ORIGINAL PAPER

The effect of invasive fall armyworm abundance on native species depends on relative trophic level

Pengxiang Wu[1,2] · Kai Shi[1,2] · Tianhao Zhang[1,2] · Megan L. Head[3] · Runzhi Zhang[1,2]

Abstract

Fall armyworm (FAW) has posed a significant threat to Chinese agriculture and native species since its presence was first reported in 2019. To better understand the impacts of FAW, however, information on how FAW abundance affects native abundance and communities and whether these effects are dependent on the trophic level of native species relative to FAW is needed. Here, we studied the direction, strength, and shape of the relationship between FAW abundance and responses of native abundance and community-level metrics (mean value of unit-scaled richness, diversity, and evenness). We then tested how relative trophic position influenced these relationships. Across 25 study sites in Yunnan province, we recorded FAW abundance ranging from 0 to 715 individuals per 2666.8 m^2. Across this range, native abundance declined nonlinearly by 14.6%, on average, and community metrics declined linearly by 18.1%. For lower trophic levels, FAW caused a significant nonlinear decline in native abundance (20.7%) and community metrics (28.6%), with the greatest declines occurring at low FAW abundance. At the same trophic level, native abundance (9.1%) and community metrics (14.5%) declined nonlinearly and linearly, respectively. In contrast, FAW had no significant impact on native abundance or community metrics at higher trophic levels. At the community level, negative impacts were stronger for evenness and diversity than for richness. The results of our analyses suggest native responses to FAW invasion rely strongly on FAW abundance and trophic position. The FAW abundance–native response relationships reveal how FAW impacts may develop during the invasion process and when to best manage them.

Keywords *Spodoptera frugiperda* · Invasion · Abundance · Community metrics · Trophic position

Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is an invasive noctuid moth that damages more than 180 plant species but prefers maize (Fan et al. 2021; Garcia et al. 2019; Cruz-Esteban et al. 2018). For maize alone, the

✉ Runzhi Zhang
zhangrz@ioz.ac.cn

1   State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, 1-5 Beichen West Rd., Chaoyang, Beijing 100101, China

2   University of Chinese Academy of Sciences, Beijing 100049, China

3   Division of Ecology and Evolution, Australian National University, Canberra, ACT 2600, Australia

economic losses of crop yield from FAW can reach between 15 and 73% worldwide (Guo et al. 2018; Hruska and Gould 1997). Native to the Americas, FAW lives year-round in tropical and subtropical regions and undergoes seasonal migrations as far north as temperate North America (Jiang et al. 2019; Westbrook et al. 2016). Outside of their native distribution FAW is highly invasive. After recent introductions into West Africa in 2016 (Cock et al. 2017; Koffi et al. 2020), and India in 2018 (Sharanabasappa et al. 2018; IPPC 2018, 2019), FAW has spread to neighboring countries at an alarming rate (NATESC 2019a, b; Stokstad 2017). In January 2019, FAW was first reported in China (Yunnan province, southwest China), and by September 2019, it had reached almost all southern Chinese provinces (Wu et al. 2019; NATESC 2019c, d). China is the world's second-largest maize producer where maize is grown in all provinces (Li et al. 2020). Therefore, Chinese crop production and native species would be seriously threatened if FAW were to reach the main maize-growing regions annually. Given the rapidly

escalating economic influence of FAW, understanding how its impacts are likely to develop during the invasion process is important for determining the best timing for pest management.

Invasive species are well known to have negative impacts on the abundance of native species as well as on the composition of native communities (i.e., reduction in richness, diversity, and evenness) (Bezemer et al. 2014; Kenis et al. 2009). These adverse effects can be seen for a broad range of invasive taxa, across a variety of ecosystems (Cameron et al. 2016; Gallardo et al. 2016; Thomsen et al. 2011). However, research evaluating the impact of invasive taxa has generally focused on the presence or absence of invasive species and ignored how this impact may change over the course of an invasion, as invader abundance increases (Strayer et al. 2006). Increased understanding of how the abundance of invasive species impacts native species abundance and native communities (species diversity) will be valuable for predicting the threat they pose to native communities (Cassey et al. 2006; Gilbert and Levine 2013), estimating the costs and benefits of control strategies (Yokomizo et al. 2009), and prioritizing management activities (Byers et al. 2002).

Evaluating threat levels of invasive species relies on the assumed relationship between invader abundance and impact. Some studies have shown that impacts increase linearly with invasive abundance, with no density-dependent relationship (Parker et al. 1999). More recently, others have proposed a density-dependent relationship, with impacts increasing or decreasing nonlinearly with invader abundance (Thiele et al. 2010; Barney et al. 2013). For a new invader, invasive abundance–impact relationships are likely to be determined by the trophic position of native species relative to invasive species (Bradley et al. 2019). Therefore, variation in the relationship between invader abundance and impacts on native species may, in part, be driven by their relative trophic level (Ricciardi et al. 2013; Thomsen et al. 2014).

Ecological theory suggests that for native species that occupy a lower trophic level than invaders, biological invasion may have strong, negative, nonlinear effects on abundance due to density-dependent effects (Volterra 1926). During the initial stages of invasion, when the density of the invading species is low, native species may show a rapid decline in numbers. However, later during invasion, when the density of the invading species is higher, the abundance of native species may stabilize at a smaller size, thus leading to a nonlinear relationship between native species abundance and invader abundance (Strayer 2010; Benkwitt 2015). Moreover, invasive species could also affect the composition of lower trophic levels in native communities; however, the shape of responses needs further study (Moyle and Light 1996; Estes et al. 2011). For native species that occur at the same trophic level as an invading species, relationships

between invader abundance and native species abundance are primarily driven by competition (Levine et al. 2003). The abundance of native species typically shows a linear decline when effects of competition are not density-dependent; however, field studies often find that competition is density-dependent and thus may cause a nonlinear decline in the abundance of native species (Law and Watkinson 1987). Further, research has shown that species diversity of the native community that occupies the same trophic level as an invader may vary with the spatial scale of analysis, but these studies are rarely followed up with further analyses of the shape of the responses to invader abundance (Powell et al. 2011). When native species occupy a higher trophic level than invasive species, increasing invader abundance could be positively or negatively related to the abundance of native species (Volterra 1926), as the effect of invader abundance will depend on whether they remove or add resources for native consumers. However, many studies show that negative impacts of invader abundance on the abundance of native (e.g., Vilà et al. 2011; Litt et al. 2014; Tallamy 2004) suggest that this response may be more likely to occur. While the impact of invader abundance on the composition of higher trophic levels within native communities is hard to determine, some studies assert that invasive species could have no impact or just a small positive impact at this level (Thomsen et al. 2014; Gallardo et al. 2016).

A recent meta-analysis by Bradley et al. (2019) supports the idea that the relationship between invader abundance and impact on native species and communities is dependent on their relative trophic level. Their study showed that across all the invasive species studied on average lower trophic levels showed a nonlinear decline in native populations and communities, and same trophic levels showed a linear decline, while higher trophic levels show non-significant relationships. However, as noted earlier there is also variation among invasions in how relative trophic level interacts with invader abundance to affect impact on native communities. This variation between invasive and native species in the abundance–impact relationship means that empirical assessment is necessary to accurately predict the impact of any particular invasive species (Sofaer et al. 2018). Thus, further study, especially on highly invasive species, which proliferate quickly, is needed to determine the role of trophic level in driving abundance–impact relationships in specific systems.

Here, we describe how native abundance and communities respond to increasing abundance of the invasive FAW, quantifying the direction (negative or positive), strength, and shape (linear or nonlinear) of this relationship for different trophic interactions. We study FAW impacts based on empirical evidence of how FAW abundance–impact relationship varies between response level (abundance or community), among trophic categories (lower, same, higher), and among community-level metrics (evenness, diversity, richness).

This analysis of highly invasive pest also provides a test of ecological theory associated with native species' abundance and community responses to novel species interactions.

Materials and methods

Study site

In China, FAW was first reported in Yunnan Province—a region that is considered a biodiversity hotspot (Wu et al. 2021a). Because of the diverse agroecosystems and climates in Yunnan, FAW can survive over winter and breed year-round throughout the Province. We selected 25 study sites representing a broad geographic area and range of altitudes (from 619 to 2710 m) in the mountainous area of Huize County, Yunnan Province, China, between latitudes 103°03′E—103°55′E and longitudes 25°48′N—27°04′N (Fig. S1 in Supporting Information). Study site were spaced 13.1 to 128.6 km apart.

Survey design

Each study site was surveyed monthly from April to October 2019 (i.e., 6 survey rounds). During each survey round, 4 new plots (each plot covers 1 mu, 666.7 m^2), covering a total area of 2666.8 m^2 (4 mu), were sampled in each site (i.e., over the whole study 24 independent plots were sampled per site). Within sites and survey rounds, plots were spaced 0.3 to 2.2 km apart and were located in areas with high crop diversity and no pesticide use to ensure a large species pool. The surveys within each round were conducted within a period of 7 days to minimize impacts of phenology. In each study site, every crop plant was surveyed (total number of plants $= 7459 \pm 540$ plants per site), and all plant species were identified. The number of uninfested plants per species was recorded, and the data were included in this analysis of unaffected native species. Once infested plants were identified, arthropods (including adult, larvae, and eggs) were dissected from inside the plants and collected. We dissected 1558 ± 164 infested plants per study site. We then used a gasoline-powered reversible leaf blower (Burkard Vortis EA0001) with a fabric bag securely inserted into the vacuum end, to sample arthropods in the areas surrounding the plants. This "insect vac" was passed over a 9×9 m area for 60 s until no arthropod activity was detected. Once an area had been vacuumed, the specimens were removed from the vacuum and emptied into a ziplock bag (40×50 cm) containing cotton balls soaked with ethyl acetate. This was repeated until the whole plot had been vacuumed. All specimens from the dissections and vacuums were stored in a freezer and then sent to Institute of Zoology, Chinese Academy of Sciences for identification.

Arthropod specimens were identified to the species level using appropriate taxonomic keys and direct comparison with voucher specimens that were expertly identified. Identified species were then counted and assigned to trophic groups: detritivore, herbivore, predator, parasitoid, or omnivore. Detritivores (mostly collembolans) were not counted in all study sites due to their overwhelming abundance, and omnivores (mostly muscoid flies) were not identified to a sufficient level. Thus, detritivores and omnivores were excluded from trophic analyses. According to published literature (Zhang and Zhao 1996), herbivores were classified as the "same" trophic level as FAW, while predators and parasitoids were placed in a "higher" category and plants were placed into a "lower" category. The plant and arthropod species surveyed are listed in Table S1 in Supporting Information.

Calculating abundance and community-level metrics

Averaged responses of native abundance and community metrics to FAW by transforming the mean value of unit-scaled native responses at lower, the same, and higher trophic levels to the unit scale (Fig. 1). For each trophic level, we calculated native species abundance (i.e., the total number of all individuals across native species) and native community metrics (the mean value of unit-scaled richness, diversity, and evenness) (Fig. 2). Margalef richness (R), Shannon–Wiener diversity (D), and Pielou evenness (E) were used as the native community-level metrics (Lu et al. 2020). The equations for the metrics are as follows:

Margalef richness metrics:

$$R = \frac{(S - 1)}{\ln N} \tag{1}$$

Shannon–Wiener diversity metrics:

$$D = -\sum_{i=1}^{S} P_i \log_2 P_i \tag{2}$$

Pielou evenness metrics:

$$E = \frac{D}{\ln S} \tag{3}$$

where S is the number of species in an area; N is the total number of all types of individual species; and P_i is the relative abundance of each species.

Statistical analyses

Native abundance and community responses to increasing FAW abundance were evaluated through two complementary meta-analyses (Bradley et al. 2019). Both meta-analyses
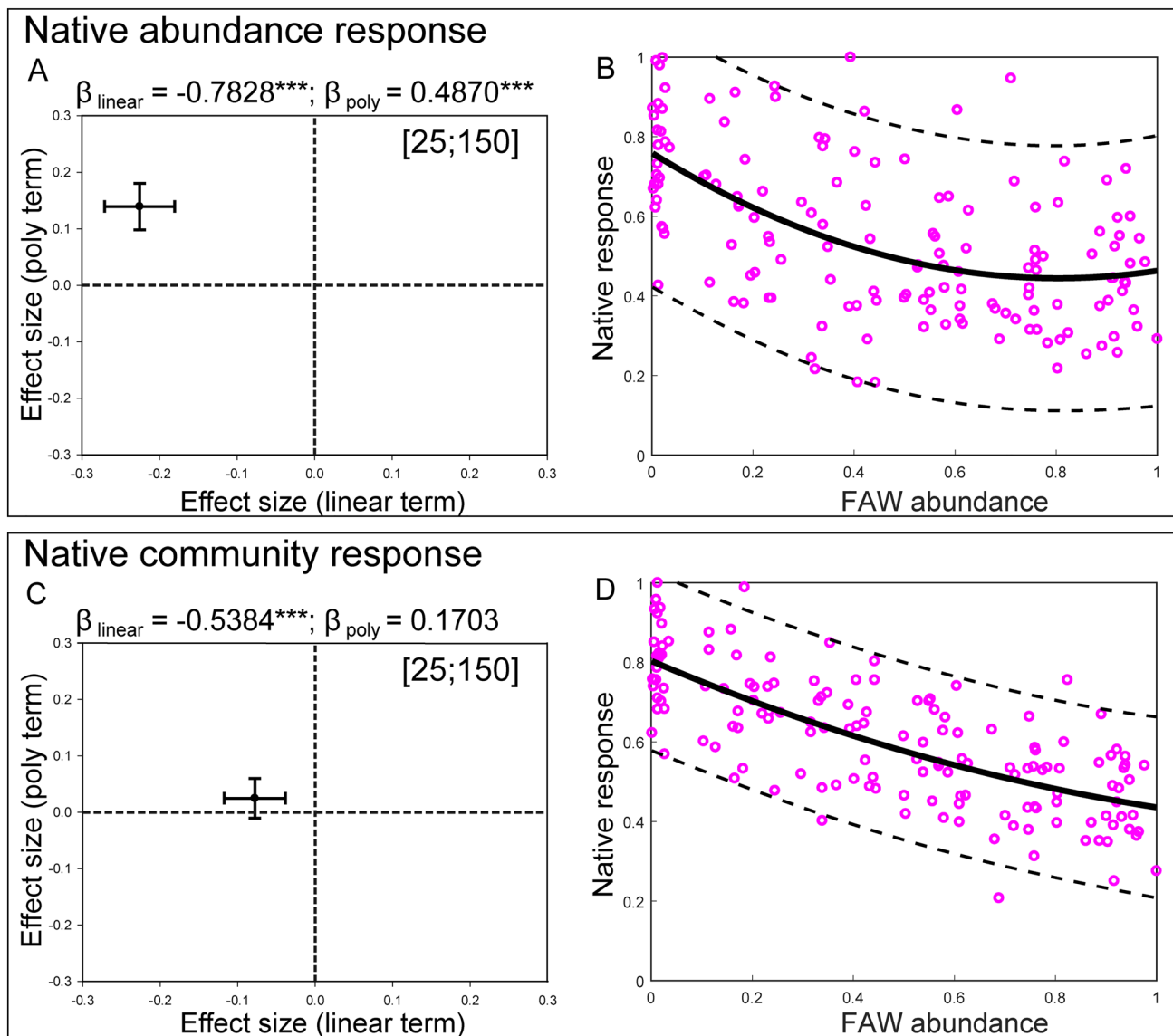
Fig. 1 Averaged native responses to FAW abundance by transforming the mean value of unit-scaled native responses at lower, the same, and higher trophic levels to the unit scale (0, 1). Native abundance response is nonlinear (**A** and **B**), while native community-level response is linear (**C** and **D**), according to both the partial-r analyses (**A** and **C**) and the slope analyses (**B** and **D**). Numbers in brackets are total study sites and data analyzed. Effect size estimates in **A** and **C** are statistically supported when 95% credible interval bars do not cross the zero lines. Black lines show model predictions with area between dotted lines indicating the 95% credible zone. Asterisks indicate significant linear (β_{linear}) or polynomial (β_{poly}) regression terms (***$P < 0.001$)

were used to determine the direction and strength of linear and polynomial components to the relationship between FAW abundance and native responses. The second meta-analysis was additionally used to reconstruct the average shape of this relationship. Both meta-analyses extracted information on response direction, strength, and shape (curvature) from the raw FAW abundance–native response data (Table S3) via a regression model:

$$y = \beta_0 + \beta_{linear}x + \beta_{poly}x^2 \qquad (4)$$

where y is the native response, x is the FAW abundance, β_0 is the intercept, β_{linear} is the linear regression term, and β_{poly} is the second-order polynomial regression term. The regression model was fit separately to raw data for each study site.

The first meta-analysis (i.e., partial-r meta-analysis) derived effect sizes from Fisher-transformed partial correlation coefficients associated with each regression term from Eq. 4 (Nakagawa and Cuthill 2007):
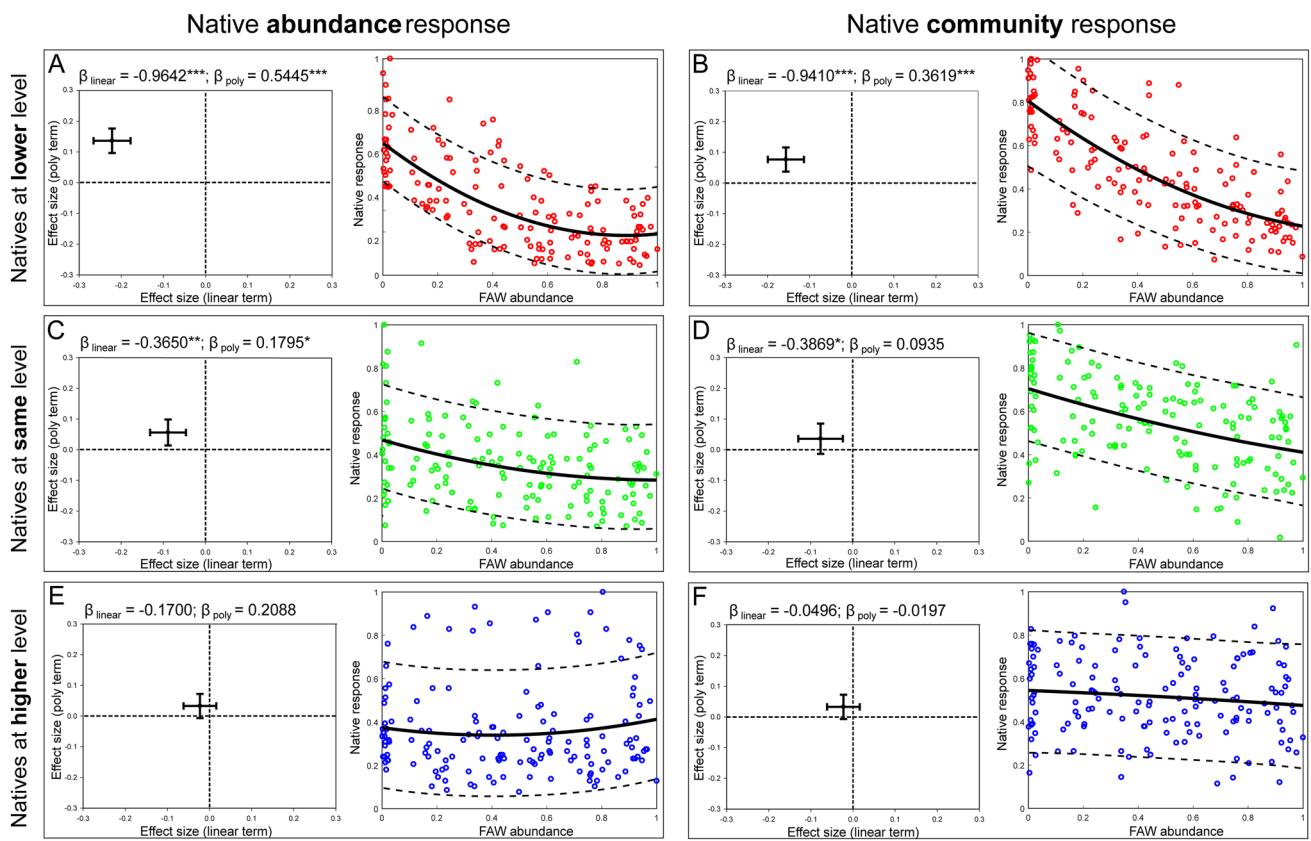
Native **abundance** response

Native **community** response

Fig. 2 Native responses to FAW abundance across different trophic categories. Responses of native abundance (the total number of all individuals across native species) at lower (**A**), the same (**C**), and higher (**E**) trophic levels. Responses of native community-level metrics (the mean value of unit-scaled richness, diversity, and evenness) at lower (**B**), the same (**D**), and higher (**F**) trophic levels. The shape and strength of FAW impacts on native abundance and communities rely largely on relative trophic position, based on both the partial-r analyses (left panel) and the slope analyses (right panel). Asterisks indicate significant linear (β_{linear}) or polynomial (β_{poly}) regression terms (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

$$r = \frac{t}{\sqrt{t^2 + df}} \tag{5}$$

$$\text{Effect size} = 0.5 * \ln\left(\frac{1 + r}{1 - r}\right). \text{(Fisher transformation)} \tag{6}$$

where r is the partial correlation coefficient for β_{linear} or β_{poly} in Eq. 4, t is the corresponding model t value, and df are the degrees of freedom associated with the same regression coefficient (Nakagawa and Cuthill 2007). Partial-r effect sizes were calculated separately for β_{linear} and β_{poly} for each study site. Effect size measurement error variance (mev) was calculated as $1/(n-3)$, where n is the sample size for a study site (Borenstein et al. 2011). We mean-centered the FAW abundance (x) for each study site before fitting Eq. 4. Repositioning of the x-axis to a mean of zero did not affect FAW abundance–native response shape, but reduced dependence between linear and polynomial effect sizes within study sites (Schielzeth 2010). Meta-analysis of the partial-r effect sizes

determined the strength and direction of linear and polynomial components of the regression fit.

The second meta-analysis (i.e., slope meta-analysis) derived effect sizes from β_0, β_{linear} or β_{poly} in Eq. 4. Nevertheless, an analysis of the three regression terms requires that FAW abundance (x) and native responses (y) be on a comparable scale as regression terms are scale dependent (Becker and Wu 2007; Koricheva et al. 2013). Therefore, we rescaled the raw data (both x and y variables) by dividing by the maximum raw data value to create an unit scale of 0–1. Here, averaged native abundance or community responses (y) were obtained by transforming the mean value of unit-scaled native responses at lower, the same, and higher trophic levels to the unit scale (0, 1) (Fig. 1). In each trophic category, native abundance response was obtained by transforming the native species abundance ($y_{\mathrm{abundance}}$) to the unit scale, while native community response ($y_{\mathrm{community}}$) was obtained by transforming the mean value of unit-scaled diversity, richness, and evenness to the unit scale (Fig. 2). Native responses of

diversity, richness, and evenness were obtained by transforming the mean value of the three community-level metrics across all trophic categories to the unit scale (Fig. 3). Subsequently, we mean-centered the rescaled FAW abundance values before analysis using Eq. 4 to generate β_0, β_{linear}, and β_{poly} effect sizes. We used the regression model-reported SE for each regression term as an estimate of effect size *mev* (Koricheva et al. 2013). The slope meta-analysis allowed us to determine the shape of the FAW abundance–native response relationship, which provided an additional test of the magnitude of β_{linear} and β_{poly}. Native abundance or community change as FAW abundance increased from 0 to 715 per study site (2666.8 m^2) was calculated using Eq. 7.

$$\text{Native response to FAW abundance} = \left(\frac{y_{x=0} - y_{x=1}}{y_{x=0}}\right) \times 100\%$$
(7)

We used Bayesian mixed-effects models (MCMCglmm in R version 4.0.5; Hadfield 2010) for all meta-analyses of the relationship between FAW abundance and native responses, to examine how FAW–native response relationship varies between response level (abundance or community), among trophic categories (lower, same, higher), and among community-level metrics (evenness, diversity, richness). More analytical details are presented in Supporting Information Part 1.
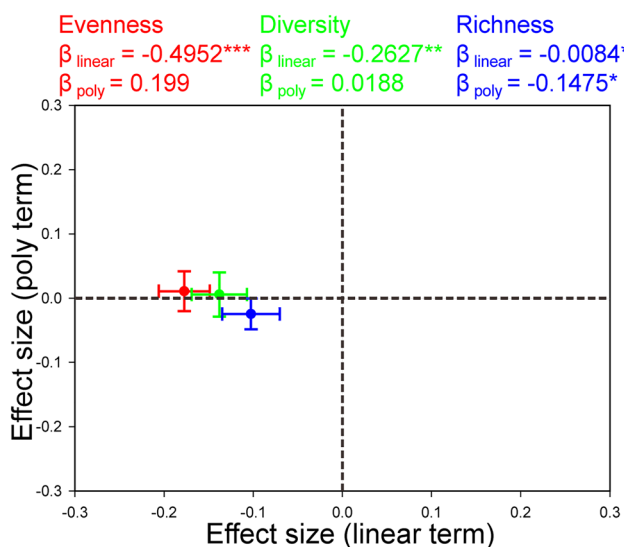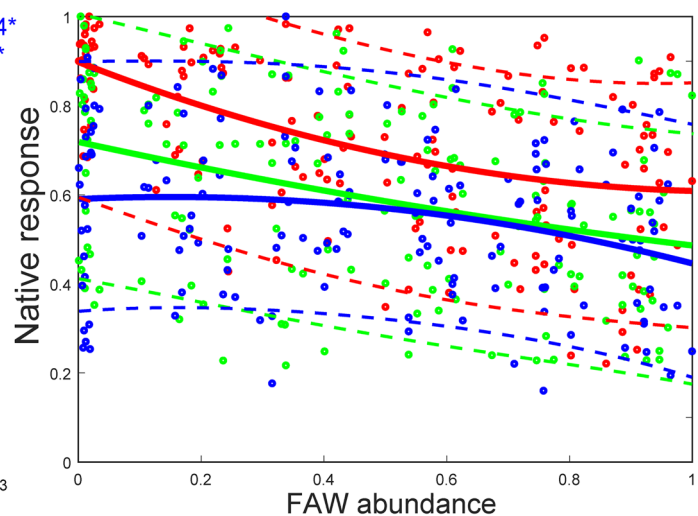
Results

Our data from 150 surveys (25 study sites × 6 survey rounds) showed a total of 15 species (a total of 824,000 individuals) at lower trophic levels, 9 species (13,688 individuals) at the same trophic level, and 14 species (6336 individuals) at higher trophic levels (Table S1). A total of 50,489 FAW individuals were recorded from across all the study sites (Table S3). In each study site (2666.8 m^2), on average, FAW abundance was 336.6 ± 18.6 individuals, with a range of 0–715 individuals per study site. Native species abundance for lower, the same, and higher trophic levels was 5493.3 ± 287.6 [765–16,532] individuals, 91.3 ± 3.9 [18–257] individuals, and 42.2 ± 2.0 [9–117] individuals, respectively. For our community-level metrics, mean native species richness for each of the trophic levels was 0.93 ± 0.05 (lower), 1.37 ± 0.07 (same), and 1.89 ± 0.09 (higher) across the study sites. Mean native species diversities for each of the trophic levels were 1.32 ± 0.07 (lower), 1.18 ± 0.05 (same), and 1.1 ± 0.05 (higher). And mean native species evenness was 0.46 ± 0.02 (lower), 0.51 ± 0.02 (same), and 0.36 ± 0.02 (higher).

As FAW abundance increased from 0 to 715 individuals per study site (2666.8 m^2), native species abundance declined dramatically. Significant linear and polynomial effects indicate that this decline was steepest at low FAW abundance, but stabilized at higher FAW abundance (Fig. 1A and B; summary statistics for model contrasts are given in Table S2). Our analysis showed an average of 14.6% decline

Fig. 3 Responses of native community-level metrics to FAW abundance. FAW has strongly negative linear impacts on evenness (red) and diversity (green), and significantly negative nonlinear impacts on richness (blue). There were significant differences between community-level responses for both linear and polynomial terms, according to the partial-r analyses (left panel) and the slope analyses (right panel). Colored lines show model predictions, with area between dotted lines indicating the 95% credible zone. Asterisks indicate significant linear (β_{linear}) or polynomial (β_{poly}) regression terms (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

in native abundance as FAW abundance increased (Fig. 1B). In contrast, a significant linear effect but non-significant nonlinear effect indicated that native community metrics showed a strong, negative linear response to increased FAW abundance with no reduction in effect at higher FAW abundance (Fig. 1C and D). Increasing FAW abundance caused native community metrics decreased by an average of 18.1% (Fig. 1D).

Native abundance and community responses to FAW abundance were dependent on the relative trophic level of native species being considered (Fig. 2; Table S2). When native species were at a lower trophic level than FAW, the relationships between FAW abundance and native abundance and the community-level metrics were significantly negative and nonlinear (Fig. 2A and B). Overall, native abundance at lower trophic levels decreased by 20.7% (Fig. 2A) and native community metrics by 28.6% (Fig. 2B) as FAW abundance increased. However, as the relative trophic position of native species shifted from lower to higher, their negative responses gradually weakened (Fig. 2). When native species were same trophic level perspective, we still found an overall drop in native abundance, and native community metrics (Fig. 2C and D), but the declines were weaker (9.1 and 14.5%, respectively) and for the community responses shifted from being nonlinear to being linear (Fig. 2D). When native species were at a higher trophic level, FAW abundance showed no significant effects on native abundance or communities, with a 1.9% increase in abundance and a 3.4% decrease in community metrics (Fig. 2E and F).

At the community level, three metrics including Pielou evenness (33.2%), Shannon–Wiener diversity (34.1%), and Margalef richness (23.3%) declined markedly as FAW abundance increased (Fig. 3; Table S2). Linear impacts were dramatically more negative for evenness ($P_{linear} = 0.0004$) and diversity ($P_{linear} = 0.0037$) than for richness ($P_{linear} = 0.0271$). Moreover, FAW abundance did not show a significant nonlinear relationship with evenness ($P_{poly} = 0.0559$) or diversity ($P_{poly} = 0.6055$), but did with richness ($P_{poly} = 0.0267$), indicating a relatively weak influence of FAW on richness at low abundance.

Discussion

Our study investigated general trends in the direction, shape, and strength of the relationship between FAW abundance and responses of native abundance and community-level metrics across three trophic categories. It is generally believed that invasive alien species have adverse effects on native species, especially at lower or the same trophic levels (Bradley et al. 2019; Baiser et al. 2010; France and Duffy 2006). Across our study sites in the Yunnan, we recorded FAW abundance ranging from 0 to 715 per 2666.8 m^2.

Within this range, we found that native abundance and community metrics decreased by an average of 14.6 and 18.1%, respectively (Fig. 1). Regardless of trophic level, FAW abundance did not positively impact native abundance and communities (Fig. 2). Rather, we found that native responses to FAW invasion tended to be strongly negative and often nonlinear, showing a convex relationship (Fig. 2A, B and C), implying that FAW abundance has the strongest impact at low levels and early in the invasion process.

Effects of FAW on native abundance and community metrics of lower trophic levels were strongly negative and consistently nonlinear (Fig. 2A and B). As illustrated with the native abundance response example (Fig. 2A), nonlinear effects on native abundance are common in ecological theory considering interactions between invasive herbivores and native plants (Volterra 1926). Similar to native abundance, native communities at lower trophic levels are also more likely to suffer from adverse effects compared with those at other trophic levels (Moyle and Light 1996). Invasive herbivores are more likely to impact native communities at lower trophic levels via nonlinear effects, and the impacts tend to be strongest at low invader abundance (Mcewan et al. 2009), as with the FAW example (Fig. 2B). From a biological invasion viewpoint, low invader abundance typically occurs at initial stages of invasion (Bradley et al. 2019). Therefore, in invaded areas where invaders tend to impose nonlinear effects, the most effective way to reduce invasive impacts is to provide timely early detection and rapid response to new invasions (Westbrooks 2004; Crall et al. 2012). The assumption is that once FAW establishes in an invaded area, eradicating it may be a more appropriate and valid approach to protecting native species than just reducing FAW abundance. However, FAW eradication is impractical. Many current control strategies are nonspecific to FAW and affect non-target species (e.g., pesticides such as chlorpyrifos, chlorfenapyr, and spinosad), throwing up a major barrier to practical application (Campos et al. 2011). Our analysis provides an explanation why FAW has a rapidly escalating impact on agriculture: If eradication is impossible, once invasive FAW reaches high abundance, control strategies would work poorly in mitigating impacts.

However, FAW impacts weakened as native species' trophic position shifted from lower to higher (Fig. 2; Table S2). When native species were at the same trophic level, the FAW invasion showed a significantly negative effect on native abundance and community metrics, but both declines were weaker. Additionally, we found that there was a nonlinear component to the effect on abundance but not the community response (Fig. 2C and D). From native abundance perspective, at the same trophic level density-dependent competition is indeed common in invasive animals (Hairston et al. 1960; Barney et al. 2013; Law and Watkinson 1987). At the community level, for native species

(e.g., competitors of FAW), management of FAW abundance at any stage of invasion would likely prove effective for promoting the richness, diversity, and evenness of native communities.

In contrast, higher trophic levels of native abundance and communities did not show a significant and consistent response to FAW (Fig. 2E and F). However, previous studies have shown that influences of invasive species can cascade up to higher trophic levels (Gallardo et al. 2016; Vilà et al. 2011; Litt et al. 2014). Given the small though not negligible impacts of FAW, we further found that native abundance responses were non-significantly positive (increased by 1.9%; Fig. 2E). Some biological invaders could act as foundation species forming new habitat structure, increasing physical resources and space for native consumers (Gutiérrez 2017). Contrary to abundance responses, native community responses to FAW were slightly negative (decreased by 3.4%; Fig. 2F). FAW may be a foundation species, but is more likely to result in a loss of resources for native consumers. For instance, suppression of native insects resulting from competition with invasive species could adversely affect communities of native consumers at higher trophic levels because many native consumers tend to be specialists of native insects (Litt et al. 2014; Tallamy 2004). Our study reveals that to some extent native consumers may suffer both positive and negative impacts from FAW. In summary, higher trophic levels of native responses are not particularly positive or even slightly negative, indicating that FAW is more likely to reduce resources for native consumers rather than increase them. As such, native species at higher trophic levels would profit from management aimed at reducing FAW abundance at any stage of invasion.

At the community level, although all three metrics (evenness, diversity, and richness) were negatively related to FAW abundance, there were differences between the metrics in the strength and shape of this relationship (Fig. 3; Table S2). Increasing FAW abundance had a greater negative effect on evenness and diversity than on richness. Although species richness is by far the most commonly reported community-level metric, it is a relatively conservative method assessing community changes based on species removal or addition. Invasive species generally spend a very long time removing native species (seem like local extinctions) (Gilbert and Levine 2013), which explains a smaller decline in richness. In addition, our analysis showed that richness tends to decline more slowly during the initial stages of invasion and more rapidly at higher levels of FAW abundance, whereas evenness and diversity decline in a linear fashion. There is a tendency that biological invaders are more likely to impact common native species at the early stages of invasion and rare native species only later (Powell et al. 2013). Our results indicate that lower richness resulting from species removal may not become fully apparent until later stages of FAW

invasion (possibly because common species often have high abundance and thus are difficult to remove), whereas declines in evenness and diversity may occur more quickly and appear to be more sensitive metrics of community change.

Predicting the ecological impact of a species without known invasion history or previous economic impact is extremely challenging because it is likely to be unknown before invading new regions (Paini et al. 2016; Zhang et al. 2009). Although the economically significant pest FAW is a known invasive species and a global threat to agriculture, it has been only a year since FAW was first detected in China, and so we are cautious with our conclusions. Due to its short invasion history in China, our analysis focuses on the establishment phase of FAW invasion, prior to spread and impact. More regions in China will suffer from the substantial ongoing FAW threat over the coming years, so our analysis is still far from "saturated" and "homogenized." Nevertheless, we expect the patterns uncovered in this analysis to be sufficiently robust to meet the expectations of long-term prediction.

In conclusion, our results show that overall, increasing FAW abundance has clear negative effects on native abundance and community metrics (including richness, diversity, and evenness) and that these negative effects are strongest for lower trophic levels. Further, significant nonlinear responses indicate a rapid decrease in native abundance and community-level responses at low FAW abundance, which are likely to correspond to early stages of FAW invasion. These results highlight the value of early detection and rapid responses to FAW invasion—a management strategy which has proven cost effective for eradicating early infestations in the past (Leung et al. 2002). However, FAW eradication via early detection and rapid response looks unfeasible practically, because many current control strategies such as pesticides are nonspecific to this highly invasive species (who can spread rapidly from a restricted range up to a widespread range). Rather than eradicating FAW, we tend to emphasize the importance of good pre-border biosecurity. A stronger commitment to proactive policies preventing new invasions is essential to avoiding the economic and ecological impacts of alien species (Early et al. 2016). As China continues to expand international trade, it will also consistently increase its crop production, which could make stronger connections between China and other countries (Hulme 2009; Levine and D'Antonio 2003). Therefore, the pressures from FAW will only intensify (Early et al. 2018; Wu et al. 2021b). And, of course, it requires a greater coordination and cooperation between countries. From China's perspective, the formation of a national body responsible for FAW (e.g., National Agro-Tech Extension and Service Center, NATESC) could not only enable the FAW management at the early stages of invasion but also provide those regions most vulnerable to

FAW with more accurate and timely information. NATESC would provide all necessary support and available resources to protect the Chinese border and limit the further spread of FAW.

Author contributions

PW and RZ conceived and designed research. PW and KS conducted experiments. PW, KS, TZ, and MLH analyzed data. PW, MLH, and RZ wrote the manuscript. All authors read and approved the manuscript.

Declarations

Conflicts of interest The authors declare no conflict of interest.

References

Baiser B, Russell GJ, Lockwood JL (2010) Connectance determines invasion success via trophic interactions in model food webs. Oikos 119:1970–1976. https://doi.org/10.1111/j.1600-0706.2010.18557.x

Barney JN, Tekiela DR, Dollete ES, Tomasek BJ (2013) What is the "real" impact of invasive plant species? Front Ecol Environ 11:322–329. https://doi.org/10.1890/120120

Becker BJ, Wu MJ (2007) The synthesis of regression slopes in meta-analysis. Stat Sci 22:414–429. https://doi.org/10.1214/07-STS243

Benkwitt CE (2015) Non-linear effects of invasive lionfish density on native coral-reef fish communities. Biol Invasions 17:1383–1395. https://doi.org/10.1007/s10530-014-0801-3

Bezemer TM, Harvey JA, Cronin JT (2014) Response of native insect communities to invasive plants. Annu Rev Entomol 59:119-U740. https://doi.org/10.1146/annurev-ento-011613-162104

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2011) Introduction to MetaAnalysis. John Wiley and Sons, West Sussex

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019) Disentangling the abundance–impact relationship for invasive species. Proc Natl Acad Sci USA 116:9919–9924. https://doi.org/10.1073/pnas.1818081116

Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Hayes EC (2002) Directing research to reduce the impacts of nonindigenous species. Conserv Biol 16:630–640. https://doi.org/10.1046/j.1523-1739.2002.01057.x

Cameron EK, Vilà M, Cabeza M (2016) Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Glob Ecol Biogeogr 25:596–606. https://doi.org/10.1111/geb.12436

Campos MR, Picanco MC, Martins JC, Tomaz AC, Guedes RNC (2011) Insecticide selectivity and behavioral response of the earwig *Doru luteipes*. Crop Prot 30:1535–1540. https://doi.org/10.1016/j.cropro.2011.08.013

Cassey P, Blackburn TM, Lockwood JL, Sax DF (2006) A stochastic model for integrating changes in species richness and community similarity across spatial scales. Oikos 115:207–218. https://doi.org/10.1111/j.2006.0030-1299.15223.x

Cock MJW, Beseh PK, Buddie AG, Giovanni C, Crozier J (2017) Molecular methods to detect *Spodoptera frugiperda* in Ghana, and implications for monitoring the spread of invasive species in developing countries. Sci Rep 7:4103. https://doi.org/10.1038/s41598-017-04238-y

Crall AW, Renz M, Panke BJ, Newman GJ, Chapin C, Graham J, Bargeron C (2012) Developing cost-effective early detection networks for regional invasions. Biol Invasions 14:2461–2469. https://doi.org/10.1007/s10530-012-0256-3

Cruz-Esteban S, Rojas JC, Sánchez-Guillén D, Cruz-López L, Malo EA (2018) Geographic variation in pheromone component ratio and antennal responses, but not in attraction, to sex pheromones among fall armyworm populations infesting corn in Mexico. J Pest Sci 91:973–983. https://doi.org/10.1007/s10340-018-0967-z

Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Gonzalez P, Grosholz ED, Ibanez I, Miller LP, Sorte CJB, Tatem AJ (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Commun 7:12485. https://doi.org/10.1038/ncomms12485

Early R, Gonzalez-Moreno P, Murphy ST, Day R (2018) Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm. NeoBiota 40:25–50. https://doi.org/10.3897/neobiota.40.28165

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soule ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet Earth. Science 333:301–306. https://doi.org/10.1126/science.1205106

Fan JY, Haseeb M, Ren QL, Tian TQ, Zhang RZ, Wu PX (2021) Factoring distribution and prevalence of Fall armyworm in southwest China. J Appl Entomol 145:295–302. https://doi.org/10.1111/jen.12852

France KE, Duffy JE (2006) Consumer diversity mediates invasion dynamics at multiple trophic levels. Oikos 113:515–529. https://doi.org/10.1111/j.2006.0030-1299.14140.x

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. Glob Change Biol 22:151–163. https://doi.org/10.1111/gcb.13004

Garcia AG, Ferreira CP, Godoy WAC, Meagher RL (2019) A computational model to predict the population dynamics of *Spodoptera frugiperda*. J Pest Sci 92:429–441. https://doi.org/10.1007/s10340-018-1051-4

Gilbert B, Levine JM (2013) Plant invasions and extinction debts. Proc Natl Acad Sci USA 110:1744–1749. https://doi.org/10.1073/pnas.1212375110

Guo JF, Zhao JZ, He KL, Zhang F, Wang ZY (2018) Potential invasion of the crop-devastating insect pest fall armyworm *Spodoptera frugiperda* to China. Plant Prot 44:1–10

Gutiérrez JL (2017) Modification of habitat quality by non-native species. In: Vilà M, Hulme PE (eds) Impact of biological invasions on ecosystem services, Invading nature-springer series in invasion ecology. Springer International Publishing, Cham, pp 33–47. https://doi.org/10.1007/978-3-319-45121-3_3

Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J Stat Softw 33:1–22. https://doi.org/10.18637/jss.v033.i02

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425. https://doi.org/10.1086/282146

Hruska AJ, Gould F (1997) Fall armyworm (Lepidoptera: Noctuidae) and *Diatraea lineolata* (Lepidoptera: Pyralidae): impact of larval population level and temporal occurrence on maize yield in Nicaragua. J Econ Entomol 90:611–622. https://doi.org/10.1093/jee/90.2.611

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

IPPC (2018) First detection of fall army worm on the border of Thailand. IPPC Official Pest Report, No. THA-03/1. FAO: Rome, Italy. https://www.ippc.int/. Accessed 19 December 2018

IPPC (2019) First detection report of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on Maize in Myanmar. IPPC Official Pest Report, No. MMR-19/2. FAO: Rome, Italy. https://www.ippc.int/. Accessed 11 January 2019

Jiang XF, Zhang L, Cheng YX, Song LL (2019) Advances in migration and monitoring techniques of the fall armyworm, *Spodoptera frugiperda* (J E Smith). Plant Prot 45:12–18

Kenis M, Auger-Rozenberg MA, Roques A, Timms L, Pere C, Cock M, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45. https://doi.org/10.1007/s10530-008-9318-y

Koffi D, Agboka K, Adenka DK, Osae M, Tounou AK, Anani AMK, Fening KO, Meagher RL (2020) Maize infestation of fall armyworm (lepidoptera: noctuidae) within agro-ecological zones of Togo and Ghana in west Africa 3 yr after its invasion. Environ Entomol 49:645–650. https://doi.org/10.1093/ee/nvaa048

Koricheva J, Gurevitch J, Mengersen K (2013) Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton. https://doi.org/10.1515/9781400846184

Law R, Watkinson AR (1987) Response-surface analysis of two-species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. J Ecol 75:871–886. https://doi.org/10.2307/2260211

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc Biol Sci 269:2407–2413. https://doi.org/10.1098/rspb.2002.2179

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326. https://doi.org/10.1046/j.1523-1739.2003.02038.x

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc Biol Sci 270:775–781. https://doi.org/10.1098/rspb.2003.2327

Li XJ, Wu MF, Ma J, Gao BY, Wu QL, Chen AD, Liu J, Jiang YY, Zhai BP, Early R, Chapman JW, Hu G (2020) Prediction of migratory routes of the invasive fall armyworm in eastern China using a trajectory analytical approach. Pest Manag Sci 76:454–463. https://doi.org/10.1002/ps.5530

Litt AR, Cord EE, Fulbright TE, Schuster GL (2014) Effects of invasive plants on arthropods. Conserv Biol 28:1532–1549. https://doi.org/10.1111/cobi.12350

Lu J, Li Z, Gao T, Tang X (2020) Seed bank characteristics in a *Pinus densata* forest and its relationship with vegetation diversity in Southeast Tibet, China. Ecol Evol 10:9214–9222. https://doi.org/10.1002/ece3.6603

Mcewan RW, Rieske LK, Arthur MA (2009) Potential interactions between invasive woody shrubs and the gypsy moth (*Lymantria dispar*), an invasive insect herbivore. Biol Invasions 11:1053–1058. https://doi.org/10.1007/s10530-008-9316-0

Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. Biol Conserv 78:149–161. https://doi.org/10.1016/0006-3207(96)00024-9

Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev Camb Philos Soc 82:591–605. https://doi.org/10.1111/j.1469-185X.2007.00027.x

National Agricultural Technology Extension Service Center (NATESC) (2019a) Recent reports of fall armyworm in China and neighbouring countries. Plant Pathogen and Pest Information, No. 13/2019a–4–4. NATESC: Beijing, China. https://www.natesc.org.cn/. Accessed 4 April 2019a

National Agricultural Technology Extension Service Center (NATESC) (2019b) Recent reports of fall armyworm in China. Plant Pathogen and Pest Information, No. 16/2019b–4–28. NATESC: Beijing, China. https://www.natesc.org.cn/. Accessed 6 May 2019b

National Agricultural Technology Extension Service Center (NATESC) (2019c) Major pest *Spodoptera frugiperda* have invaded in Yunnan, and all areas should immediately strengthen investigation and monitoring. Plant Pathogen and Pest Information, No. 7/2019c–1–18. NATESC: Beijing, China. https://www.natesc.org.cn/. Accessed 29 January 2019c

National Agricultural Technology Extension Service Center (NATESC) (2019d) *Spodoptera frugiperda* harms winter corn in 3 cities and states in southwestern Yunnan. Plant Pathogen and Pest Information, No. 8/2019d–1–31. NATESC: Beijing, China. https://www.natesc.org.cn/. Accessed 1 February 2019d

Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP, Thomas MB (2016) Global threat to agriculture from invasive species. Proc Natl Acad Sci USA 113:7575–7579. https://doi.org/10.1073/pnas.1602205113

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19. https://doi.org/10.1023/A:1010034312781

Powell KI, Chase JM, Knight TM (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. Am J Bot 98:539–548. https://doi.org/10.3732/ajb.1000402

Powell KI, Chase JM, Knight TM (2013) Invasive plants have scale-dependent effects on diversity by altering species-area relationships. Science 339:316–318. https://doi.org/10.1126/science.1226817

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282. https://doi.org/10.1890/13-0183.1

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1:103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Sharanabasappa D, Kalleshwaraswamy CM, Asokan R, Swamy HM, Maruthi MS, Pavithra HB, Hegde K, Navi S, Prabhu ST, Goergen GE (2018) First report of the fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India. Pest Manag Hortic Ecosyst 24:23–29

Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader abundance and impact. Ecosphere 9:e02415. https://doi.org/10.1002/ecs2.2415

Stokstad E (2017) New crop pest takes Africa at lightning speed. Science 356:473–474. https://doi.org/10.1126/science.356.6337.473

Strayer DL (2010) Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshw Biol 55:152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21:645–651. https://doi.org/10.1016/j.tree.2006.07.007

Tallamy DW (2004) Do alien plants reduce insect biomass? Conserv Biol 18:1689–1692. https://doi.org/10.1111/j.1523-1739.2004.00512.x

Thiele J, Kollmann J, Markussen B, Otte A (2010) Impact assessment revisited: Improving the theoretical basis for management of invasive alien species. Biol Invasions 12:2025–2035. https://doi.org/10.1007/s10530-009-9605-2

Thomsen MS, Olden JD, Wernberg T, Griffin JN, Silliman BR (2011) A broad framework to organize and compare ecological invasion impacts. Environ Res 111:899–908. https://doi.org/10.1016/j.envres.2011.05.024

Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Mar Ecol Prog Ser 495:39–47. https://doi.org/10.3354/meps10566

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarosik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pysek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Volterra V (1926) Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560. https://doi.org/10.1038/118558a0

Westbrook JK, Nagoshi RN, Meagher RL, Fleischer SJ, Jairam S (2016) Modeling seasonal migration of fall armyworm moths. Int J Biometeorol 60:255–267. https://doi.org/10.1007/s00484-015-1022-x

Westbrooks RG (2004) New approaches for early detection and rapid response to invasive plants in the United States. Weed Technol 18:1468–1471. https://doi.org/10.1614/0890-037X(2004)018[1468:NAFEDA]2.0.CO;2

Wu QL, Jiang YY, Wu KM (2019) Analysis of migration routes of the fall armyworm *Spodoptera frugiperda* (J.E. Smith) from Myanmar to China. Plant Prot 45:1–6

Wu PX, Ren QL, Wang W, Ma Z, Zhang RZ (2021a) A bet-hedging strategy rather than just a classic fast life-history strategy exhibited by invasive fall armyworm. Entomol Gen 4:337–344. https://doi.org/10.1127/entomologia/2021/1154

Wu PX, Wu FM, Fan JY, Zhang RZ (2021b) Potential economic impact of invasive fall armyworm on mainly affected crops in China. J Pest Sci 94:1065–1073. https://doi.org/10.1007/s10340-021-01336-9

Yokomizo H, Possingham HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: The value of knowing the density-impact curve. Ecol Appl 19:376–386. https://doi.org/10.1890/08-0442.1

Zhang SM, Zhao YX (1996) The geographical distribution of agricultural and forest insects in China. China Agriculture Press, Beijing

Zhang RZ, Zhang YP, Jiang YX (2009) Threat and management strategies of potentially invasive insects in China. Sci China Life Sci 52:903–910. https://doi.org/10.1007/s11427-009-0126-0

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.