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Rewiring after knockout: using network structure to inform insect responses to flower removal

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Abstract

Human activities are driving unprecedented species losses, and predicting the consequences of these losses for the stability of the remaining community is a major challenge for ecologists. Ecosystems can buffer species loss through interaction rewiring either by adjusting interaction strength or the emergence of novel interactions. A community's ability to rewire depends on the flexibility, specialization, and network position of the remaining species, particularly the extent of shared interactions. Although widely explored theoretically, this response has rarely been tested experimentally. We perform a knockout experiment in a flower-thrips (Insecta: Thysanoptera) visitation network on Réunion island, a hot-spot of diversity in the Indian Ocean. To inform how the insect community shifts in response, we combine this experiment with analyses of community clustering structure, insect specialisation and visitation overlap among plants. We removed flowers of the plant *Solanum mauritianum,* which was identified in the network as a central species, and assessed the impact of its removal on insect communities visiting two other plants that share many visiting insects (*Ipomea indica* and *Lantana camara*). The experiment did not alter insect diversity, total abundance or community composition, but it triggered changes in the density of some species. Interaction strength rewiring thus buffered the loss of insect diversity and overall abundance, in a network dominated by specialist species. By linking experimental data and a well-defined network, we provide evidence of the importance of considering the larger community context to understand how subtle habitat degradations may trigger changes in species interactions.

Keywords

community composition - experimental community ecology - habitat loss - indirect effects - flower removal - Mascarene islands - pollinator network - rewiring

Introduction

In ecological communities, interactions between species form complex networks of interdependent species (Dunne 2006; Montoya et al. 2006; Bascompte and Jordano 2007). When a species goes extinct, so do its interactions with other species, leading to knock-on effects for other directly and indirectly linked species (Paine 1966; Borrvall et al. 2000; Solé and Montoya 2001; Dunne et al. 2002; Koh et al. 2004; Memmott et al. 2004; Ebenman and Jonsson 2005; Eklöf and Ebenman 2006; Pires et al. 2020). This can result in extinction cascades, which have been reported in most ecosystems on Earth as a result of species invasions, habitat loss, overexploitation of resources, and climate change. This can lead to accelerated biodiversity loss and dramatic consequences for the ecosystem services that natural communities provide (Colwell et al. 2012; Brondizio et al. 2019; Almond et al. 2020; Kehoe et al. 2020). Therefore, predicting the consequences of species losses for the stability of the remaining community is an important challenge for ecologists. Two mechanisms may buffer the loss of species and their interactions: (1) topological rewiring, whereby lost interactions are replaced by new ones, and (2) interaction strength rewiring, the adjustment in interaction strength of remaining interactions (Kondoh 2003; Staniczenko et al. 2010; Valdovinos et al. 2010, 2013; Thierry et al. 2011; Ramos-Jiliberto et al. 2012; Pearse and Altermatt 2013; Sanders et al. 2018; Sheykhali et al. 2020), but see (Gilljam et al. 2015). The possibility for topological and interaction strength rewiring, however, vary as a function of species morphological and phenological trait matching, specialisation and abundances, which mediate the probability of encounter between potential partners (Futuyma and Moreno 1988; Devictor et al. 2010; Ramos-Jiliberto et al. 2012; Valdovinos et al. 2013; Brodie et al. 2014; Grass et al. 2018). Trophic specialisation of consumers, for example, is an important trait determining species' ability to persist in eroded networks (Futuyma and Moreno 1988; Devictor et al. 2010; Poisot et al. 2011; Poisot 2020). Relative to generalists, specialist species are more likely to go extinct if the few partners they rely on disappear (Warren et al. 2001; Bascompte and Jordano 2007; Fonseca 2009; Valdovinos et al. 2013; Grass et al. 2018). When the extinct species is a basal resource, like a plant, cascading effects for the rest of the community are usually strong because many species depend on that resource (Fonseca 2009; Schleuning et al. 2016), which is particularly true for specialist consumers. Consequences are even stronger if the lost species is a generalist or keystone species, i.e. a species that engages in a disproportionate number of interactions in the community (Carson and Root 2000; Dunne

et al. 2002; Ebenman and Jonsson 2005; Kadoya et al. 2018; Narango et al. 2020). This means generalist species are often pillars of the structure and stability of ecological communities.

Communities of herbivorous arthropods are among the most diverse in terrestrial ecosystems with the loss of resource plants being an important driver of their decline (Tews et al. 2004; Koh et al. 2004; Gandhi and Herms 2010; Fox 2013; Schleuning et al. 2016; Wagner 2020; Kehoe et al. 2020). In agricultural or timber-producing lands, plant species are often lost due to overexploitation of species with high economic value, or when plants go locally extinct because they cannot cope with increased nitrogen in the soil, invasive herbivores and pathogens, or toxic chemicals (Tilman and Lehman 2001). The consequences of plant loss on topological and interaction strength rewiring have been largely studied using theoretical modelling, or by comparing areas with or without a particular species (Bascompte and Jordano 2007; Schleuning et al. 2016; Grass et al. 2018). Experimental removal of species, or knockout experiments, however, remain the ideal approach to get a mechanistic understanding of post-extinction community rewiring. This approach is however still rarely used due to its technical complexity. Experiments that removed invasive plants (Lopezaraiza–Mikel et al. 2007; Ferrero et al. 2013; Kaiser-Bunbury et al. 2017), generalist flowering plants (Biella et al. 2019, 2020) or herbivores (Carson and Root 2000) suggest dramatic changes in communities, even if some studies report a lack of effect (Ferrero et al. 2013; Goldstein and Zych 2016). These discrepancies are evidence of the importance that network structure has in determining the consequences of species extinctions, and call for experimental designs tailored to test these theoretical predictions.

These experimental designs should reflect the central role that network structure plays in determining how extinctions and rewiring cascade through the network, for example by coupling knockout experiments with network analyses. Considering clustering structure is particularly important to understand how species (network nodes) form densely connected groups through interactions (network links), and how such organization influences the spread of disturbances like extinctions (Stouffer and Bascompte 2011). Clustering methods (or community detection methods) coupled with graph representations are therefore ideal to detect groups of tightly-connected species or clusters that have loose connections with species in other groups (Girvan and Newman 2002; Fortunato 2010). These methods allow identifying central or keystone species that interact with the largest number of species, or species functions, and their dependencies on other groups (Fortunato 2010; Leger et al. 2014, 2015). Bipartite ecological networks like plant-insect interaction networks, are often described with clustering approaches. Whether this approach is capable of informing how the loss of a central plant triggers community rewiring or cascading extinctions, however, is a question that

106 remains little explored. Coupling this statistical method with knockout experiments can be particularly useful given that species dependency to others is a function of the position of the
108 cluster they belong to. Peripheric clusters of highly interacting species that weakly interact with generalist species, for instance, are likely to be less impacted by the loss of generalists
110 (Stouffer and Bascompte 2011).

In this work, we use a knockout experiment in a flower-thrips (Insecta: Thysanoptera)
112 visitation network to explore how insect species densities and diversity change following the experimental removal of floral resources. We specifically consider shifts in species relative
114 abundances and diversity as a metric of community rewiring. We combine this experiment with an analysis of the community clustering structure to target the plant species more likely
116 to be impacted by the experiment. We performed this study in Reunion, a tropical island considered a diversity hotspot located in the south-west of the Indian Ocean. Thrips are minute
118 insects, whose larvae feed on plants, fungi, or other insects. Most adults migrate to flowers to feed on pollen or to mate, with few species known to be strict pollinators (Mound 2005). We
120 analyse a previously described thrips-plant visitation network that included the whole island (Dianzinga et al. 2020). In this network we identify clusters of highly-interacting species, or
122 communities, using the stochastic block model algorithm (Mariadassou et al. 2010), currently the most reliable clustering approach for weighted networks (Fortunato 2010; Leger et al.
124 2014, 2015). In the second part of the study, we used the results from the block model analysis to set-up a flower-head removal experiment. We tested the hypothesis that removal of a
126 highly-connected generalist plant (the treatment species) would alter insect communities on two neighbouring plants (the focal species), with which it shares an important number of
128 insect species. We specifically hypothesise that removal of the treatment plant will reduce thrips diversity (species richness and evenness), and total abundance on the focal plants due to
130 loss of an important resource. We also hypothesise that the flower-head removal will particularly impact specialist insect species, and species on focal plants that are more often
132 shared with the removed generalist plant. The previously described network included the whole island, but the experiment was performed in a smaller area (Fig 1). To assess the
134 influence of these two different scales, we compare the output of the clustering method, and its relationship with the experiment by analysing the network both at the regional (the whole
136 island), and at the local (experimental sites) scale.

138 **Materials and methods**

Characterization of the insect-plant visitation network

We performed this study in Reunion, a diversity hotspot located at 55°39’ E, 21°00’ S in the south-west of the Indian Ocean between Madagascar and Mauritius (Strasberg et al. 2005). A recent study on this island revealed that flowers are an important habitat for adult thrips, and that some thrips species are highly specialized on certain plant species (Dianzinga et al. 2020). Thrips is an insect order with 6.000 extant species described worldwide. Although thrips larvae feed on plants, fungi or on other insects, many species migrate to flowers as adults to feed on flower tissues and pollen, or to mate, with few species known as strict pollinators (Mound 2005). Thrips have short development times, and several generations per year, making them an ideal group to study multi-generational community dynamics, and to assess the timescale at which interaction rewiring may occur (CaraDonna et al. 2017). In our previous study we described the network of thrips visiting flowers by setting up in 2017 a total of 120 sites along seven elevational transects from 0 to 1600 m.a.s.l (Dianzinga et al. 2020). These transects run in winter and summer and covered the whole island. In each site we sampled flowers of several plant species, each during ten minutes with the beat-sheet technique. We identified collected insects using morphological characters that we further verified through molecular barcoding. We identified a total of 4279 individuals of 41 different thrips species collected from 106 plant species. Here, we use these insect assemblages to build insect-plant bipartite visitation networks based exclusively on winter data. We use winter samples because we conducted the flower-head removal experiment (see below) during this season, and because Dianzinga et al. (2020) revealed significant seasonal differences in insect diversity and community composition. To assess which plants are central, and whether such centrality depends on the scale at which the network is built, we applied the clustering method at two different scales including a regional scale that included the whole island, and a local scale that included the area where we performed the experiment - a subset of the regional network (Fig 1).

We assessed the clustering structure using the stochastic block model (SBM) with the R package sbm *(Chiquet et al. 2024)* coupled with a graph representation of the flower-thrips network using the R package igraph (Csardi et al. 2025). This method is currently the most reliable approach to infer groups in weighted networks, and is based on similarity in interaction patterns (Leger et al. 2015). Stochastic block models are also useful because they allow for a rearrangement of the matrix thus allowing the identification of clusters of species in a hierarchical manner (Fortunato 2010; Leger et al. 2014) that can be later plotted as a graph object. In SBMs inference is based on the maximization of the likelihood that is obtained through a Variational version of the Expectation- Maximization algorithm. Groups are then identified based on an iterative algorithm that selects the best model using the ICL

(penalized likelihood criterion) metric that penalises for an increasing number of groups (Leger et al. 2015; Chiquet et al. 2024). We used this approach to identify the best species to be used in the flower-head removal experiment.

To further understand which insect species are more likely to be impacted by the flower-head removal experiment, we estimated for the most abundant insect species found in the flower-head removal experiment, their degree of ecological specialization on plants. We used the Paired Difference Index following Poisot et al. (2011) because our network was quantitative. We implemented it with the function *specieslevel* in the Bipartite package (Dormann 2011). This metric ranges between 0 (perfect generalist) and 1 (perfect specialist). We also estimated for each species a species-level index of overlap (or sharedness) between treatment and focal plants. We estimated it as the proportion of individuals on a focal plant divided by the sum of individuals on both the focal and treatment plant. This metric ranges between 0 (all individuals on the treatment plant) and 1 (all individuals on the focal plant), a 0.5 value indicating a similar number of individuals on both plants.

Experimental removal of the central plant

Based on the results from the SBM analysis, which we present in the results section, we selected as treatment species (the plant from which we experimentally removed flowers) the central plant *S. mauritianum,* and as focal plants (those in which rewiring was assessed) *L. camara* and *I. indica*. By measuring changes in abundance through time, we assess how insect–plant visitation networks rewire, using shifts in relative abundances and species diversity as our metric. We selected the focal plants based on the fact that (1) they share a different number of insect species with the treatment plant, (2) they are exotic (and often invasive) and can be manipulated without ethical concerns, (3) they are very abundant and often co-ocur with the treatment plant. *S. mauritianum*, in particular, is very abundant and invasive, and is a central plant species in this system because it has large flowers that host the most abundant thrips assemblages (Dianzinga et al. 2020). Between August and September 2018, we established a total of 36 sites located at elevations between 200 and 1300 m.a.s.l in the municipalities of Entre-Deux and Le Tampon, both located in the south-central part of the island (Fig 1). This area was originally a semi-dry forest of sclerophyllous tree species that once covered the leeward western side of the island (Strasberg et al. 2005). This area was transformed by the early European colonization and is currently strongly altered by urbanization and agriculture, with remnants of natural vegetation. Despite these alterations, the current plant and insect communities likely represent long-term associations established since the sugar cane industry settled at the beginning of the 19th century. For instance, two

plant species used in the flower-head removal experiment were introduced in the island during early human colonisations: *L. camara* was introduced in 1840 as ornamental, and *S. mauritianum* likely via the Portuguese trade routes in the early 16th century (www.foretseche.re, www.cabi.org). We established experimental sites through visual selection of areas containing both *S. mauritianum* and either *L. camara* or *I. indica,* leading to a total of 20 *L. camara* and 16 *I. indica* sites. For each of the two focal plants, we selected sites in such a way that we could establish a spatial block design by pairing two similar nearby sites. Within each pair, we assigned control and treatment conditions at random, which determined whether we removed *S. mauritianum* flowers or not. We therefore had a total of 10 pairs (10 treatment and 10 control sites) for *L. camara*, and eight (8 treatment and 8 control sites) for *I. indica.* We used such a spatial block design to minimize habitat differences and distance between pairs, that allowed us to isolate the effects of environmental heterogeneity (such as species composition and landscape effects) from the impact of our experimental treatment. Sites were usually composed of large and isolated patches of 0.2 to 0.5 hectares of vegetation out of which at least one third of the aboveground biomass was composed of the plants of interest. Our treatment implied flower removal because flowers are the habitat for adult thrips. To emulate the loss of this resource, we experimentally removed all *S. mauritianum* flowers in treatment sites. We removed between 20 to 600 *S. mauritianum* flower heads per site and week. This design ensured that when we removed *S. mauritianum* flowers we were able to alter the dynamics of an isolated local population.

We aimed at assessing how removal of flowers of a generalist plant (the treatment species *S. mauritianum*) impacts insect communities on two other plants (the focal plants *L. camara* and *I. indica*) through time. These changes are likely to be different between focal plants because they share a different number of insect species with the treatment plant. Before any flower-removal treatment, we therefore described the initial insect assemblages in the different study sites on each of the studied plant species to compare them with the communities after the treatment. Once we removed flowers in treatment sites, and every week during three consecutive weeks we sampled insects on flowers of the two focal plants *L. camara* and *I. indica.* At each sampling event, we also removed from treatment sites any regrown *S. mauritianum* flower. The experiment thus lasted four weeks, encompassing several thrips generations given thrips' short generation times (Mound 2005). We collected insects using the beat-sheet technique and a mouth aspirator. Following the protocol by Dianzinga et al. (2020), we sampled each plant species during five minutes to standardize sampling effort. We considered the insects obtained from each site as an independent species assemblage.

Sampling was always carried out by the same two persons blocking for the focal plant species. Insect identification was carried out by the first author of the study.

Statistical analyses

We performed all statistical analyses with R software version 4.5.0. In the flower-head removal experiment, and for each sampling event and plant species, we estimated alpha diversity using abundance-based rarefaction methods to estimate Hill numbers (effective number of species) and to consider potentially undetected species (Chao and Jost 2012). We estimated species richness and evenness (i.e. Shannon index) as Hill numbers of order q = 0 and q = 2, respectively, using the *iNEXT* function from the package *iNEXT* (Hsieh et al. 2016). We tested the effect of the elimination of *S. mauritianum* flowers independently for each of the two focal species. We tested the impact of the flower-head removal on overall thrips abundance, species richness and evenness, on the abundance of each individual thrips species, and on thrips community composition. To test treatment effects on insect richness and evenness we built linear mixed-effects models with a Gaussian error distribution using the function *lmer* from the package *lme4* (Bates et al. 2015). In these models, response variables were changes relative to initial conditions in each site. For insect abundance (for each independent species and for overall thrips abundance), we built a generalized linear mixed-effects models with a Binomial error distribution using the function *glmer* from the package *lme4* (Pinheiro et al. 2020). In these models, the response variable was insect abundance during the three weeks after flower removal, relative to the initial densities in the same site. In all these models we included as fixed categorical predictor the treatment. To account for the spatial block design and the non-independence of the three repeated sampling events, we built a nested random intercept model by including as a random factor sampling event nested within pair identity. To prevent overdispersion in binomial models we also included an observational-level random factor. In Gaussian models, we assessed model fit by visual inspection of the residuals. In addition, we used the lmerControl and glmeControl functions with the optmizer *nloptwrap* from the package *nloptr* to improve model performance (Bates et al. 2015). We tested the effect of flower removal on thrips community composition during the three weeks after the treatment effect with the function *Adonis* from the package *vegan (Oksanen et al. 2020)*. Adonis is a method to partition sums of squares of multivariate data and is similar to a multivariate analysis of variance (MANOVA) (Anderson 2001). This function evaluates terms sequentially so a variable indicating the three sampling events (i.e. three weeks) was added as first term followed by the treatment term. We assessed the significance of these using a

permutation analysis (9999 repetitions). To plot the results, for each species and focal plant we extracted the effect of the treatment as the estimate of the mixed-effects models.

Results

Clustering of species in the regional and local network

The stochastic block model (SBM) clustering method applied to the regional network determined seven plant clusters (Fig 2). *S. mauritianum* was a central plant in the network that strongly interacted with many species (Fig 2 and 3A; Table 1), and hosted abundant communities of insects, particularly the endemic thrips *Thrips bourbonensis.* This thrips was also found on the focal plants studied in the flower-head removal experiment. This species was particularly abundant on *L. camara*, but we only sampled one individual on *I. indica. S. mauritianum* flowers often hosted the insect *Frankliniella schultzei* morphotype 1, which was particularly abundant on *I. indica* too. The thrips *Haplothrips gowdeyi* was common on *L. camara,* but had low abundances on *S. mauritianum* and *I. indica*. The thrips *Frankliniella occidentalis* was quite common in the flower-head removal experiment (see below), albeit relatively rare in the regional network studied one year before. *S. mauritianum* shared several insect species with the endemic plant *Dombeya ficulnea* and the recently-described endemic thrips *Thrips reunionensis* (Goldarazena et al. 2020). The interaction matrix shows that *S. mauritianum* shares a large number of insect species with both *L. camara* than with *I. indica.* The slightly closer distance between *S. mauritianum* and *L. camara* in the graph representation, suggests that insect communities on these two plant species are likely more similar to each other than to those on *I. indica.* The cluster where *L. camara* is placed, also includes the plant *Hedychium gardnerianum* both with strong interactions with the insects *T. bourbonensis, H. gowdeyi, Haplothrips articulosus, Megalurothrips sjostedti* and *Thrips candidus. I. indica* is located in an independent cluster that strongly interacts with the thrips *F. schultzei.* The generalist plant *S. mauritianum* and the two focal plants thus belong to different clusters, but even in different clusters they share several insects. Based on the bipartite network, the two insect species most likely to be negatively impacted by removal of the treatment plant *S. mauritianum* are *F. schultzei* and *H. gowdeyi.* The main reasons are that they are very abundant, and they have species-level overlap indexes that are often close to 0.5 (Table 1). For all main thrips species found in the flower-head removal experiment, the Paired Difference Index (PDI) was always close to one, which suggests that these species are highly specialised. With a PDI index of 0.96, and as can be seen in Figure 3A, *H. gowdeyi* is the most generalist species. The clustering method applied to the local network (i.e. the area where the flower-head removal experiment was performed, Fig 1) reveals similar clusters (Fig 2). The

main difference with the regional network is that in the local network the plant *D. ficculnea*, and its associated thrips disappear because these two species are mostly present at higher elevations. Based on the clustering structure of the local network, species abundances and the species-level overlap index, the insect species *H. gowdeyi* is the most likely to be impacted by removal of *S. mauritianum* flowers, particularly on the focal plant *L. camara* (Table 1).

Description of the thrips community during the flower-head removal experiment

Before removing *S. mauritianum* flowers, we collected a total of nine flower-visiting thrips species from our experimental plant species: nine on *S. mauritianum,* six on *L. camara*, and four on *I. indica* (Fig 3B, 3C and ESM-3). Before the flower-head removal treatment, most thrips species were shared between plant species, except for *Thrips quilici, Thrips palmi* and *Thrips tabaci* that were exclusively found on *S. mauritianum*. We only found *T. palmi* at the beginning of the experiment but not in subsequent sampling events, and we collected *T. quilici* and *T. tabaci* in small numbers after the first week of flower removal, the former on *L. camara,* and the latter on both *L. camara* and *I. indica*. We found *Thrips parvispinus* at the beginning of the experiment (first week) on both *S. mauritianum* and *L. camara* but not in subsequent sampling events. Finally, we only found *Megalurothrips sjostedti* once on *I. indica* during the third sampling event. The rest of the species were much more abundant and persisted throughout the four weeks of the experiment. In the plant pair including *S. mauritianum* and *I. indica* common species were *Frankliniella occidentalis* and *F. schultzei* (Fig 3B). In the pair including *S. mauritianum* and *L. camara,* common species were *F. occidentalis, Haplothrips gowdeyi, Thrips bourbonensis* and *Hercinothrips patersonii* (Fig 3C).

Effect of flower-head removal on thrips diversity, abundance and composition

After removal of *S. mauritianum* flowers, we assessed thrips abundance, diversity and community composition during the following three weeks, and compared them to initial densities at the same site. Elimination of *S. mauritianum* flowers significantly affected the abundance of one of the two thrips species studied on *I. indica,* and of two of the four studied on *L. camara* (Fig 4) thus revealing interaction strength rewiring. Elimination of *S. mauritianum* flowers increased the abundance of *F. occidentalis* on *I. indica* (χ^2=9.24, d.f.=1,43, *P*=0.0023), but decreased it on *L. camara* ($\chi^2_{1,55}$=5.00, d.f.=1,55, *P*=0.0253). The treatment also increased the abundance of *H. patersonii* on *L. camara* (χ^2=13.67, d.f.=1,55, *P*=0.0002). The treatment did not significantly alter the densities of *F. schultzei* on *I. indica* (χ^2=0.07, d.f.=1,43, *P*=0.7858), or of either *H. gowdeyi* (χ^2=0.01, d.f.=1,55, *P*=0.9254) or

348 *T. bourbonensis* (χ^2=0.09, d.f.=1,55, *P*=0.7519) on *L. camara*. As shown by flat lines through time in almost all replicates, for some species like *F. occidentalis* and *H. patersonii* rewiring
350 was very consistent because it occurred quickly after the first flower-head removal experiment and persisted over the three weeks of the experiment.

352 Despite these differences, and as shown in Figure 5, on both *I. indica* and *L. camara*, the flower-head removal did not affect thrips total abundance (*I. indica*: χ^2 =0.62, d.f.=1,43,
354 *P*=0.4299; *L. camara*: χ^2=0.14, d.f.=1,55, *P*=0.7082), species evenness (*I. indica*: χ^2=0.67, d.f.=1,43, *P*=0.4123; *L. camara*: χ^2=0.58, d.f.=1,55, *P*=0.4453), species richness (*I. indica*:
356 χ^2=2.22, d.f.=1,43, *P*=0.1361; *L. camara*: χ^2=0.40, d.f.=1,55, *P*=0.5244) or species community composition (*I. indica*: *F*=0.39, d.f.=1,44, *P*=0.8981; *L. camara*: *F*=1.01, d.f.=1,55,
358 *P*=0.4106).

360 **Discussion**

In this study we tested the hypothesis that in a network of flower-visiting insects,
362 experimental removal of the central and highly-connected resource plant *S. mauritianum* would affect the diversity and abundance of insects on two other plants *I. indica* and
364 *L. camara*, potentially triggering insect extinctions and community rewiring. We coupled this knockout experiment with a well-defined visitation network that allowed us to delimit clusters
366 of highly interacting species, and to design the experiment in a way that removal of flowers of the central plant would have the largest effect possible on insect assemblages on the two other
368 plants. The network analysis revealed that the removed species *S. mauritianum* was central because it hosted the largest abundance and diversity of insects, which were shared with many
370 other plant species. This network also allowed us to predict which insects were likely to be more impacted by the flower-head removal experiment based on the amount of individuals
372 shared among focal and the treatment plants, and their degree of specialisation. We worked with thrips, an insect order that relative to other flower-visiting groups like flies, lepidopterans
374 and bees, has been little studied. Even if many thrips species are known to be efficient flyers and strict pollinators (Mound 2005), the dispersal and pollination capabilities of many species
376 are still not well understood. This group of minute insects, however, is well suited for the study of the dynamics of flower-inhabiting insects because most species have short generation
378 times, and flowers are an important habitat for them. In addition, there are both generalist and specialist species. In our study, extreme examples of specailisation are *T. bourbonenesis* and
380 *F. occidentalis*. The former is a Reunion endemic that mostly colonises flowers of the endemic plant *D. ficulnea* (Mound 2005; Goldarazena et al. 2020; Dianzinga et al. 2020), but also the
382 invasive *S. mauritianum.* The later is considered as polyphagous, and often reported as a pest.

Such a gradient of specialisation is important to monitor knock-on effects in eroded networks: specialists are more likely to go extinct while generalists may be better suited at allowing rewiring, and connecting the whole community (Futuyma and Moreno 1988; Devictor et al. 2010; Ramos-Jiliberto et al. 2012; Valdovinos et al. 2013; Brodie et al. 2014). In our study, removal of flowers of the plant *S. mauritianum* triggered dramatic changes in the abundance of some of the most abundant insect species, but not in the direction that we anticipated. We expected the thrips *F. schultzei* and *T. bourbonensis* to be among the most strongly affected by the treatment, but they were unaffected by it. The species *F. occidentalis,* however, responded to the treatment on both *L. camara* and *I. indica* plants (even if in different directions), and *H. pattersoni* only on *L. camara*. The observed changes could simply reflect a collapse of insect communities after the loss of an important floral resource, but frequency-based rewiring or interaction readjustment at the community level is more likely. First, because we monitored several insect generations so that the observed changes were likely driven by shifts in species dynamics and adult recruitment within the studied network. Second, because flower removal did not trigger a significant decrease in insect richness, evenness, or total abundance. Instead, some species decreased in abundance, while some others increased. A clear example of such effect is the thrips *F. occidentalis* that decreased in abundance in one plant, while increasing on another (a result that we discuss below). Frequency-based rewiring or interaction readjustment within the studied ecological network thus buffered changes in species composition or diversity, as many previous studies have shown (Kondoh 2003, Staniczenko et al. 2010, Valdovinos et al. 2010, 2013, Thierry et al. 2011, Ramos-Jiliberto et al. 2012, Sanders et al. 2018, Sheykhali et al. 2020). The weak community-wide impact of the flower-head removal treatment, may also reflect that even if the studied plants share many insects, most species are highly specialised, and plants belong to independent clusters or communities. This conditions may imply that extinctions were contained within the cluster. To confirm this hypothesis, it would be interesting to perform a flower-head removal experiment comparing plants that are either located in the same network cluster, or not. Since our study assessed the flower-head removal experiment on only two plant species, future studies examining the dynamics across the full network would provide a deeper understanding of the mechanisms driving changes in species density.

There are many features determining how knock-on effects are transmitted through ecological networks (Dunne 2006; Bascompte and Jordano 2007). For instance, network nestedness increases robustness in mutualistic networks because many interactions are redundant, and abundant generalist species (i.e. species that link the whole network) can buffer the loss of specialist ones (Olesen et al. 2007; Thébault and Fontaine 2010; Stouffer and

418 Bascompte 2011). It is likely that this was the case in our study because even if the main thrips species found in the flower-head removal experiment were highly specialised, the three plant
420 species we worked with were found in a highly entangled part of the network. We observed that the flower-head removal experiment decreased the abundance of the thrips *F. occidentalis*
422 on one plant, but it increased its density on another. The increased density was an unexpected output of our treatment because removal of resources (and plants in particular) usually triggers
424 reductions in abundance and diversity of herbivores and pollinators [e.g. (Lopezaraiza–Mikel et al. 2007; Biella et al. 2019, 2020)]. Yet, this observation provides evidence for the effect
426 that Gilljam et al. (2015) reported by implementing a knockout extinction model. This report demonstrated that species loss and subsequent rewiring can lead to species switching to
428 available resources, an indirect phenomenon that can even trigger the extinction of resource species when they become overexploited. In a situation where *S. mauritianum* would become
430 extinct, or intentionally removed [this species is an important invasive plant in some tropical areas (Cowie et al. 2018)] it is thus possible that other plant species would experience
432 increased insect densities with potential effects on insect-plant visitation networks and pollination output (Artamendi et al. 2025). Even if the density changes observed may seem
434 subtle, they are likely to change insect encounters with conspecifics and impair mating opportunities. These changes can also modulate competitive interactions for the pollen
436 resource, and indirectly plant fitness if different flower-associated species vary in their ability to pollinate (e.g. Brosi and Briggs 2013).

438 Theoretical advances in network ecology are increasing our ability to predict knock-on effects of extinctions in networks (Paine 1966; Dunne et al. 2002; Memmott et al. 2004; Pires
440 et al. 2020; Kehoe et al. 2020), but experimental approaches to validate theory are needed to better understand diversity loss and global insect decline. In a recent example Bartomeus et al.
442 (2021) manipulated a community composed of three plants and three pollinators, and parameterized a theoretical model with experimental data. This study reported that removal of
444 a bumblebee-plant interaction triggered the extinction of a plant species in the network, which revealed how the complex interactions found in plant-pollinator networks are important to
446 understand species persistence. These types of integrative approaches are very powerful to test hypotheses into the precise mechanisms operating after the loss of a species or an interaction.
448 In the study by Bartomeus et al. (2021) the interaction manipulated was a strict mutualism in which both partners (the plant and the pollinator) are interdependent for survival. In our study,
450 whether thrips pollinate plants, act as pollen robbers, or feed on plant tissues is a question that needs to be elucidated. The intimacy of the interaction may therefore be important to

452 determine how removal of a node in a network is likely to impact other distantly-related species in the network.

454 We report a case of rewiring of interaction strengths that we measured as changes in species relative abundances in a very diverse tropical community with concomitant buffering 456 consequences for species extinctions, and diversity decline. Such rewiring occurred quickly following the removal of the focal plant, which evidences the efficiency of rewiring in 458 buffering the loss of important resources. As mentioned above, in our system whether the flower-inhabiting insects act as pollinators, or antagonistic herbivores, remains to be fully 460 understood. If purely pollinating, our study would provide evidence of the importance of rewiring in preventing the loss of plant reproductive output, with likely consequences for the 462 composition of plant communities (Brosi and Briggs 2013; Bartomeus et al. 2021; Artamendi et al. 2025). By coupling the experiment with a network analysis, we also show how recent 464 analytical techniques can help understanding the resilience of bipartite systems to cascading extinctions. We used a regional network spanning the whole Reunion island, and compared 466 that to a local network limited to the area where we performed the experiment. Although the local network clearly had fewer species, its interactions and clusters remained largely 468 unchanged. The clustering method thus proves robust in delimiting insect-plant communities, and our results are likely generalizable to other areas of the island, or to similar low-elevation 470 tropical ecosystems. Since many thrips species like *F. occidentalis* are pests, such generalisations may provide novel information into how changes in plant communities can 472 trigger outbreaks of problematic thrips species in agricultural habitats. Our study can also help to better understand the decline in diversity and abundance of insects (Hallmann et al. 2017; 474 Seibold et al. 2019; Montgomery et al. 2020; Wagner 2020). Habitat loss due to urbanization, intensive livestock production or mining usually deprive ecosystems from plants, whereas 476 agriculture usually leads to habitats dominated by few species. In these different scenarios, declines of insect herbivores are usually a direct consequence of deep changes in natural plant 478 communities (Schleuning et al. 2016; Kehoe et al. 2020). Insect extinctions, however, are often driven by more subtle effects, for example through the degradation or loss of critical 480 resources needed for species to persist (Samways et al. 2010). Our experiment shows that these subtle effects may be the loss of a single plant species in an ecosystem, but arrival of a 482 new invasive plant or loss of a single insect species may have similar consequences.

484 **Conflict of interests**

We declare no conflict of interests. The funders had no role in study design, data acquisition or 486 analysis, and any further steps in the publication process.

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Author contributions

KT and EF conceived the idea and designed the study. KT and M-LM performed the experiment. NTD, M-LM and EF built the interaction web. KT and NTD identified the insects. KT and EF analysed data. KT, DS, KPM and EF wrote the manuscript with input from all authors.

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Figure 1. Map of Reunion island with solid dots representing sites where we sampled insects to build the regional bipartite network. The size of the dot is relative to the amount of insects sampled in each site. Contour lines represent clines of 500m of elevation. The rectangular inset limits the sites used to build the local web. Inside this rectangle the two empty circles show the two areas where we performed the flower-head removal experiment.

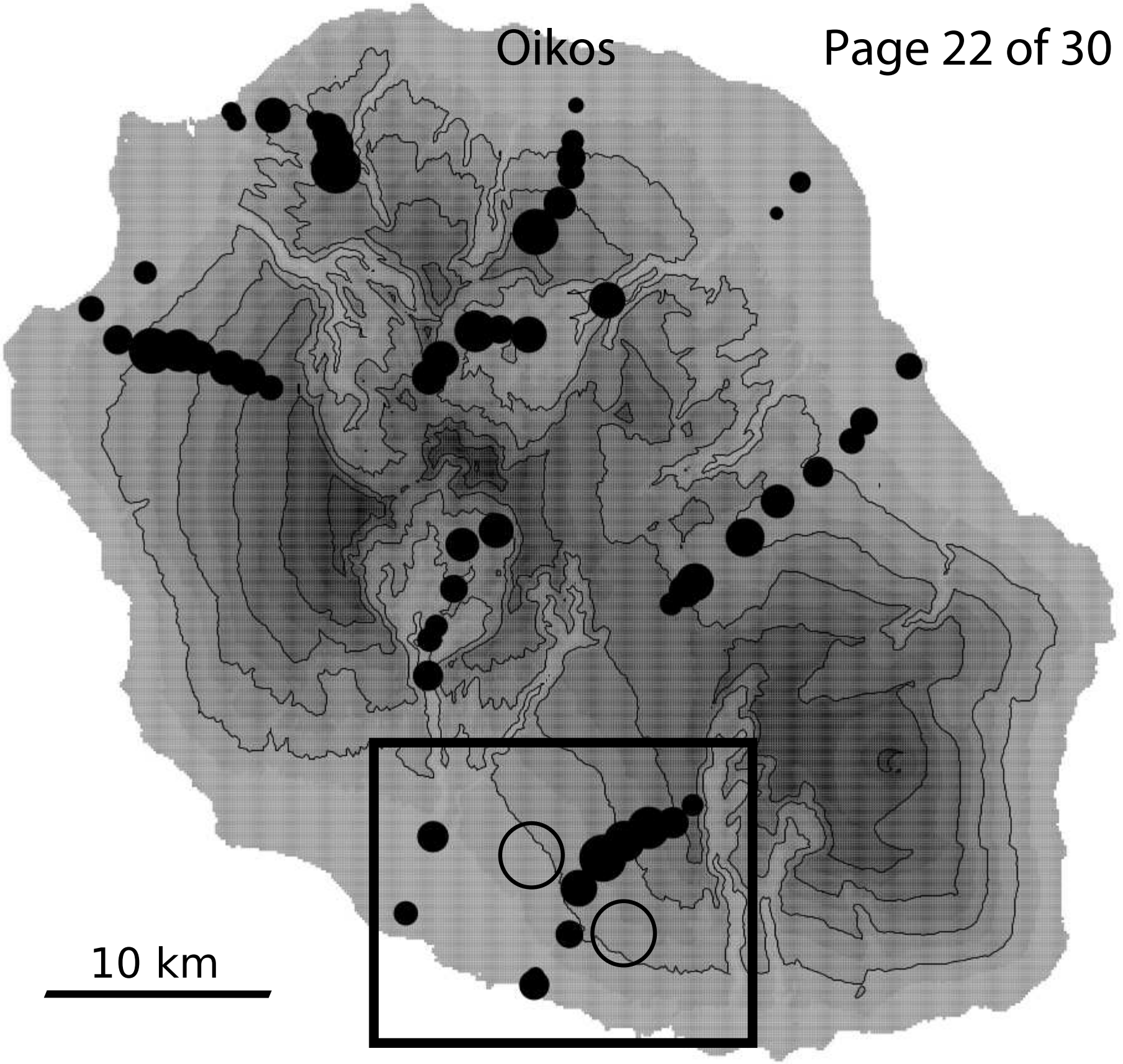
Figure 2. Representation of regional (top) and local (bottom) networks clustered with the stochastic block model (SBM). A and C. Interaction matrix with plants as columns, and insects as rows. The intensity of the gray coulor in the square is proportional to interaction strength (i.e. number of interactions reported). Clusters determined by the SBM clustering method are delimited with vertical and horizontal black lines. The insect *Frankliniella occidentalis* is highlighted in blue as this species was unexpectedly impacted in the flower-head removal experiment. B and D. Graph representation of the bipartite network with plants as nodes coloured as the clusters delimited by the SBM algorithm, and connections representing shared insect species. Plants located at the centre of the graph share a large proportion of species with other plants. Distance among species positively relates with the number of shared species. Species abbreviations can be found in ESM-1 and ESM-2.

Figure 3. Quantitative bipartite flower-visiting networks between plants and thrips in the regional network and in the flower-head removal experiment. The length of the bars (plants at the bottom and insects on top) and the polygons connecting them are relative to the abundances of insects on plants. A. Regional network. Coloured plants are those that we selected for the flower-head removal experiment. Insects that we found in the experiment are also coloured, and have horizontal labels. B and C. Network of insect species that we found in the flower-head removal experiment before removal of *Solanum mauritianum* flowers, in sites with either *Ipomea indica* (B), or *Lantana camara* (C). Colours of the different species are the same in all three networks. Species that we found in the experiment are abbreviated as follows (see the full list of abbreviations in the ESM-1 and ESM-2): *Solanum mauritianum* (SolMau), *Ipomea indica* (IpoInd), *Lantana camara* (LanCam), *Frankliniella occidentalis* (FraOcc), *F. schultzei* (FraSch), *Haplothrips gowdeyi* (HapGow), *Hercinothrips pattersoni* (HerPat), *Thrips bourbonensis* (ThrBou), *T. palmi* (ThrPal), *T. parvispinus* (ThrPar), *T. quilicii* (ThrQui) and *T. tabaci* (ThrTab).

Figure 4. Effect of *Solanum mauritianum* removal on the abundance of the most abundant thrips species: *Frankliniella occidentalis, F. schultzei, Haplothrips gowdeyi, Thrips bourbonensis* and *Hercinothrips patersonii* on *Ipomea indica* and *Lantana camara* plants. Top panels represent overall treatment effects. Light grey dots represent model partial residuals averaged per study site (i.e. a single point per site is shown instead of one per sampling event) jittered along abscissa. Mean (±SE) of these points are represented in black. We calculated partial residuals with the *visreg* package in R and show unexplained variation in the data associated with the plant removal treatment after accounting for other sources of variation in the models including random effects. We also provide significance of effects associated with the generalized mixed-effects models used to test the hypothesis that *S. mauritianum* removal will lead to differences in abundance. Bottom panels show the effect observed at each study site through time. Black lines represent model predicted values from control sites and grey ones from treatment sites. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; n.s.: non-significant.

Figure 5. Effect of *Solanum mauritianum* removal on thrips species richness, evenness and total abundance on *Ipomea indica* and *Lantana camara* plants. Light grey dots represent model partial residuals averaged per study site (i.e. a single point per site is shown instead of one per sampling event) jittered along abscissa. Mean (±SE) of these points are represented in black. Partial residuals were calculated with the *visreg* package in R and show unexplained variation in the data associated with the plant removal treatment after accounting for other sources of variation in the models including random effects. We also provide significance of effects associated with the generalized mixed-effects models used to test the hypothesis that *S. mauritianum* removal will lead to differences in richness, evenness and abundance. n.s. non significant p-value.

Table 1. Table showing for each of the most abunndant thrips species found in the flower-head removal experiment, information extracted from both the regional and local network including: specialisation (measured as the Paired Difference Index), total insect abundance in the whole network, abundance on *Solanum mauritianum, Ipomea indica,* and *Lantana camara* plants, and the species-level overlap index (between the tretment plant *S. mauritianum* and either *I. indica* or *L. camara*).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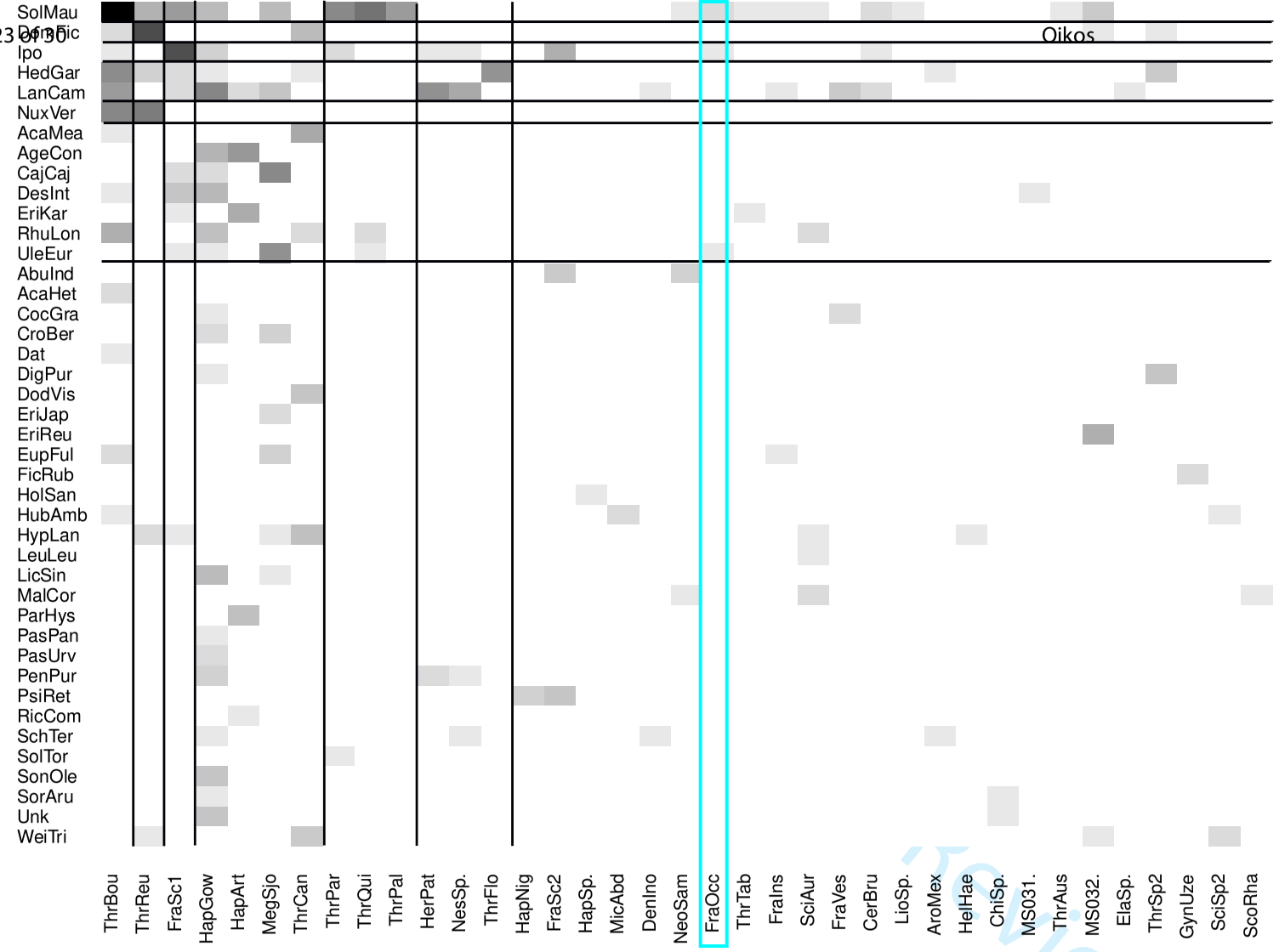
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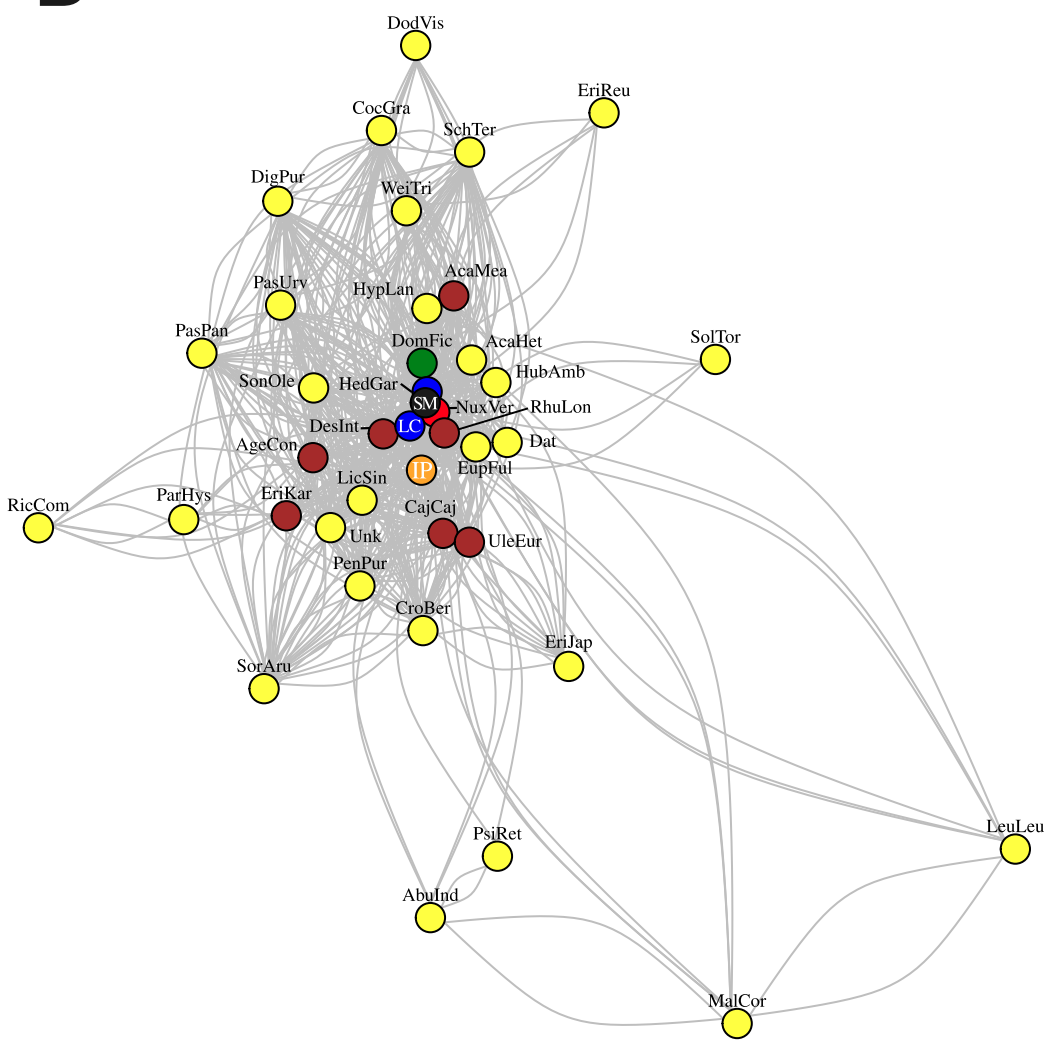
UleEur
AbuInd
AcaHet
CocGra
CroBer
Dat
DigPur
DodVis
EriJap
EriReu
EupFul
FicRub
HolSan
HubAmb
HypLan
LeuLeu
LicSin
MalCor
ParHys
PasPan
PasUrv
PenPur
PsiRet
RicCom
SchTer
SolTor
SonOle
SorAru
Unk
WeiTri
ThrBou
ThrReu
FraSc1
HapGow
HapArt
MegSjo
ThrCan
ThrPar
ThrQui
ThrPal
HerPat
NesSp.
ThrFlo
HapNig
FraSc2
HapSp.
MicAbd
DenIno
NeoSam
FraOcc
ThrTab
FraIns
SciAur
FraVes
CerBru
LioSp.
AroMex
HelHae
ChiSp.
MS031.
ThrAus
MS032.
ElaSp.
ThrSp2
GynUze
SciSp2
ScoRha

B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HubAmb
SonOle
HedGar
SM
NuxVer
RhuLon
DesInt
LC
AgeCon
Dat
EupFul
IP
LicSin
RicCom
ParHys
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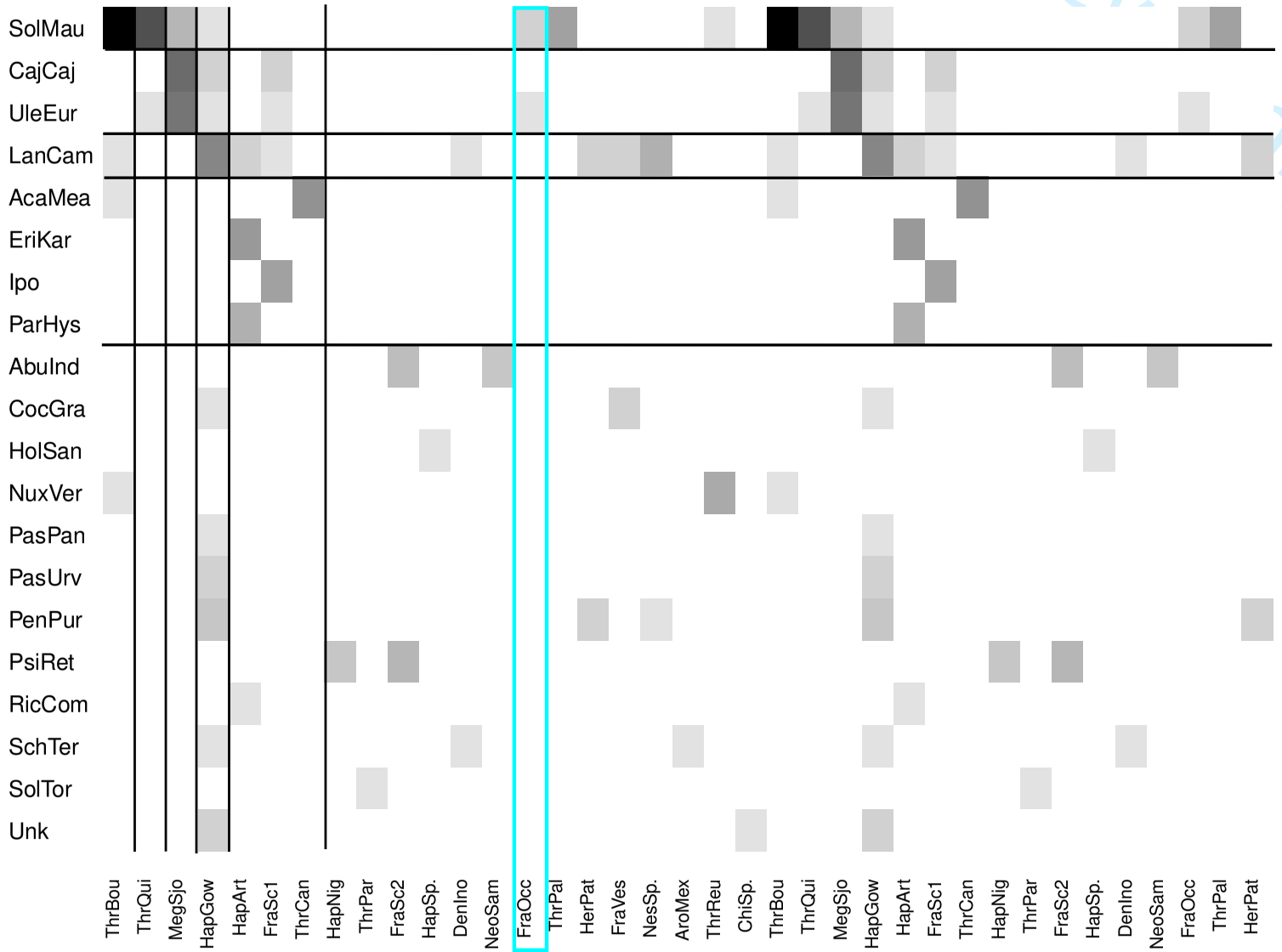
AbuInd
MalCor

C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PasUrv
PenPur
PsiRet
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SchTer
SolTor
Unk
ThrBou
ThrQui
MegSjo
HapGow
HapArt
FraSc1
ThrCan
HapNig
ThrPar
FraSc2
HapSp.
DenIno
NeoSam
FraOcc
ThrPal
HerPat
FraVes
NesSp.
AroMex
ThrReu
ChiSp.
ThrBou
ThrQui
MegSjo
HapGow
HapArt
FraSc1
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ThrPar
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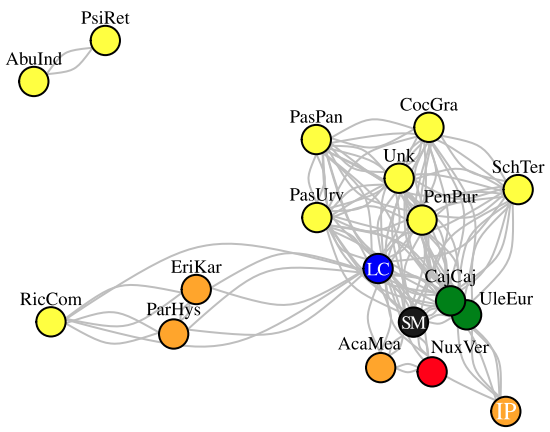
HapSp.
DenIno
NeoSam
FraOcc
ThrPal
HerPat

D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SM
AcaMea
NuxVer
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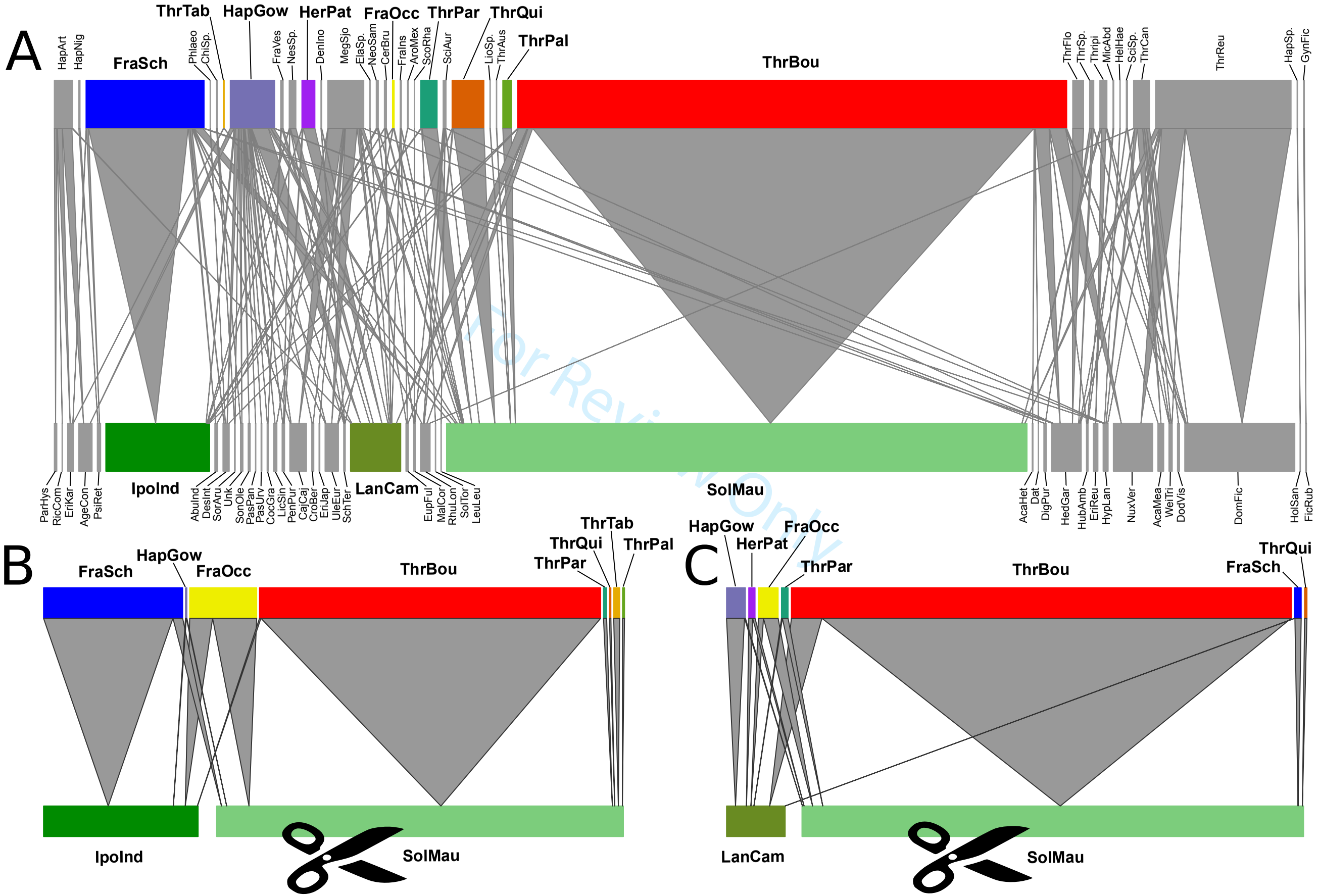
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ChiSp.
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NesSp.
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ElaSp.
NeoSam
CerBru
FraOcc
FraIns
AroMex
ScoRha
ThrPar
SciAur
LioSp.
ThrAus
ThrQui
ThrPal
ThrBou
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ThrSp.
Thripi
MicAbd
HelHae
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GynFic
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RicCom
EriKar
AgeCon
PsiRet
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DesInt
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LeuLeu
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AcaHet
Dat
DigPur
HedGar
HubAmb
EriReu
HypLan
NuxVer
AcaMea
WelTri
DodVis
DomFic
HolSan
FicRub
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HapGow
FraOcc
ThrBou
ThrPar
ThrQui
ThrTab
ThrPal
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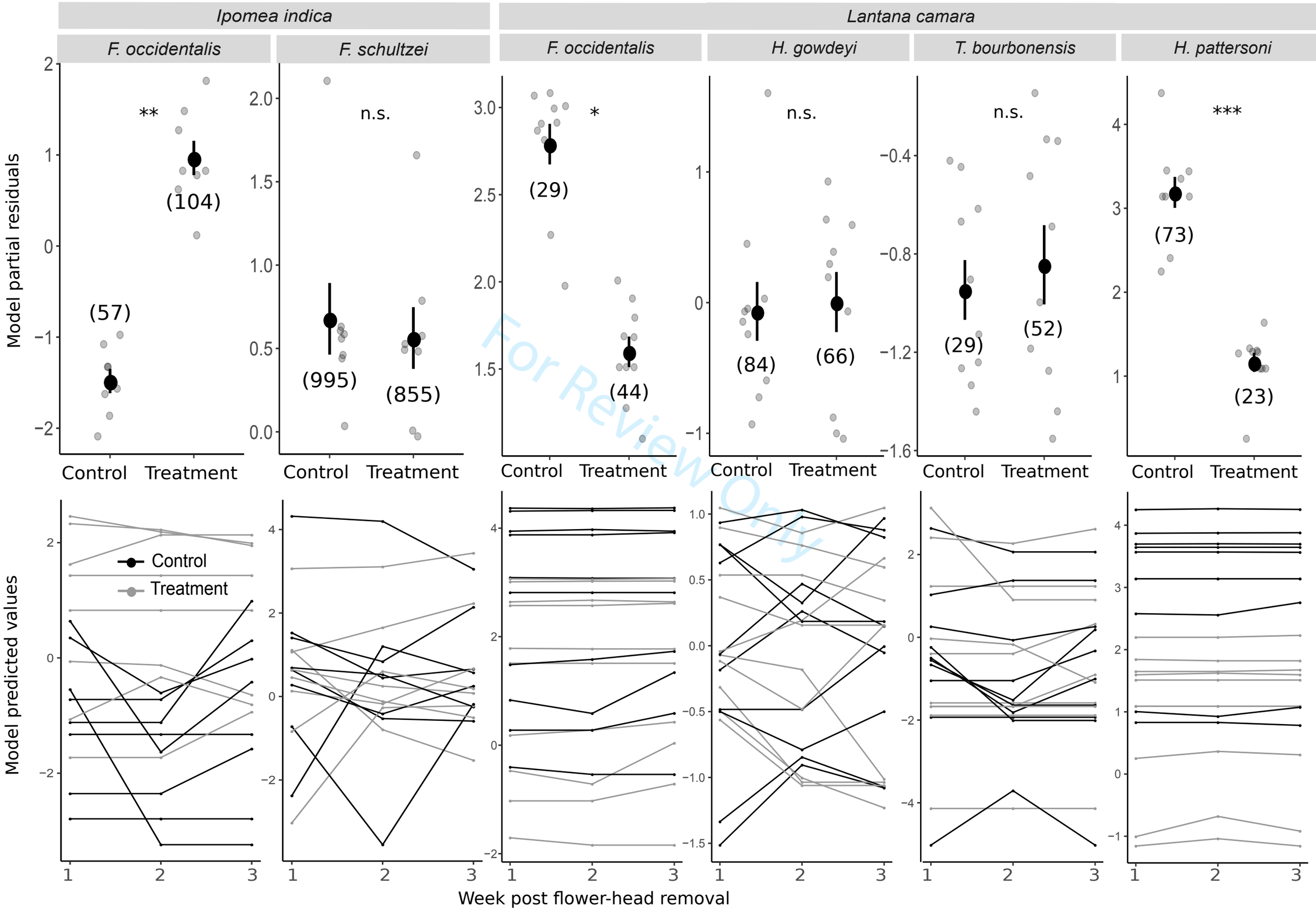

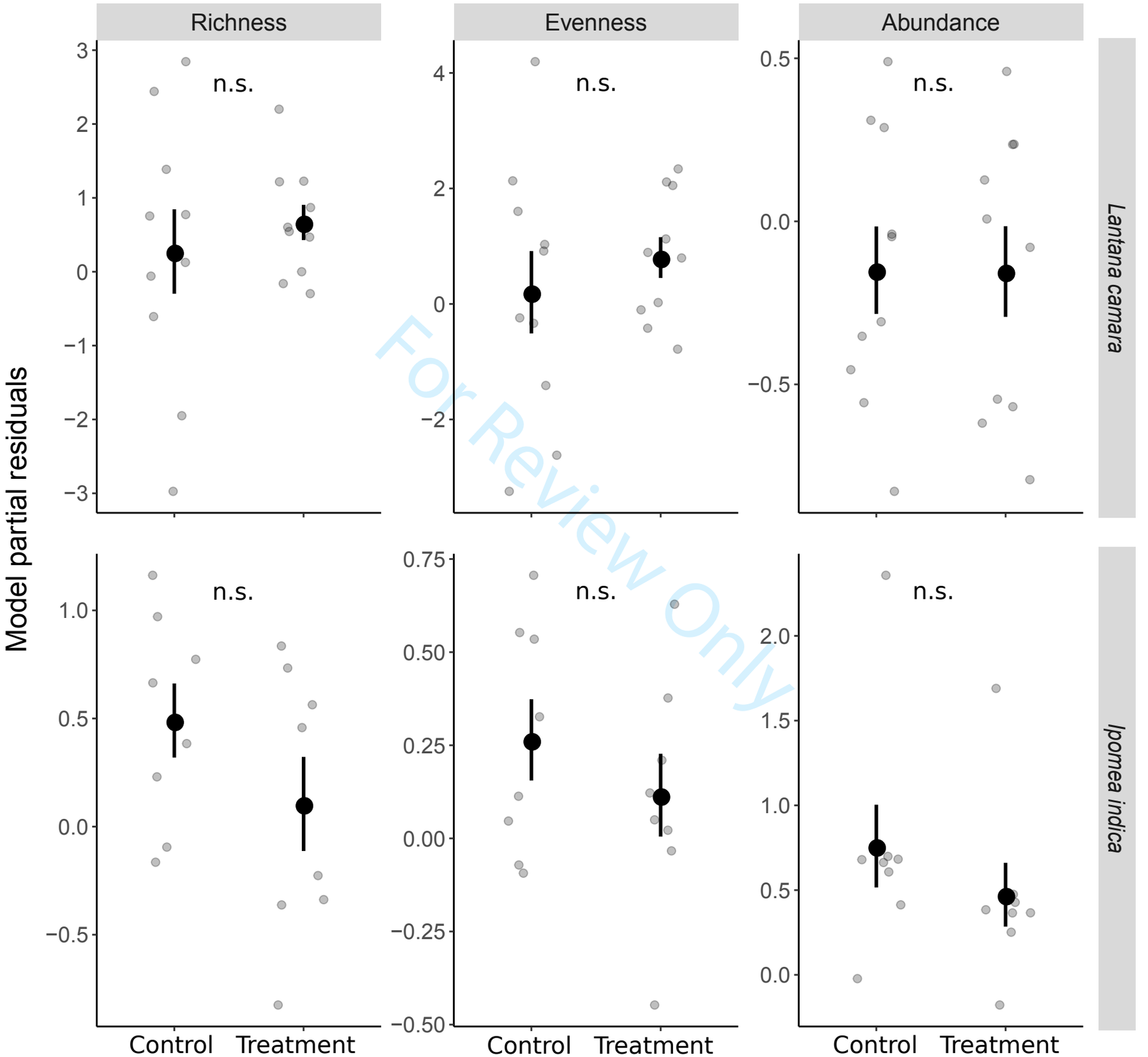

Table 1

	Frankliniella occidentalis	*Frankliniella schultzei*	*Haplothrips gowdeyi*	*Thrips bourbonensis*	*Hercinothrips patersonii*
Regional network					
Specialisation (Paired Difference Index)	0.976	0.996	0.960	0.998	0.997
Total abundance on Solanum mauritianum	2	21	7	1198	0
Total abundance on Ipomea indica	1	227	3	1	1
Total abundance on Lantana camara	0	2	40	21	28
Species-level overlap (I. Indica)	0.333	0.915	0.300	0.001	1.000
Species-level overlap (L. camara)	0.000	0.087	0.851	0.017	1.000
Total abundance in regional network	4	262	106	1312	31
Local network					
Specialisation (Paired Difference Index)	0.974	0.977	0.959	0.999	0.947
Total abundance on Solanum mauritianum	2	0	1	276	0
Total abundance on Ipomea indica	0	9	0	0	0
Total abundance on Lantana camara	0	1	18	1	2
Species-level overlap (I. Indica)	0.000	1.000	0.000	0.000	0.000
Species-level overlap (L. camara)	0.000	1.000	0.947	0.004	1.000
Total abundance in local network	3	13	32	279	4

Figure and table legends

ESM-1. Abbreviations of the plant species found in Figure 2 and 3, and the family they belong to.

ESM-2. Abbreviations of the thrips species found in Figure 2 and 3, and the sub-order they belong to.

ESM-3. Table showing raw insect counts on the four sampling events. Species abbreviations can be found in ESM-1 and ESM-2.

ESM-1

Family	**Genus**	**Species**	**Abbreviation**
Malvaceae	*Abutilon*	*indicum*	AbuInd
Fabaceae	*Acacia*	*heterophylla*	AcaHet
Fabaceae	*Acacia*	*meanrsii*	AcaMea
Asteraceae	*Ageratum*	*conyzoides*	AgeCon
Fabaceae	*Cajanus*	*cajan*	CajCaj
Cucurbitaceae	*Coccinia*	*grandis*	CocGra
Fabaceae	*Crotalaria*	*berteroana*	CroBer
Solanaceae	*Datura*	sp.	Dat
Fabaceae	*Desmodium*	*intortum*	DesInt
Plantaginaceae	*Digitalis*	*purpurea*	DigPur
Sapindaceae	*Dodonaea*	*viscosa*	DodVis
Malvaceae	*Dombeya*	*ficulnea*	DomFic
Ericaceae	*Erica*	*reunionensis*	EriReu
Asteraceae	*Erigeron*	*karvinskianus*	EriKar
Rosaceae	*Eriobotrya*	*japonica*	EriJap
Euphorbiaceae	*Euphorbia*	*fulgens*	EupFul
Moraceae	*Ficus*	*rubra*	FicRub
Zingiberaceae	*Hedychium*	*gardnerianum*	HedGar
Lamiaceae	*Holmskioldia*	*sanguinea*	HolSan
Asteraceae	*Hubertia*	*ambavilla*	HubAmb
Hypericaceae	*Hypericum*	*lanceolatum*	HypLan
Convolvulaceae	*Ipomoea*	indica	IpoInd
Verbenaceae	*Lantana*	*camara*	LanCam
Fabaceae	*Leucaena*	*leucocephala*	LeuLeu
Sapindaceae	*Licthi*	*sinensis*	LicSin
Malvaceae	*Malvastrum*	*coromandelianum*	MalCor
Stilbaceae	*Nuxia*	*verticillata*	NuxVer
Asteraceae	*Parthenium*	*hysterophorus*	ParHys
Poaceae	*Paspalum*	*urvillei*	PasUrv
Poaceae	*Paspalum*	*paniculum*	PasPan
Poaceae	*Pennisetum*	*purpureum*	PenPur
Asteraceae	*Psiadia*	*retusa*	PsiRet
Anacardiaceae	*Rhus*	*longipes*	RhuLon
Euphorbiaceae	*Ricinus*	*communis*	RicCom
Anacardiaceae	*Schinus*	*terebinthifolia*	SchTer
Solanaceae	*Solanum*	*mauritianum*	SolMau
Solanaceae	*Solanum*	*torvum*	SolTor
Asteraceae	*Sonchus*	*oleraceus*	SonOle
Poaceae	*Sorghum*	*arundinaceum*	SorAru
Fabaceae	*Ulex*	*europaeus*	UleEur
Cunoniaceae	*Weinmannia*	*trinctoria*	WeiTri

ESM-2

Sub-order	**Genus**	**Species**	**Abbreviation**
Terebrantia	*Arorathrips*	*mexicanus*	AroMex
Terebrantia	*Ceratothripoides*	*brunneus*	CerBru
Tubulifera	*Chirothrips*	sp.	ChiSp.
Terebrantia	*Dendrothripoides*	*innoxius*	DenInn
Tubulifera	*Elaphothrips*	sp.	ElaSp.
Terebrantia	*Frankliniella*	*insularis*	FraIns
Terebrantia	*Frankliniella*	*occidentalis*	FraOcc
Terebrantia	*Frankliniella*	*schultzei*	FraSch
Terebrantia	*Franklinothrips*	*vespiformis*	FraVes
Tubulifera	*Gynaikothrips*	*ficorum*	GynFic
Tubulifera	*Haplothrips*	*articulosus*	HapArt
Tubulifera	*Haplothrips*	*gowdeyi*	HapGow
Tubulifera	*Haplothrips*	*nigricornis*	HapNig
Tubulifera	*Haplothrips*	sp.	HapSp.
Terebrantia	*Heliothrips*	*haemorrhoidalis*	HelHae
Terebrantia	*Hercinothrips*	*pattersoni*	HerPat
Tubulifera	*Liothrips*	sp.	LioSp.
Terebrantia	*Megalurothrips*	*sjostedti*	MegSjo
Terebrantia	*Microcephalothrips*	*abdominalis*	MicAbd
Terebrantia	*Neohydatothrips*	*samayunkur*	NeoSam
Tubulifera	*Nesothrips*	sp.	NesSp.
Terebrantia	*Scirtothrips*	*aurantii*	SciAur
Terebrantia	*Scirtothrips*	sp.	SciSp.
Terebrantia	*Scolothrips*	*rhagebianus*	ScoRha
Terebrantia	*Thrips*	*australis*	ThrAus
Terebrantia	*Thrips*	*bourbonensis*	ThrBou
Terebrantia	*Thrips*	*candidus*	ThrCan
Terebrantia	*Thrips*	*florum*	ThrFlo
Terebrantia	*Thrips*	*palmi*	ThrPal
Terebrantia	*Thrips*	*parvispinus*	ThrPar
Terebrantia	*Thrips*	*quilicii*	ThrQui
Terebrantia	*Thrips*	*reunionensis*	ThrReu
Terebrantia	*Thrips*	sp.	ThrSp.
Terebrantia	*Thrips*	*tabaci*	ThrTab
Tubulifera	Phlaeothripinea	sp.	Phlaeo
Terebrantia	Thripinae	sp.	Thripi

ESM-3

Plant	Week	Treatment	HapGow	ThrPar	ThrQui	FraSch	FraOcc	MegSjo	ThrPal	ThrTab	ThrBou	HerPat
Solanum mauritianum	0 (before flower removal)	NA	5	30	13	55	203	0	7	21	2756	8
Lontana camara			60	3	0	1	17	0	0	0	102	13
Ipomea indica			3	0	0	452	80	0	0	0	5	0
L. camara	1	c	25	0	0	2	6	0	0	0	15	14
I. indica		c	16	0	0	426	31	0	0	0	2	1
L. camara		t	33	0	0	0	10	0	0	0	39	4
I. indica		t	4	0	0	302	34	0	0	1	4	0
L. camara	2	c	30	0	2	0	7	0	0	0	5	20
I. indica		c	2	0	0	326	6	0	0	0	0	0
L. camara		t	16	0	3	7	9	0	0	2	6	11
I. indica		t	4	0	0	276	43	1	0	0	0	0
L. camara	3	c	29	0	0	1	16	0	0	3	9	39
I. indica		c	5	0	0	243	20	0	0	0	0	0
L. camara		t	17	0	4	1	25	0	0	0	7	8
I. indica		t	1	0	0	277	27	0	0	0	0	0