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Joint species distributions reveal the combined effects of host plants, abiotic factors and species competition as drivers of community structure in fruit flies

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Abstract

The relative importance of ecological factors and species interactions for phytophagous insect species distributions has long been a controversial issue. Using field abundances of eight sympatric Tephritid fruit flies on 21 host plants, we inferred flies' realized niches using joint species distribution modelling and network inference, on the community as a whole and separately on three groups of host plants. These inferences were then confronted to flies' fundamental niches estimated through laboratory-measured fitnesses on host plants. Community structure was mainly determined by host plants followed by climatic factors, with a minor role for competition between species sharing host plants. The relative importance of these factors was mildly modulated by host plants. Despite overlapping fundamental niches, specialists and generalists flies almost behaved as separate communities, with possible competitive exclusion of generalists by specialists on Cucurbitaceae and different assembly rules: specialists were mainly influenced by their adaptation to host plants while generalist abundances varied regardless of their fundamental host use.

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Introduction

The search for fundamental processes underlying species distributions and community structure is among the oldest challenges in ecology (Diamond 1975, Gotelli and Graves 1996). Understanding assembly processes could also be crucial for coping with global changes and habitat loss currently affecting both abiotic conditions and species distributions (Adler and HilleRisLambers 2008). Community structure can be determined by several factors such as environmental filtering, interspecific interactions, regional species pool and dispersal (Müller et al. 2011, D'Amen et al. 2018, Nakadai et al. 2018, Jabot et al. 2020). Despite decades of research, estimating the relative importance of these processes on species distributions has proven particularly complex (Pollock et al. 2014). Most of these processes imprint species distributions in a scale-dependent manner (Meynard et al. 2013). For instance, abiotic factors are generally thought to determine large-scale species ranges, whereas interspecific interactions would influence species distributions at smaller spatial scales (Heikkinen et al. 2007, Thuiller et al. 2015, but see Gotelli et al 2010 and Araújo and Rozenfeld 2014).

Phytophagous insects are among the most diverse and abundant groups of terrestrial animals and a major component of ecosystems due to their tight interaction with primary producers. Some species have important economic impacts given their great invasive potential and their impact on crops (Roy et al. 2015). Knowledge of the main determinants of insect occurrence on particular plant species and their potential to colonize and persist in a given area is still limited. In particular, the importance of interspecific competition in structuring phytophagous insect communities has been a controversial issue (Kaplan and Denno 2007). Many experimental studies conclude that interspecific competition plays a primary role (Denno et al. 1995, Kaplan & Denno 2007), but the consistent absence of negative co-occurrence patterns in natural phytophagous insect communities suggests otherwise (Tack et al. 2009, Brazeau & Schamp 2019). This apparent discrepancy could result from the regulation of phytophagous insect populations below competitive levels through shared predators or parasites (Hairston et al. 1960). Phytophagous insects would also rarely overexploit their hosts, leaving sufficient plant material for competition with other species to be mild (Kaplan & Denno 2007). Finally, ecological

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differences between species could lower the intensity of competition (Stewart et al. 2015). The importance of competition relative to environmental characteristics in shaping phytophagous insect distributions remains thus an open question and demands appropriate testing (Augustyn et al. 2016, Nakadai et al. 2018).

In community ecology, co-occurrences have long been used to identify possible biotic interactions. Checkerboard patterns are classically interpreted as signs of competition, but species co-occurrences also result from common or diverging species dependence on confounding environmental factors. Species that share the same abiotic niche may frequently co-occur without necessarily interacting (Wisz et al. 2013, Blanchet et al. 2020). Deciphering the effects of species interactions and environmental variables on species distributions has long represented a methodological challenge (Pollock et al. 2014), which is being overcome by joint species distribution modeling (JSDM) approaches (Ovaskainen et al. 2016). JSDM are multivariate regression methods that infer the relationships between multiple species abundances and environmental variables, explicitly accounting for the interdependence of species distributions (Pollock et al. 2014). In these approaches, residual covariances between species abundances, i.e., covariances not explained by environmental factors, encapsulate species interactions (Zurell et al. 2018). Recent methods now allow deciphering which of these residual covariances represent significant species associations (Chiquet et al. 2018, 2019). Environmental factors that feed JSDM, in turn, represent significant abiotic filtering of realized species niches. In the case of phytophagous insects an obvious feature of the environment to account for is host plant identity.

Host plants can be treated as any environmental cofactor, and their effects on species abundances can be inferred directly from adequate abundance data (Ferrier and Guisan 2006). Host plants impose a specific challenge because modelling a phytophagous community as a whole relies on the assumption that interactions (encapsulated into residual covariances) are similar among host plants. Since species interactions mostly occur in/on plant organs, they may be modulated by plant species identity, with possibly important consequences for patterns of species occurrences (Ulrich et al. 2017). Analyzing

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competition patterns on different plants or groups of plants could therefore allow detecting the role of host plants in modulating species interactions.

In addition, a growing body of literature pleads for using independent knowledge of species traits in species distribution modelling (Lavorel et al. 1997, Kraft et al. 2008, Poisot et al. 2015), which is still seldom done. For phytophagous insects, independent information on species niche could be drawn from laboratory measures of insect fitness on their host plants. Interestingly, such fitness measures are generally conducted under optimal abiotic conditions in absence of antagonists, and therefore can be considered as estimates of fundamental host use, as opposed to abundance data, which reveal realized host use. Comparing species distribution models with and without laboratory-measured host use information could shed new light on the gap between fundamental and realized niches and the importance of species interactions in shaping species distributions.

Here we aim at disentangling the roles of host plant species, abiotic factors, and interspecific interactions on the distributions of eight fruit fly species (Tephritidae) occurring in sympatry on a diversity of host plants and in highly variable abiotic conditions. The study system, which comprises four generalist species, three specialists of *Cucurbitaceae*, and one specialist of *Solanaceae*, presents key advantages to tackle community assembly questions. First, the community is a rather closed system as it occupies a small French island in South-western Indian Ocean (Réunion, 2512 km^2). Second, the local environment is characterized by important variability in elevation (from 0 to 3000m.a.s.l), climatic conditions, land use, and plant distributions (Duyck et al. 2006a). Observational and experimental studies have suggested that climatic factors could influence local Tephritid distributions (Duyck et al. 2004). Climatic factors were even found more influential than host plant diversity in allowing coexistence in an analysis of the distributions of the four generalist species on four host plants on Réunion (Duyck et al. 2008). Lastly, there is indirect evidence that competition may shape this community. First, host-use strategies largely overlap, opening possibilities of competition (Quilici & Jeuffrault 2001, Duyck et al. 2008). Second, the arrival of one generalist species on the island has constrained the host ranges of some resident species, without complete exclusion (Charlery de la

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Masselière et al. 2017a, Moquet et al. in press). Third, larval competition experiments in a subset of plant species and abiotic conditions have evidenced hierarchical competition interactions among the four generalist species (Duyck et al. 2006b).

Here we confronted a long-term field dataset describing abundances of the eight fly species on 21 host plants with laboratory measures of fundamental host use obtained for seven of the fly species on the same plants. We first modelled joint species distributions using Poisson-LogNormal (PLN) modelling (Chiquet et al. 2019) and conducted model selection among various combinations of host plant species and ecological covariates (representing temperature, rainfall, elevation, land use and date). Residual correlations estimated under the best model were further searched for signs of species interactions. Second, we assessed whether knowledge on fundamental host use was sufficient to explain field species abundances by accounting for host plant species either directly or through estimates of female preference and larval performance in laboratory conditions. Finally, we tested for a potential dependence of community structuring factors on host plants by replicating the analyses on three subsets of plants: *Cucurbitaceae*, *Solanaceae* and the pool of the other plants.

Materials and Methods

Species abundance table

Field campaigns were conducted over a period of 18 years, between 1991 and 2009, to identify potential host plants for Tephritidae on Réunion on the whole island including orchards, gardens, and natural areas. These surveys were assembled in a previous study (Charlery de la Masselière et al. 2017a), and used here as our species abundance table. Each observation corresponds to the number of individual flies of the eight species recorded from a set of fruits sampled in one location at a specific date. For each sample, the collected fruits were counted and weighted, before being stored until adult fly emergence. Of the 12872 initial samples, only those with GPS coordinates, with at least one individual fly and belonging to one of the 21 host plants characterized in the laboratory (see below) were kept. This resulted in 4918 samples and a total of 97351 individual flies. Samples covered 104

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field sessions all year round over the study period (Tables S1 and S2) and originated from 380 sites well distributed over the whole island (Figure 1A). Additional details on sample collection can be found in Appendix S1.

Ecological covariables

The GPS coordinates of each sample were used to retrieve ecological and climatic characteristics from GIS information available on the CIRAD Agricultural Web Atlas for Research (AWARE, https://aware.cirad.fr). Each sample was associated with a month and a year, a land use category, an elevation, three pluviometry descriptors (minimal rainfall in the 20% most humid years, minimal rainfall in the 20% driest years, and median annual rainfall between 1986 and 2016) and three temperature variables (minimal, mean and maximal annual temperature over the 1987-2017 period) (Figure 1A, Appendix S1). To account for the correlations between some of the variables, a FAMD (factorial analysis of mixed data) was conducted on all 10 variables using *FactoMineR* (Lê et al. 2008). Ten uncorrelated dimensions were obtained and subsequently used as ecological covariables in the following analyses (see Figure S2 for details on the FAMD).

Species traits

For all species but *D. ciliatus*, fundamental host use, i.e., fly fitness on host plants in optimal abiotic conditions and in absence of antagonists, was characterized using four traits describing larval performances and female preferences for 21 plant species. Female preferences were the numbers of eggs laid by females during 24h on each of the 21 fruit species in the 'no-choice' experiment of Charlery de la Masselière et al. (2017b). Larval performances (survival probability until maturity s, development time T, and pupal weight w) were obtained from Hafsi et al. (2016) for 17 plant species, and in the current study for *Coffea arabica*, *Solanum mauritianum*, *Syzygium jambos*, and *S. samarangense*, using the same methods. The three larval performance traits were combined into a single performance trait using the formula:

$$Perf = s \times w/T.$$

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Both preference and performance traits were log-transformed before being included as covariates in statistical models.

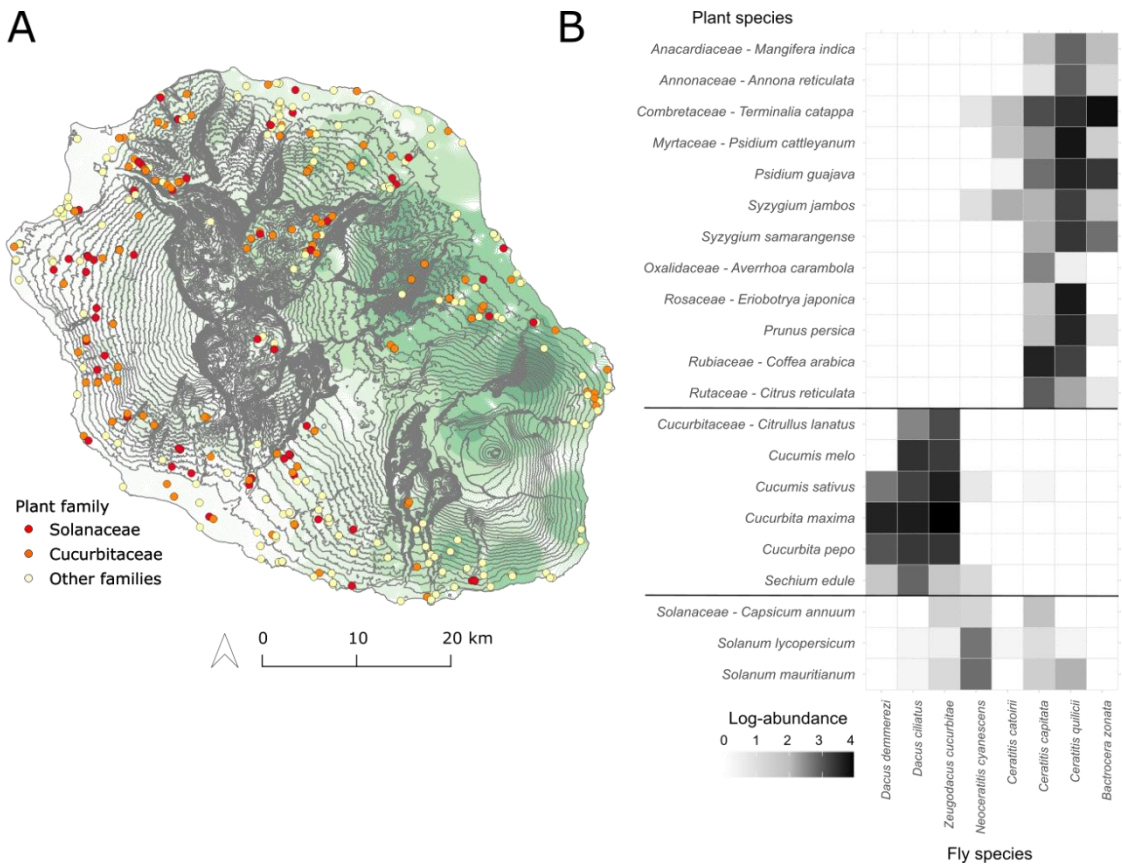

Figure 1: Characteristics of the species abundance dataset. A) Sampling sites in Réunion. Dot colors refer to the family of the sampled plant (Solanaceae n=259, Cucurbitaceae n=2347, other families n=2285). Elevation, represented by grey isoclines, ranges from 0 along the coast, to >3000 m, in the center of the island, and strongly correlates with annual temperature. Pluviometry (here median rainfall over 1986-2016) is represented by green isohyets. The island is separated into two contrasted rainfall regimes: very humid all year round in the east, and drier, especially during winter, in the west. B) Fly species abundances on the 21 sampled plant species.

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Statistical analysis

Datasets

To account for the possibility that, despite having overlapping fundamental host ranges, these fly species behave as distinct communities on different plants, we replicated all analyses on the full 21-plants dataset, and on the following three sub-datasets: (i) Cucurbitaceae only (3 fly species x 6 plant species, 2347 samples), (ii) Solanaceae only (3 fly species x 3 plant species, 259 samples), (iii) other plant families (4 fly species x 12 plant species, 2285 samples).

Statistical modelling

Joint variations in fly species abundances were modelled using Poisson-LogNormal (PLN) models with the *PLN*() function in the *PLNmodels* R package (Chiquet et al. 2018, 2019). A PLN model is a multivariate mixed generalized linear model, where each species count is assumed to arise from a Poisson distribution with a parameter resulting from fixed effects of covariates and a random log Normal effect. Random effects associated to all species observed in a sample are jointly sampled from a multivariate Log Normal distribution. The variance-covariance of the multivariate distribution potentially reveals species interactions, after controlling for confounding environmental covariates and differences in sampling efforts. Samples differed in fruit number and weight, inducing uncontrolled variation in sampling effort among samples potentially leading to spurious associations between fly species. As a consequence, the (log-transformed) total fruit weight of each sample was added as an offset to every tested model, thus controlling for the simple fact that more fruit material could shelter more fly larvae. Using fruit number in each sample as an offset was also tested and did not affect conclusions (results not shown). Direct statistical associations between species were looked for using the *PLNnetwork*() function, which adjusts the considered model under a sparsity constraint on the inverse of the variance-covariance matrix, i.e., constraining the number of edges in the resulting estimated network. This sparsity level is controlled by a penalty parameter, for which 40 values are systematically tested and confronted using model selection.

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Model selection design

The importance of plant species identity, ecological covariates and species interactions to explain species abundances was evaluated by model selection using the extended BIC criteria (Chen & Chen 2008). First we focused on species response to environmental variables and compared models (listed in Table 1) including either no covariate (Model 1-0), plant species identity as a cofactor (Model 1-1), ecological variables (all 10 FAMD dimensions described above, Model 1-3) or both plant species and ecological variables (Model 1-5). Second, we evaluated the importance of species interactions. *PLNmodels* enables fitting models where the residual variance-covariance matrix is constrained to be diagonal. Such models assume no possible interaction between fly species. We therefore compared all models with their diagonal counterpart (Models 1-2, 1-4 and 1-6) as a way to evaluate the importance of species interactions. After model selection, network inference was conducted on the selected model with *PLNnetwork*(). In the selected sparse underlying network, the stability of each association of the selected network was calculated as its selection frequency (range 0-1) in bootstrap subsamples of the StARS model selection procedure (Liu et al. 2010). Third we estimated how well knowledge of the fundamental niche, here laboratory-measured preferences and performances, explained field abundances. In its present form, *PLNmodels* does not allow accounting for species traits (covariates describe samples but not species within samples). To cope with this limitation, we considered that assuming that species distribute according to their fundamental niche implies that species interactions are negligible, and species distribute independently from one another. Using this assumption we fitted models separately for each fly species, obtained their likelihoods and numbers of parameters, and computed the BIC of the seven-species dataset as:

$$BIC = kln(n) - 2ln(L),$$

where *k* and *L* are the sums of the numbers of parameters and likelihoods over the seven single-species datasets and *n* the number of samples. Following this principle, we built models where the host plant cofactor is replaced by either preference (Model 2-7 without ecological covariates and 2-8 with ecological covariates), or performance (Models 2-9 and 2-10), or both preference and performance

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(Models 2-11 and 2-12). In addition, all previous models were reevaluated on the datasets excluding *D. ciliatus* (Models 2-0 to 2-6).

Results

All plants

The variance-covariance structure of the complete dataset including 21 plant species was first inferred by fitting a PLN model without any covariate (Model 1-0). The obtained residual variance-covariance matrix (Figure 2A) revealed a sharp distinction between three groups of flies: (i) the four generalist fly species (*B. zonata*, *C. capitata*, *C. catoirii*, and *C. quilicii*), (ii) the three specialists of Cucurbitaceae (*D. ciliatus*, *D. demmerezi* and *Z. cucurbitae*), and the specialist of Solanaceae (*N. cyanescens*). While *N. cyanescens* abundances showed very low covariances with those of other species, the two other groups showed positive within-group covariances and negative among-group covariances. This variance-covariance structure suggested strong separation of the realized niches of the three groups, likely mediated by host plants.

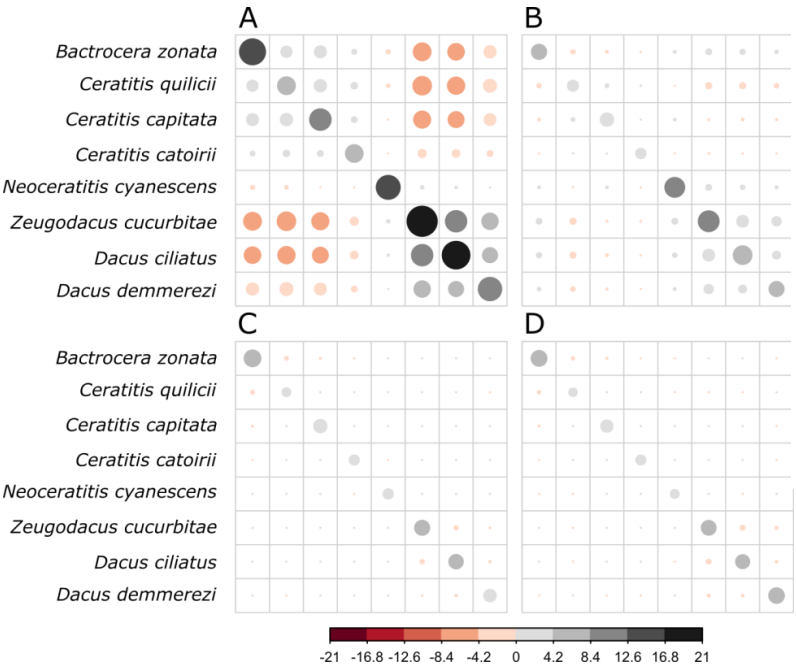

Figure 2: Residual variance-covariance matrices obtained after PLN model fitting on species abundances. A) Without any covariate (Model 1-0). B) With ecological covariates (Model 1-3). C) With plant species as a cofactor (Model 1-1). D) With both plant species and ecological covariates (Model1-5).

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Considering model selection between models without species traits, i.e., models including combinations of plant species and ecological covariates (Table 1), model ranking was equivalent on the eight-species (Models 1-0 to 1-6) and seven-species (Models 2-0 to 2-6) datasets, except that diagonal models tended to be slightly better than their full-matrix counterparts on the latter. For both datasets, the selected model included both ecological variables and host plant species as covariates (Models 1-5 and 2-6), which strongly improved the BIC (Δ_{BIC} = 17087.4 and 18935.7 respectively) as compared to the basic model (no covariate, Models 1-0 and 2-0). Models with host plant species ranked close to the selected model with a moderately inflated BIC relative to the selected model (Model 1-2: Δ_{BIC} = 971.1, Model 2-2: Δ_{BIC} = 933.2) and an important reduction in residual covariances relative to the basic model (compare Figures 2A and 2C). In comparison, including ecological variables alone deteriorated model fit with a greatly increased BIC (Model 1-3: Δ_{BIC} = 15088.8, Model 2-4: Δ_{BIC} = 11387.9) and a mild reduction of residual covariances (compare Figures 2A and 2B).

The selected model showed a good fit, with a tendency to overestimate low abundance values (Figure S3). The coefficients relative to host plant species, which represent the response of species abundances to host plants, had a bimodal distribution, i.e., some plant species were inferred as host plants and others as non-host plants (Figure 3A, right panel), in good agreement with patterns of field abundances (Figure 1B). Comparing these inferences with laboratory measures of fly species host use (Figure 3A, left panel) showed that the inferred realized host range was narrower than the laboratory-measured fundamental host range, particularly for generalists. Among plants inferred as possible hosts from species abundance patterns (i.e., those with high coefficient values), coefficients correlated positively with fly laboratory-measured fitness for specialists but not for generalists (Figure 3B).

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Model	Covariates	Residual matrix	*K*	*L*	BIC	Δ_{BIC}
A) Model set 1 (21 plants x 8 flies)						
Model 1-5	Plant + Eco	Full	284	-27664.3	57742.8	0.0
Model 1-6	Plant + Eco	Diagonal	256	-27997.8	58171.7	428.9
Model 1-2	Plant	Diagonal	176	-28608.9	58713.9	971.1
Model 1-1	Plant	Full	204	-28784.0	59302.1	1559.2
Model 1-3	Eco	Full	124	-35888.8	72831.6	15088.8
Model 1-4	Eco	Diagonal	96	-36598.4	74012.9	16270.1
Model 1-0	None	Full	44	-37228.1	74830.3	17087.4
B) Model set 2 (21 plants x 7 flies)						
Model 2-6	Plant + Eco	Diagonal	224	-20753.9	43374.1	0.0
Model 2-5	Plant + Eco	Full	245	-20723.1	43487.5	113.4
Model 2-2	Plant	Diagonal	154	-21563.1	44409.4	1035.3
Model 2-1	Plant	Full	175	-21504.7	44467.5	1093.4
Model 2-12	Preference + Performance + Eco	Diagonal	98	-23924.4	48665.3	5291.2
Model 2-10	Performance + Eco	Diagonal	91	-24387.4	49533.0	6158.9
Model 2-11	Preference + Performance	Diagonal	28	-25689.9	51613.0	8238.9
Model 2-8	Preference + Eco	Diagonal	91	-25516.9	51792.1	8418.0
Model 2-9	Performance	Diagonal	21	-26443.3	53061.6	9687.5
Model 2-4	Eco	Diagonal	84	-27082.1	54864.0	11489.9
Model 2-7	Preference	Diagonal	21	-27628.9	55432.8	12058.7
Model 2-3	Eco	Full	105	-27321.5	55517.8	12143.7
Model 2-0	None	Full	35	-31060.1	62411.8	19037.7

Table 1: Model selection on the 21-plant dataset n = 4918). Models are ranked by increasing BIC (from best to worst). k is the number of parameters. L is the log-likelihood. Δ_{BIC} is the BIC difference between any focal model and the best one.

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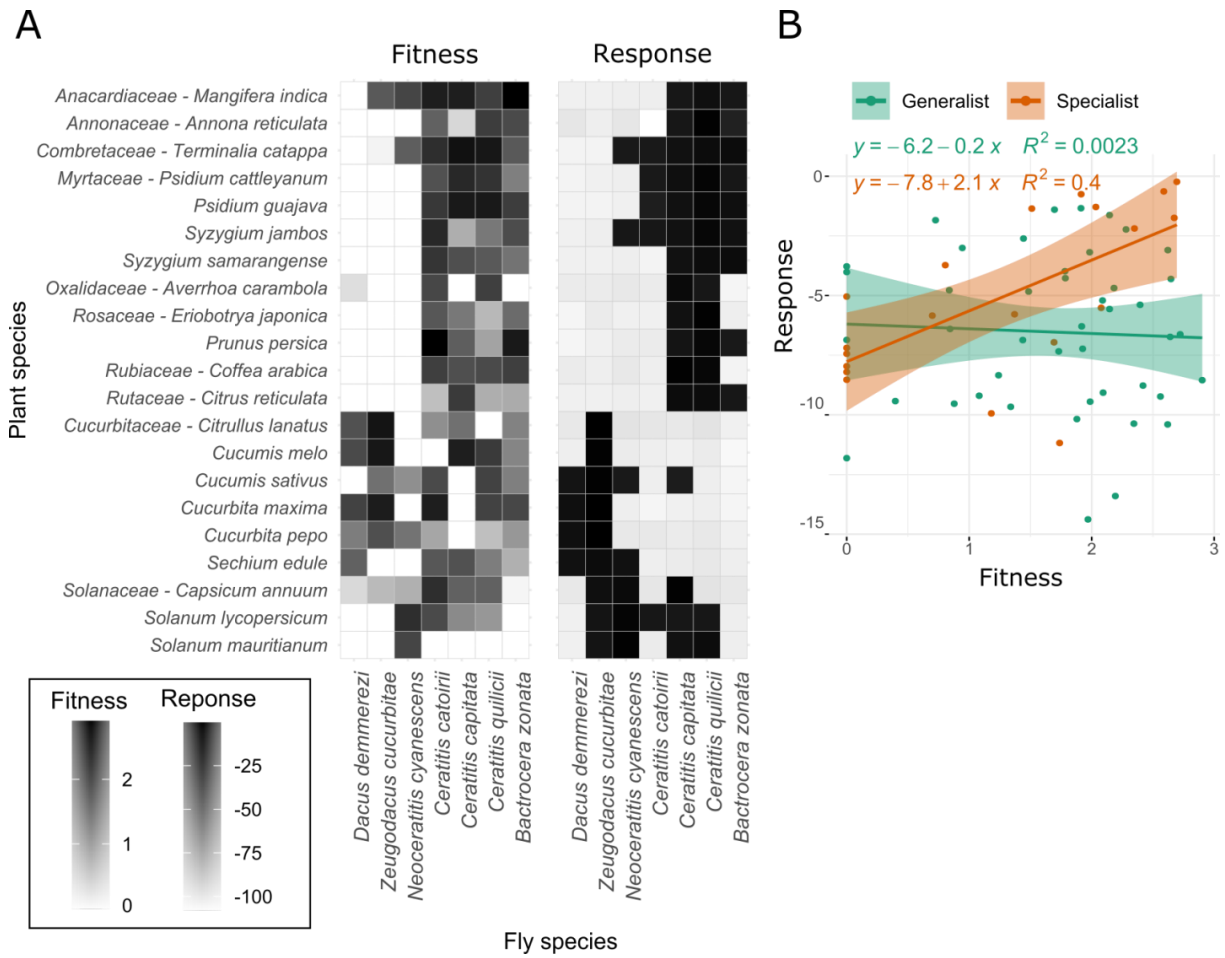

Figure 3: Comparison of fly species' fundamental and realized host use. A) Fundamental host use as measured in the laboratory (left panel – fitness is the logarithm of the product preference and performance) and realized host use as inferred from regression coefficients relative to host plants in the selected model (right panel – response is obtained from Model 2-6 on the seven-species dataset). B) Relationship between inferred responses to host plants and laboratory-measured fitness for specialists in orange and generalists in green on hosts detected as such in the field.

The coefficients relative to the first two axes of the FAMD on ecological covariates could be interpreted as responses of fly abundances to rainfall, temperature, and elevation (Figure 4). Rainfall had a low effect on the abundances of *B. zonata*, *C. capitata, C. quilicii*, and *D. demmerezi*. *Ceratitis catoirii, N. cyanenscens,* and *Z. cucurbitae* showed a propensity towards warm high-rainfall areas, while *D. ciliatus* seemed to prefer colder drier climates. *Ceratitis quilicii* and *C. catoirii* were not much affected by temperature. *Bactrocera zonata*, *C. capitata*, *D. ciliatus,* and *Z. cucurbitae* should thrive in low-elevation warm climates. *Dacus demmerezi* and to a lesser extent *N. cyanescens* seemed to prefer colder higher-elevation climates.

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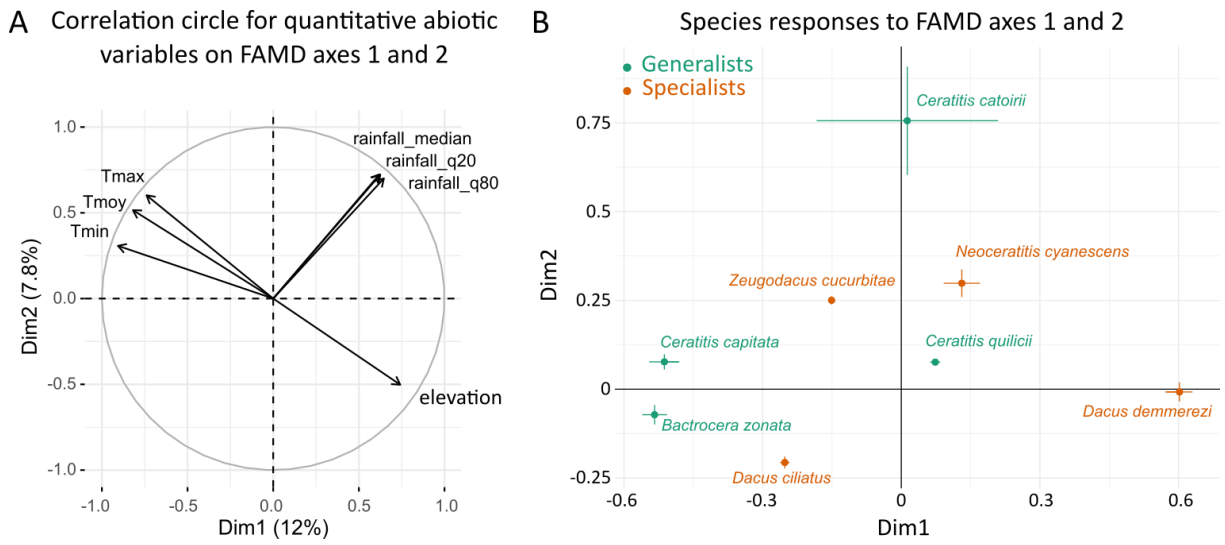

Figure 4: Species abundance responses to ecological variables. A) Correlation circle on the first and second axes of the FAMD (factorial analysis of mixed data) on ecological variables (Dim1 and Dim2, respectively). The first axis contrasts warm low-altitude sites and colder high-altitude sites. The second axis is a gradient of rainfall and maximal temperature (see Supplementary figure S3 for details on axes contributions). B) Regression slopes relative to Dim1 and Dim2, inferred under the selected model on the full 21 plant x 8 fly species dataset (Model 1-5). Error bars represent approximate confidence intervals (1.96 x standard errors). For the first axis (Dim1), negative slopes (e.g., *B. zonata* and *C. capitata*) can be interpreted as a positive effect of temperatures and a negative effect of elevation on species abundances. For the second axis (FAMD 2), positive slopes (e.g., *C. catoirii*) can be interpreted as a positive effect of rainfall on species abundances.

The selected model had full residual variance-covariance matrix on the eight-species dataset and diagonal residual variance-covariance matrix on the seven-species dataset. On the eight-species dataset its diagonal version ranked second with Δ_{BIC} = 428.9. Congruently, the residual variance-covariance matrix inferred under the selected model (Figure 2D) had very low covariance values for all pairs of fly species, all covariances being negative. This suggested possible, though weak, antagonist interactions. The largest residual correlations were observed between the three specialists *D. demmerezi, D. ciliatus* and *Z. cucurbitae* (residual correlations ranging from -0.031 to -0.112) and between the generalists *B. zonata*, *C. quilicii* and *C. capitata* (residual correlations from -0.025 to -0.090). Network inference, applied to the selected model, converged to one significant interaction

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between *D. ciliatus* and *Z. cucurbitae*, with a stability of 0.99 (i.e., detected in 99 out of 100 network inferences on bootstrapped data). Overall these results suggested that at the scale of the whole community competitive interactions between fly species only weakly affected their joint distributions and that fly species abundances were mainly explained by environmental covariates.

Considering models accounting for species fundamental niche (Table 1B), the best model with species traits included female preference, larval performance and ecological variables (Model 2-12, Δ_{BIC} = 5189.2). It ranked intermediate between the model with ecological variables alone and the best model. Such good performance of models with species traits suggests that the fundamental host range of fly species is an important determinant of fly species joint distributions. Whether in combination with ecological covariates or not, models with larval performance were slightly better than models with female preference.

Cucurbitaceae

Focusing on Cucurbitaceae and the three fly species they hosted, *D. ciliatus*, *D. demmerezi* and *Z. cucurbitae*, the selected model was again the one including both host plant species and ecological covariates (Model 1-5, Table S5A). Its BIC was lower than the one of the basic model (Model 1-0, Δ_{BIC} = 1208.0). It assumed a full residual variance-covariance matrix and performed better than its diagonal version (Δ_{BIC} = 190.6). Network inference yielded two significant negative interactions between *D. ciliatus* and *Z. cucurbitae* (stability = 1.0) and between *D. demmerezi* and *Z. cucurbitae* (stability = 0.56). For all other models, versions with full residual matrix performed better than their diagonal counterparts. Besides, models including plant species alone or ecological covariates alone performed equivalently (Δ_{BIC} = 515.3 vs. Δ_{BIC} = 653.2). This is congruent with the idea that plant species are more similarly affecting fly distributions within the Cucurbitaceae family than at the scale of the 21-plant dataset, so that the influence of plant identity is less important for species distributions among Cucurbitaceae than on a wider set of plants.

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For *D. demmerezi* and *Z. cucurbitae,* for which traits were available, models with species traits alone had poor performance, and displayed higher BIC than the basic model (Table S5B). However, the model with both species traits and ecological covariates ranked third just after the diagonal version of the selected model (Model 2-10, Δ_{BIC} = 124.9).

Solanaceae

For Solanaceae and their associated fly species, *N. cyanescens, C. capitata,* and *C. quilicii*, the selected model included host plant species, ecological covariates and a diagonal residual variance-covariance matrix (Model 1-6, Table S6). It improved the BIC of the basic model by 201.8. It performed better than its full residual matrix version (Δ_{BIC} = 15.8) and congruently, applying network inference to the latter yielded no significant interaction between fly species. On this dataset all models with a diagonal matrix performed better than their full residual matrix counterpart, further confirming the absence of detected interactions. Models with ecological covariates alone performed poorly (Model 1-3 Δ_{BIC} = 176.4 and Model 1-4 Δ_{BIC} = 162.0, respectively). Models with species traits were almost as good as their equivalent with host plant as a cofactor. For instance, the model with species traits and ecological covariates (Model 2-10) ranked second with Δ_{BIC} = 9.5. Female preference and larval performance performed equally well (Δ_{BIC} = 44.6 and Δ_{BIC} = 38.5 respectively) and almost as good as both traits together (Δ_{BIC} = 33.4), suggesting important correlation between the traits.

Other plant families

The last dataset considers all families other than Cucurbitaceae or Solanaceae with *B. zonata*, *C. capitata*, *C. catoirii*, and *C. quilicii* (Table S7). The selected model included host plant species and ecological covariates (Model 1-5, Δ_{BIC} = 2639.7 with the basic model 1-0). It assumed a full residual variance-covariance matrix and performed slightly better than its diagonal version (Δ_{BIC} = 55.8). All models with a full residual matrix performed better than their diagonal counterpart. Network inference yielded one significant interaction between *B. zonata* and *C. quilicii* (stability = 1.0).

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The model with only ecological covariates performed well (Model 1-3, Δ_{BIC} = 967.3), and almost as good as the model with host plant alone (Model 1-1, Δ_{BIC} = 684.1), suggesting redundancy between ecological information and plant identity. Models that included species traits without ecological covariates performed badly (Δ_{BIC} > 2220), and the model with species traits and ecological covariates (Model 2-10, Δ_{BIC} = 814.3) performed only slightly better than the model with ecological covariates only (Model 1-3, Δ_{BIC} = 967.3). Of the two traits, only female preference really improved model fit (Model 2-8 Δ_{BIC} = 888.9 vs. Model 2-12 Δ_{BIC} = 1050.0).

Discussion

The determinants underlying the structure of a community of eight Tephritid fly species were deciphered. Modelling joint species abundances without accounting for any covariate (only intercepts and an offset) confirmed a major role of host use strategy on fly species abundances. Species abundances co-varied positively among generalists and among specialists and negatively between species from these two groups. Common responses to environmental factors may cause positive residual correlations in species abundances, while divergent responses will imply negative correlations, potentially leading to incorrect interpretations of species interactions (Ovaskainen et al. 2016, Dormann et al. 2018). Accounting for environmental covariates strongly improved model fit and made all residual covariances almost completely vanish, particularly among groups, suggesting that no important environmental factor structuring the community has been missed.

Detection of competitive interactions

Some residual covariances remained non-negligible after accounting for fly species' response to host plants between some generalists and between some specialists of Cucurbitaceae. They were all negative, suggesting a possible minor role of antagonistic interactions within specialists and within generalists. Only one of these possible associations resisted the network inference process on the whole dataset (*D. ciliatus* - *Z. cucurbitae*, the two most abundant specialists of Cucurbitaceae). Two more significant associatons were detected when focusing on Cucurbitaceae (*Z. cucurbitae* - *D.*

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demmerezi) and on other plant families (*B. zonata* - *C. quilicii*) suggesting some dependence of species interactions on host plants. On Cucurbitaceae, although qualitatively congruent with other independent empirical measures of host range (Vayssieres et al. 2008) and climatic niche (Vayssières & Carel 1999), host plant species and abiotic factors only moderately improved model fit. All three specialist flies found on Cucurbitaceae are able to thrive on any plant of this family (Charlery de la Masselière et al. 2017b) and competitive interactions between these fly species are highly plausible (Vayssieres et al. 2008). On other plant families, both host plants and abiotic factors clearly improved model fit, congruently with former interpretations of the system (Duyck et al. 2006a, Duyck et al. 2008). Responses of generalist species to abiotic factors were strikingly congruent with former independent laboratory experiments (Duyck & Quilici 2002, Duyck et al. 2004, Duyck et al. 2006a). There was redundancy between host plants and abiotic factors. Many of these plants are exploited but not planted (e.g., Myrtaceae). Their distributions are therefore more dependent on ecological factors than those of Solanaceae and Cucurbitaceae, which are mainly cultivated throughout the year in Réunion. On Solanaceae, no species association was detected. Plant identity was the main determinant of species abundances, congruently with the idea that Solanaceae impose adaptive challenges on their fruit consumers through a variety of toxic compounds (Brévault et al. 2008), rendering host adaptation the main factor driving species abundances.

The ghost of competition past

Among-group covariation between specialists and generalists were mainly attributable to fly species' adaptation to host use with a minor contribution of abiotic factors. Previous studies have highlighted differences in host adaptation between these fly species (Hafsi et al. 2016). Contrary to the specialists, which are mainly able to use their preferred hosts, the four generalists can thrive in numerous plant species, and have weak female preferences (Charlery de la Masselière et al. 2017b). Accordingly, specialists were seldom found in plants other than Cucurbitcaeae or Solanaceae. However, these results do not explain why generalists were so rarely found on Cucurbitaceae and Solanaceae. Competitive exclusion with specialists would be a natural hypothesis to explain this absence (Nakadai

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et al. 2018). Here, no competition among groups was detected. It is possible, however, that competition has operated and that competitive exclusion has been so strong that generalists cannot be found on Cucurbitaceae. In PLN modelling, such absence could be interpreted as negative response of generalist abundances to Cucurbitaceae and be encapsulated in plant cofactor slope rather than in species interactions. It is precisely when competition is intense enough to cause niche partitioning that it can no longer be detected, a well-known paradox in ecology formerly termed ''the ghost of competition past'' (Connell 1980).

To escape the paradox, knowledge about the fundamental niches of species could help settle whether species interactions are an important driver of species assemblages (Augustyn et al. 2016, Dormann et al. 2018). Laboratory measurements of larval performance and female preference on all host plants were used in replacement of plant identity. Congruently with the community being essentially driven by host use, preference and performance clearly improved model fit. Interestingly, performance was more informative than preference, which was expected from previous knowledge that generalists' preferences are uncorrelated to their performances (Charlery de la Masselière et al. 2017b). If competition truly shapes species abundances and has not been detected, it is to be found in the difference between models with plant identity as a cofactor and models with species traits instead. Here we found a difference suggesting that competitive exclusion is at work. In terms of importance, from model rankings, host use patterns were the most important factor shaping species abundances, followed by abiotic factors and possibly a dose of competition.

This predominance of host plants as a structuring factor of phytophagous insect communities has been much debated, but congruent studies exist. In analyses of insect communities along road verges, Schaffers et al. (2008) found that the composition of plant communities was a much better predictor of insect and spider assemblages than environmental variables. Similarly Nakadai et al. (2018) found that sharing of host species was predominant among butterflies of the Japanese archipelago, suggesting that interspecific resource competition may not effectively determine community assembly patterns at regional scales. In an earlier review on the importance of competition in insects, Denno et

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al. (1995) pointed that only weak to moderate effect of competition should certainly be expected in phytophagous insects such as Tephritids due to their high mobility and weak aggregation behaviors. Experimental manipulations of competitive interactions in the field could offer a promising way to test the validatity of the present inferences. These experiments would also be useful to unveil the role of other biotic interactions (e.g., natural enemies), as forces capable of modulating interspecific competition between fruit flies.

Generalists vs. specialists

Overall specialists and generalists almost behaved as separate communities with different assembly rules. That specialists and generalists form separate interaction networks has already been highlighted, e.g., among soil microbial species (Barberan et al. 2012). It is well known that the predictability of assemblages differs between host-plant generalists and specialists (Müller et al. 2011). This has led to the hypothesis that specialists would have assemble according to the species-sorting paradigm of metacommunity ecology (Leibold et al. 2004), whereby species occurrences are mainly driven by habitat heterogeneity and local adaptation. Generalists' assembly rules, on the other hand, would rather follow a mass-effect paradigm (Shmida & Wilson 1985), according to which sink populations, where the species is maladapted, can persist through a migration influx from source populations (Müller et al. 2011). Our results confirm this hypothesis. For specialists, a good agreement between the inferred host plant effects on species abundances and the laboratory measures of host adaptation suggested that specialists were mainly filtered by host plant characteristics. In contrast, generalists displayed no relationship between inferred and laboratory-measured host plant effects, suggesting that generalists were found on some hosts where their fitness is low and at low density on good hosts. Besides generalists use fruits whose availability is highly variable over time. Contrary to specialists, most of their hosts are not available all year long (Figure S4). This temporally variable habitat may trigger a dynamics of local extinction and recolonization, in which the roles of migration and stochasticity become more important than that of host adaptation and in which coexistence is possible despite fundamental niche overlap (Connell 1980, Chesson 2000).

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Data and script accessibility

Data and script are available online: http://doi.org/10.5281/zenodo.4309264

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Supplementary material

Appendix S1: Additional materials & methods

Details on species table

Among the 12872 initial samples, only samples that fulfilled to following conditions were kept: (i) GPS coordinates could be retrieved (n=9715 in 41 plant species), (ii) at least one Tephritid fly emerged (n=6455 in 41 plant species), (iii) from plant species which had been successfully sampled at least 10 times in the dataset (n=6434 in 36 plants), and (iv) from plant species that were also characterized in the laboratory (n=4918 in 21 plants). In the resulting dataset, 97351 individual flies were counted. Samples covered 104 field sessions all year round over the 1991-2009 period (Tables S1 and S2).

Table S1: Number of samples (*n*) by year in the full 21-plant dataset

Year	1991	1992	1993	1994	1995	1996	1997	1998	2001	2002	2003	2004	2005	2008	2009
n	4	15	31	52	80	38	434	1143	83	523	634	19	205	191	1466

Table S2: Number of samples (*n*) by month in the full 21-plant dataset

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	447	818	708	458	328	182	594	252	222	238	242	429

The number of samples per plant species (Table S3) varied from 12 (*Averrhoa carambola*) to 1105 (*Cucurbita maxima*). The most represented plant families were the Cucurbitaceae (six plant species and 2374 samples), the Myrtaceae (four plant species and 1102 samples) and the Combretaceae (one plant species with 853 samples).

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Table S3: Number of samples (*n*) for each of the 21 plant species retained in the study

Family	Species	Common English name	*n*
Anacardiaceae	*Mangifera indica*	Mango	36
Annonaceae	*Annona reticulata*	Custard apple	27
Combretaceae	*Terminalia catappa*	Indian almond	853
Cucurbitaceae	*Citrullus lanatus*	Water melon	175
	Cucumis melo	Melon	30
	Cucumis sativus	Cucumber	440
	Cucurbita maxima	Pumpkin	1105
	Cucurbita pepo	Zucchini	504
	Sechium edule	Chayote	120
Myrtaceae	*Psidium cattleyanum*	Strawberry guava	422
	Psidium guajava	Guava	398
	Syzygium jambos	Rose apple	255
	Syzygium samarangense	Java apple	27
Oxalidaceae	*Averrhoa carambola*	Star fruit	12
Rosaceae	*Eriobotrya japonica*	Loquat	61
	Prunus persica	Peach	99
Rubiaceae	*Coffea arabica*	Coffee	81
Rutaceae	*Citrus reticulata*	Mandarin	14
Solanaceae	*Capsicum annuum*	Chilli	29
	Solanum lycopersicum	Tomato	68
	Solanum mauritianum	Bugweed	162

Plant species differed in terms of the patterns of occurrence of the eight fly species (Figure S1). In particular, Cucurbitaceae were mostly used by the three species known as specialists of this plant family, *D. ciliatus* (14047 flies in 1264 samples), *D. demmerezi* (6335 flies in 276 samples) and *Z. cucurbitae* (21830 flies in 1463 samples). Other fly species were detected in fewer than 10 Cucurbitaceae samples. Solanaceae mainly hosted the specialist species *N. cyanescens* (1205 flies in 225 samples). They were also, to a lesser extent, hosts of *C. capitata* (116 flies in 32 samples), and *C. quilicii* (131 flies in 22 samples). Other fly species were detected in less than 5 Solanaceae samples. The other plant species (12 plant species) were mainly used by the four generalist species, i.e., *B. zonata* (11517 flies in 728 samples), *C. capitata* (8735 flies in 537 samples), *C. quilicii* (33149 flies in 1583 samples), *C. catoirii* (291 flies in 65 samples). Other fly species were detected in less than 5 samples.

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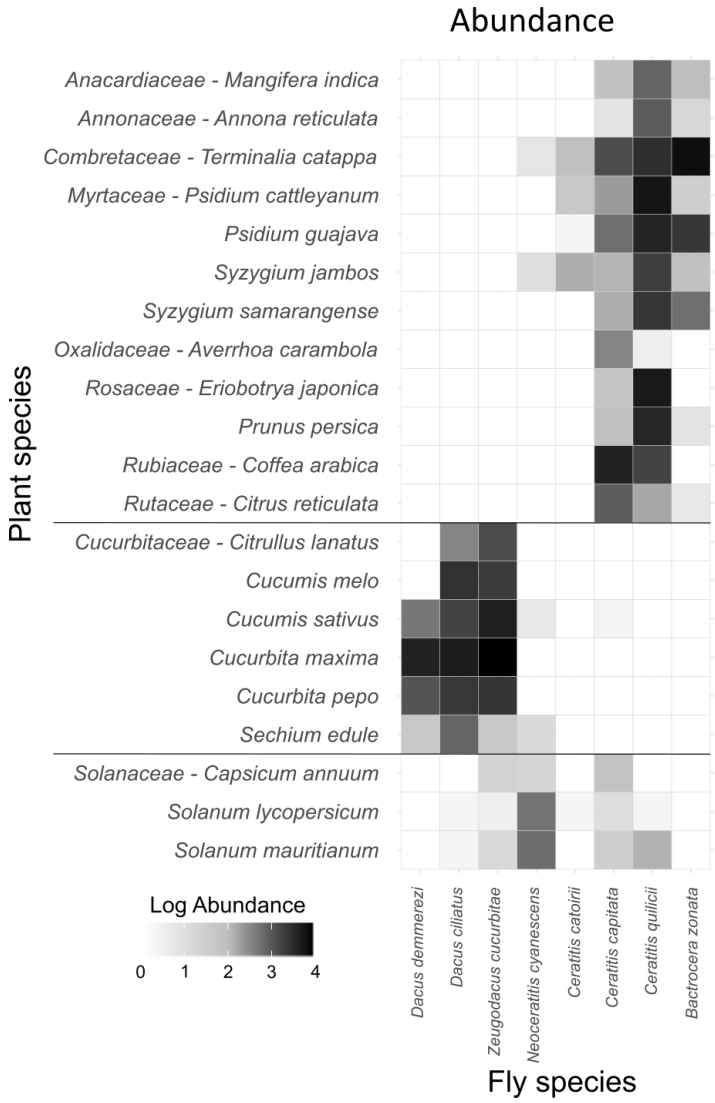
Figure S1: Fly species realized host use in the field (log-abundance)



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Co-occurrences between fly species were therefore much structured by whether the considered plant species belonged to Cucurbitaceae, Solanaceae or other families (Table S4).

Table S4: Species co-occurences in the full 21-plant dataset (*n* = 4918 samples)

	Bactrocera zonata	*Ceratitis quilicii*	*Ceratitis capitata*	*Ceratitis catoirii*	*Neoceratitis cyanescens*	*Dacus ciliatus*	*Dacus demmerezi*	*Zeugodacus cucurbitae*
Bactrocera zonata	728	198	120	1	0	0	0	0
Ceratitis quilicii	198	1605	309	57	12	1	0	1
Ceratitis capitata	120	309	570	31	15	1	0	2
Ceratitis catoirii	1	57	31	66	1	1	0	1
Neoceratitis cyanescens	0	12	15	1	237	3	1	5
Dacus ciliatus	0	1	1	1	3	1266	107	454
Dacus demmerezi	0	0	0	0	1	107	276	133
Zeugodacus cucurbitae	0	1	2	1	5	454	133	1467

Ecological covariables

Elevation (in meters) of each sample was obtained from the Digital Elevation Model Litto3D® co-produced by the French IGN (National Geographic Institute) and the SHOM (Marine Oceanographic Hydrographic Service). Pluviometry was obtained from layers produced by M. Mezino from 143 CIRAD and Meteo-France meteorological stations, containing isohyets of (i) the minimal rainfall observed in the 20% most humid years of the 1986-2016 period (ii) the minimal rainfall observed in the 20% driest years of the 1986-2016 period and (iii) the median annual rainfall over the 1986-2016 period. For each sample, the value of closest isohyet was retained for each of the three variables. Temperature was characterized by the (i) minimal, (ii) mean and (iii) maximal annual temperature over the 1987-2017 period as interpolated by M. Mezino from 73 CIRAD and Meteo-France meteorological stations raw data. Land use around each sample location was obtained from a 12-categories layer produced by supervised classification of Pléiades 2018 images (Dupuy and Gaetano, 2019 doi:10.18167/DVN1/WKAJZO, CIRAD Dataverse, V1).

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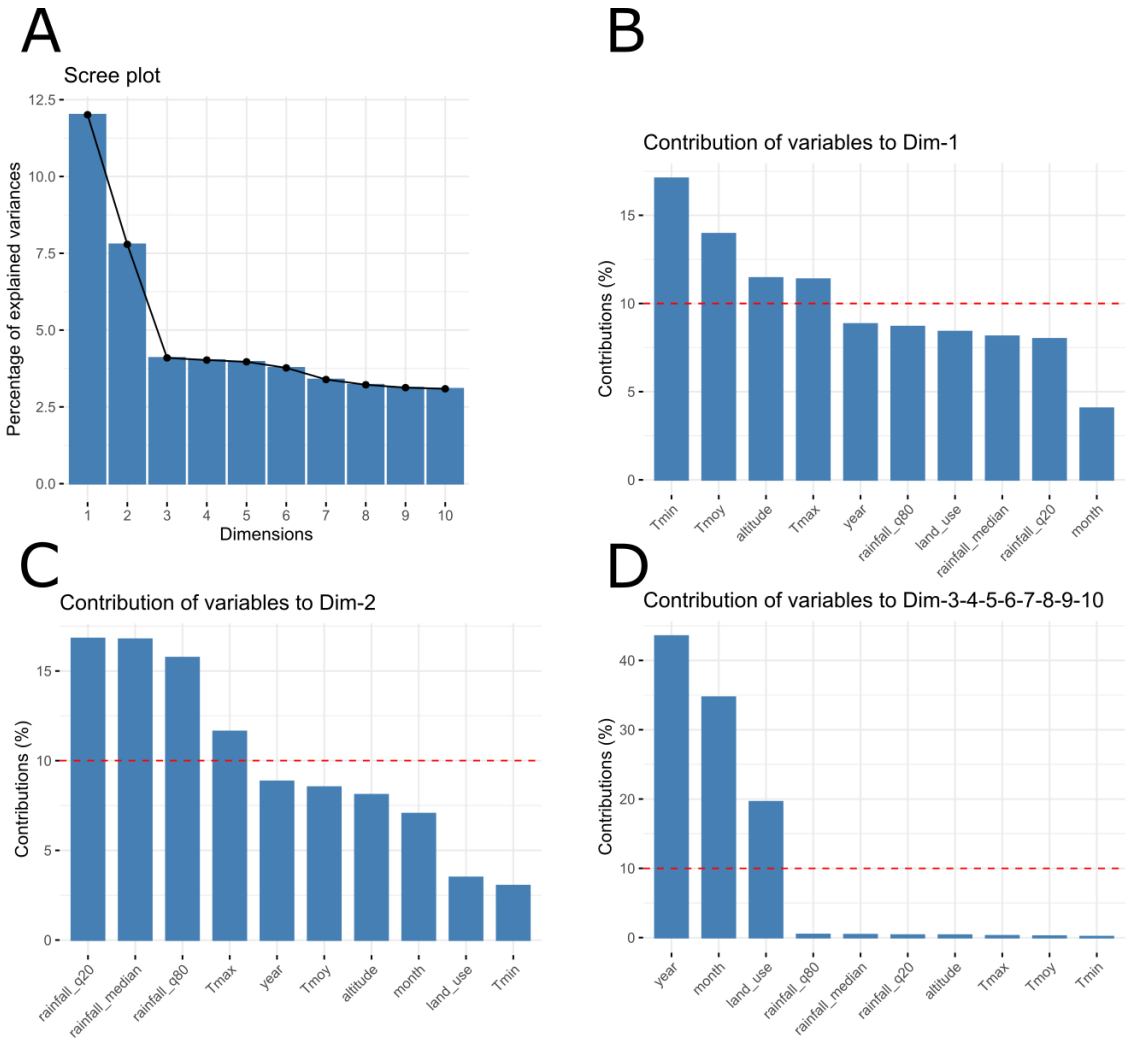
Additional details on FAMD on ecological covariables

Figure S2: Interpretation of the axes of the FAMD on ecological covariables. A) Percentage of variance explained by each of the 10 axes of the FAMD. The first and second FAMD axes explain 19.8 % of the variance. C-D) Contribution of individual ecological covariates to Axis 1, 2 and other axes, respectively. Axis 1 is mainly contributed by temperature and elevation. Axis 2 is mainly contributed by rainfall and maximal temperature. Other axes are contributed by qualitative variables (year, month and land use).



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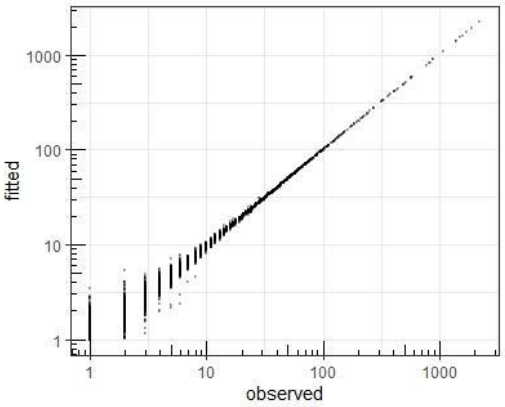
Appendix S2: Complementary results

Goodness of fit of the selected model

Figure S3: Relationship between observed and fitted species abundances (log scale) in the selected model on the full 21 plant x 8 fly species dataset (Model 1-5, Table 1A).



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Model selection on the three sub-datasets

Cucurbitaceae

Table S5: Model selection on the Cucurbitaceae dataset (*n* = 2347). Models are ranked by increasing BIC (from best to worst). *k* is the number of parameters. *L* is the log-likelihood. Δ_{BIC} is the BIC difference between any focal model and the best one.

Model	Covariates	Residual matrix	*k*	*L*	BIC	Δ_{BIC}
A) Model set 1 (6 plants x 3 flies)						
Model 1-5	Plant + Eco	Full	54	-14168.3	28756.3	0.0
Model 1-6	Plant + Eco	Diagonal	51	-14275.3	28947.0	190.6
Model 1-1	Plant	Full	24	-14542.5	29271.6	515.3
Model 1-3	Eco	Full	39	-14553.2	29409.5	653.2
Model 1-2	Plant	Diagonal	21	-14661.3	29485.7	729.4
Model 1-4	Eco	Diagonal	36	-14649.7	29579.2	822.8
Model 1-0	None	Full	9	-14947.2	29964.3	1208.0
B) Model set 2 (6 plants x 2 flies)						
Model 2-5	Plant + Eco	Full	35	-7311.6	14881.6	0.0
Model 2-6	Plant + Eco	Diagonal	34	-7361.7	14974.4	92.8
Model 2-10	Preference + Performance + Eco	Diagonal	28	-7399.9	15006.5	124.9
Model 2-3	Eco	Full	25	-7419.8	15024.2	142.6
Model 2-8	Preference + Eco	Diagonal	26	-7421.5	15035.1	153.5
Model 2-12	Performance + Eco	Diagonal	26	-7423.9	15039.8	158.2
Model 2-4	Eco	Diagonal	24	-7461.8	15100.9	219.3
Model 2-1	Plant	Full	15	-7570.5	15251.8	370.2
Model 2-2	Plant	Diagonal	14	-7654.1	15411.5	529.9
Model 2-0	None	Full	5	-7722.3	15481.6	600.0
Model 2-7	Preference	Diagonal	6	-7739.0	15522.4	640.8
Model 2-9	Preference + Performance	Diagonal	8	-7745.6	15550.4	668.7
Model 2-11	Performance	Diagonal	6	-7801.2	15646.7	765.1

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Solanaceae

Table S6: Model selection on the Solanaceae dataset (n = 259). Models are ranked by increasing BIC (from best to worst). k is the number of parameters. L is the log-likelihood. Δ_{BIC} is the BIC difference between any focal model and the best one.

Model	Covariates	Residual matrix	k	L	BIC	ΔBIC
Model 1-6	Plant + Eco	Diagonal	42	-824.2	1881.7	0.0
Model 2-10	Preference + Performance + Eco	Diagonal	42	-829.0	1891.2	9.5
Model 1-5	Plant + Eco	Full	45	-823.8	1897.5	15.8
Model 2-12	Performance + Eco	Diagonal	39	-842.6	1901.7	20.0
Model 2-8	Preference + Eco	Diagonal	39	-846.5	1909.5	27.8
Model 1-2	Plant	Diagonal	12	-922.3	1911.2	29.4
Model 2-9	Preference + Performance	Diagonal	12	-924.2	1915.1	33.4
Model 2-11	Performance	Diagonal	9	-935.1	1920.2	38.5
Model 1-1	Plant	Full	15	-921.1	1925.6	43.8
Model 2-7	Preference	Diagonal	9	-938.2	1926.3	44.6
Model 1-4	Eco	Diagonal	36	-921.9	2043.8	162.0
Model 1-3	Eco	Full	39	-920.8	2058.1	176.4
Model 1-0	None	Full	9	-1016.8	2083.5	201.8

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Other plant families

Table S7: Model selection on the dataset with other plant families. Models are ranked by increasing BIC (from best to worst). *k* is the number of parameters. *L* is the log-likelihood. Δ_{BIC} is the BIC difference between any focal model and the best one.

Model	Covariates	Residual matrix	*k*	*L*	BIC	Δ_{BIC}
Model 1-5	Plant + Eco	Full	98	-12218.5	25195.0	0.0
Model 1-6	Plant + Eco	Diagonal	92	-12269.6	25250.8	55.8
Model 1-1	Plant	Full	58	-12715.3	25879.1	684.1
Model 1-2	Plant	Diagonal	52	-12796.6	25995.3	800.3
Model 2-10	Preference + Performance + Eco	Diagonal	56	-12788.1	26009.3	814.3
Model 2-8	Preference + Eco	Diagonal	52	-12840.9	26083.9	888.9
Model 1-3	Eco	Full	54	-12872.4	26162.4	967.3
Model 2-12	Performance + Eco	Diagonal	52	-12921.4	26245.1	1050.0
Model 1-4	Eco	Diagonal	48	-12968.4	26308.1	1113.1
Model 2-9	Preference + Performance	Diagonal	16	-13650.6	27424.9	2229.8
Model 2-7	Preference	Diagonal	12	-13855.9	27804.7	2609.7
Model 1-0	None	Full	14	-13863.2	27834.7	2639.7
Model 2-11	Performance	Diagonal	12	-13905.2	27903.1	2708.1

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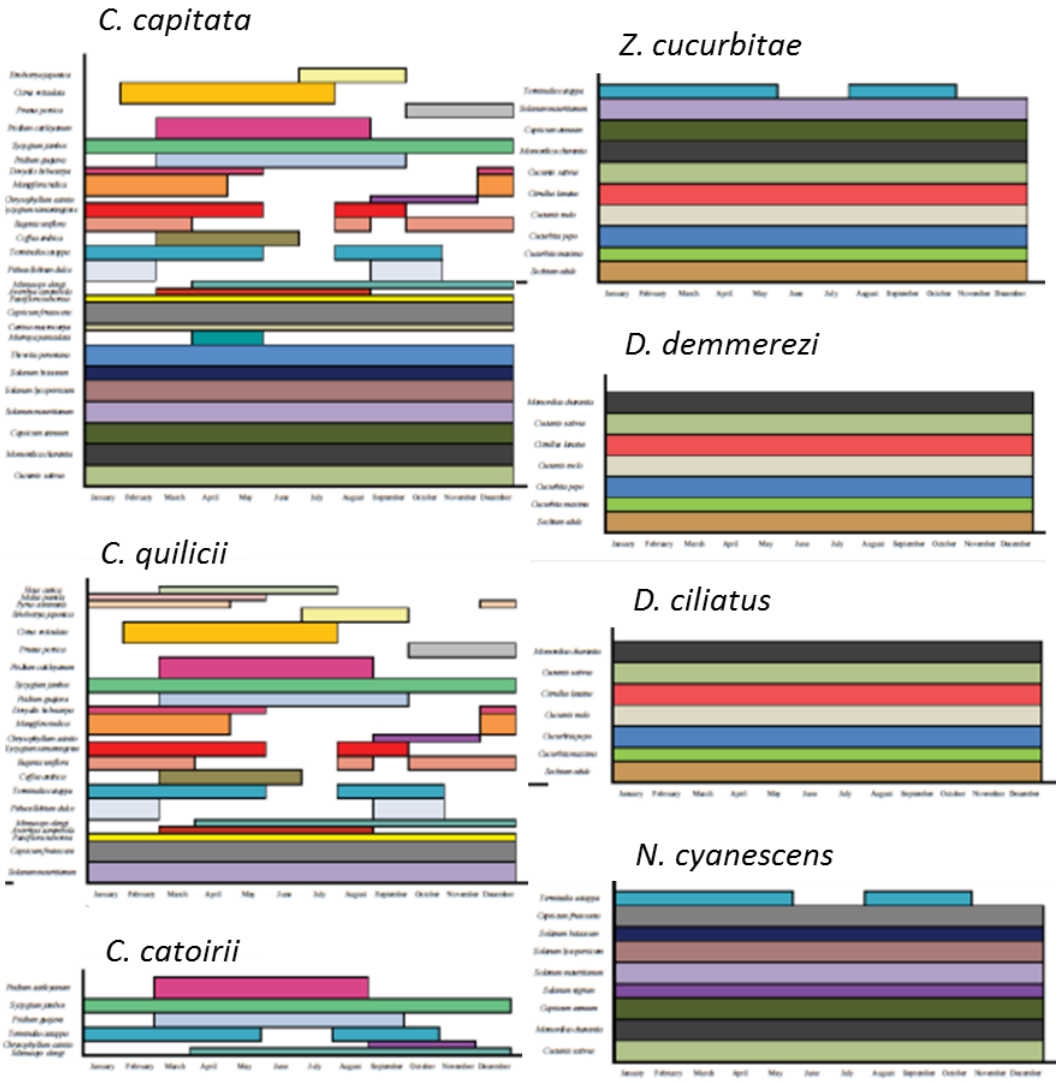
Figure S4: Availability of host plants along the year for seven fly species from Charlery de la Masselière et al. (2017a, Supplementary material Figure S1). Only major host plants are reported. Specialist species tend to rely on hosts with year-long availability, while generalists also have host with short fructification periods in their diet.