	15		8	11	12	7	18	40	93	0.0313
<i>obliqua</i>	Grapefruit	7	8	13				8	1	7	4	2	3	0.0070
	Mango	1376	432	575	315	56	55	219	238	157	232	692	1950	0.6287
	Sapodilla	303	126	851	145	58	44	263	140	114	256	926	1189	0.4408
<i>pallens</i>	Grapefruit		1					1				1	1	0.0005
	Mango		5	1			1			2	1	2	3	0.0015
	Sapodilla		4	6			1	1		2	6	3	9	0.0032
<i>pastrana</i>	Grapefruit													
	Mango								1		1	1	2	0.0005
	Sapodilla										1	1		0.0002
<i>robusta</i>	Grapefruit													
	Mango													
	Sapodilla	1										1		0.0002
<i>serpentina</i>	Grapefruit	15	3	18	5		1	29	9	16	19	3	134	0.0333
	Mango	1808	55	1830	1004	143	358	218	38	2000	274	2547	2177	1.2432
	Sapodilla	1830	78	4377	1082	400	1015	524	84	1393	574	4893	2028	1.8249
<i>spatulata</i>	Grapefruit				1									0.0001
	Mango	5	224	34	2	2	4	1	4	13		4	8	0.0301
	Sapodilla	1	28	16			3		3	5	1	8	12	0.0077
<i>striata</i>	Grapefruit		1		1			2		5		1		0.0013

Table 1 continued

Species	Orchard	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	Relative abundance ^a
<i>zuelaniae</i>	Mango	8	17	23	2	1		5	1	2	1	4	6	0.0070
	Sapodilla	4	3	24				9	8	3	21	8	6	0.0086
	Grapefruit							1	1					0.0003
	Mango													
	Sapodilla									1				0.0001
Relative abundance ^b		0.218	0.094	0.342	0.133	0.035	0.062	0.136	0.051	0.152	0.122	0.368	0.303	
Number of species		12	13	10	10	9	7	12	12	11	11	13	13	

^a Relative abundance calculated as number of captured fruit flies per orchard divided by the number of samples per orchard (grapefruit: 7,560 samples; mango and sapodilla: 10,016 samples each)

^b Relative abundance calculated as number of captured fruit flies per year divided by the total number of samples (27,592)

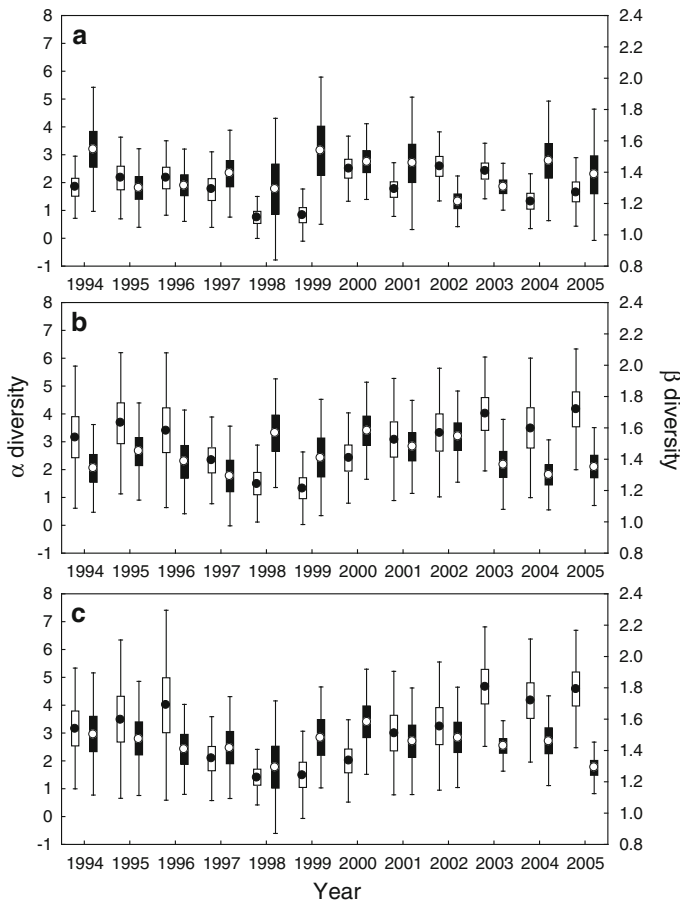


Fig. 1 Yearly variation of α (number of species; white boxes, black points) and β (Whittaker; black boxes, white points) diversity of *Anastrepha* fruit fly species across 12 years in grapefruit (a), mango (b), and sapodilla (c) orchards of Veracruz, Mexico. Points represent means, boxes are standard errors and whiskers depict standard deviation

However, no difference was found among years (grapefruit = global $R = -0.008$, $P = 0.55$; mango = global $R = 0.002$, $P = 0.453$; sapodilla = global $R = 0.008$, $P = 0.4$). Removing season as a nested factor, showed that the ensemble structure changed significantly among years (grapefruit = global $R = 0.053$, $P = 0.007$; mango = global $R = 0.053$, $P = 0.003$; sapodilla = global $R = 0.05$, $P = 0.006$), that together with the previous analysis above showed, indicates that variation in ensemble structure among years is due to seasonal differences among years. A second analysis revealed that almost all seasons showed a particular ensemble structure, with the greatest differences between spring and autumn (Table 3). Following differences among seasons, the grapefruit orchard appeared structurally different from the mango and sapodilla orchards, with the lowest values of R (Table 3). Only spring and winter in the grapefruit orchard were similar (not significantly different) in terms of composition and structure (Table 3).

Table 2 Seasonal profile along 12 years of weekly fruit fly captures in three orchards of Veracruz, Mexico

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Grapefruit												
Fruit availability	a	a							a	a	a	a
Mean total richness	1.92	1.67	1.83	1.75	2.17	2.33	1.75	1.50	1.75	2.33	1.33	1.42
Non-pest mean richness	0.25	0.08	0.33	0.00	0.08	0.50	0.33	0.08	0.08	0.00	0.08	0.08
Pest mean relative abundance	0.91	1.00	0.91	1.00	1.00	1.00	0.91	0.75	0.83	0.92	0.66	0.66
Non-pest mean relative abundance	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01
Mango												
Fruit availability					a	a	a					
Mean total richness	3.67	5.75	4.67	3.75	3.17	3.67	3.33	2.50	1.33	0.33	0.50	2.33
Non-pest mean richness	0.58	1.83	1.17	0.50	0.42	1.00	0.25	0.17	0.08	0.00	0.08	0.25
Pest mean relative abundance	0.90	0.86	0.86	0.96	1.00	0.99	1.00	0.99	0.74	0.33	0.39	0.65
Non-pest mean relative abundance	0.01	0.14	0.14	0.04	0.00	0.01	0.00	0.01	0.01	0.00	0.03	0.02
Sapodilla												
Fruit availability											a	a
Mean richness	4.17	5.08	4.67	3.75	3.33	4.08	3.33	2.33	1.08	0.83	0.50	2.33
Non-pest mean richness	0.92	1.67	1.17	0.67	0.58	1.08	0.58	0.08	0.08	0.08	0.08	0.17
Pest mean relative abundance	0.82	0.87	0.89	0.98	1.00	0.98	1.00	1.00	0.73	0.40	0.33	0.65
Non-pest mean relative abundance	0.18	0.13	0.11	0.02	0.00	0.02	0.00	0.01	0.27	0.60	0.67	0.35

Maximum values per variable are in bold, minimum ones in italic. Relative abundance calculated as number of captured fruit flies per month divided by the total number of samples per orchard per month. The sum of averages of relative abundance of pest and non-pest species does not sum one when there are zero values in any year

^a Indicates the period of high fruit availability in each orchard

Do temporal dynamics of fruit fly pest species and non-target species covariate?

Cross-correlation functions showed that non-pest abundance (FTD) covariated with pest abundance (FTD) in different ways in each orchard. In the sapodilla orchard, pest and non-pest abundance covariated positively at lag zero with $R = 0.18$ ($P = 0.0083$); which indicates that in any month, pest and non-pest species abundance covariated in the same direction. Also, total richness covariated mainly with non-pest abundance, and non-pest richness equally covariated with pest abundance (Table 4). As it is hoped, non-pest richness was mostly a reflection of non-pest abundance, evidenced by the positive cross-correlation at lag zero, and by a negative cross-correlation at lag of 5 months (Table 4). This last result indicates that a high non-pest species richness in any month was preceded by a season (i.e., around 5 months) with a low non-pest abundance. Also, in sapodilla, the significant cross-correlation between non-pest abundance and richness was two times

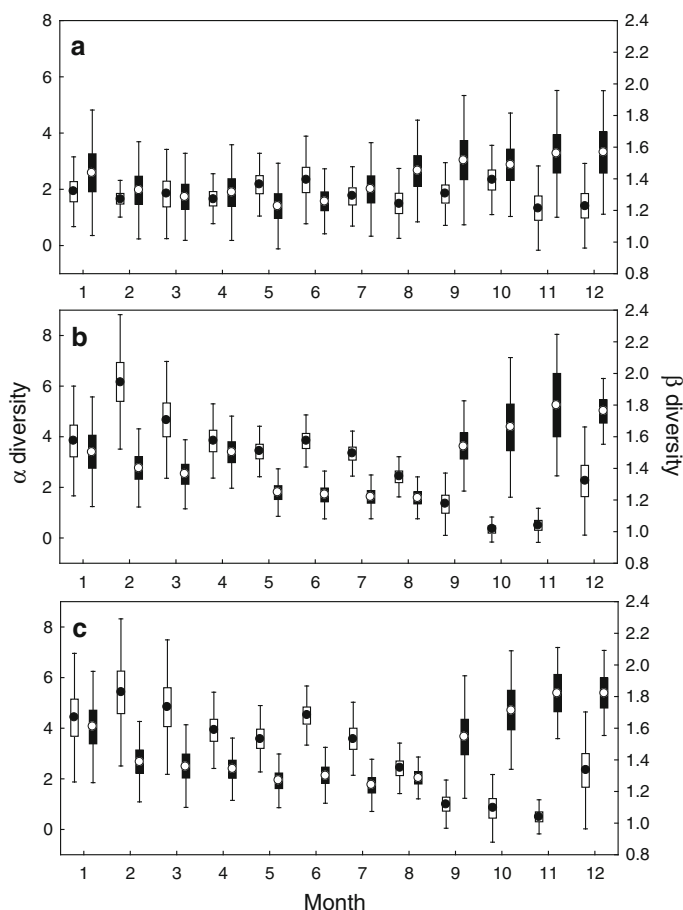


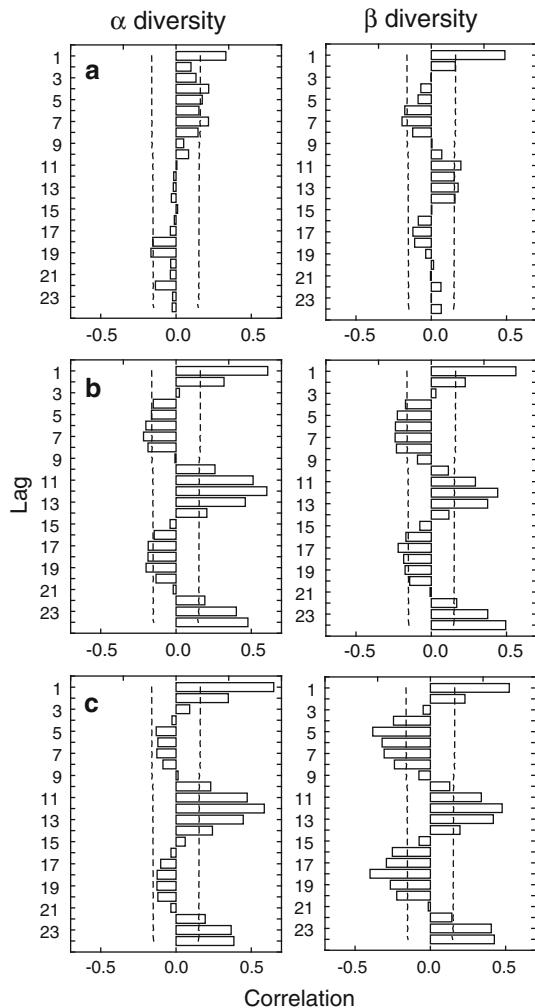
Fig. 2 Monthly variation of α (number of species; white boxes, black points) and β (Whittaker; black boxes, white points) diversity of *Anastrepha* fruit fly species from January 1994 to December 2005 in grapefruit (a), mango (b), and sapodilla (c) orchards of Veracruz, Mexico. Points indicate means, boxes are standard errors and whiskers depict standard deviation

greater than those between pest abundance and richness, indicative of a higher contribution of non-pest abundance to diversity dynamics through time, but the two positive and significant correlations also indicate that temporal dynamics in diversity at lag zero (any current month) are a combination of pest and non-pest abundance, which corresponds to a relatively higher species turnover in sapodilla.

In the mango orchard, the relationship pattern was slightly different (Table 4). Non-pest abundance covaried negatively with pest abundance with a lag of 3 months, indicating that if in any month non-pest abundance was high, 3 months before pest abundance was low, and viceversa (Table 4). In the mango orchard, diversity dynamics were a clear contribution of non-pest abundance (i.e., significant positive values at lag zero, Table 4). Total richness and non-pest richness were unrelated to pest abundance and covaried positively with non-pest abundance in any month of the time window examined (Table 4).

Finally, in the grapefruit orchard the relationship between pest and non-pest abundance is indicative of positively correlated fluctuations, if non-pest abundance was low, it was

Fig. 3 Autocorrelation function plots for the α (number of species) and β (Whittaker) diversity values of *Anastrepha* fruit fly species from captures in grapefruit (a), mango (b), and sapodilla (c) orchards in Veracruz, Mexico. Pointed lines indicate 95 % confidence bands for autocorrelations. Note the strong seasonal pattern revealed by ACF



preceded by a low pest abundance 2 months before, and when pest abundance was higher at any month, non-pest abundance was higher 2 months later. In grapefruit, total richness was the result of both pest and non-pest abundance (positive cross-correlation), indicating a relatively higher importance of pest abundance fluctuations (Table 4). Overall, from a management perspective, these results indicate that the covariation between temporal dynamics of pest and non-pest species was more relevant in the sapodilla orchard, followed by the mango orchard and was less important in the grapefruit orchard.

Discussion

Current integrated pest management (IPM) programs attempt to consider the impact of management actions on non-pest species, with the underlying idea that implementing this approach would produce returns as both environmentally friendly and productive (Kogan

Table 3 Comparisons of the *Anastrepha* fruit fly ensemble structure and composition between seasons

	Winter	Spring	Summer
Grapefruit			
Spring	0.015 (0.15)		
Summer	0.115 (0.001)	0.178 (0.002)	
Autumn	0.287 (0.001)	0.336 (0.001)	0.071 (0.011)
Mango			
Spring	0.267 (0.001)		
Summer	0.135 (0.001)	0.118 (0.002)	
Autumn	0.269 (0.001)	0.55 (0.001)	0.237 (0.001)
Sapodilla			
Spring	0.343 (0.001)		
Summer	0.16 (0.001)	0.077 (0.008)	
Autumn	0.251 (0.001)	0.579 (0.001)	0.26 (0.001)

R statistics and its corresponding *P* values (in parentheses) from ANOSIM pairwise tests are indicated

Table 4 Matrix of cross-correlations among filtered *Anastrepha* fruit fly time series showing the degree of influence of fruit fly abundance (pest and non-pest species) on fruit fly non-pest abundance, total richness and non-pest richness at lag indicated within brackets

Response series	Lagged series					
	Grapefruit		Mango		Sapodilla	
	Pest abundance	Non-pest abundance	Pest abundance	Non-pest abundance	Pest abundance	Non-pest abundance
Non-pest abundance	0.21 [lag 2]		−0.34 [lag 3]		0.18 [lag 0]	
Total richness	0.46 [lag 0]	0.46 [lag 0]		0.32 [lag 0]	0.24 [lag 0]	0.47 [lag 0]
Non-pest richness		0.82 [lag 0]		0.42 [lag 0]	0.20 [lag 0]	0.65 [lag 0]
						−0.20 [lag 5]

A significant correlation at lag zero is indicative of covariation among the two contrasted series in the same sampling date. Other lag means that the lagged series affects the response series with the lag indicated in months. All cross-correlations values were significant at $P = 0.0083$ after Bonferroni correction

and Lattin 2004). Here, we revealed explicitly by means of time series analysis and for the first time, that the potential negative impact of fruit fly pest management actions may be elucidated and minimized in a specific orchard with knowledge on the patterns of variation in fruit fly diversity, the seasonal dynamics of ensemble structure, and the relationship between the temporal dynamics of pest and non-pest species.

Fruit fly ensembles in the three orchards evaluated here (grapefruit, mango, and sapodilla), appeared as being stable, with strong seasonal dynamics in terms of number of species, species turnover, and ensemble composition and structure. The fact of that ensemble structure was markedly seasonal is consistent with the seasonal dynamics of

species turnover (β diversity) depicted by time series and ACF. The major variations in species turnover occurred in the mango and sapodilla orchards, according with the observed significant differences in terms of species composition and structure among seasons in these two orchards.

The temporal dynamics of abundance of pest and non-pest species covariated depending of the orchard type. The significant influence of lags of 2 and 3 months of the pest abundance series in grapefruit and mango orchards respectively, are consistent with a lack of detection of a cross-correlation between pest abundance and non-pest fruit fly species richness in these two orchards. This is an expected result, because the type of resources and refuge available in each orchard (Aluja and Birke 1993; Aluja et al. 1997).

Use of broad spectrum chemicals for pest control has been shown to cause, among others, negative impacts on non-targets including pollinators, beneficial, and rare or endangered species (Paoletti and Pimmentel 2004). If our time series models are good proxies to represent the essential variability of temporal dynamics of *Anastrepha* fruit fly species, consequently we may draw up some recommendations specific to each orchard in order to minimize the impact of pest control practices on non-target fruit fly species.

In the grapefruit orchard, which was regularly sprayed with chemicals, cross-correlation results suggest that potential pest abundance depression presumably by chemical action will also have a detrimental impact on non-pest fly abundance 2 months later. It is obvious that intervention experiments designed to corroborate the impact of chemical sprays on non-target species may directly elucidate the degree of the impact on non-target species. However, the analytical tools here applied are indicative that non-pest fly abundance tracks those of pest abundance with a lag of one or two generations (depending on the fruit fly species). In this case a recommendation aimed at mitigating the potential impact of pest control practices on non-target flies, could consider to spray in 1 month in which it can be predicted that 2 months later the abundance of non-pest species should be low based on the monitoring program established in the orchard. We must emphasize that these recommendations might only be considered at the orchard level and the viability of a decision in that way, should also consider other agronomic factors. For instance, the beginning of the grapefruit fruiting period appeared as a period where spray applications would have a minor impact on non-pest abundance.

In the mango orchard we detected the particularity that non-pest abundance tracked pest abundance with a negative lag of 3 months (i.e., significant cross-correlation between filtered time series). This is a good scenario to implement IPM practices because when there is a high non-pest outbreak, it was preceded 3 months before by a low pest outbreak, a pattern that allows for implementation of actions to control high pest outbreaks with a minor impact on non-pest species. It is important to note that fairly large numbers of *Anastrepha spatulata* were captured in the mango orchard in February, roughly 3 months before the mango fruiting period. *Anastrepha spatulata* is therefore a non-pest species on which natural enemy populations (i.e., parasitoids) could build up during periods of low pest species abundance and later exert control on pest species populations (Aluja et al. 2012). We ignore if the presence of this species is due to proximity of host plants in the orchard, a fact worth exploring to foster effective biological control by promoting within orchard plant diversity. Along these lines, *A. fraterculus* was found in all orchards in large numbers in March. Although this species can be considered a pest of guavas, in México it does not infest citrus, mango, or sapodilla (Aluja et al. 2003b), and could also function as a parasitoid reservoir near orchards with such fruit.

Complementary management practices could improve the approach here proposed. Because most fruit fly parasitoids attack immature stages (Ovruski et al. 2000), their effect

on pest species occurs once commercial fruit has been infested and consequently once it has lost its value. Use of parasitoids needs therefore to be targeted outside orchards, before the fruiting period of commercial hosts, as part of an area-wide effort. Predation on adult flies, by contrast can be targeted to pest species both, within and outside the orchard. Ants cause substantial mortality of fruit fly larvae on fallen fruit (Aluja et al. 2005), and could contribute in cleaning the orchard of infested fruit after harvest. Additionally, some arboreal ant species have been shown to deter ovipositing fruit fly females from fruit (Van Mele et al. 2009). Through management of plant diversity within and around orchards, and considering results on temporal dynamics of pest and non-pest fruit fly species identified in our study, host plants of key non-pest fruit fly species such as *A. spatulata* and *A. fraterculus*, could be used to foster establishment and growth of predator and parasitoids populations in orchards. Fostering propagation of vegetation that can serve as animal refuges that render ecological services to agriculture is a common practice in Mediterranean areas where high human population densities have co-existed with diverse fauna for a long time (Ascensao et al. 2012). Such practices should also be fostered in tropical environments under pressure by recent exacerbated population growth.

In turn, in the sapodilla orchard, according to our results, we face a sensitive scenario, because non-pest abundance and richness track pest abundance, and any treatment implemented to control pests is expected to cause a correlated impact on non-pest *Anastrepha* species. Consequently, in sapodilla orchards, pest control practices could be improved by developing host resistance through plant breeding programs or other strategies that do not rely on broad spectrum insecticide application. In that particular crop, which has a relatively long fruiting period, early destruction of infested fallen fruits can significantly reduce second generation fruit fly inoculum and facilitate pest control. From a conservation perspective, this is particularly important, because sapodilla was the most diverse orchard where we recorded captures from one to three individuals of rare species such as *A. bahiensis*, *A. hamata*, *A. robusta* and *A. zuelanie* over the entire 12 year trapping period. These rare species of *Anastrepha*, can remain undetected in orchards for periods encompassing up to 10 years (the case of *A. robusta*), a fact highlighting the value of performing long term studies. In some cases, the host plants of these species are not known, may be rare, and may not grow in the proximity of orchards. However, in a worst case scenario, as for example *A. hamata*, whose sole individual was captured almost 20 years ago, we could have documented a case of local extinction. In any case, these species, if naturally existing at low densities, may be particularly sensitive to pesticide application and should be the target of conservation efforts. Additionally, their presence in orchards could be used as an indicator of responsible use of pesticides or of permanent damage to rare insects due to deforestation or severe habitat fragmentation.

Several species of rare *Anastrepha* species were sporadically detected in the course of this study, such is the case of *A. bahiensis*, *A. cordata*, *A. hamata*, *A. zuelanie*, *A. pastrana*, *A. chichayae* and *A. robusta*. Although none of these species is commonly known to use sapodilla, mango or citrus as hosts, they may be using the orchard habitat for other purposes (e.g., shelter, food) and are susceptible, along with many species in other insect taxa, to control measures employed against abundant pest species (e.g. Uchida et al. 2006; Vayssieres et al. 2007; Leblanc et al. 2009). It can be argued that conservation of rare species may be targeted by protecting pristine areas of original vegetation (Pimm et al. 2001), where tephritid diversity has been found to be high (Aluja et al. 2003a). We argue that since agricultural settings occupy an enormous proportion of terrestrial landscapes, particularly in the state of Veracruz (Toledo-Aceves et al. 2011) it is also important to focus conservation efforts in agroecosystems and anthropized landscapes.

In a previous paper (Aluja et al. 2012) we have shown that population dynamics of *A. ludens* in grapefruit, *A. obliqua* in mango, and *A. serpentina* in sapodilla orchards, are stable and seasonal outbreaks apparently track the period of crop fruiting and also are significantly affected by local and global weather effects. Here, our results indicate that the pattern revealed by the dynamics of diversity in these same orchards is considerably more complex, with the important consequences that might allow decoupling pest control actions from their potential negative impacts on non-target fruit fly species. This is an important result, because generally, pest control actions do not consider the impact impeding in non-pest species, and here we showed a possible analytical way to visualize it.

The stability of pest species outbreaks detected by Aluja et al. (2012) also implies that fruit fly populations in commercial orchards decimated by insecticide applications, are quickly replaced by individuals flying from neighbouring groves or native vegetation and that unless control measures are applied on an area-wide scale to lower overall fruit fly populations, any local effort will not be sustainable. We have shown here, that using a conventional pest control approach could have a negative impact on diversity and that studying the temporal dynamics of non-pests species populations can also contribute in establishing viable ecologically based strategies for an effective regional pest control approach.

Acknowledgments We are grateful to the Bigurra-Armida family (Martínez de la Torre, Veracruz) and Doña Leticia Lagunes Rivera (Apazapan, Veracruz) for allowing us to work in their orchards. We thank Gemma Quintero, Andrea Birke-Biewendt, Isabel Jácome and Jaime Piñero for technical support. We thank Isabel Jácome, Jaime Piñero, Víctor Pavón, Oscar Palafox, Darío García, Martín Pale and Emilio Acosta for supervising and servicing traps on a weekly basis over the 12-year study period. This project was funded by grants by the Mexican Campaña Nacional Contra Moscas de la Fruta (DGSV-SAGARPA-IICA) to M. Aluja. Additional funds were provided by the Mexican Consejo Nacional de Ciencia y Tecnología (CONACyT Grant Nos. D111-903537 [1990–1991], 0436P-N9506 [1996–1998] and 46846-Q [2004–2008]), the International Foundation for Science (IFS Grant No. C/1741-1), the Mexican Comisión para el Conocimiento y Uso de la Biodiversidad (CONABIO Project H-296), and the Sistema de Investigación Regional del Golfo de México (SIGOLFO-CONACyT, Project 96-01-003-V) to M. Aluja.

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