



Standing on an invasion front: predicting potential impacts of praying mantids using fuzzy interaction webs

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Abstract Developing tools for rapidly predicting which introduced species will become invasive is essential for effective species management. It's also notoriously difficult. Quantitative models exist but often require extensive data, precluding timely application. A qualitative modeling approach, Fuzzy Interaction Webs (FIW), offers a practical alternative. FIWs hold the potential to predict impacts, guide early responses, and identify research needs using the limited data commonly available on an invasion front. As a case study, we applied FIWs to predict effects of introduced European praying mantis (*Mantis religiosa*) populations in grassland communities of western Montana, USA. Using available field data, published data, and expert opinion, we modeled mantid impacts on this community. We also explored how abiotic conditions (winter severity) and natural enemies (parasitoids) might independently and interactively

influence mantid abundance. Our model predicted that current mantid densities, which are comparatively low, produce negligible impacts. At increased mantid densities, our model predicted declines across invertebrate guilds, with the greatest impacts at highest densities, especially on invertebrate predators, herbivores, and pollinators. Mantids were also predicted to reduce songbird abundance via indirect effects. However, if wild parasitoids establish, our model predicted they would maintain mantids below these impact levels, even under mild winter conditions. The potential adverse effect of parasitoids on native mantids is unknown, warranting additional study. We recommend monitoring *M. religiosa* populations within the study area and suggest that our predictions may help guide management decisions. More broadly, our case study demonstrates the potential usefulness of FIWs for evaluating invasion fronts.

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Introduction

Species that are introduced outside of their native range can diminish biodiversity, degrade habitat, and impair ecosystem services (Pyšek and Richardson 2010; Bacher et al. 2023). However, only a subset of introduced species becomes problematic

(Williamson and Fitter 1996; Pearson et al. 2016). Rapidly determining which of the many introduced species are likely to generate significant impacts is critical because management is most effective in the early stages of establishment and invasion (Hulme et al. 2009). Yet, predicting invader impacts is notoriously difficult, because impacts can derive from a wide range of direct and indirect effects (Mack et al. 2000; Crooks 2002; Pyšek et al. 2012). This challenge increases at the community level where complex and cryptic interactions may spread across multiple trophic levels. There is a need in invasion ecology for modeling tools that can accommodate such complexity to rapidly predict potential impacts of newly introduced species, while also being accessible to practitioners.

Traditional quantitative models are often impractical for these fast-paced, real-world applications (Özesmi and Özesmi 2004). These models require precise empirical data (e.g., demographic rates, interaction coefficients) that are often unavailable early in an invasion, particularly for understudied organisms, multiple trophic levels, and non-trophic interactions (Montoya et al. 2009; Novak et al. 2011; Clark-Wolf et al. 2022; Pearson and Clark-Wolf 2023). This limitation justifies the need for more flexible modeling tools that can be rapidly applied using a wide range of available data. Fuzzy interaction webs (FIW), a qualitative modeling approach, was adapted from the social sciences (Kosko 1992) to address challenging questions in ecology and conservation (Hobbs et al. 2002; Ramsey and Veltman 2005; Baker et al. 2016; Clark-Wolf et al. 2022; Pearson and Clark-Wolf 2023). For species abundance and interaction strength parameters, FIW can accept a variety of data, ranging from empirical measurements to qualitative rankings. These rankings (e.g., low, moderate, high) may be based on limited data or expert opinion (Hobbs et al. 2002; Ramsey and Veltman 2005). Vetted against empirical case studies of species introductions with known outcomes, FIWs reasonably predict the direction and qualitative magnitude of changes in species abundance (Clark-Wolf et al. 2022). Hence, FIWs offer potential for predicting invasion outcomes and the efficacy of management interventions.

Here, we illustrate the functionality of FIWs for assessing biological invasions by evaluating European praying mantis (*Mantis religiosa*) introductions in western Montana, USA. *Mantis religiosa* was first

observed in North America in 1899 (Gurney 1950) and has since spread across the continent. Its arrival in western Montana's intermountain grasslands is relatively recent, being first documented in 2006 (Montana Natural Heritage Program). Local observations, mostly made by citizen scientists using the online platform iNaturalist (iNaturalist community 2025), were rare initially but have increased sharply over the past ten years, reaching a recent peak in 2022. This trend suggests that *M. religiosa* is now established and increasing in western Montana. This species is a large generalist invertebrate predator, the largest terrestrial invertebrate in our system, capable of a wide range of ecological impacts (Hurd 1999; Snyder and Evans 2006). Hence, *M. religiosa*'s presence in our system possibly reflects an invasion in its early stages, an "invasion front", with potentially significant impacts that warrant evaluation.

Methods

Study Area

In western Montana, the semi-arid grasslands being invaded by *M. religiosa* occur at valley and foothill elevations (700–1650 m) with a climate defined by cold winters and hot, dry summers (Montana Natural Heritage Program). Recent anthropogenic uses have created a patchwork of grazed rangeland, irrigated cropland, old-field habitat, and exurban development. Nutrient-poor soils are derived from Pleistocene glacial depositions and alluvium, which today support a mix of native and non-native plant communities, including annual (*Bromus tectorum*, *Bromus japonicus*) and perennial grasses (*Poa spp.*, *Festuca idahoensis*, *Pseudoroegneria spicata*, *Agropyron cristatum*), forbs (*Centaurea stoebe*, *Euphorbia esula*, *Balsamorhiza sagittata*, *Lupinus argenteus*), and shrubs (*Artemisia tridentata*, *Purshia tridentata*) (Durham et al. 2017). These grasslands support diverse invertebrate communities of pollinators (e.g., native bees, butterflies, moths), herbivores (e.g., grasshoppers, sap feeders), and predators (e.g., spiders, wasps, hemipterans) (Kuhlman and Burrows 2017; Doherty et al. 2021; Bullington et al. 2021). Various bird species that nest and/or forage in these grasslands (e.g., sparrows, thrushes, blackbirds, catbirds, Blake et al. 2023) rely heavily on invertebrate

prey during breeding and migratory periods (Elphick et al. 2001). Small mammals, including omnivorous deer mice (*Peromyscus maniculatus*), also consume invertebrates (Pearson 2000; Pearson et al. 2000), and, through granivory, alter grassland plant community structure and function (Pearson et al. 2022b).

Mantis *religiosa* natural history

Here, we provide a brief natural history background and community assessment as the basis for constructing and parameterizing our model (see Clark-Wolf et al. 2022; Pearson and Clark-Wolf 2023). *Mantis religiosa* is a dominant generalist predator that sits at the apex of its trophic guild due to its large body size, near-instantaneous reflexes, and broad feeding habits (Gurney 1950; Prete et al. 1999). Generalist invertebrate predators like *M. religiosa* can generate powerful and widespread impacts on ecosystems (Snyder and Evans 2006), including direct effects on prey (Fagan and Hurd 1991; Fagan et al. 2002), intraguild predation or displacement of other predators (Polis and Myers 1989; Moran et al. 1996; Crowder and Snyder 2010), and herbivore suppression sufficient to cause trophic cascades (Moran and Hurd 1997). Although mantids' negative direct effects on all insect groups would be reasonable to assume, negative indirect effects are plausible (e.g., exploitative competition, *sensu* MacArthur 1970) and positive indirect effects have been observed (e.g., competitive release, Fagan and Hurd 1994; Moran and Hurd 1997). Impacts on invertebrate predators may be most severe due to a combination of negative direct (i.e., predation) and indirect (i.e., competition) effects (Snyder and Evans 2006).

Adult mantids are sometimes eaten by birds, small mammals, and lizards (Gurney 1950; Nyffeler et al. 2017), but lizards are rare in western Montana grasslands (Ortega and Pearson 2001). Because of its cryptic coloration, sit-and-wait hunting strategy, and preference for roosting low in the vegetation canopy (Gurney 1950; Rathet and Hurd 1983; Battiston and Fontana 2023), predation seems unlikely to act as a strong control on adult *M. religiosa*. Birds may damage oothecae (egg cases) and eat eggs, as documented in a similar mantid species (*Stagomantis limbata*, Arizona, USA, Fagan 2002). Yet, *M. religiosa* oothecae occur low in dense vegetation (often grass), making them difficult for birds to find and attack (Rose

and Hurd 2016). Rodents may depredate mantids, but we could find no information to support this.

Alternatively, parasitism can cause substantial mortality to mantids. Among the several parasites of *M. religiosa*, *Podagrion* spp. wasps are well-studied (Breland 1941). These circumboreal parasitoid wasps are thought to be generalists attacking several genera of mantids and known to infect *M. religiosa* (Gurney 1950; Helfer 1987; Bolu and Özaslan 2015). Female wasps oviposit in mantid ootheca and wasp larvae develop as external parasites on mantid eggs. They produce multiple generations per year and are active in the winter, amplifying parasitism rates when conditions are favorable (Breland 1941). Indeed, 79–94% of *S. limbata* oothecae were parasitized by *Podagrion* spp. wasps, reducing mantid emergence by 35–37% (Fagan and Folarin 2001; Fagan 2002), but it is unclear if *Podagrion* wasps have reached western Montana. Inspection of dozens of oothecae has revealed no evidence (e.g., emergence holes or hatching adults, B.L. personal observation). However, a student recently hatched wasps from an *M. religiosa* ootheca bought online, suggesting one way that the wasps could be introduced (P. Leach, personal communication).

Besides predation and parasitism, certain abiotic conditions can limit mantid populations. *Mantis religiosa* produces only one generation per year and requires a lengthy developmental period until reaching maturity (95 days on average, Hideg 1995). Mantid nymphs and adults cannot survive freezing, and local populations may be extirpated where freezing temperatures occur before females have oviposited. Eggs of *M. religiosa* can withstand extreme cold, but some mortality occurs at temperatures below -25 °C, increasing as the temperature falls further (Salt and James 1947). Temperatures in this range have sporadically occurred in western Montana since 1949 (Appendix S1, Fig. S1), suggesting that overwinter survival of mantids could vary from year to year, and could be influenced by climate change.

Evidence of mantid colonization

The first recorded observation of *M. religiosa* in western Montana dates to 2006 (Montana Natural Heritage Program). To our knowledge, no formal monitoring has been conducted for this species in the region. To examine anecdotal trends in mantid populations,

we queried iNaturalist (iNaturalist), an online platform for citizen scientist observations. We retrieved records of insects (class Insecta) from 1976 (when records on the platform in this region begin) to 2024 within a rectangular area of 6,325,075 ha in western Montana (southwest corner: 45.8394 latitude, -115.5397 longitude; northeast corner: 48.6433 latitude, -112.8590 longitude). To ensure data quality we filtered results to research-grade observations which require a verifiable location, date, and agreement from at least two other users on species identification. Observations of captive individuals were excluded. From these records, we created two datasets: one for *M. religiosa* ($n=230$) and another for all other insects ($n=16,582$). We mapped *M. religiosa* locations (Fig. 1) within the study area and then summed

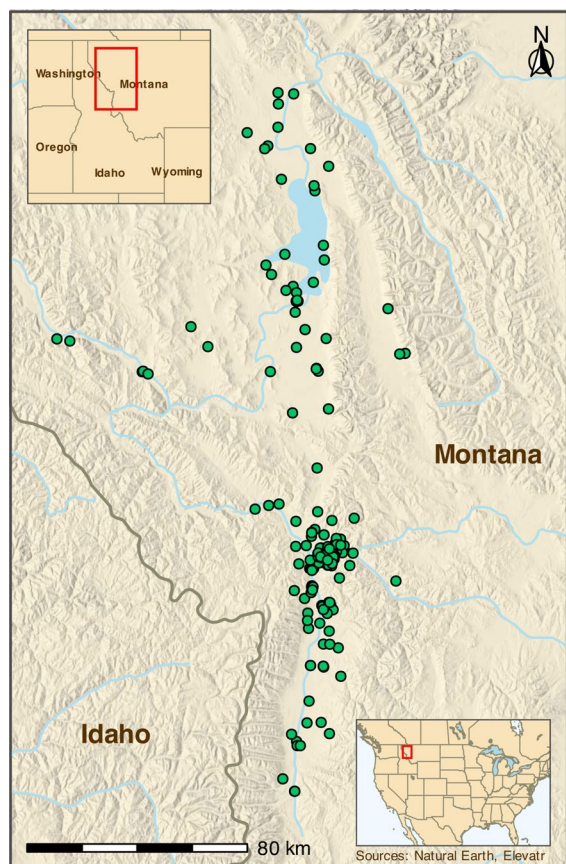


Fig. 1 Map displaying the focal area in western Montana under invasion by *Mantis religiosa*. Inset maps show the focal area enclosed in a red box. Green points show locations of *M. religiosa* observations made by citizen scientists from 2015–2024 and downloaded from iNaturalist

observations per year for the past ten years. Maps were produced using R (R Core Team 2012) and data from the rnatualearth (Massicotte and South 2023) and elevatr (Hollister et al. 2023) packages.

Because the number of citizen scientists using iNaturalist likely increased during the years under consideration, survey effort was presumed to also increase in time. To correct for this, we calculated mantid observations per 1,000 insect observations per year. We then performed a linear regression, using year as the independent variable and the relativized mantid observation rate as the dependent variable, to test whether mantid abundance changed over time. A Shapiro–Wilk test confirmed that regression residuals did not deviate from normality ($W=0.92$, $p=0.35$). The regression and diagnostics were done in R (R Core Team 2012) using the tidyverse package (Wickham et al. 2019). Over the past ten years, observations of *M. religiosa* have increased significantly ($R^2_{Adj}=0.66$, $p<0.01$, Fig. 2).

Fuzzy interaction webs

Constructing a FIW begins by defining the nodes that reflect an ecological network. Nodes commonly represent species, but they may also represent functional or taxonomic groups, abiotic elements like precipitation or cold, or concepts like management actions.

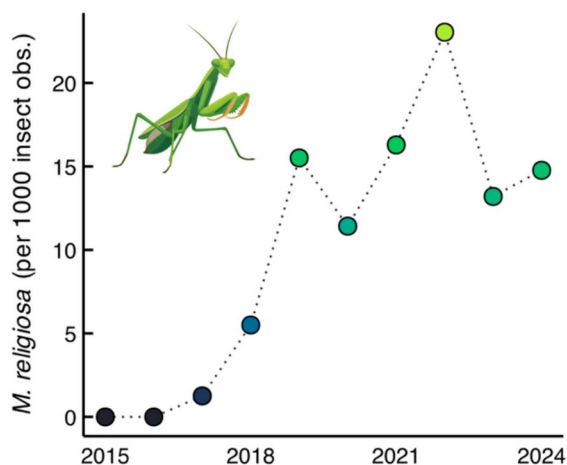


Fig. 2 Points represent observations of *Mantis religiosa* per 1000 insect observations per year in the focal area shown on Fig. 1. Data for mantid and insect observations were downloaded from iNaturalist. The color gradient corresponds to the observation rate (y-axis value)

This flexibility allows for the integration of ecological and human processes in one model. Each node, once defined, is assigned an abundance value, drawn from empirical data, literature, or expert opinion. The modeler defines a minimum, mode, and maximum abundance for each node, then sets a current value within that range. These values are transformed into the unit interval $[0, 1]$ using fuzzy logic (McNeill and Thro 1994; Nguyen et al. 2018), allowing abundances with diverse ranges, distributions, or units to be handled uniformly.

Interactions between nodes (e.g., predation, facilitation) are represented by linkages, which are further defined by numeric values from -1 to 1 , with sign indicating direction (positive or negative) and magnitude indicating the interaction's strength. These interaction strengths are stored in a square matrix, where each row-column pair defines the effect of one node on another. As with abundances, interaction strengths are drawn from empirical data, literature, or expert opinion, and they can be bidirectional, but need not be reciprocal. Once abundances, linkages, and interaction strengths are set, a fixed-point iterative method solves the system to equilibrium (Kosko 1992; Ramsey and Veltman 2005). These equilibrium abundances—still on $[0, 1]$ —are back-transformed to the original units using the same fuzzy logic previously described. This solution defines a baseline FIW. Experiments are conducted on a FIW by designating input nodes, which affect but are not affected by the system. Changing the abundance of an input node yields a new equilibrium among all other nodes, resulting in new abundance values (“outputs”). The difference in node abundances between the baseline and experimental FIWs reveals the magnitude of perturbation effects. For a more thorough description of fuzzy logic, FIW modeling, and its application to ecological systems, we refer the reader to the supplementary materials in Clark-Wolf et al. (2022).

Constructing the mantis FIW

We explored the ongoing invasion by *M. religiosa* in western Montana using the MPG Matrix, a web-based tool with a graphical user interface (<https://matrix.mpgranch.com>) designed for creating and analyzing FIWs (Clark-Wolf et al. 2022). From the MPG Matrix, we leveraged the existing MPG Grasslands FIW (<https://matrix.mpgranch.com/#/>

[matrices/bd9880](https://matrix.mpgranch.com/#/)), which was built to model the habitat where we find *M. religiosa* in western Montana (Clark-Wolf et al. 2022). Using the community assessment framework proposed by Pearson et al. (2022a), we pruned the MPG Grasslands FIW to only those nodes and interactions germane to *M. religiosa*. After pruning, 11 nodes remained. For these, we retained the existing abundance estimates, which were derived from the literature (1/11 nodes) or long-term monitoring conducted by MPG Ranch, a private conservation area (10/11 nodes, <https://www.mpgranch.com>). To this set of 11, we added three new nodes: one for *M. religiosa*, one for its parasitoid wasp, and one for winter severity.

To set the abundance of *M. religiosa*, we began with local survey results. We estimated *M. religiosa* density at 1.25 mantids/1000 m² in our system in 2024 using area census and mark-recapture methods (Rathet and Hurd 1983; Hurd et al. 1994, 2020; Appendix S2). We believe this estimate is conservatively low for our system because the population is relatively new and iNaturalist data suggest that our mantid populations declined by roughly 32% from 2022–2024 concomitant with winter cold snaps (see below and Fig. 2). Accordingly, we also used published density estimates for introduced mantids in other parts of North America where they have been established long enough to reach equilibrium abundances (introduced in the northeastern United States in 1899, Gurney 1950). In long-established populations in Delaware, *M. religiosa* densities averaged 60 mantids/1000 m² (Rathet and Hurd 1983) and the nonnative mantid *Tenodera sinensis* averaged 158 mantids/1000 m² (Hurd et al. 2020). Because old-field habitat in Delaware is more productive than our system, we set the modal abundance for mantids at a conservative value of 30 mantids/1000 m², or half of the published values for *M. religiosa* in Delaware. We set the maximum abundance at 158 mantids/1000 m², acknowledging that even higher densities may be possible in productive systems, so that we could investigate the effect of what we would consider very high mantid density in Montana. The minimum potential abundance was set to zero, resulting in a minimum, mode, and maximum abundance of $\{0, 30, 158\}$. Finally, we extracted the measured densities from individual plots in the Delaware studies (Rathet and Hurd 1983; Hurd et al.

2020) and calculated the 15th and 85th percentile values for later use in experimental scenarios.

With the abundance parameters for mantids set, we linked the mantid node to invertebrate herbivore, invertebrate predator, pollinator, small mammal, and songbird nodes. The next step was to set interaction strengths for these linkages while allowing for the fact that interactions are commonly asymmetric, i.e., the interaction strength of mantids to pollinators may differ from pollinators to mantids. We began by setting the interaction strengths for mantid predation on prey nodes. To do this, we used data from experiments conducted at the University of Delaware with *M. religiosa* and various invertebrate groups (Fagan and Hurd 1991, 1994). These experiments provided data from control and treatment enclosures, from which we calculated per capita interaction strengths following the method of Paine (1992). Interaction strengths for specific prey taxa, usually grouped at the order or family level, were then summed into the insect guilds represented as nodes in our FIW. However, these studies (Fagan and Hurd 1991, 1994) applied predator augmentation (sensu Price 1987) at mantid densities greater than those observed in the field, potentially resulting in upward biased interaction strengths (Wootton and Emmerson 2005). To address this situation, we scaled down the interaction strengths to levels consistent with our FIW, maintaining their relative proportional values across nodes. We also included data from another study in Delaware that used *T. sinensis* at field-relevant densities (Moran and Hurd 1997). These data were already calculated as interaction strengths and summarized in a figure from which we visually estimated the values. Sometimes, the assignment of interaction strengths from these studies to specific linkages in our FIW was ambiguous. For example, Fagan and Hurd (1991) demonstrated an effect of mantids on insects in the order Coleoptera, but they did not differentiate mantids' effects on predatory versus herbivorous beetles. In cases like this, interaction strengths were assigned evenly among possible linkages.

With the interaction strengths of mantids on prey nodes set, we then turned to the opposite interaction by setting prey nodes' influence on mantids. No published data were available for these interaction strengths. For nodes representing the insect prey, we used dietary data from a gut content analysis of *M. religiosa* (Shmerling et al. 2022), reasoning that

prey frequencies reflect the relative contribution of each taxon to mantid abundance. From Fig. 15 of that study, we visually estimated the frequencies of prey taxa and grouped them into the guilds used in our FIW. As before, we split interaction strengths evenly among guilds when these taxonomic order-based data were ambiguous. To normalize the values, we divided each guild's sum by the maximum, yielding relative proportions. We then scaled these proportions to levels consistent with our FIW, maintaining their relative proportional values as previously described. For nodes with no empirical data—such as birds or small mammals—we estimated low interaction strengths based on natural history understandings as described above (e.g., birds likely exert only minor effects on mantids).

For parasitoid wasp abundance, published estimates were unavailable. We estimated wasp abundance relative to that of mantids by using counts of *Podagrion* spp. parasites emerging from *Stagomantis carolina* oothecae collected in nature by Breland (1941): mean $\cong 28$ wasps per parasitized ootheca, $n=6$. Not all oothecae are parasitized. In grassland sites occupied by both *S. limbata* and *Podagrion* spp., the parasitism rate across oothecae was 79% (Fagan and Folarin 2001), implying a mean of $28 \times 0.79 \cong 22$ wasps per ootheca when all ootheca are considered. For the next step in this calculation, we needed to estimate the number of oothecae per mantid. Conservatively, we assumed that female mantids oviposit only once, implying 22 wasps per female mantid. Since only females oviposit, this value was halved to 11 to estimate the ratio of wasps to all mantids, based on an even sex ratio of hatching mantids (*T. sinensis*, Hurd et al. 1994). Finally, since not all female wasps survive long enough to reproduce (Fagan and Folarin 2001), we adjusted the ratio of wasps to mantids at 6:1, a value we consider conservative, resulting in a modal abundance of $(6 \text{ wasps} \times 30 \text{ mantids}/1000 \text{ m}^2 = 180 \text{ wasps}/1000 \text{ m}^2)$ and a maximum abundance of $(6 \text{ wasps} \times 158 \text{ mantids}/1000 \text{ m}^2 = 948 \text{ wasps}/1000 \text{ m}^2)$. Because we have no evidence that wasps have colonized western Montana yet, we set their minimum abundance to zero, resulting in abundance parameters of {0, 180, 948}. To set the interaction strength of wasps on mantids, we again considered data from a grassland site with *S. limbata* colonized by *Podagrion* spp. wasps. On average, 37% of emergents from parasitized ootheca were wasps (Fagan

and Folarin 2001), but, since only 79% of ootheca were parasitized, we set the interaction strength at $(79\% \times -0.37 / 100) = -0.29$ for the linkage between parasitoid wasps and mantids.

To set parameters for the winter severity node, we used data from a growth chamber study where exposure to -31.5°C killed 30% of mantid eggs (Salt and James 1947). This suggests an interaction strength of -0.3 on mantid recruitment whenever this temperature is reached. Using this data point, we defined winter severity as the number of days per winter with a minimum temperature at or below -31.5°C . To set the abundance function for winter severity, we made several assumptions. First, we retrieved daily weather data from two international airports in western Montana (Missoula and Kalispell, NCEI 2025; Appendix S1). Between the winters of 2014–15 and 2021–22, no temperatures below -31.5°C occurred (Fig. S1), implying a minimum winter severity abundance of zero. During this period, *M. religiosa* observations steadily increased (Fig. 2). Then, in the winters of 2022–23 and 2023–24, there were one and two cold events, respectively, followed by a 32% decline in mantid observations (Fig. 2). Based on this crude correlation, we speculated that the recent window of warm winters favored *M. religiosa* invasion and recent cold snaps may have reduced mantid populations, partly leading to the low density we censused in 2024. Accordingly, we set the modal abundance of cold events to two so that it was consistent with the measured abundance of mantids. However, these cold events are historically rare. Since 1948, temperatures at or below -31.5°C have been recorded in only 13 winters in our low-elevation study area. For such events to occur in consecutive winters, as just happened in 2022–23 and 2023–24, is rarer still, having occurred just once before in 1948–49 and 1949–50 (Fig. S1). That these extreme cold events are both rare and (recently) associated with a major decline in mantid observations suggests they should be accounted for in our model. Finally, since 1948, the most severe winters occurred in 1949–50, with five cold events, and in 1978–79, with seven. Based on this, we set the maximum winter severity at six, resulting in abundance parameters of $\{0, 2, 6\}$.

With the FIW's topology finished, we used an iterative process to tune the interaction strengths (Clark-Wolf et al. 2022). This step is necessary because true interactions strengths are rarely known

and extremely difficult to experimentally derive (Wootton and Emmerson 2005; Novak et al. 2011; Kleinhesselink et al. 2022). First, we set the parasitoid wasp, winter severity, and mantid node abundances to zero in alignment with pre-introduction conditions. Then, we incrementally adjusted interaction strengths among the original MPG Grassland FIW nodes until their abundances approximated the original estimated values for this system to within 5% (see Clark-Wolf et al. 2022 for details). Ratios among interaction strength estimates were maintained as much as possible during tuning. Constraining the tuning process by the field abundance estimates and the proportionality of interaction strengths greatly limits the number of viable combinations of interaction strengths that can generate a similar empirically defined FIW. The interaction strength matrix is available in the supplementary material (Appendix S3, Table S1).

Once tuning was finished, the baseline FIW representing pre-introduction conditions of western Montana's grasslands was complete. In this FIW, the mantid node was designated an "input" and set to zero, representing the community without mantids present. This allowed us to run experimental scenarios, manipulating mantid abundance and evaluating system responses. The results from these scenarios were then compared with the pre-introduction baseline FIW to determine how increasing mantid abundance influenced other nodes. However, because we also planned to examine how altered abiotic conditions and natural enemies might influence current mantid populations, it was necessary to generate a second baseline FIW. This FIW uses the same topology and interaction strength matrix as the pre-introduction baseline, but two changes were required to model post-introduction conditions. First, the mantid node was set to "output" so that it would respond to other nodes in the FIW. Second, because the post-introduction conditions measured in 2024 followed two consecutive years of severe cold snaps, we set the number of severe winter events to two. Under these conditions, the mantid node reached an equilibrium abundance of $27.55/1000\text{ m}^2$. We designated this FIW as the post-introduction baseline. This allowed us to run experimental scenarios manipulating the abundance of parasitoids and incidence of severe winter events, which affect mantids directly, producing an indirect system response.

Impacts of increased mantid abundance

Using our two baseline models, we explored nine scenarios relevant to the invasion of *M. religiosa* (Table 1). The first four scenarios are experiments based on the pre-introduction baseline FIW. In these scenarios, we manipulate the abundance of mantids to examine impacts on the invaded community.

Scenario 1: Observed-Low. Mantid abundance was set at 1.2 mantids/1000 m², close to the density we observed in local surveys.

Scenario 2: Predicted Equilibrium. Mantid abundance was set at ~28 mantids/1000 m², which approximates the equilibrium density predicted in the post-introduction baseline FIW.

Scenario 3: Observed-Mid. In this scenario, we increased mantid abundance to ~40 mantids/1000 m², which is approximately the 15th percentile of densities measured in individual plots in Delaware (Rathet and Hurd 1983; Hurd et al. 2020).

Scenario 4: Observed-High. In this scenario, we tested the effect of a high density of mantids by ramping their abundance to ~132, which is approximately the 85th percentile of densities measured in individual plots in Delaware (Rathet and Hurd 1983; Hurd et al. 2020).

Table 1 List of experimental scenarios and abundance values used in two sets of models depicting *Mantis religiosa* influences in western Montana grasslands. The first model set portrays the pre-introduction baseline FIW, which evaluates the effects of *Mantis religiosa* on the community as its abundance is increased from zero in scenarios 1–4. The second model set

Effects of abiotic filters and natural enemies

These scenarios are based on the post-introduction baseline FIW where mantid abundance has reached equilibrium with the modeled system. Here, we adjusted the intensity and abundance of abiotic filters and natural enemies independently and interactively (Table 1) to see how these changes affect mantid abundance and propagate through the community. Increased and decreased winter severity were both modeled because future conditions are uncertain due to climate change. Climate volatility, caused by Arctic amplification (Cohen et al. 2021), may increase the frequency of winter cold events despite long-term warming (Doss-Gollin et al. 2021). Increased cold events should suppress mantid populations. Alternatively, long-term warming could support mantid population growth if it produces longer summers and milder winters. Longer summers at higher latitudes correlated with *M. religiosa*'s expanding range in Europe (Steger et al. 2020).

Scenario 5: No Cold Snaps, No Wasps. We examined the effect that reducing the number of cold events may have on the system by setting winter severity to zero. This scenario assumes the absence of mantids' natural enemies (parasitoid

portrays the community with mantids present at equilibrium abundance, represented by the post-introduction baseline FIW. This set predicts how mantids respond to natural enemies and abiotic conditions as these pressures are varied in scenarios 5–9 and, indirectly, how the mantids' response propagates through the community

Model set and scenario	Mantids (per 1000 m ²)	Parasitoid wasps (per 1000 m ²)	Winter severity (number of days)
Pre-introduction baseline FIW	0	0	0
1. Observed-Low	1.2	0	0
2. Predicted Equilibrium	27.42	0	0
3. Observed-Mid	40.24	0	0
4. Observed-High	132.40	0	0
Post-introduction baseline FIW	27.55	0	2
5. No Cold Snaps, No Wasps	33.23	0	0
6. Four Cold Snaps, No Wasps	24.53	0	4
7. No Cold Snaps, 6X Wasps	26.04	267.55 [†]	0
8. Two Cold Snaps, 6X Wasps	22.46	219.94 [†]	2
9. Four Cold Snaps, 6X Wasps	19.16	195.36 [†]	4

[†]Parasitoid wasp abundance was calculated at 6× the initial mantid abundance as described in the methods

wasp abundance also set to zero). This scenario reflects potential future warming or historically common abiotic conditions that have been exceeded in the two winters before this study.

Scenario 6: Four Cold Snaps, No Wasps. We examined the effect of increased winter severity in the absence of natural enemies by doubling the incidence of cold events.

Scenario 7: No Cold Snaps, 6X Wasps. In this scenario, we contrasted how mantids are controlled by enemies while being released from abiotic control. First, winter severity was reduced from 2 to 0 events and the mantid node reached a temporary equilibrium of 45 mantids/1000 m². Then, parasitoid wasps were ramped from zero to 270 wasps/1000 m², maintaining the 6:1 ratio with mantids.

Scenario 8: Two Cold Snaps, 6X Wasps. This scenario maintained winter severity from the baseline FIW and introduced parasitoid wasps into the system at the 6:1 ratio with mantids. Here, mantids' abundance at equilibrium before introducing wasps was ~37, resulting in a wasp abundance of ~220 wasps/1000 m².

Scenario 9: Four Cold Snaps, 6X Wasps. We examined the effect of maximal controls on the system. First, we increased the number of cold events from 2 to 4. The mantid node reached a temporary equilibrium of 33 mantids/1000 m². Then, we ramped parasitoid abundance to ~195 wasps/1000 m², again maintaining the 6:1 ratio with mantids.

For each scenario, we used the MPG Matrix's sensitivity analysis tool to test for uncertainty in modeled interaction strengths. For each permutation in the sensitivity analyses, we randomly varied the interaction strengths between experimentally manipulated "input" nodes and their direct linkages by $\pm 50\%$ (the lone exception is described in Appendix S4, see Table S2 for specific ranges for each node). The sensitivity analysis used 10,000 permutations, and the median value of the permuted distribution is reported along with 95% confidence intervals in the figures. If a confidence interval did not overlap zero (zero indicates no change in abundance), we inferred strong support that the node is likely to change as predicted due to the scenario's manipulation(s). When confidence intervals slightly overlapped zero, but the

median remained far from zero, we inferred moderate support for change. If confidence intervals overlapped zero substantially, with the median close to zero, we inferred weak support for change. Sensitivity analysis results were compared across scenarios using the same criteria (i.e., non-overlapping CIs are presumed to reflect differences in abundance estimates). The results of sensitivity analyses were summarized using R (R Core Team 2012) and the tidyverse (Wickham et al. 2019), ggplot2 (Wickham 2016), and knitr (Xie 2025) packages.

Results

Constructing the Mantis FIW

The baseline FIWs comprised 14 nodes and 76 linkages (Fig. 3). The pre-introduction baseline FIW is publicly available on the MPG Matrix website (<https://matrix.mpgranch.com/#/matrices/bf3590>) and the post-introduction baseline FIW is shared at (<https://matrix.mpgranch.com/#/matrices/e096f7>). Links to the FIWs for each scenario are available in the supplementary material (Appendix S5, Table S3). The baseline and scenario FIWs may be discovered, duplicated, and modified by anyone with internet access. To manipulate the FIWs, users should reference the *How to Use* guide and *FAQ* page, both accessible via conspicuous headings on the website.

Impacts of increased mantid abundance

In Scenario 1 (Observed-Low), increasing mantid abundance from zero to the current estimated density resulted in negligible impacts (Fig. 4). In Scenarios 2–4, incremental increases in mantid abundance caused incremental declines in the invertebrate nodes' abundances when compared to the pre-introduction baseline condition. These declines were strongly supported by the sensitivity analyses (Fig. 4). Scenario 4 (Observed-High) produced declines of the greatest magnitude, with invertebrate predators declining the most, followed by invertebrate herbivores and pollinators (Fig. 4). The pattern was similar in Scenarios 2 (Predicted Equilibrium) and 3 (Observed-Mid), where invertebrate predators were most impacted, followed by invertebrate herbivores and pollinators, all with strong support (Fig. 4). The abundance of grassland

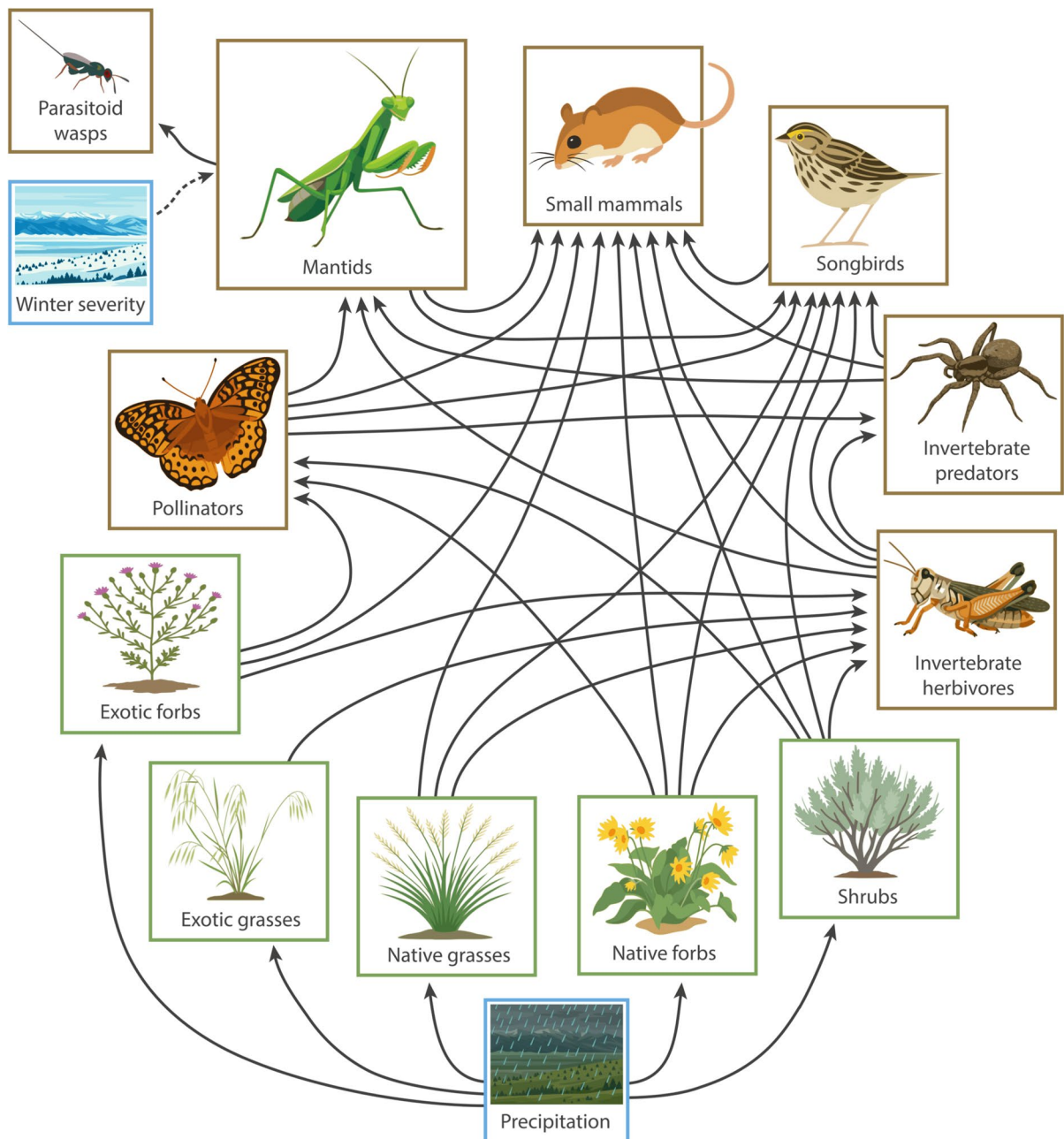


Fig. 3 Network diagram of the food web topology used to model the invasion of *Mantis religiosa* in western Montana, USA. Linkages and arrows show trophic energy or resource flows through the web, with one exception. The linkage between Winter severity and Mantids, shown with a dashed line, points in the direction of the direct negative effect of this node on mantids. For clarity, linkages of other non-trophic interactions (e.g., plant-plant competition) are not shown. This

topology is the same across scenarios: the pre-introduction scenarios, where altered mantid abundance produces changes in other nodes, and the post-introduction scenarios, where winter severity and parasitoids affect mantids, indirectly affecting other nodes. Box color indicates the ecosystem component or trophic group: blue for abiotic elements, green for primary producers, and brown for consumers. See the FIWs online for additional detail (links in Table S3)

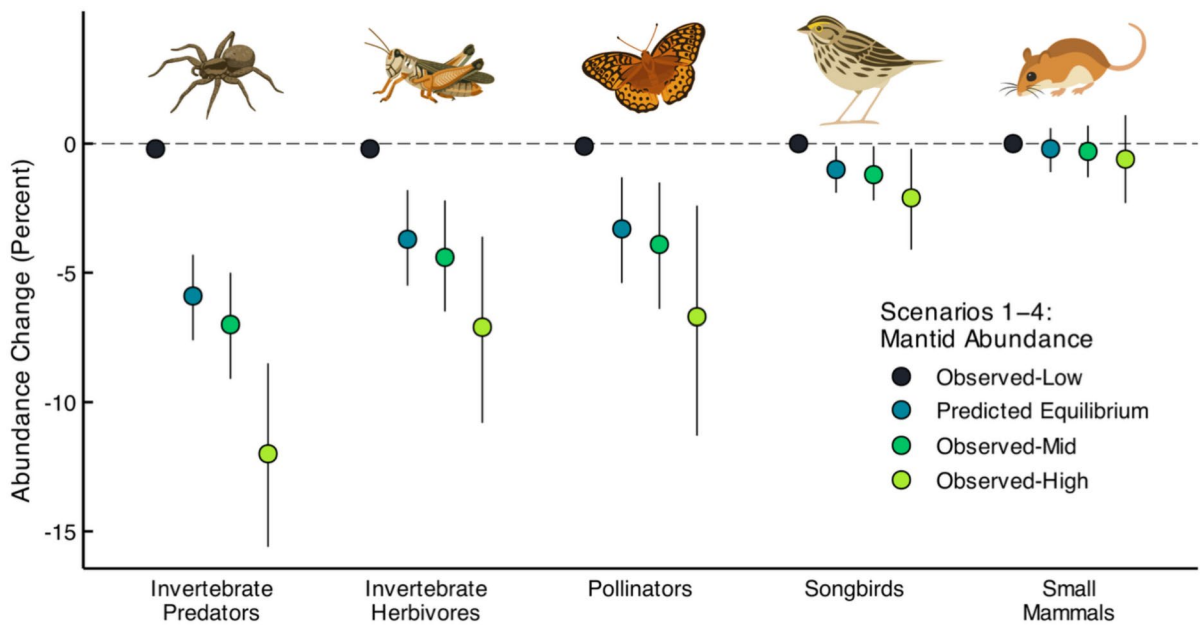


Fig. 4 Percentage abundance change for target nodes in Scenarios 1–4, each corresponding with incrementally increased *Mantis religiosa* abundance, from a starting abundance of zero, based on the pre-introduction baseline FIW. Scenario 1 (Observed-Low) reflects field-estimated abundance in western Montana (1.2 mantids/1000 m²). Scenario 2 (Predicted Equilibrium) uses the equilibrium mantid abundance predicted by the post-introduction baseline FIW (27.4 mantids/1000 m²). Mantid abundance in Scenario 3 (Observed-Mid) is based on

an estimate from Delaware (40.2 mantids/1000 m², the 15th percentile of individual plots). Mantid abundance in Scenario 4 (Observed-High) is also based on an estimate from studies in Delaware (132.4 mantids/1000 m², the 85th percentile of individual plots). Points show median percent change. Vertical lines encompass 95% confidence intervals; these are derived from a sensitivity analysis (10,000 permutations). Point color indicates scenario and the color gradient reflects increasing mantid abundance from least (black) to most (light green)

songbirds was also predicted to decline slightly due to increased mantid abundance, with moderate support (CIs were near but did not overlap zero). We saw negligible support for a change in small mammal abundance with all median estimates near zero and CIs overlapping zero.

Comparing across scenarios, the largest negative responses were produced in Scenarios 3 and 4, which predicted impacts associated with the 15th or 85th percentile mantid abundances as measured in studies from Delaware. Between these scenarios, responses separated by a relatively wide margin, with negative response of invertebrate predators in Scenario 4 exceeding that in Scenario 3 by 42%, with strong support (Fig. 4). The separation between Scenarios 3 and 4 was moderately supported for invertebrate herbivores, pollinators, and songbirds (Fig. 4). However, affected guilds showed only small abundance differences when comparing Scenario 2 (mantids at

predicted equilibrium for Montana) and Scenario 3 (15th percentile abundance measured in Delaware, Fig. 4).

Effects of abiotic filters and natural enemies

With mantids present in the system at equilibrium abundance (i.e., the post-introduction baseline condition), and winter severity and parasitoid wasp abundance set to zero (Scenario 5: No Cold Snaps, No Wasps), the abundance of mantids increased 11%, with moderate support (Fig. 5a). However, this was the only scenario in this set where the abundance of mantids grew from an already established population. In contrast, mantid abundance declined by 14% when winter severity was increased in Scenario 6 (Four Cold Snaps, No Wasps), again with moderate support (Fig. 5a). When parasitoids were present and winter severity was reduced to zero (Scenario 7: No Cold Snaps, 6X Wasps), the change

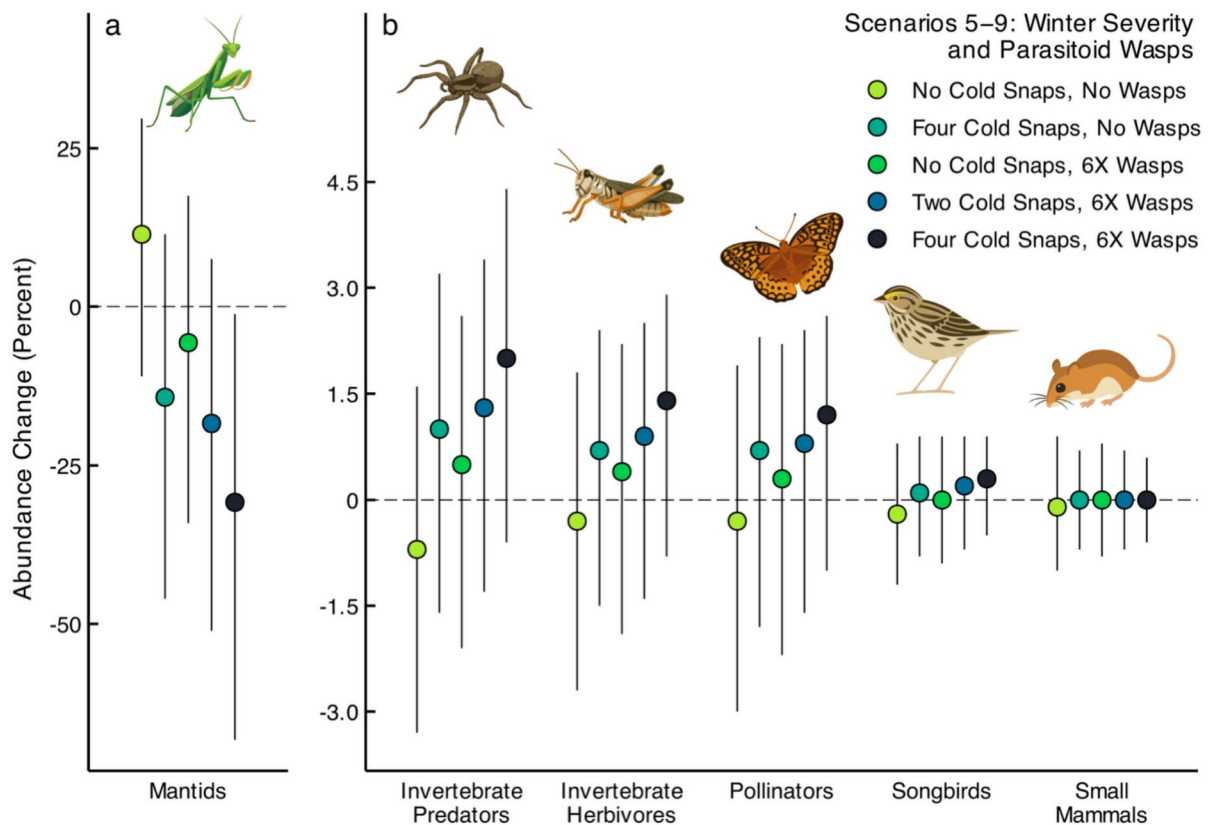


Fig. 5 Percentage abundance change for **a** *Mantis religiosa* and **b** target nodes in Scenarios 5–9. These scenarios correspond to altered winter severity and presence/absence of parasitoid wasps. They are based on the post-introduction baseline FIW with mantid populations already established. Scenario 5 (No Cold Snaps, No Wasps) sets winter severity and parasitoids at zero. Scenario 6 (Four Cold Snaps, No Wasps) increases winter severity while holding parasitoids at zero. Scenario 7 (No Cold Snaps, 6X Wasps) sets winter severity to zero and increases parasitoids (to 6×the initial mantid

abundance, see methods). Scenario 8 (Two Cold Snaps, 6X Wasps) uses baseline winter severity and increases parasitoids. Scenario 9 (Four Cold Snaps, 6X Wasps) increases both winter severity and parasitoids. Points show median percent change. Vertical lines encompass 95% confidence intervals; these are derived from a sensitivity analysis (10,000 permutations). Point color indicates scenario and the color gradient reflects increasing mantid abundance from least (black) to most (light green)

in mantid abundance was still negative, but smaller, and with only slight to moderate support (Fig. 5a). The combined effects of increased winter severity and parasitoids produced larger declines in mantids. With winter severity held at baseline conditions and parasitoids introduced into the FIW (Scenario 8: Two Cold Snaps, 6X Wasps), mantid abundance fell further, with moderate to strong support, and when conditions for mantids were at their most severe (Scenario 9: Four Cold Snaps, 6X Wasps), mantid abundance declined 31%, with strong support (Fig. 5a).

Comparing across scenarios, mantid abundance differed greatly, with moderate to strong support, between the positive effects of reduced winter severity (Scenario 5) and the strong negative effects of severe winters and parasitoids combined (Scenario 9). In contrast, the difference in mantid abundance when influenced only by severe winters (Scenario 6) or only by parasitoids (Scenario 7), was small, with only slight support (Fig. 5a).

The effects of winter severity and parasitoid abundance on mantids exerted ramifying indirect effects on other nodes. The increase in mantids due to reduced winter severity (Scenario 5) was associated

with slight declines in invertebrate predator, herbivore, and pollinator nodes, with moderate to slight support (Fig. 5b). In all other scenarios, these nodes tended to increase in abundance, consistent with a release from predation or competition. When winter severity was increased to four cold events, but without parasitoids present (Scenario 6), the recovery of invertebrate nodes was modest, with slight to moderate support (Fig. 5b). The smallest positive effects occurred under the opposing effects of reduced winter severity and abundant parasitoids (Scenario 7), with invertebrate predators, herbivores, and pollinators recovering slightly, with moderate to slight support. However, when the effects of winter severity and parasitoids were aligned—in Scenarios 8 and 9—we observed the largest positive effects on invertebrate nodes. In Scenario 8, invertebrate recovery was moderately supported, and in Scenario 9, with four cold events plus abundant parasitoids, invertebrate recovery was substantial, with moderate-strong support for invertebrate predators and moderate support for herbivores and pollinators (Fig. 5b). In all scenarios, cascading effects on birds and small mammals were negligible.

With parasitoid wasps alone (Scenario 7) or in combination with increased winter severity (Scenarios 8 and 9), predicted invertebrate abundances diverged substantially from the mantid-favoring scenario with reduced winter severity and no wasps (Scenario 5). Support for the contrasting outcomes of these scenarios varied. Compared with Scenario 5, invertebrate recovery had slight support in Scenario 7 and moderate support in Scenarios 8 and 9. However, high winter severity without parasitoids (Scenario 6) produced a negligible recovery in invertebrate nodes. Similarly, the difference in invertebrates' predicted outcomes between Scenario 6, with increased cold alone, and Scenario 7, with parasitoids but no cold, was negligible (Fig. 5b).

Discussion

Proactive management of biological invasions requires the ability to rapidly predict which introduced species might cause serious ecological impacts. However, predicting impacts of introduced species in complex ecological systems remains a challenge. Here, we applied a qualitative modeling approach,

adapted from the social sciences, to assess the potential impacts of the European praying mantis in western Montana grasslands. Our model suggests that at current abundances, mantid impacts are likely negligible. However, if mantids reach the modest to high densities observed in other introduced ranges, they could cause substantive reductions in key invertebrate guilds, with potentially ramifying effects on native grassland songbirds. Importantly, the model also predicted that native North American parasitoids could suppress mantid populations below these impact levels if they establish naturally or are introduced. Finally, this suppression was predicted to persist even if future winters become milder—a condition otherwise predicted to favor mantid population growth. While we emphasize that these are model-based predictions, FIWs like the one applied here have performed well when tested against empirical data from species introductions in complex communities (Clark-Wolf et al. 2022). Below, we explore the implications of our findings and discuss the potential for applying FIWs for predicting impacts on invasion fronts.

Two key predictions from our model are 1) current mantid populations likely have negligible impacts in our system, but 2) if they increase to moderate or high densities observed elsewhere, they could have substantive impacts on specific taxa. The finding that *M. religiosa*'s impacts scale with its abundance is consistent with invasion theory and empirical studies (Parker et al. 1999; Pearson et al. 2016; Dick et al. 2017; Sofaer et al. 2018). While we cannot speak to whether these relationships are linear or nonlinear (Thiele et al. 2010; Barney et al. 2013), our models predict that declines could average 7–12% (with estimate boundaries reaching as high as 11–16%) at high mantid abundance for important taxa like pollinators and other invertebrates that have already experienced dramatic global declines (Goulson 2019; Wagner et al. 2021). This information is valuable to managers because it allows them to see how increased abundance levels of the introduced species are linked to predicted impacts on specific taxonomic groups, providing a barometer for deciding if and when to intervene. The importance of acting before introduced species become serious pests is well-documented to be the most cost-effective and logistically feasible strategy for invasive species management (Venette et al. 2021; Ahmed et al. 2022). Hence, providing barometers for monitoring and triggering management of

introduced species is a powerful tool for invasive species management.

The potential consequences of mantid impacts could be substantive for some taxa. For example, the potential for declines in pollinators due to mantid predation is concerning given the ecological importance of pollinators (Klein et al. 2007; Ollerton et al. 2011). The presence of at least 229 bee species, many of them rare, in the area of western Montana under invasion by *M. religiosa* provides one example of the threat posed by nonnative mantids (Kuhlman and Burrows 2017). Also, in our model, mantid predation on pollinators and invertebrate herbivores resulted in a loss of prey for other consumers, including both invertebrate predators and grassland birds. Of the affected guilds, invertebrate predators were predicted to decline the most, a counterintuitive outcome driven by both direct (intraguild predation) and indirect (competition) effects (Fig. 4). These findings are consistent with unanticipated indirect effects that have been predicted and documented in other systems involving generalist insect or arthropod predators (Polis and Myers 1989; Snyder and Evans 2006; Crowder and Snyder 2010) and are potentially additive to the declines already documented for invertebrate predators (Samu et al. 2023). The extension of competitive effects to grassland songbirds was unexpected, but decreased abundance of insectivorous birds has previously been attributed to declining insect foods (Lister and Garcia 2018; Møller 2018; Tallamy and Shriver 2021). In our model, predicted reductions in birds occurred when mantid populations were substantially elevated. While the predicted declines were small (2–3%), grassland bird species have experienced long-term declines (Rosenberg et al. 2019), making additive effects of invader impacts potentially concerning.

The likelihood of mantids causing these or other impacts may depend in part on future abiotic conditions. If extreme winter events become less frequent or dissipate in a warming climate, the model predicts that *M. religiosa* populations will increase, generating increased ecological impacts. This prediction aligns with previous observations in western Montana. From 2015 to 2022, a period of mild winters, citizen scientist observations of *M. religiosa* grew by an average of 118% per year (Fig. 2). In 2022, adult male mantids—conspicuous because they fly—were so abundant that the local newspaper attributed the

population surge to recent mild winters and predicted further growth due to climate change (Erickson 2022). Populations of *M. religiosa* may have continued to increase had such mild winters persisted, but in 2022–2024, observations declined by 32% following two consecutive winters with severe cold snaps (Fig. 2). These anecdotal data seemingly corroborate our purported relationship between mantid populations and winter severity, supporting the inclusion of winter severity as an abiotic filter in the FIW. However, temperatures near the ground, where oothecae rest, may differ from above-ground air temperatures. For example, deep snow traps heat from the ground and protects it from desiccating wind (Pauli et al. 2013). Reduced snow accumulation in future milder winters may counterintuitively expose oothecae to colder temperatures and increased desiccation (Zhu et al. 2019). Future research on how microclimate affects ootheca hatch rates and mantid densities will be necessary to refine our understanding of how weather affects *M. religiosa* populations.

Perhaps our most significant finding is the prediction that parasitoid wasps native to North America could prevent mantid populations from causing serious impacts—regardless of future winter conditions. In a future with benign winters, our conservatively estimated density of parasitoids is sufficient to produce a small but negative change in mantid abundance (Fig. 5a). Based on this model, we predict the combination of constant pressure from parasitoids and occasional severe winters would make the strongest impacts seen in Scenarios 3 and 4 unlikely. This combination may also prevent mantids from reaching the equilibrium abundance modeled in Scenario 2. This prediction is good news, especially because this prospective biocontrol agent already exists on the continent, avoiding the logistically and financially demanding, ecologically risky, but sometimes necessary, process of importing a nonnative biocontrol agent (Simberloff 2012; Lee et al. 2024). Also, given the lack of restrictions on ootheca transport across state lines, the arrival of *Podagrion* spp. wasps seems inevitable. These wasps are well-adapted to cold winters, as one congener has been observed as far north as 52.75° latitude in Russia (iNaturalist community 2024), a latitude 5° north of our study area in western Montana. However, we caution that Montana hosts two rarely observed native mantids in the genus *Litaneutria*. Although the potential for *Podagrion* spp.

wasps to parasitize them is unknown, the wasp's host range is broad among mantids, with hosts from four genera already known (Gurney 1950; Helfer 1987; Bolu and Özaslan 2015). The potential risk to our native mantid species via apparent competition suggests an immediate need to test whether *Podagrion* spp. wasps can parasitize ootheca of *Litaneutria* spp. mantids, and if so, to assess the potential harm the parasitoids may cause should they establish, particularly if their population is augmented by the introduced *M. religiosa*.

Tools to evaluate invader impacts and potential management solutions are critical given the ongoing threats and costs associated with introduced species (Pimentel et al. 2000). At least 11,000 nonnative species have established in the United States (Simpson and Eyler 2018), and the pace of introductions is likely accelerating. When nonnative species are first detected on an invasion front, ecologists and land managers must quickly predict which ones are likely to become invasive. This task can seem overwhelming given limited resources (Pimentel et al. 2000). Traditional quantitative models carry stringent data requirements that can be difficult to meet, especially with organisms and systems that are understudied (which is likely in most systems), or where species abundance estimates and interaction strengths are difficult to obtain. FIWs provide an actionable alternative, with growing applications in ecology and conservation (Ramsey and Veltman 2005; Baker et al. 2018; Clark-Wolf et al. 2022; Pearson and Clark-Wolf 2023; Pearson et al. 2025). The critical advantage of FIWs for application to new invasions is not a difference in the amount of data required; rather, it is the capacity to integrate a range of data types and varying data precision (Clark-Wolf et al. 2022). Our modeling exercise demonstrates how FIWs can be used to quickly assess potential invader impacts on an invasion front while also evaluating the influence of abiotic conditions and the potential efficacy of management actions (i.e., natural enemies for biological control). However, as with any model, predictions obtained with FIWs are only as reliable as the data used to parameterize them. Accordingly, data can—and should—be updated via monitoring and experimentation in the modeled system where possible. In this regard, the tool is highly amenable to adaptive management. Importantly, the FIWs we built and the tool we used are publicly available via a user-friendly

online interface (<https://matrix.mpgranch.com>) that allows users to modify and deploy FIWs even if they lack substantial experience with the code that generates the model. It is our hope that this tool will benefit both prediction of invader impacts and invasive species management actions for improved conservation.

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Author contributions All authors contributed to the study conception, design, and preliminary literature review. Material preparation, data collection and analysis were performed by Beau G. Larkin and Dean E. Pearson. The first draft of the manuscript was written by Beau G. Larkin and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Data and annotated code are available on GitHub at <https://github.com/bglarkin/mantrix.git>

Declarations

Conflict of interest The authors' declared that they have no conflict of interest.

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