Seasonal variation of Drosophilidae communities in viticultural landscapes.

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Abstract

Studies at the landscape scale are important to understand insect population and community dynamics. Despite numerous studies on the effects of landscape context on phytophagous insect communities, few studies were conducted on fruit flies and the seasonal variation in the effects of landscape context remains poorly explored. Here, we investigate how landscape composition affects Drosophilidae communities in vineyards and how these effects vary over time. To do this, we sampled Drosophilidae communities in 20 vineyards selected along a gradient of proportion cover of semi-natural habitats in the landscape over a whole year in southwestern France. We found an overall positive effect of increasing proportion of semi-natural habitats in the landscape on abundance of drosophilid species but not on the rarefied species richness. We also found strong seasonal changes in community composition with a major temporal differentiation between the two dominant species of the community, *Drosophila subobscura* and *Drosophila suzukii*. Our study revealed that the composition of the Drosophilidae communities in vineyards is strongly influenced by the proportion of semi-natural habitats and the time of year. Our results suggest that the variation in space and time of key resources such as host plants or overwintering habitats in the landscape is a key factor affecting community composition of Drosophilidae in crops.

Keywords

Drosophilidae, Grapevine, Biodiversity analysis, Community ecology, Semi-natural habitat, Landscape

Introduction

Agricultural intensification manifested by the intensive use of agrochemical inputs, the fragmentation of semi-natural habitats or low crop diversity is a major factor affecting biodiversity dynamics in agricultural landscapes. Semi-natural habitats like grasslands, forests or hedgerows, are often seen as key habitats for a wide range of animal species such as for birds (Mühlner et al., 2010), insects (Ellis et al., 2017) and spiders (Clough et al., 2005). These habitats provide key resources for these organisms such as nesting or overwintering sites, refuges from disturbance, as well as food or host sources (Rusch et al., 2010). It is now well demonstrated that exploring how landscape structure, both in terms of composition and configuration, affects population and community dynamics in agricultural landscapes provides relevant information about how species exploit their resources and disperse through their environment (Fahrig et al., 2011).

Recent studies showed that phytophagous insects and their natural enemies very often respond to the proportion of semi-natural habitats in agricultural landscapes (Chaplin-Kramer et al., 2011). However, controversial results about the effects of landscape context on pests and beneficials have recently been highlighted, making it difficult to generalize conclusions about how phytophagous insects respond to change in landscape structure (Karp et al., 2018). Increasing landscape complexity (defined as the proportion of semi-natural habitats in the landscape) usually promotes top-down control of phytophagous insects by their natural enemies (Chaplin-Kramer et al., 2011). However, landscape complexity can also directly affect phytophagous insects either through positive bottom-up effects mediated by the provision of key resources such as overwintering sites or alternative food (Rusch et al., 2010) or through negative bottom-up effects mediated by inadequate habitats or barriers to their dispersal (Gustafson & Gardner, 1996). Most insects are able to move around patches of suitable resources and to use different habitats to find an environment suitable for their development. Species traits such as dispersal abilities or diet breadth can shed light about how species respond to landscape structure (Martin et al., 2019). However, very few studies have examined how communities of phytophagous insects respond to change in landscape composition especially in the case of Generalist species that can use several host plant species in the landscape. Generalists species often perform better than specialists in complex and variable environments due to their global plasticity (Wang et al., 2017), often inducing the replacement of specialist species and a functional homogenization at the community level (Clavel et al., 2011).

Studies investigating the effect of landscape context on arthropod communities rarely explore the temporal variability in landscape effects (but see Raymond et al., 2015). However, top-down and bottom-up forces that shape population or community dynamics are not constant in time (Kindlmann & Burel, 2008). Disruptions in temporal continuity in resources can have major effects on dynamics of a target organism (Schellhorn et al., 2015). Resource continuity is thus assumed to be a critical factor driving the magnitude and the direction of spillovers through complementation (i.e. different types of habitats provide different types of resources) or supplementation (i.e. different types of habitats provide similar resources but of different quality) (Dunning et al., 1992). Complex landscapes with high and more continuous resources are thus expected to support more abundant and diverse phytophagous communities than simple landscapes. However, to our knowledge, no empirical study examined the temporal variability in the effects of landscape structure on a community of phytophagous insects that are potential threats to crops.

Here, we investigated how landscape composition shapes the Drosophilidae community in vineyards and how these effects vary over time. In our study system, the Drosophilidae community is interesting because it is associated with grape, a crop of major economic importance in the world and with key environmental issues as it is highly treated with pesticides. Drosophilids are associated with grape, infesting both maturating fruits but also vine in cellars (Capy et al., 1987). In recent years, the invasive polyphagous species *Drosophila suzukii* entered this community in European grapevine (Rouzes et al., 2012). We expected that abundance and richness of Drosophilidae would increase with the complexity of the landscape, particularly for generalist species including the invasive *D. suzukii*. Moreover, we hypothesized that this effect would vary through time and between species due to differences in resource availability in time.

Materials and methods

Study sites

The Bordeaux wine-grape growing region covers an area of approximately 125,000 ha which is about 16% of the French viticulture, and receives about 16 pesticide treatments a year per unit area. We selected our study area in the Saint-Emilion wine-growing zone located 40 km east of Bordeaux (approx. 44°54'N, 0°09'W). This 12,000 ha "Appellation d'Origine Contrôlée" area represents homogeneous climate and cultural practices. Our study system consisted of 20 vineyards selected along a landscape complexity gradient. We calculated the proportion of Semi-Natural Habitat (SNH) as the percentage of land consisting of woodland, grasslands, hedgerows and shrubs. SNH ranged from 0 to 31.7% in our experimental design. The proportion of SNH was calculated using ArcGis sofware (Version 10.4, ESRI) in a 100 m radius around each vineyard plot. This radius is suitable to calculate the effect of the landscape on drosophilid flies in vineyards (Delbac et al., 2018). We only use SNH for the analyses because it is the descriptor that structures our landscapes and is a commonly used variable in landscape analyses. This proxy of landscape composition is relevant to describe how landscapes affect processes at the population level (Dunning et al., 1992).

Monitoring and identification of the Drosophilidae

For the monitoring of Drosophilidae populations, adults were caught using the attractive model trap recommended by the French Agriculture authority on vines. It consists of a 1-L mineral water bottle pierced laterally with twenty 5 mm holes in the upper part and filled with 125 ml of bait (1/3 red wine, 1/3 cider vinegar, 1/3 water and a few drops of wetting agent). For each plot, we set up three traps 10 m apart and located in the center of the plot. They were set up for a period of 7 days each month from January to December 2017 (i. e. 12 capture sessions). After each session, the trap contents were analyzed in the laboratory and the caught individuals were stored in 70% ethanol. Adults were then identified to species using a fauna of Drosophilidae (Baechli et al., 2004) and criteria published for *D. suzukii* (Withers & Allemand, 2012).

Statistical analysis

To test the effect of landscape complexity and time of trapping on abundance and species richness of drosophilid species, we used Generalized Linear Mixed Models (GLMMs). We fitted GLMMs with appropriate error distribution to examine the effects of SNH and the trap session, and their interaction, on individual and total abundance of drosophilid species (Poisson error distribution) and on community rarefied species richness (Gaussian error distribution). The trapping session and SNH were included as fixed variables. SNH in the landscape was scaled (by substracting the mean from each value and then dividing by the standard deviation) before analyses to help with model convergence. The sites and traps within each site were included as nested random factors. We also included an observation-level random effect to correct for overdispersion in the count data. Diagnostic residual plots of all full models were confirmed using the DHARMa package (Hartig, 2019). Spatial autocorrelation in the residuals was explored using variograms, and no spatial autocorrelation was detected. Prior to these analyses, we also calculated the rarefied richness. We compared the model outputs of the two modes of calculating species richness, and present only the results from the rarefied richness.

To further explore the temporal changes in community composition we used distance-based Redundancy Analysis (db-RDA) on Drosophilidae communities using the trap session and SNH as explanatory variables (Legendre & Legendre, 2012). We used Bray-Curtis dissimilarity matrices.

In the analysis, we discarded data from February because of 35% of missing data. Three other traps failed in April and May but these data were included as missing values. The analyses were performed in R version 3.5.1 (R Core Team 2018) using the *lme4* (Bates, 2019), the *emmeans* (Lenth et al., 2020) and the *vegan* (Dixon, 2003) packages.

Results

Overall Drosophilidae community

In total, 686 baited traps were surveyed and 47,881 individuals belonging to 17 species were caught (see Appendix A: Fig. 1). Thirty-three individuals could not be identified (thus 0.06%). Ten species are rather rare taxa (each species representing less than 0.1% of the total number of individuals): *Chymomyza ameona*, *Drosophila ambigua*, *Drosophila bifasciata*, *Drosophila busckii*, *Drosophila kuntzei*, *Drosophila testacea*, *Drosophila transversa*, *Drosophila tristis*, *Hirtodrosophila cameraria* and *Phortica variegata*. The other seven species represented 99.6% of the total number of individuals: *Drosophila hydei*, *Drosophila immigrans*, *Gitona distigma*, *Drosophila melanogaster*, *Drosophila simulans*, *D. suzukii* and *Drosophila subobscura*. These last two species were largely dominant as they represented 90% of the individuals caught. Interestingly, the abundance peaks of these two dominant species were different with high number of individuals of *D. subobscura* caught in winter while *D. suzukii* peaked in late summer-early fall (see Appendix A: Fig. 2 and Table 1). Over the entire trapping period, the number of species varied from 7 to 14 species per plot depending on the site.

Effect of landscape on Drosophilidae community

GLMMs revealed that SNH, the trap session and their interaction all had a significant effect on total abundance of Drosophilidae and the abundance of the two dominant species (Fig. 1: A1, A2 and A3 and see Appendix A: Table 2). The significant effect of the interaction between the trap session and SNH (ANOVA effect for all three models: $p < 0.001$) indicated that the positive effects of SNH on abundance varied over time; the effect of this variable was always positive. The strongest effect was found for December and January and the weakest in march and from August to October (Fig. 1: B1, B2 and B3). For rarefied species richness there was no effect of SNH (ANOVA effect: $p = 0.954$) since it was positive at the beginning of the year, then null and finally negative in October (see Appendix A: Fig. 3).

Temporal change in the drosophilid community

The redundancy analysis showed distinct Drosophilidae communities (db-RDA: F=4.084, p <0.001, Fig. 2). We found significant effects of trap session, SNH as well as their interaction on community composition (Table 1). Species composition of catches made in January to May differed considerably from the catches made later in the year (Fig.2). On this ordination graph, there is a significant shift in the position of the community between May and June. The projection of drosophilid species on the biplot clearly shows that the two species explain this community evolution well: *D. subobscura* is linked to the winter community, occurring in with January to April, while *D. suzukii* belongs to the fall community, especially September and October. These two dominant species drive the temporal evolution of the community. Also these two dominant species were positively associated with SNH, variable with the highest score on the CAP2 axis. The significant interaction between the trap session and SNH (p <0.001) shows that the effect of these two variables varies over time. Axis CAP1 can be likened to a temporal effect while axis CAP2 can be likened to a landscape effect.

Discussion

Our study reveals that the composition of the Drosophilidae communities in wine-growing landscapes is strongly influenced by the proportion of semi-natural habitats in the landscape and the time of year. We found an overall positive effect of increasing proportion of semi-natural habitats in the landscape on overall abundance of Drosophilidae as for some individual species. Our data also show strong seasonal changes in community composition with a major niche temporal differentiation between the two dominant species, *D. subobscura* and *D. suzukii*. *D. subobscura* strongly dominates in the community at the beginning of the year while *D. suzukii* dominates the community later in the year.

Positive effect of semi-natural habitats on the Drosophilidae community

The positive effect of SNH in the landscape on fly abundance may be explained by the presence of alternative resources for the different species in these habitats. Habitats such as forests, grasslands or hedges support key resources for a wide range of arthropod species (Chaplin-Kramer et al., 2011; Rusch et al., 2010). Increasing the proportion of these habitats in the landscape increases the spillover of individuals from semi-natural habitats to crops through complementation and/or supplementation processes (Dunning et al., 1992). Although these have been described for different taxa, our study shows that Drosophilidae communities are shaped by spillover between semi-natural habitats and crops.

Semi-natural habitats are able to provide multiple resources to drosophilid species including alternative food and host plants, as well as shelters or overwintering areas harboring beneficial micro-climatic conditions for Drosophilidae communities. Concerning nutritive resources, the species we captured in our study are divided into three different diets (see Appendix A: Table 3):fungivorous (e.g. *D. kuntzei* or *D. testacea*), frugivorous (e.g. *D. suzukii*, *D. melanogaster* or *D. simulans*) or both (e.g. *D. subobscura*). Basidiomycetes found mainly in forests serve as a major nutritional basis for fungivorous drosophilids (Shorrocks & Charlesworth, 1980). Several Ascomycetes classically develop on leaves or bunches of grapes and this could explain supplementation processes and spillover of fungivorous species from semi-natural habitats to vineyards (Dubos, 1999). These fungi emit a characteristic mushroom odor (La Guerche et al., 2006) and can attract adults to such infected grapes.

Moreover, the presence of fruit resources in the landscape may drive the spillover of frugivorous drosophilids. For instance, semi-natural habitats provide different alternative fruit sources to *D. suzukii* (Cahenzli et al., 2018; Santoiemma, Mori, et al., 2018; Tonina et al., 2018). Several studies have shown that this polyphagous species feed on a large range of wild or cultivated host plants (Kenis et al., 2016; Poyet et al., 2015). In another complementary study conducted during the same period on the same survey plots, we confirmed the presence of *D. suzukii* on the fruits of plant species monitored in the vineyard margins, especially on blackberry which represents the most abundant wild resource (Delbac et al., 2020). The presence of blackberry in the field margin, like other fruit host species, influenced the abundance of *D. suzukii* in the crop (Tonina et al., 2018). The presence of these resources can promote a spillover effect.

Moreover, it is assumed that vineyards offer different microclimates than forests (Fort et al., 2016). Indeed, it has been shown that forests offer lower temperatures (Karlsson, 2000) and mitigate extreme climatic events (Potter et al., 2001). Such a refuge effect could explain why semi-natural habitats are a source of drosophilid flies in the landscape. For instance, we know that semi-natural habitats provide climatic conditions suitable for the development of *D. suzukii* (Cahenzli et al., 2018; Santoiemma, Mori, et al., 2018), particularly during cold, hot or dry periods (Tonina et al., 2018). It has also been shown that blackberry bushes maintain *D. suzukii* through microclimatic effects (Diepenbrock & Burrack, 2017). *Drosophila suzukii* is mostly found in SNH during winter in cold periods and then in crops with large amounts of forest edges during summer (Santoiemma, Trivellato, et al., 2018). The insect shows a much reduced activity during warm temperatures and low relative humidity in summer (Tochen et al., 2016) which results in a high daily mobility of adults between crops and woodland habitats (Tait et al., 2019).

The impact of land-use on species diversity is known for many biological models (Katayama et al., 2019; Newbold et al., 2015). In the case of predominantly wine-growing landscapes, our results are similar to studies that show a positive effect of SNH on species diversity, such as plant (Nascimbene et al., 2016) or bird communities (Guyot et al., 2017) but not carabid communities (Rusch et al., 2016). For Drosophilidae communities there are very few studies that have examined this effect and this has never been done for predominantly wine-growing landscapes outside our study.

Seasonal variation of the Drosophilidae community

Our study shows seasonal variation in the landscape effects on drosophilid species. The temporal dynamics found in our study are in line with the already known temporal dynamics of *D. subobscura*, *D. simulans* and *D. melanogaster* (Begon, 1978; Bombin & Reed, 2016). The temporal changes in the effect of the landscape on Drosophilidae communities may come from the fact that landscape composition is not constant in time (Kindlmann & Burel, 2008; Schellhorn et al., 2015). Indeed, the phenology of host plants can partly explain the structure of a community of species (Charlery de la Masselière et al., 2017).

Our db-RDA clearly showed a habitat and a temporal axis where the two dominant species, *D. subobscura* and *D. suzukii*, are located in opposite directions on the temporal axis. The concomitance between these two species could be explained by niche partitioning in time (Stuble et al., 2013). Although *D. subobscura* is recognized as fungivorous, it is also frugivorous (Appendix: Table S3). These two species can also be found on fallen or decaying fruits (Bal et al., 2017; Capy et al., 1987) and therefore sometimes compete on fruit. In addition, they are spatially segregated with *D. suzukii* in the canopy of trees (Tanabe, 2002) while *D. subobscura* will be found on the ground (Shorrocks, 1977).

Time segregation can be explained by food availability (Stuble et al., 2013):

i) The temporal dynamics of fungal resources could impact the fungivorous Drosophilidae community (Worthen & McGuire, 1990). *Basidiomycota* fungi are seasonal nutrient sources with a limited presence in time from summer to fall (Worthen & McGuire, 1990). In the absence of these resources, it can be assumed that the fungivorous species disperse and their low abundance in vineyards might be explained by dispersal to search for food. In our study, we observe *D. subobscura* in post-harvest when only crop residues remain, after its nutrient activity on mushrooms in the forest from June to September (Shorrocks & Charlesworth, 1980).

ii) The temporal availability of fruits impacts the population dynamics of frugivorous drosophilids. In the case of *D. suzukii*, this species is observed from early summer to autumn, i.e. from the beginning of grape berry formation in the vineyard plot (Ioriatti et al., 2015). This early presence is explained by the different responses to plant odor of this insect (Pham & Ray, 2015), sensitive to various odors such as Beta-cyclocitral, released at the beginning of berry formation in summer.

Close to grape harvest time, in autumn, the quantity of host plants in SNH is very limited, e.g. blackberry fruits become rare (Briem et al., 2018), and grapes are the only abundant host plant for females (Delbac et al., 2020). After the harvest period, the abundance of *D. suzukii* is decreasing. This change can be attributed to the movement of this species from the cultivated plot to a physical site more suitable for wintering (Kaçar et al., 2016). These overwintering sites are located in the litter of forest leaves (Zerulla et al., 2015), a place where climatic conditions are favorable to this insect (Rossi-Stacconi et al., 2016).

Our work shows that Drosophilidae communities in vineyards are strongly shaped by landscape composition and temporal succession of the resource. Our results therefore suggest that a higher proportion of semi-natural habitats around wine-growing areas, providing more resources in the landscapes, is a key driver of community composition mediated by spillover effects between habitats and vineyards. Moreover, our results suggest that invasive drosophilid species, such as *D. suzukii*, could be favored by landscape complexity.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Fig. 1. Graphical representations obtained from Generalized Linear Mixed effects Models (GLMM) calculated to test the effect of landscape complexity (measured as a proportion of semi-natural habitat (SNH), scale variable) and trapping session on the total abundance of: 1: Drosophilidae; 2: *Drosophila subobscura*; 3: *Drosophila suzukii*. The top graphs (A) represent the predictor effects corresponding to the response of each of the abundances (1, 2 or 3) to SNH for each of the 11 months of surveys. For each month, the x-axes corresponds to the SNH scale values; for graphical clarity, the values have only been shown on the graph line (A3) and only 1 out of 2 months. The y-axes are logarithmic due to the Poisson error model used in the GLMMs; the values shown correspond to the values estimated by the models. In each graph, the magenta circles represent the partial residuals for each of the 20 plots and the blue line represents the fitted partial-regression line with its confidence interval in shaded area. Bottom graphs (B) represent the estimated slopes (with 95% confidence interval) relative

to SNH of each of the abundances (1, 2 or 3) for each survey month. The y-axes value correspond to the estimated slope scale value for SNH; the redder the color, the higher the value. There is no value for the x-axes. SNH was scaled by substracting the mean from each value and then dividing by the standard deviation.

Fig. 2. Canonical ordination plot obtained by distance-based redundancy analysis (dbRDA) for the occurrence of the Drosophilidae community composition data for the 20 sites. Months correspond to sampling sessions and are marked by black characters at the respective centroids of all sites and with the 60% coverage ellipses. The green arrow indicates the significant interaction between the trap session and the proportion of semi-natural habitat (SNH) (p <0.001). The blue open circles indicate the respective centroid of the main drosophilid species. The axes (canonical analysis of principal coordinates (CAP) 1 and CAP 2) represent a Euclidean space on which are positioned the values of coordinates obtained by analysis on each axis (centroids of all site scores for each factor in the month of sampling variable and for species; correlation scores for SNH). For ease of presentation, the SNH values have been multiplied by 5; it does not affect the analysis.

Table 1. Effect of the trap session (TS), the proportion of semi-natural habitat (SNH) and their interaction on drosophilid species composition in our 20 vineyard plots. Relationships were tested with distanced-based Redundancy Analysis (db-RDA).

Predictors	F	p
TS	6.613	**<0.001**
SNH	3.818	**<0.001**
TS x SNH	1.581	**<0.001**

Explained variance: constrained= 30.22%; unconstrained= 69.78%

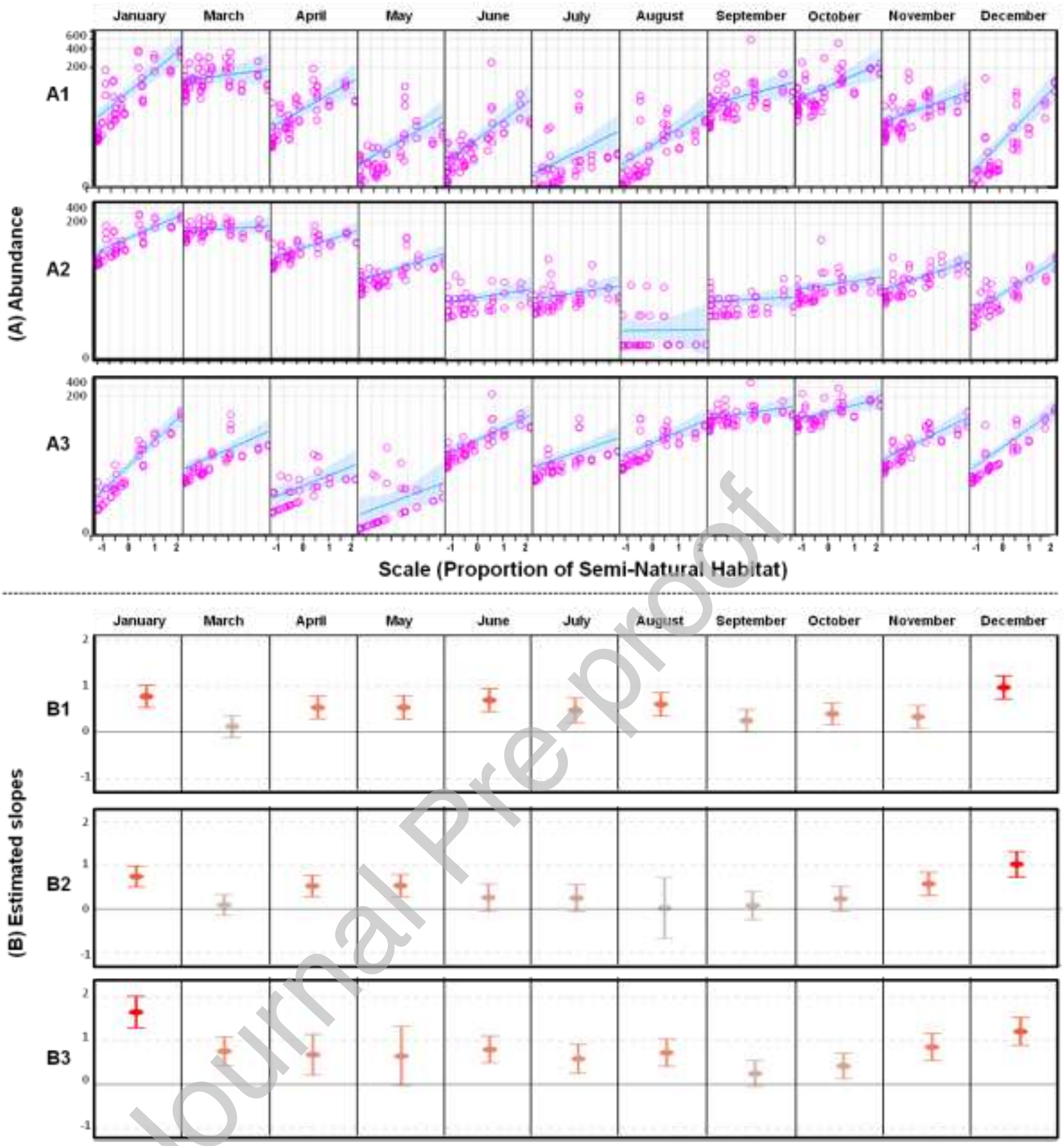
January
March
April
May
June
July
August
September
October
November
December
A1
A2
A3
(A) Abundance
600
400
200
0
-1
0
1
2
Scale (Proportion of Semi-Natural Habitat)
B1
B2
B3
(B) Estimated slopes
2
1
0
-1

Fig. 1

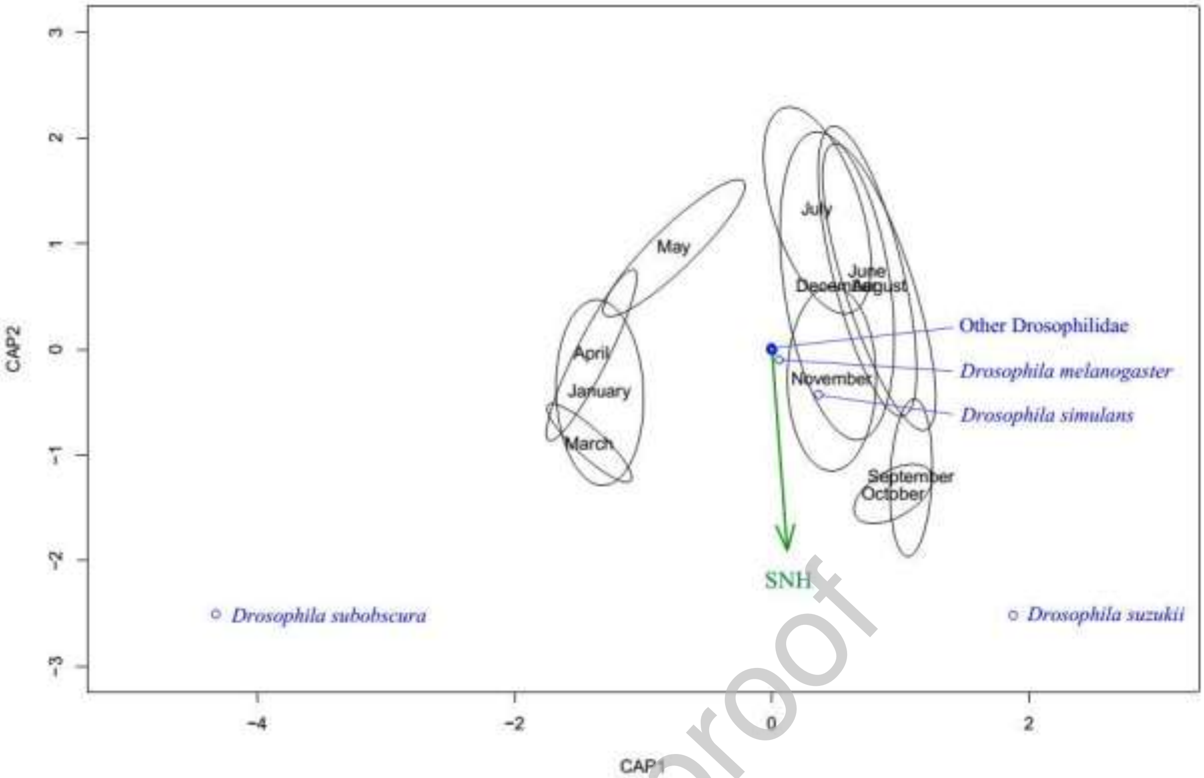
CAP2
CAP1
3
2
1
0
-1
-2
-3
-4
-2
0
2
May
April
January
March
July
June
December
August
November
September
October
SNH
Other Drosophilidae
Drosophila melanogaster
Drosophila simulans
Drosophila subobscura
Drosophila suzukii

Fig. 2