Kent Academic Repository

Metacommunity robustness of plant–fly–wasp tripartite networks with specialization to habitat loss

Jinbao Liao [1,4] Xinqiang Xi, [2] Daniel Bearup, [3] and Shucun Sun [2]

[1] *Ministry of Education's Key Laboratory of Poyang Lake Wetland and Watershed Research, School of Geography and Environment, Jiangxi Normal University, Ziyang Road 99, 330022 Nanchang, China*
[2] *Department of Ecology, School of Life Science, Nanjing University, 163 Xianlin Avenue, Nanjing 210023 China*
[3] *School of Mathematics, Statistics and Actuarial Sciences, University of Kent, Parkwood Road, Canterbury CT2 7FS United Kingdom*

Abstract. Recent observations have found plant-species-specific fly-host selection (i.e., specialization) of wasp parasitoids (wasps) in plant–fly–wasp (P–F–W) tripartite networks, yet no study has explored the dynamical implications of such high-order specialization for the persistence of this network. Here we develop a patch-dynamic framework for a unique P–F–W tripartite network with specialization observed in eastern Tibetan Plateau and explore its metacommunity robustness to habitat loss. We show that specialization in parasitoidism promotes fly species diversity, while the richness of both plant and wasp decreases. Compared to other two null models, real network structure favors plant species coexistence but increases the extinction risk for both flies and wasps. However, these effects of specialization and network structure would be weakened and ultimately disappear with increasing habitat loss. Interestingly, intermediate levels of habitat loss can maximize the diversity of flies and wasps, while increasing or decreasing habitat loss results in more species losses, supporting intermediate disturbance hypothesis. Finally, we observe that high levels of habitat loss initiate a bottom-up cascade of species extinction from plants to both flies and wasps, resulting in a rapid collapse of the whole tripartite networks. Overall, this theoretical framework is the first attempt to characterize the dynamics of whole tripartite metacommunities interacting in realistic high-order ways, offering new insights into complex multipartite networks.

Key words: habitat loss; higher-order interactions; metacommunity robustness; parasitism/parasitoidism; patch-dynamic model; specialization; tripartite networks.

Introduction

A key issue in ecology is to explore how the stability of a community is influenced by the structural properties that arise from species interactions. To date, numerous studies have already explored the structure and dynamics of bipartite plant–animal networks, and significant advances have been made in understanding the structure–stability relationship (Fortuna and Bascompte 2006, Bastolla et al. 2009, Thébeault and Fontaine 2010). For example, almost all the bipartite network structures observed in nature are highly nested irrespective of whether the network is mutualistic or antagonistic (Bascompte et al. 2003, Jordano et al. 2003, Lewinsohn et al. 2006, Tylianakis and Morris 2017). These nonrandom network patterns associated with asymmetrical interactions are proven to favor community stability (Bastolla et al. 2009, Thébeault and Fontaine 2010).

Despite these advances, the focus on bipartite networks alone is insufficient to fully interpret the evolution of

interactions in general and the coevolutionary process in particular, as the potential important influence of species interactions among three or more trophic groups is completely overlooked (Fontaine et al. 2011, Kéfi et al. 2012, Staniczenko et al. 2013, Sauve et al. 2014, 2016). Recently, a few studies have begun to consider community dynamics by combining both mutualistic and antagonistic interactions (Allesina and Pascual 2008, Melián et al. 2009, Mougi and Kondoh 2012, Sauve et al. 2014, 2016). By analyzing observational data, several studies found that the way plants connect pollination and herbivory is not randomly structured, and their nested and modular structures strongly affect the stability of pollination and herbivory communities in isolation but not when these networks are connected together (Thébault and Fontaine 2010, Sauve et al. 2014, 2016). However, even these models for tripartite networks still considered the structures of mutualistic and antagonistic networks separately (Sauve et al. 2016). In addition, these species-based tripartite networks do not reflect reality in natural communities, as many indirect interactions (e.g., high-order interactions, meaning one species can modulate the direct interactions between two others) among multitrophic groups are largely ignored (Bairey et al. 2016, Grilli et al. 2017, Mayfield

and Stouffer 2017). For example, the interactions of plant species with pollinators and herbivores are not independent from each other. Herbivory can reduce pollination by altering floral display or activating chemical defenses of plants (Strauss 1997, Adler et al. 2006). Reciprocally, several floral traits involved in pollinator attraction have been shown to attract herbivores as well, such as corolla size and color (Strauss et al. 2002), nectar sugar concentration (Adler and Bronstein 2004), and floral scent (Theis 2006). In plant–host–parasitoid tripartite networks, host selection of parasitoids is often plant-species-specific (i.e., specialization), since parasitoids can only parasitize their herbivorous hosts if their ovipositors are long and strong enough to penetrate the plant organs they feed on (Godfray 1994, Memmott et al. 2004, Xi et al. 2017). These observed high-order interactions can further influence network patterns by changing nestedness and asymmetry in linking degree (Stang et al. 2007). To capture the full community complexity, future study thus should consider high-order interactions by involving multiple species from multipartite networks, while not focusing solely on bipartite networks.

Despite the mounting evidence of high-order interactions, to our best knowledge, no study has yet explored the dynamical implications of such high-order effects on tripartite network persistence in a spatial context. Recently, metacommunity theory has become increasingly prevalent in exploring regional network patterns, as this framework can offer important insights into general understanding of the negative consequences of habitat loss for biodiversity, for example, interaction disruption and biodiversity decline (Fortuna and Bascompte 2006, Pillai et al. 2010, 2011, Jabot and Bascompte 2012, Liao et al., 2016, 2017a–c). By integrating metacommunity and network approaches, we thus develop a patch-dynamic framework for an observed plant–fly–wasp (P–F–W) tripartite network involving high-order interactions. Different from our model describing changes in species abundance, previous models of host–parasite interactions mainly characterize the dynamics of a host and a parasite, and very few have addressed the concept of diffuse coevolution by considering sets of interacting species as well as their interacting network structure (Boots and Sasaki 2000, 2002, Duffy and Sivars-Becker 2007, Vogwill et al. 2010, Boots et al. 2012). With the model, we assess to what degree specialization and network structure separately affect the metacommunity robustness to habitat loss (defined as the degree of habitat loss that can be tolerated without one or more species going extinct).

METHODS

Data set

The unique plant–fly–wasp (P–F–W) tripartite network (illustrated in Fig. 1) is extracted from sample data collected in Hongyuan County (32°48′ N, 102°33′ E) on the eastern Tibetan Plateau by deleting those P–F links without any interactions with wasps (more details in Xi et al. 2013, 2017; see Data S1). It is composed of $n_i = 19$ plants, $n_j = 19$ flies, and $n_k = 19$ wasps, with total triple links $L = 201$ (see nodes in Fig. 1d). In this tripartite system, the flies, as seed predators, can parasitize their host plants by laying eggs within the flower heads, wherein hatched larvae grow and mature by consuming immature seeds (parasitism in Fig. 1b). Some of the larvae are parasitoidized by wasps through penetrating their ovipositors into larvae host flies (parasitoidism in Fig. 1c). Specifically, only those wasps with sufficiently long ovipositors, longer than radius of the plant flower heads, can parasitoidize larvae successfully (Xi et al. 2017), thereby revealing the plant-species-specific fly host selection in parasitoidism (i.e., specialization). Based on the observed P–F–W system, we further configure another two tripartite networks randomized by means of two different null models in the following subsections.

Null models

Null models are pattern-generating models that deliberately exclude a mechanism of interest, allowing for randomization tests of ecological data (Gotelli 2001). By comparing real networks with null models, we can assess to what extent network structure alters metacommunity responses to habitat loss.

Null model 1.—This model intends to preserve the total number of triple P–F–W links (L) in the observed network while discarding other aspects of network structure (Fig. 2a). To achieve this, the probability of a triple link $L/(n_i \times n_j \times n_k)$ in that network is computed. Random interaction networks are generated using this link probability as the probability that a link occurs between any given triple of P–F–W species. In practice, this means that the mean number of triple links within a random interaction network is fixed with some variation (Appendix S1: Fig. S1).

Null model 2.—This model intends to preserve the total number of triple links (L) and the number of triple links per species (degree D) in the observed network (Fig. 2b). Thus, this approach maintains interspecific differences in vulnerability to parasites and generalism in host choice. We calculate the proportion of links in which each plant i is involved as $P_i = D_i/L$, each fly j with $F_j = D_j/L$ and each wasp k with $W_k = D_k/L$. Thus, assuming that each species forms links independently, the probability of a triple link between plant i, fly j and wasp k is given by $P_i \times F_j \times W_k$. We then generate random interaction networks using this link probability distribution in place of the link probability used in null model 1. In order to approximately keep the total number of links, it is necessary to scale this distribution by L. In practice, this approach produces slightly fewer total links than
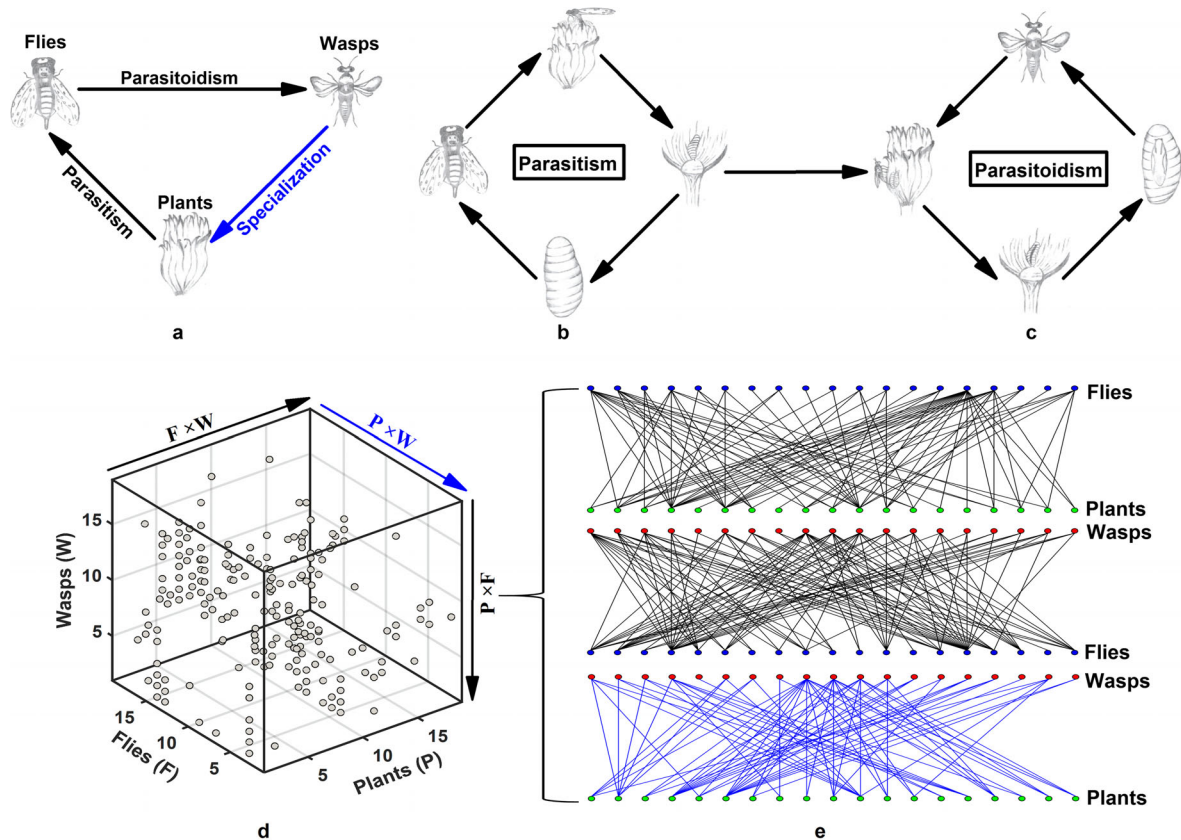
FIG. 1.   Real plant–fly–wasp (P–F–W) tripartite networks observed in eastern Tibetan Plateau. (a) Different interactions (arrows) in a P–F–W system, including parasitism, parasitoidism, and specialization (blue; i.e., plant species-specific host selection of wasps in parasitoidism); (b) fly parasitism; (c) wasp parasitoidism; (d) three-dimensional graph depicting triple interactions in real networks (denoted by gray nodes); (e) bipartite networks of P–F, F–W, and P–W mapped from panel d, with species interactions linked by lines.

expected, and slightly underestimates the degree of extreme generalists (Appendix S1: Fig. S1).

Note that, it is certainly possible to simply reshuffle the interaction matrix to produce the null model that perfectly preserves the observed number of links. Yet, such approach to preserve degree for each species becomes increasingly computationally expensive as the network size increases (e.g., Gotelli and Entsminger 2001, 2003). The probability distribution approach outlined above is, by contrast, very fast and has been used widely in other studies (e.g., Bascompte et al. 2003, Thébault and Fontaine 2010). Thus, we prefer to use the same basic approach of probability distribution in both null models (see their statistical behaviors in Appendix S1).

Metacommunity models

We consider the P–F–W tripartite networks inhabiting in a landscape consisting of an infinite number of well-mixed patches with two habitat types: *suitable habitat* (S patches), which can be colonized by any species; and *unsuitable habitat* (U patches), which is not suitable for any species establishment. Each S patch can accommodate many populations of distinct species at the same time. As all S patches have the same size, it is justified to assume that they can support the equal maximum population for a given species. As such, the number of S patches occupied by a species (i.e., patch occupancy) can be considered as a measure of its total populations (i.e., species regional abundance). We use S to represent the proportion of suitable patches in the landscape, thus it is immediately clear that S is a measure of habitat availability, directly related to the level of habitat loss $U = 1 - S$, i.e., the fraction of U patches in the landscape, such as patches with poor nutrition resulting from land use change, pollution, over-exploitation, or climate change.

Several assumptions are made to simplify the theoretical framework. (1) The fitness or fecundity of a parasitized species (i.e., plant or fly colonization rate) is decreased (e.g., via loss of seeds or pupae). (2) Parasitic species (flies and wasps) are unable to survive in an S patch without a suitable host. (3) We disregard resource competition among plants, flies or wasps in a local patch
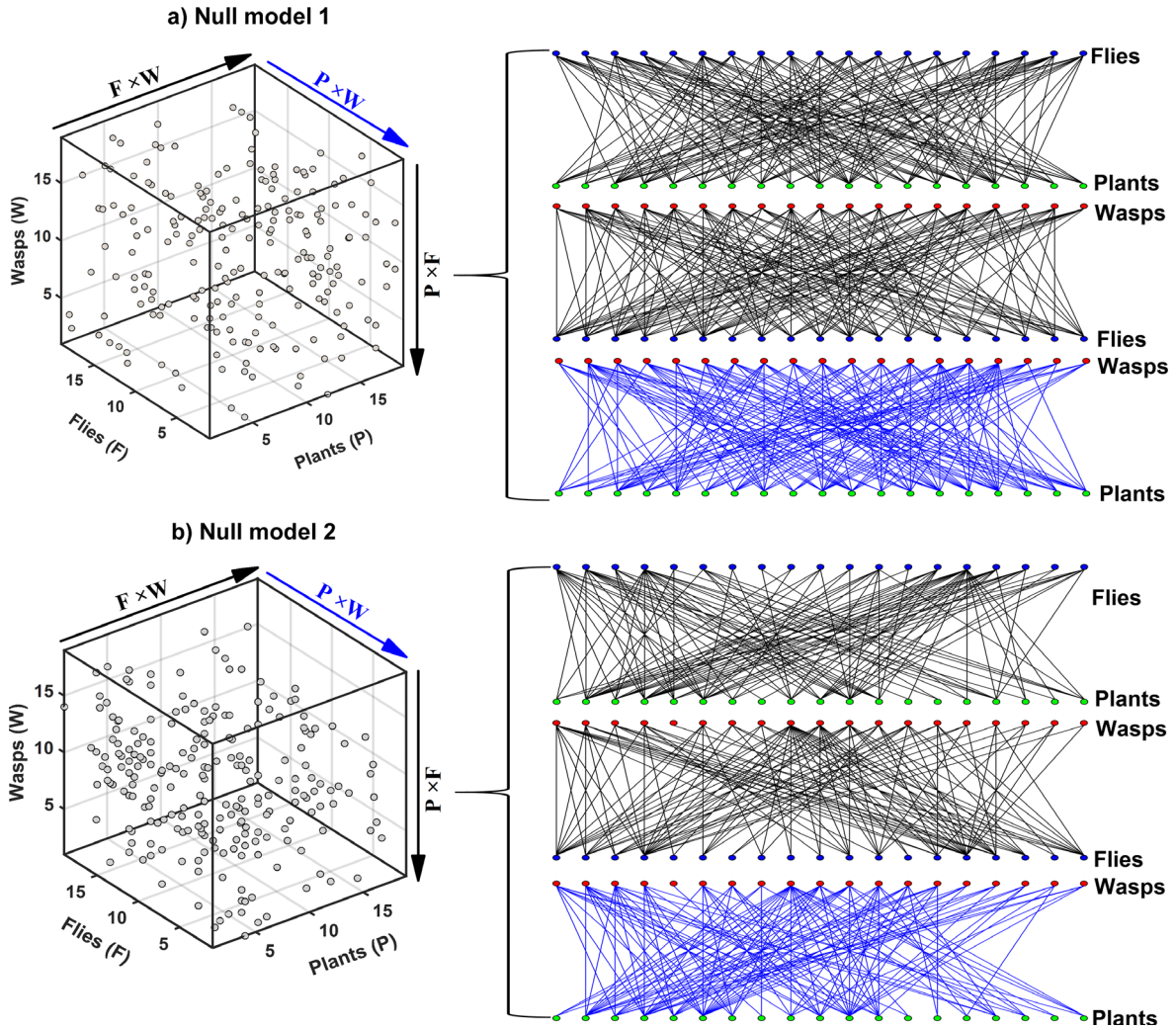
Fig. 2. Tripartite networks structured separately using (a) null model 1 and (b) 2 based on real tripartite networks (gray node, species interaction). Each bipartite network is mapped from null models, linked by lines.

(e.g., Fortuna and Bascompte 2006). (4) Each species (including plants, flies, and wasps) can access any suitable patch freely (via seed dispersal or flying across the landscape). (5) Effects of parasitism or parasitoidism between species are cumulative, e.g., a plant would perform worse when multiple parasitic flies are present in the same patch.

Following Fortuna and Bascompte (2006), we characterize the patch dynamics for the focal plant i as

$$\frac{dp_i}{dt} = \underbrace{c_i p_i (1 - U - p_i)}_{\text{Colonization}} \underbrace{- e_i p_i}_{\text{Extinction}}. \quad (1)$$

Parameter interpretations are seen in Table 1. As assumed above, parasitism can reduce species colonization rate, and such effects are synergistic when multiple fly parasites are present in a local patch. In addition, the

flies with strong reproductive capacity (i.e., producing large number of eggs per life cycle) can access to any suitable patch freely via flying, and lay eggs into the flower heads of plant hosts. According to Gross (2008), we thus have the per-capita colonization rate for plant i

$$c_i = c_i^0 - b_i + \frac{2b_i}{1 + \exp\left(\sum_{j=1}^{n_j} \gamma_{ij} p_j\right)}. \quad (2)$$

The coefficient γ_{ij} denotes the interaction strength of the fly j on the plant i. In particular, parasitism can decrease plant species intrinsic colonization rate (c_i^0) with a maximum amount b_i, determined by the cumulative parasitic impacts from all n_j fly species ($\sum_{j=1}^{n_j} \gamma_{ij} p_j$; note $\gamma_{ij} = 0$ – no interaction between species i and j). As such, $c_i = c_i^0 - b_i$ if $\sum_{j=1}^{n_j} \gamma_{ij} p_j \to \infty$, while $c_i = c_i^0$ when $\sum_{j=1}^{n_j} \gamma_{ij} p_j = 0$.

TABLE 1. Parameter interpretations.

Symbols	Interpretations
p_i	patch occupancy of the plant species i (=1, 2, 3...n_i)
p_j	patch occupancy of the fly species j (=1, 2, 3...n_j)
p_k	patch occupancy of the wasp species k (=1, 2, 3...n_k)
U	habitat patch loss in the landscape (so-called habitat loss)
c	species per-capita colonization rate (c_i, plant; c_j, fly; c_k, wasp)
c^0	species intrinsic colonization rate (c_i^0, plant; c_j^0, fly; c_k^0, wasp)
e	species per-capita extinction rate (e_i, plant; e_j, fly; e_k, wasp)
b	parasitism (or parasitoidism) can decrease the per-capita colonization rate of the plant i (or the fly j) by a maximum amount b_i (plant) or b_j (fly), depending on the cumulative impacts from all potential parasitic n_j flies (or n_k wasps)
θ	species interaction coefficient, with $\theta = 1$ if species can interact (otherwise $\theta = 0$)
γ	coefficient of species interaction strength

Similarly, we can characterize the patch occupancy dynamics for the fly j as

$$\frac{dp_j}{dt} = c_j p_j (\Phi_j - p_j) - e_j p_j, \qquad (3)$$

where Φ_j is the union of all potential patches (occupied by host plants) accessible for the fly j, since the fly cannot survive in a local patch without any plant host. Thus

$$\Phi_j = (1 - U)\Big[1 - \prod_{i=1}^{n_i}\Big(1 - \theta_{ji}\frac{p_i}{1 - U}\Big)\Big], \qquad (4)$$

in which n_i is the total number of plant species, and θ_{ji} (=0 or 1) indicates whether the fly j can parasitize the plant i. The term in the square bracket represents the fraction of suitable patches occupied by at least one plant accessible for the fly j, as these plant species that cannot establish in the unsuitable patches are randomly distributed in the suitable patches instead of the whole landscape. Then this union should be converted as global union by multiplying (1-U) for consistency.

Likewise, the wasps with strong reproductive capacity (i.e., producing many generations per year) can parasitoidize any suitable fly freely via flying, thus the intrinsic colonization rate of the fly j (c_j^0) can be decreased by the parasitoid wasp k

$$c_j = c_j^0 - b_j + \frac{2b_j}{1 + \exp\big(\sum_{k=1}^{n_k} \gamma_{jk} p_k\big)}. \qquad (5)$$

However, the wasps in nature often display plant-species-specific fly host selection (i.e., specialization), that is, plant species can restrict the parasitoidism of the wasp if the wasps' ovipositors are not long and strong enough to penetrate into the plant organs that the flies

feed on. As such, a given wasp can parasitize some but not all populations of their host fly species (Godfray 1994, Xi et al. 2017). Considering the effects of high-order specialization, we modify Eq. 5 as

$$c_j = c_j^0 - b_j + \frac{2b_j}{1 + \exp\big(\sum_{i=1}^{n_i} \sum_{k=1}^{n_k} \gamma_{jik} p_i p_k\big)}. \qquad (6)$$

The term $p_i p_k$ is the intersection of patches occupied by both plant i and wasp k, as both can disperse globally.

In a similar way, we have the patch dynamics for the wasp k

$$\frac{dp_k}{dt} = c_k^0 p_k (\Phi_k - p_k) - e_k p_k. \qquad (7)$$

If plant species do not restrict the parasitoidism (i.e., no specialization), then

$$\Phi_k = (1 - U)\Big[1 - \prod_{j=1}^{n_j}\Big(1 - \theta_{kj}\frac{p_j}{1 - U}\Big)\Big], \qquad (8)$$

otherwise

$$\Phi_k = (1 - U)\Big[1 - \prod_{i=1}^{n_i} \prod_{j=1}^{n_j}\Big(1 - \theta_{kij}\frac{p_i}{1 - U}\frac{p_j}{1 - U}\Big)\Big], \qquad (9)$$

with the indirect restriction from plant species. Similarly, the coefficient θ_{kij} (= 0 or 1) indicates whether the wasp k can parasitize the fly j hosted in the plant i, and the term $(p_i/[1 - U])(p_j/[1 - U])$ approximately represents the intersection of suitable patches occupied by both the plant i and the fly j (i.e., fraction of suitable patches occupied by both plant i and fly j).

Numerical simulations

To get insights into the complex P–F–W tripartite networks, we first make a systematic comparative analysis of species persistence under generalization vs. specialization in a simple four-species system consisting of two plants, one fly, and one wasp (Appendix S2: *Model analysis* and Fig. S1). With the spatially implicit model described above (Eqs. 1–9), we then use numerical methods to derive the non-trivial stable equilibrium states for this complex tripartite multispecies system, thereby determining which species survive and which go extinct (Appendix S3: Fig. S1). All species are assumed to be equally abundant initially. To our knowledge, tripartite networks at the regional scale have not yet been parameterized using realistic biological estimates, we thus choose similar parameter ranges to previous metacommunity models (Fortuna and Bascompte 2006), and parameter values (e.g., species colonization and extinction rates) are randomly drawn from appropriate uniform distributions within the defined ranges. Note that

drawing parameter values from normal distributions yields the similar outcomes. Simulations are run long enough for initial transients to dissipate and reach a steady state (Appendix S3: Fig. S1). Species are assumed to be extinct if their patch occupancy falls below 0.00001. Each case is run for 100 replicates to reduce stochastic errors (mean ± SD). A broad range of biologically reasonable parameter combinations are explored and found to yield qualitatively consistent community patterns (Appendix S3: Fig. S2). In order to focus on the effect of interaction network structure, we assign all species the same relative extinction rate ensuring that no species has a direct competitive advantage as a result of its life-history traits.

Since using deterministic differential equations (DDEs) to draw conclusions on an intrinsically stochastic process could be problematic and misleading (e.g., Van Kampen 1992, Allen 2010, Azaele et al. 2010), we additionally apply a discrete-time, stochastic cellular automaton (CA) model (with 100×100 patches) to simulate the stochastic dynamics of the P–F–W system (cf. Liao et al. 2013*a*,*b* , Shen et al. 2019), in order to examine the accuracy of the DDEs described above (see

codes in Data S2). To find the steady state, the CA simulations are initially run for a long time, and normally 10,000 time steps are enough to achieve system stability with small fluctuations around the average global patch occupancy for each species (Appendix S3: Fig. S3). As such, a population goes extinct when its number is exactly zero, and then we count how many species survive at steady state in each simulation. Similarly, each case is run with 100 replicates yields the fraction of surviving species (mean ± SDs) at steady state. We find that, although the DDEs overestimate species diversity especially for wasps compared to the CA simulations, both approaches yield similar biodiversity patterns following habitat loss (comparing Figs. 3, 4 and Appendix S3: Figs S4, S5), thereby demonstrating the validity of using the DDEs to model the stochastic process of the P–F–W system.

RESULTS AND DISCUSSION

This study is one of very few modelling a community-wide P–F–W tripartite networks with plant-species-specific host selection of parasitoids (i.e., specialization)
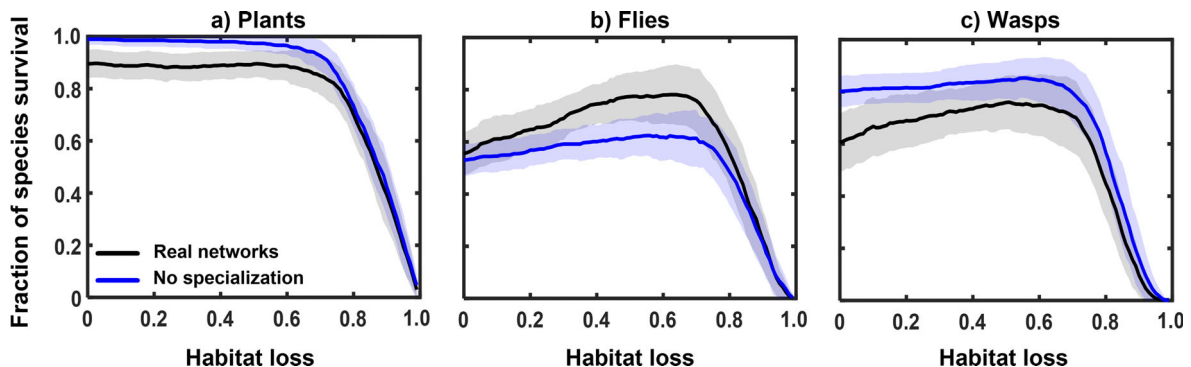

FIG. 3. Effect of habitat loss on the fraction of surviving species (mean ± SD of 100 replicates) in real P–F–W tripartite meta-communities with (black) vs. without (blue) specialization (i.e., plant species-specific host selection of parasitoids). Parameters for each species are randomly drawn from uniform distributions unifrnd[a_1, a_2] with the range between $a_1 \sim a_2$ (mean $(a_1 + a_2)/2$ and variance $(a_2 - a_1)^2/12$): $e_i = e_j = e_k \sim$ unifrnd[0, 0.2], $c_i^0 = c_j^0 = c_k^0 \sim$ unifrnd[0.6, 1], $b_i = c_i^0$, $b_j = c_j^0$, species interaction coefficient $\theta = 1$ if species can interact ($\theta = 0$ otherwise), and coefficient of interaction strength $\gamma \sim$ unifrnd[0.5, 1.5].
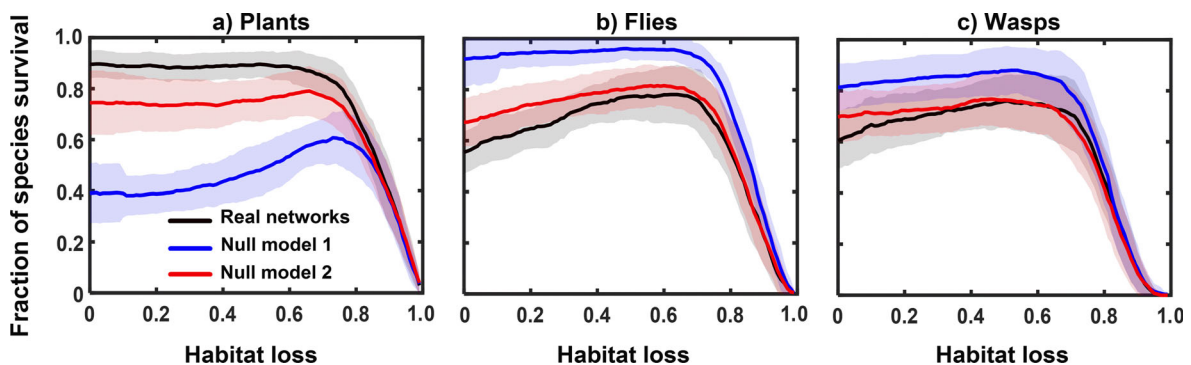

FIG. 4. Effect of habitat loss on the fraction of species surviving (mean ± SD of 100 replicates) in real tripartite networks vs. two null models 1 (blue) and 2 (red). Parameter values: see Fig. 3.

in landscapes subject to habitat loss. Our model predicts that such high-order specialization (relative to no specialization, i.e., without plant-inhibitory effect on parasitoidism) can promote fly diversity but reduce both plant and wasp richness, though high levels of habitat loss can weaken and even eliminate such effects (Fig. 3). In fact, in such tripartite metacommunities, the flies as intermediate consumers are the most vulnerable species, as they suffer from the dual threat: habitat loss (bottom-up constraint) and parasitoidism (top-down constraint), which can have substantial negative demographic effects on fly communities. Luckily, high-order specialization greatly restricts the success of parasitoidism because of plant-inhibitory effects, thereby releasing top-down constraints on fly hosts. As such, the resulting increased fly richness promotes the cumulative parasitic pressure on plant hosts, greatly suppressing plant species persistence by reducing plant colonization ability (i.e., eating plant seeds). Thus, high specialization in parasitoidism results in more losses for both plant and wasp while promoting fly species survival, suggesting a strong association between current network structure and system robustness to habitat loss.

Relative to both null models, the structure of observed tripartite networks (more clustered points in Fig. 1e) favors plant species coexistence but reduces both fly and wasp richness (Fig. 4). Since randomized connections (more scattered points in Fig. 2) significantly increase species linking degree (i.e., the number of pairwise interactions per species, including plants, flies and wasps) in their mapped bipartite networks (including plant–fly parasitism and fly–wasp parasitoidism). This results in an increase in parasitic breadth (i.e., the number of species that can be parasitized) for both flies and wasps, thus increasing patch availability for these species; comparing Figs. 1, 2). The resulting increase in colonization opportunities enhances the persistence of parasitic species while decreasing that of the parasitized species (particularly plants). The second null model, which more accurately captures parasite specialization, does not increase parasitic breadth to the same degree and, as a consequence, we see a reduction in this effect. However, since this null model does not perfectly capture these structural properties, it does not precisely replicate the behavior of the observed community. However, the differences in community maintenance resulting from network structure would decrease and ultimately disappear at high levels of habitat loss. The overall effect of tripartite interaction structure on community richness is thus greatly mediated by habitat loss.

Interestingly, intermediate levels of habitat loss can maintain highest species diversity for flies and wasps, while increasing or decreasing habitat loss results in more species losses (Figs. 3, 4). In fact, low levels of habitat loss can maintain higher species abundances, which can increase the negative cumulative parasitic effects on host colonization rate, thereby greatly reducing host species survival. Due to the trophic cascading

effect, the decline in host richness in turn reduces the diversity of parasites. As such, parasitism is the dominant process determining species diversity at high habitat availability. In contrast, at high levels of habitat loss, only low species abundances can be maintained, decreasing the overall level of parasitism, but strongly limiting species diversity nonetheless. As such, habitat loss is the dominant process determining species diversity at low habitat availability. Moderate habitat loss can maximize overall species diversity due to the balance between negative effects of parasitism and habitat loss (with effects of parasitism greatly mediated by habitat loss), supporting the intermediate disturbance hypothesis (IDH).

The final observation is that high levels of habitat loss lead to a rapid collapse of the whole tripartite networks, thereby initiating a bottom-up cascade of species extinction from plants to both flies and wasps (Figs. 3, 4). At low levels of habitat loss, the flies, which often have high parasitic breadth (i.e., linking with several plants), can to some degree tolerate the decline in the abundances of plant hosts resulting from initial habitat loss. Similarly, the wasp parasitoids often with multiple alternative fly hosts can buffer the negative trophic cascading effects from decreased fly host abundances, likewise exhibiting strong resistance to habitat loss. Yet, very high levels of habitat loss can dramatically reduce plant species diversity, and such reductions quickly decrease the fly richness by disrupting the parasitic links, which in turn reduces the wasp richness via a trophic cascade. The bottom-up control of habitat loss that triggers cascading extinction in multipartite networks, has been also observed in other field observations (Knops et al. 1999, Kruess 2003, Petermann et al. 2010, Fenoglio et al. 2012). In particular, the wasps at highest trophic levels are most vulnerable to habitat loss, demonstrating that impacts of habitat loss can be amplified via extinction cascades from plants to flies to wasps in ecological networks (e.g., Schleuning et al. 2016). The maintenance of triple interactions in the plant–fly–wasp networks strongly depends on changes in their host abundances, ultimately determined by habitat loss. Hence, although parasites/parasitoids at higher trophic levels are not directly affected by habitat availability, reductions in available hosts can drive their extinction.

Here we are taking a step toward the integration of metacommunity and network approaches by exploring a model of tripartite networks with specialization in a spatial context. A set of differential equations are used as deterministic models for stochastic processes, by assuming that they can capture the main dynamic behaviors of the modelled population when the population is sufficiently large. Yet, we should be aware of the discreteness of population when using deterministic differential equations (DDEs) to draw conclusions on an intrinsically stochastic process, as the deterministic approximation can occasionally deviate considerably from the exact result even for large populations, and numerical solutions do not guarantee a good fit between the stochastic

scenario and its deterministic approximation (e.g., Van Kampen 1992, Allen 2010, Azaele et al. 2010). Yet, using the stochastic cellular automaton (CA) simulations, we demonstrate the effectiveness of applying the DDEs to draw general conclusions for the P–F–W system, since both approaches yield similar community responses to habitat loss though the DDEs overestimate species diversity relative to the CA model (Figs. 3, 4 vs. Appendix S3: Figs. S4, S5). In this study, we find that intermediate levels of habitat loss may maintain highest overall species diversity, which is particularly important for the design of holistic conservation strategies aiming at maintaining biodiversity. For example, a common recommendation for biodiversity conservation is to simply increase habitat amount. However, some care needs to be taken to ensure that such actions do not unintentionally increase negative cumulative parasitic impacts undergone by species within the landscape, inadvertently reducing overall biodiversity (Figs. 2, 3). The best way to avoid such outcomes is to consider realistic higher-order interactions across multiple trophic levels when designing conservation plans at landscape scales. As suggested by field observations (Kruess and Tscharntke 2000, Kruess 2003), this model provides some guidance for potential biological control attempts of flies using wasp parasitoids (i.e., natural enemies): large undisturbed habitats are necessary to preserve large populations of parasitoids, since flies would suffer more from parasitism in landscapes characterized by a high proportion of large and undisturbed habitats (Thies and Tscharntke 1999). Overall, this study demonstrates that considering multipartite interactions in a more realistic high-order way (e.g., specialization) could improve our ability to accurately predict species coexistence and community dynamics, offering a new theoretical framework for multipartite networks at regional scale.

Literature Cited

Adler, L. S., and J. L. Bronstein. 2004. Attracting antagonists: Does floral nectar increase leaf herbivory? Ecology 85:1519–1526.

Adler, L. S., M. Wink, M. Distl, and A. J. Lentz. 2006. Leaf herbivory and nutrients increase nectar alkaloids. Ecology Letters 9:960–967.

Allen, L. J. 2010. An introduction to stochastic processes with applications to biology. Chapman and Hall/CRC Press, Boca Raton, FL, USA.

Allesina, S., and M. Pascual. 2008. Network structure, predator-prey modules, and stability in large food webs. Theoretical Ecology 1:55–64.

Azaele, S., A. Maritan, E. Bertuzzo, I. Rodriguez-Iturbe, and A. Rinaldo. 2010. Stochastic dynamics of cholera epidemics. Physical Review E 81:051901.

Bairey, E., E. D. Kelsic, and R. Kishony. 2016. High-order species interactions shape ecosystem diversity. Nature Communications 7:12285.

Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. Proceedings of the National Academy of Sciences USA 100:9383–9387.

Bastolla, U., M. A. Fortuna, A. Pascual-Garcia, A. Ferrera, B. Luque, and J. Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1020.

Boots, M., and A. Sasaki. 2000. The evolutionary dynamics of local infection and global reproduction in host-parasite interactions. Ecology Letters 3:181–185.

Boots, M., and A. Sasaki. 2002. Parasite-driven extinction in spatially explicit host-parasite systems? American Naturalist 159:706–713.

Boots, M., A. White, A. Best, and R. Bowers. 2012. The importance of who infects whom: the evolution of diversity in host resistance to infectious disease. Ecology Letters 15:1104–1111.

Duffy, M. A., and L. Sivars-Becker. 2007. Rapid evolution and ecological host-parasite dynamics. Ecology Letters 10:44–53.

Fenoglio, M. S., D. Srivastava, G. Valladares, L. Cagnolo, and A. Salvo. 2012. Forest fragmentation reduces parasitism via species loss at multiple trophic levels. Ecology 93:2407–2420.

Fontaine, C., et al. 2011. The ecological and evolutionary implications of merging different types of networks. Ecology Letters 14:1170–1181.

Fortuna, M. A., and J. Bascompte. 2006. Habitat loss and the structure of plant-animal mutualistic networks. Ecology Letters 9:281–286.

Godfray, H. C. J. 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, New Jersey, USA.

Gotelli, N. J. 2001. Research frontiers in null model analysis. Global Ecology & Biogeography 10:337–343.

Gotelli, N. J., and G. L. Entsminger. 2001. Swap and fill algorithms in null model analysis: rethinking the knight's tour. Oecologia 129:281–291.

Gotelli, N. J., and G. L. Entsminger. 2003. Swap algorithms in null model analysis. Ecology 84:532–535.

Grilli, J., G. Barabás, M. J. Michalskasmith, and S. Allesina. 2017. Higher-order interactions stabilize dynamics in competitive network models. Nature 548:210.

Gross, K. 2008. Positive interactions among competitors can produce species-rich communities. Ecology Letters 11:929–936.

Jabot, F., and J. Bascompte. 2012. Bitrophic interactions shape biodiversity in space. Proceedings of the National Academy of Sciences USA 109:4521–4526.

Jordano, P., J. Bascompte, and J. M. Olesen. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. Ecology Letters 6:69–81.

Kéfi, S., et al. 2012. More than a meal. . . integrating non-feeding interactions into food webs. Ecology Letters 15:291–300.

Knops, J. M. H., et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecology Letters 2:286–293.

Kruess, A. 2003. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. Ecography 26:283–290.

Kruess, A., and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. Oecologia 122:129–137.

Lewinsohn, T. M., P. Inácio Prado, P. Jordano, J. Bascompte, and J. M. Olesen. 2006. Structure in plant–animal interaction assemblages. Oikos 113:174–184.

Liao, J., et al. 2017*a*. Robustness of metacommunities with omnivory to habitat destruction: disentangling patch fragmentation from patch loss. Ecology 98:1631–1639.

Liao, J., D. Bearup, and B. Blasius. 2017*b*. Food web persistence in fragmented landscapes. Proceedings of the Royal Society B 284:20170350.

Liao, J., D. Bearup, and B. Blasius. 2017*c*. Diverse responses of species to landscape fragmentation in a simple food chain. Journal of Animal Ecology 86:1169–1178.

Liao, J., J. Chen, Z. Ying, D. E. Hiebeler, and I. Nijs. 2016. An extended patch-dynamic framework for food chains in fragmented landscapes. Scientific Reports 6:33100.

Liao, J. B., Z. Li, D. E. Hiebeler, M. El-Bana, G. Deckmyn, and I. Nijs. 2013*a*. Modelling plant population size and extinction thresholds from habitat loss and habitat fragmentation: Effects of neighbouring competition and dispersal strategy. Ecological Modelling 268:9–17.

Liao, J. B., Z. Li, D. E. Hiebeler, Y. Iwasa, J. Bogaert, and I. Nijs. 2013*b*. Species persistence in landscapes with spatial variation in habitat quality: A pair approximation model. Journal of Theoretical Biology 335:22–30.

Mayfield, M. M., and D. B. Stouffer. 2017. Higher-order interactions capture unexplained complexity in diverse communities. Nature Ecology & Evolution 1:62.

Melián, C. J., J. Bascompte, P. Jordano, and V. Křivan. 2010. Diversity in a complex ecological network with two interaction types. Oikos 118:122–130.

Memmott, J., N. M. Waser, and M. V. Price. 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society B 271:2605–2611.

Mougi, A., and M. Kondoh. 2012. Diversity of interaction types and ecological community stability. Science 337:349–351.

Petermann, J. S., C. B. Müller, A. Weigelt, W. W. Weisser, and B. Schmid. 2010. Effect of plant species loss on aphid-parasitoid communities. Journal of Animal Ecology 79:709–720.

Pillai, P., A. Gonzalez, and M. Loreau. 2011. Metacommunity theory explains the emergence of food web complexity. Proceedings of the National Academy of Sciences USA 108:19293–19298.

Pillai, P., M. Loreau, and A. Gonzalez. 2010. A patch-dynamic framework for food web metacommunities. Theoretical Ecology 3:223–237.

Sauve, A. M. C., C. Fontaine, and E. Thébault. 2014. Structure-stability relationships in networks combining mutualistic and antagonistic interactions. Oikos 123:378–384.

Sauve, A. M. C., E. Thébault, P. Mjo, and C. Fontaine. 2016. How plants connect pollination and herbivory networks and their contribution to community stability. Ecology 97:908–917.

Schleuning, M., et al. 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. Nature Communications 7:13965.

Shen, Y., C. Zeng, I. Nijs, and J. Liao. 2019. Species persistence in spatially regular networks. Ecological Modelling 406:1–6.

Stang, M., P. G. L. Klinkhamer, and E. van der Meijden. 2007. Asymmetric specialization and extinction risk in plant–flower visitor webs: a matter of morphology or abundance? Oecologia 151:442–453.

Staniczenko, P. P., J. C. Kopp, and S. Allesina. 2013. The ghost of nestedness in ecological networks. Nature Communications 4:1391.

Strauss, S. Y. 1997. Floral characters link herbivores, pollinators, and plant fitness. Ecology 78:1640–1645.

Strauss, S. Y., J. A. Rudgers, J. A. Lau, and R. E. Irwin. 2002. Direct and ecological costs of resistance to herbivory. Trends in Ecology and Evolution 17:278–285.

Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856.

Theis, N. 2006. Fragrance of Canada thistle (*Cirsium arvense*) attracts both floral herbivores and pollinators. Journal of Chemical Ecology 32:917–927.

Thies, C., and T. Tscharntke. 1999. Landscape structure and biological control in agroecosystems. Science 285:893–895.

Tylianakis, J. M., and R. J. Morris. 2017. Ecological networks across environmental gradients. Annual Review of Ecology, Evolution, and Systematics 48:25–48.

Van Kampen, N. G. 1992. Stochastic processes in physics and chemistry. Elsevier Press, Amsterdam, Netherlands.

Vogwill, T., A. Fenton, and M. A. Brockhurst. 2010. Dispersal and natural enemies interact to drive spatial synchrony and decrease stability in patchy populations. Ecology Letters 12:1194–1200.

Xi, X., J. N. Griffin, and S. Sun. 2013. Grasshoppers amensalistically suppress caterpillar performance and enhance plant biomass in an alpine meadow. Oikos 122:1049–1057.

Xi, X., Y. Yang, Y. Yang, M. Segoli, and S. Sun. 2017. Plant-mediated resource partitioning by coexisting parasitoids. Ecology 98:1660–1670.