Ning, Z.; Chen, C.; Cui, B.; Zhang, Y.; Xie, T.; Wang, Q.; Zhu, Z.; Bai, J.; Bouma, T.J. (2022). ‘Mother knows best’: Maternal oviposition effects of a range-expanding insect herbivore degrade coastal wetlands by targeting juvenile foundation plant species. *Land Degradation & Development 33(16)*: 3023-3035. DOI: 10.1002/ldr.4369

Published version: https://dx.doi.org/10.1002/ldr.4369

NIOZ Repository: http://imis.nioz.nl/imis.php?module=ref&refid=355189

Mother knows best: maternal oviposition effects of a range-expanding insect herbivore degrade coastal wetlands by targeting juvenile foundation species

Authors: Zhonghua Ning [1], Cong Chen [1, 2*], Baoshan Cui [1, 2*], Yihui Zhang [3], Tian Xie [1], Qing Wang [1, 2], Zhenchang Zhu [4], Junhong Bai [1], Tjeerd J. Bouma [5, 6]

Affiliation: [1] School of Environment, State Key Joint Laboratory of Environmental Simulation and Pollution Control, Beijing Normal University, Beijing 100875, China

[2] Advance Institute of Natural Sciences, Beijing Normal University, Zhuhai 519087, China

[3] Key Laboratory of the Ministry of Education for Coastal and Wetland Ecosystems, College of the Environment and Ecology, Xiamen University, Fujian 361102, China

[4] School of Ecology, Environment and Resources, Guangdong University of Technology, Guangdong 510090, China

[5] Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, P.O. Box 140, 4400 AC Yerseke, The Netherlands

[6] Faculty of Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, The Netherlands

***Correspondence:** cuibs@bnu.edu.cn (B. Cui); congchen@bnu.edu.cn (C. Chen)

Running title: Novel insect herbivores accelerate salt marsh degradation

Abstract

Species range expansion induced by climate change and human activities threaten native populations and communities across the biosphere. Insect herbivores, important consumers of plants, are known to expand their range under global change, with potential consequences to the newly reached environment. The selection of oviposition sites by herbivorous insects could notably impact offspring performance. However, the role of such effects in impacting the receiving ecosystem has been rarely explored. Here, we provide the first evidence showing that a terrestrial range-expanding phytophagous wood-borer moth (i.e., *Zeuzera leuconotum* Butler) heavily attacked the saplings of a foundation plant species (i.e., *Tamarix chinensis*) in salt marshes. Long-term field surveys and laboratory behaviour experiments revealed that the oviposition preference of adult females was beneficial to their larval performance. The preference to oviposit on young branches of the new host plants, which were often softer and contained enough nutrients for larval development, indicates that females could still make the right choice on novel host-plants. This finding supports the "mother knows best" hypothesis that female insects will evolve to oviposit on hosts on which their offspring fare best. Consequently, the survival of host-plant saplings decreased dramatically under this top-down control, revealing that herbivory of this range-expanding insect has a profound negative impact on the recruitment and succession of coastal foundation species, thereby potentially leading to saltmarsh degradation. These findings highlight the importance of the maternal oviposition effects in range-expanding insects and how these populations can establish using novel host-plants and threaten coastal wetlands.

Keywords

Insect herbivory, mother knows best, optimal oviposition, preference-performance, species range expansion, wood-borer

1. Introduction

Coastal ecosystems like salt marshes, mangroves and seagrasses are among the most productive ecological hotspots. These ecosystems provide a variety of goods and services by maintaining the stability and sustainability of community structure and ecosystem functions (Barbier et al., 2011). The foundation plant species in these coastal wetlands are of key importance for maintaining stable ecosystem functions, and they mediate all kinds of interactions at various trophic levels ranging from populations to the entire communities (Jordan, 2009; Valls et al., 2015). These dynamic ecological processes can be affected by abiotic and biotic conditions through bottom-up and top-down controls, with consequences to ecosystem functioning (Daleo et al., 2015; Rosenblatt & Schmitz, 2016). As primary producers, coastal plants play key roles in regulating trophic interactions among food chains and/or webs in coastal ecosystems (Chen et al., 2019b; Sun et al., 2020). Unlike the plants found in most terrestrial ecosystems, coastal plant species have specifically evolved to cope with the harsh physical/abiotic conditions in their habitats. As such, they may be less adapted to cope with biotic stresses such as herbivory (Fornoni, 2011).

In both terrestrial and coastal ecosystems, insect herbivores are among the most important consumers that affect plant health, survival, reproduction and biomass through top-down processes (Sala et al., 2008; Chen et al., 2019a; Bonsignore et al., 2021). Plant species are often attacked by many different feeding guilds of insect herbivores, such as leaf miners, leaf suckers, leaf chewers, stem borers and root feeders (Van der Putten et al., 2001). Which group of insect herbivores is the major consumer depends on the functional traits of the plant species (Frenette-Dussault et al., 2013). For example, woody plants can be severely damaged by stem-borer insects (Moolman et al., 2014; Ning et al., 2020). Stem-borers are herbivorous insects that feed inside of the plant stem (Li & Pennings, 2017), using the stem's tough exterior structure as "natural barrier" against their natural enemies. Notably, the rapid climate changes (e.g., drought and heat waves) and intense human disturbances (e.g., trade, land-use change and reduction of enemies) have significantly increased the risk of insect pest outbreaks worldwide and host range expansion, possibly even extending from one ecosystem to another (Jepsen et al., 2008; Jactel et al., 2019). Thus, under such multiple inducements, stem-borers may be expected to become a threat to woody plant species that are critical for maintaining ecosystem functions in mangroves and salt marshes (Feller, 2002; Ong et al., 2010; He & Cui, 2015). For example, the recent arrival of a terrestrial range-expanding insect herbivore with devastating effects on native woody plants in Chinese coastal salt marshes (Ning et al., 2020; Figure 1) has emphasized the need to obtain a greater understanding of this threat.

Many studies have focused on understanding how herbivorous insects perceive and oviposit on suitable host-plants/positions. Such maternal oviposition effects ensure that their offspring have a greater chance of survival and access to sufficient accessible resources for development (Thompson & Pellmyr, 1991; Gripenberg et al., 2010). As hatched larvae are vulnerable and have limited mobility, the oviposition preference of adult females is essential for the offspring's success (Clark et al., 2011; Kohandani et al., 2017). However, differences in oviposition preference of insect herbivores are regarded to be due to species specificity of plants and/or insects (Awmack & Leather, 2002; Schoonhoven et al., 2005). For instance, some female leaf feeders prefer to oviposit on the young leaves of one specific species while others target mature leaves in another plant species, meaning that host-plant selection by adult females may not always correlate to larval performance (Valladares & Lawton, 1991). Interestingly, some stem borer females (e.g., rice borer - *Eoreuma loftini*) prefer to lay their eggs on leaves rather than stems (Beuzelin et al., 2013), even though leaves are, in principle, not a great oviposition site from the perspective of the larvae, as they do not provide good feeding sites for stem borers. Thus, understanding the impact of a range-expanding insect herbivore requires more insight into if and how such range-expanding insect can successfully colonize a new habitat by selecting a suitable host for oviposition that optimizes larval performance.

Several hypotheses have been developed regarding plant-herbivore interactions. Many studies have shown that many herbivorous insects prefer to attack vigorous plants than stressed ones (Price, 1991; Che-Castaldo et al., 2019). This is particularly applicable to galling insects and stem-borers because their larval development is closely related to plant growth (Fritz et al., 2000). From the insect perspective, two hypotheses associated with oviposition preference have been proposed related to their evolution by natural selection. The "mother knows best (MKB)" principle, also known as "preference-performance hypothesis (PPH)", states that adult females prefer to oviposit on host plants that promote the survival and development of larvae (Jaenike, 1978; Valladares & Lawton, 1991; Kohandani et al., 2017), whereas the optimal bad motherhood hypothesis suggests that herbivores prefer to lay eggs on host plants that are beneficial to the mothers themselves (Mayhew, 2001; García-Robledo & Horvitz, 2012). Although many previous studies have been conducted to examine the above-mentioned hypotheses in various ecosystems, remarkably little is known regarding whether the oviposition preference and larval feeding preference of a range-expanding wood-borer are related to these hypotheses, and how range-expanding insects may affect their new host in the new habitat.

Using the recently arrived range-expanding wood-borer moth [*Zeuzera leuconotum* Butler, hereafter *Zeuzera*] that feeds inside the stem of the new woody host-plant (*Tamarix chinensis*, hereafter *Tamari*x) with devastating effects on Chinese coastal wetlands (Ning et al., 2020, see details in *Section 2.1*), we addressed two key questions: (1) whether maternal oviposition preferences in the range-expanding wood-borer moth fits the predictions of the MKB hypothesis, and (2) if oviposition preference affects the health and recruitment of its new host-plant. Given that the pest *Zeuzera* belongs to the Cossidae family, of which some species could have oviposition preference to support their larval development (e.g., Zong et al., 2013), we hypothesize that (1) female *Zeuzera* adults preferentially oviposit on younger *Tamarix* branches over older ones to maximize the performance of their offspring, and (2) *Zeuzera* larvae would preferentially feed on younger branches over older ones, heavily damaging the healthy *Tamarix* saplings. Consequently, due to the maternal oviposition preference and larval feeding preference, the health and recruitment of *Tamarix* would be substantially suppressed by the novel wood-borer insect. To test the hypotheses, we conducted multi-year field observations and surveys combined with insect choice behaviour experiments (maternal oviposition preference & larval feeding preference). Finally, we broadened our findings by placing them in the context of phytophagous insects-host plants interactions across global ecosystems by conducting a systematic literature review of the "mother knows best (MKB)" or "preference-performance hypothesis (PPH)".

2. Materials and Methods

2.1 Study site and species

Field work was conducted on the terrestrial borders of five salt marshes in northern China: Huanghekou (37°46’N, 119°09’E), Yiqian’er (38°05’N, 118°42’E) and Dawenliu (37°43’N, 119°14’E) salt marshes in the Yellow River Delta, and Guangli (37°22’N, 119°54’E) and Changyi salt marshes (37°06’N, 119°22’E) in the Laizhou Bay coastal wetlands (Figure 1). These regions have a semi-humid temperate monsoonal climate. The long-term annual average temperature and precipitation in these regions are about 12-13 °C and 500-600 mm, respectively, with 60-70% of the rainfall distributed between July and September (Liu et al., 2017). These regions are typically characterized by high soil salinity and low soil moisture (He et al., 2012), and the vegetation comprises only a few species due to the harsh abiotic conditions. Woody tamarisk (*Tamarix chinensis*) is the dominant species, and two similar annual succulent forbs (i.e., *Suaeda salsa* and *Suaeda glauca*) and a perennial herb (i.e., *Phragmites australis*) are also widely distributed under or within the canopies of tamarisk (He et al., 2012).

Tamarix chinensis is a perennial shrubby halophyte that inhabits riparian and coastal zones in East Asia, and it also has invaded into North America and South Africa (González et al., 2017; Marlin et al., 2017). In the Yellow River Delta, the range of *Tamarix* covers high salt marshes to the terrestrial uplands, where they are less affected by tides (He et al., 2012 & 2015). This foundation species plays an important role in maintaining the habitat environment and the stability, health, and services of coastal ecosystems, as it acts as a primary producer in regulating the ecosystem structure and functions (Li et al., 2019).

The moth *Zeuzera leuconotum* Butler (Lepidoptera: Cossidae) is an extremely harmful wood-borer pest in China. Similar to most species of the Cossidae family, its larvae burrow into and feed on trunks or stems of woody plants in terrestrial ecosystems (e.g., *Fraxinus* *chinensis* Roxb., *Populus tomentosa* Carr., and *Salix babylonica* Linn.), pushing frass and debris to the outside (Liu et al., 2010; Byrne & Moyle, 2019; Figure S1). In September 2017, a small group of *Zeuzera* was observed to damage the *Tamarix* population in three sites of the Yellow River Delta, including Huanghekou, Yiqian'er and Dawenliu salt marshes (*personal observation*). It is possible that the actual occurrence time of the range expansion of *Zeuzera* could be prior to the time of the phenomenon that we observed, because the wood-borer develops inside of the woody plants and are hard to be detected by ordinary field observations. Nevertheless, it was the first report that *Zeuzera* has rapidly expanded its range from terrestrial ecosystem to coastal ecosystem, possibly due to anthropogenic disturbances (e.g., land-use change and pesticide abuse) and climate change (e.g., drought and heat waves), and *Tamarix* is now a new host plant of the wood-borer (Ning et al., 2020).

2.2 Field survey of wood-borer damage to *Tamarix*: spatial pattern & mechanisms responsible for damage

To quantitatively evaluate the spatial distribution and intensity of damage for the wood-borer insect (*Zeuzera*) feeding on the host plant (*Tamarix*), a field survey was conducted in three salt marshes in the Yellow River Delta (i.e., Huanghekou, Yiqian'er and Dawenliu) during autumn (active larval stage) in 2018 to 2019, and in Guangli and Changyi salt marshes in Laizhou Bay during late August 2020. We randomly selected eight sampling plots (50 m × 50 m, 100 m apart) for each site, and 20 *Tamarix* trees within each plot were randomly selected for damage quantification. *Tamarix* infestation by the wood-borer was distinguished by the presence of larval excreta/frass under the *Tamarix* canopy because *Zeuzera* larvae generally produce several clusters of excreta when feeding (*personal observation*, see Figure 3B-E). The damage intensity due to *Zeuzera* in each salt marsh was determined by calculating the proportion of damaged plants among the 160 sampled plants.

To understand the mechanisms that allow the wood-borer insect to damage the host-plant *Tamarix* in its life cycle, 12 fixed observation plots (50 m × 50 m) were set up in Huanghekou salt marsh of the Yellow River Delta. *Firstly*, the life history of *Zeuzera*, including the egg, larval, pupal, and adult stages, were detected and characterized by monthly field photographs and lab rearing observations (see photos in Figure 2B). *Secondly*, to characterize the feeding behaviour of the caterpillar inside of the plants, we randomly selected 10 *Tamarix* plants in the observation plots during the larval development stage and recorded the position (i.e., within stem or roots) and direction of movement (i.e., downward or upward) of the caterpillar each month (approximately 1-3 days). The two variables were estimated by the perpendicular distance of the larva excreta to the main stem of *Tamarix* (see details in Figure S2). Moreover, to elucidate the insect oviposition behaviour of adult females in the field, we visually divided the *Tamarix* tree (approximately 1~1.5 m in height) into three parts with equal length (i.e., top, middle and bottom). The oviposition positions of *Zeuzera* females were independently recorded using artificial light over five consecutive nights in late June 2019 (n = 20 replicates per night), as the adults usually mate at night in spring. *Thirdly*, to examine whether the insect damage intensity depends on the plant size of *Tamarix*, 10 *Tamarix* trees were randomly selected in each fixed observation plot (total of 120 plants) for the damage and plant size quantification in September and October 2019. We treated the *Tamarix* tree as an upside-down cone and determined the size of each plant as its volume by measuring the maximum lengths of the stem and crown axes. The damage intensity in each *Tamarix* plant was defined by dividing the number of larva-infested branches (their leaves are generally yellow) by the total number of branches.

2.3 Mesocosm experiments for testing the "mother knows best" hypothesis: maternal oviposition preference & larval feeding preference

To determine the oviposition behaviour of adult females on host plants, an oviposition-preference experiment was conducted to test the MKB hypothesis that adult females preferentially oviposited on younger branches over older ones to maximize their offspring performance. *Zeuzera* pupae (with attached *Tamarix* branch) were collected in the field during late May 2020, and each individual was kept in the vial without light at 25°C until adult emergence (approximately 10-14 days). After eclosion, males and females were released into a rearing cage to mate, where the environment had a temperature of 25°C, light photoperiod of 16 h, and relative humidity of 50%-60%. A mated *Zeuzera* female was placed at the bottom central axis of a rearing cage (50 cm × 50 cm × 50 cm), which was divided into two equal parts i.e., small diameter branches (SDB) group with diameter < 1 cm, and large diameter branches (LDB) group with diameter > 1 cm. Six branches of *Tamarix* with small diameters (< 1 cm) were distributed in the SDB part at the same distance from each other, and another six branches with large diameters (> 1 cm) were placed in the LDB part. All plant branches (length = 45 cm) were divided into three equal parts (i.e., top, middle and bottom), each section including a forked and straight section (see Figure 4D for details). Ten replicates were performed under the same conditions described above. Five days later, the oviposition position was recorded for each female in each cage, and the number of eggs in each position was counted using a wireless live-stream microscope (Leica EZ4W, Leica Microsystems, Switzerland).

A host selection experiment was conducted to examine the feeding preferences of *Zeuzera* larvae, where 12 *Tamarix* branches, each with a length of 30 cm, were placed in a circle at equal angles. A lump of moist cotton was wrapped around the top end of each branch to prevent it from losing water. The plant branches were equally divided into two groups: SDB and LDB groups. Ten caterpillars (body length ~ 1 cm, 1st - 2nd instar) were placed at the center of the circle, and they were allowed to move freely for 3 h, before counting the number of larvae in each branch group. Six replicates were performed using the procedure described above.

To further quantify whether *Zeuzera* larvae preferred feeding on younger branches over older ones, a lab feeding trial was conducted in late July 2020. Twenty *Zeuzera* larvae (body length ~ 1 cm) were captured in the field, and each was placed in a bucket that contained a *Tamarix* branch (length = 30 cm). Two groups of plant branches (i.e., the SDB and LDB that represented younger and older branches, respectively) were individually allotted into the 20 buckets (n = 10). To keep the branches fresh, moist cotton was wrapped around one end of each branch and was replaced every day. After 10 days, the larval excreta were collected from each bucket, oven-dried at 60°C for 48 h, and weighed, and the weight of larval excreta was used as a measure of larval performance. The branch diameter and the tunnel length excavated by the caterpillar were also measured using a vernier caliper. The diameter of all branches was measured at the middle position of the branch.

2.4 Common garden experiment for quantifying the damage intensity on *Tamarix* saplings

To quantify the effects of *Zeuzera* larvae herbivory on *Tamarix* saplings, a common garden experiment was conducted in early May 2020. We collected 24 *Tamarix* saplings aged < 2 years (approximately 2-4 branches with heights of 50-100 cm) from the field and transplanted them in a greenhouse. The saplings were individually planted in pots (30 L) filled with homogeneous salt marsh soil. All transplants were watered every day with fresh water for a week to alleviate the shock of transplanting. The transplants were then equally assigned to "with" and "without" larvae treatments (n = 12). In the "with" larvae treatment, 24 caterpillars (body length is about 2 cm, 4-5th instar caterpillar) were released onto a branch of each transplant (two caterpillars per transplant). We checked the performance of each caterpillar every other day in the first week, and any escaped or dead larvae were replaced. After a month, the damage intensity and survival proportion were calculated for the *Tamarix* saplings.

2.5 Statistical analysis and systematic literature review

The linear regression model was used to examine the relationship between *Tamarix* plant size and the damage intensity caused by *Zeuzera* larvae, and to test the relationships between the dry weight of larval excreta or tunnel length and the diameter of branches in the lab feeding trial. Mann-Whitney *U* test was used to compare the differences in the number of oviposited eggs, dry weight of the larval excreta, and tunnel length excavated by *Zeuzera* larvae between the two *Tamarix* branches groups (i.e., SDB & LDB), because the normality or homogeneity of variance of the data did not satisfy the assumptions of *T*-test. Differences in the host selection ratio by *Zeuzera* larvae were analyzed by paired *T*-test. One-way ANOVA (Tukey's HSD test) was used to compare the differences in oviposition positions of *Zeuzera* females in the field. Moreover, the nonparametric Mann-Whitney *U* test was also used to examine the effects of *Zeuzera* larval herbivory on the performance of *Tamarix* saplings based on the damage intensity and survival proportion. All statistical analyses were conducted using R 3.5.3 (R Core Team 2019).

To test the generality and suitability of the “mother knows best (MKB)” or the “preference-performance hypothesis (PPH)” in phytophagous insects-host plants interactions across global ecosystems, we conducted a systematic literature review. First, studies testing the MKB or PPH before 2010 that were reported in a global review (Gripenberg et al., 2010) were considered. To compile a list of the studies testing the MKB or PPH that have been published between 2010-2020, the ISI web of science database (http:// www.webofknowledge.com/) was used by querying the “TS = (“oviposition preference” OR “preference-performance” OR “host plant preference” OR “mother* know* best” OR “host selection”) AND TS = (insect* OR entomolog* OR bugolog*)” in August 2020. Then we screened and narrowed the search results by reading the title, abstract and the main text. Only the studies focused on testing the MKB or PPH in insect herbivores-host plants interactions were further considered. For each retained publication (including previous studies reported in Gripenberg et al., 2010), we recorded the following variables: (1) authors, (2) location, (3) latitude and longitude of study site, (4) ecosystem type, (5) insect name and its order, (6) feeding mode of insect, (7) preferred and less preferred host-plant for insect, (8) type of the host plant (i.e., woody or herby) and (9) whether the oviposition behaviour of the insect supports the MKB or PPH, through reading the full-text. All of the above information constituted the literature review database.

3. Results

3.1 Large-scale occurrence of the wood-borer insect damaging on the coastal *Tamarix*

In all of the salt marshes surveyed in northern China from 2018 to 2020 (i.e., Yiqian'er, Huanghekou and Dawenliu salt marshes in the Yellow River Delta, and Guangli and Changyi salt marshes in the Laizhou Bay coastal wetlands), approximately 70-85% of the *Tamarix* populations were infested by the wood-borer moth (Figure 1). Compared to the salt marshes in the Laizhou Bay coastal wetlands, the damage intensity of *Tamarix* caused by *Zeuzera* from 2018 to 2019 in salt marshes within the Yellow River Delta was higher. However, this difference between the two sites was not significant (81.3 ± 2.1% for the Yellow River Delta vs. 73.4% ± 4.3% for the Laizhou Bay coastal wetlands, Mann-Whitney U = 284.0, n_1 = 48, n_2= 16, P = 0.12; Figure 1).

3.2 How does the life-history of the wood-borer insect affect *Tamarix* and the phenological match between them?

Field observations showed that the adults emerged from late June to early July, and they were usually active during the night due to their mating behaviour (photo a in Figure 2B). The fertilized females oviposited a cluster of eggs in/on the bark cracks of *Tamarix* branches (photo b in Figure 2B). In terms of oviposition preference, over 70% of females laid eggs on the top section of plants in the field, which was significantly higher than that oviposited on the middle and bottom section of the *Tamarix* branches (i.e., 16% and 13%, respectively; one-way ANOVA, F = 112.2, P < 0.001, Figure 2C). The development time of the moth from eggs to larvae ranged from approximately 14 to 21 days (*lab rearing observation*). The caterpillars fed inside *Tamarix* stems and roots throughout the larval stage, and excavated a tunnel network for their movements, which can substantially damage the health and survival of their host-plant (photos c & d in Figure 2B). During summer and autumn, which are the growing season of

Tamarix, more than 90% of the early-instar caterpillars fed downward on the plant branches. When *Tamarix* was dormant in winter, the late-instar caterpillars continuously consumed downward from hollowed branches to *Tamarix* roots for overwintering. By the arrival of spring, the time the plant begins to grow, surviving caterpillars (~ 87%) re-selected a healthy branch of the same plant for their upward feeding until they reached the final instar (Figure 2D).

Field surveys showed that the larvae had about five instars, and the pupal development time was approximately 10 to 14 days. During pupation, a cocoon was formed inside the tunnel by the final instar caterpillar using its excreta and sawdust. An oval emergence hole was chewed by the caterpillar on the surface of the cocoon to leave only a thin layer of bark membrane as the cover of the hole (photo e in Figure 2B). After completing pupation, the adult emerged from the emergence hole with the help of the sea wind, which often broke off damaged *Tamarix* branches. In general, the life span of the adults was about 1 to 2 weeks (*personal observation*), and they completed mating and reproduction during this short period. In addition, the sex of the adult insect could be distinguished by the shape of the antennae, where the female had thread-like antennae, and the male had comb-like antennae (photo f in Figure 2B).

3.3 Does the wood-borer insect preferentially damage the younger *Tamarix* over older ones?

In the field survey, a significantly negative correlation was observed between the damage intensity of *Tamarix* infested by *Zeuzera* and the plant size index ($R^2 = 0.1$, $n = 120$, $P < 0.001$, Figure 3A), indicating that small *Tamarix* saplings were more likely to be infested by the wood-borer insect than large plants. Field photos also showed that *Tamarix* saplings with fine and fresh branches were heavily exploited by *Zeuzera* to potentially cause their death (Z. Ning, *personal observation*; see Figs 3B and 3D). Similarly, the health of large *Tamarix* plants was greatly affected by *Zeuzera* because the fine and fresh branches infested by the wood-borer also died (Figs 3C and 3E).

3.4 Does the mother know the best principle explain the damage pattern: maternal oviposition preference, larva feeding preference & damaged intensity?

Heterogeneous distribution of oviposition sites by *Zeuzera* females was observed in the oviposition preference experiment but most preferentially selected the top forked sections (i.e. TF) of *Tamarix* branches in the SDB group as their oviposition site (Mean ± SE: 60.0% ± 4.0%; Figure 4A). Likewise, the number of eggs laid on the TF of SDB predominated over any other oviposition position of *Tamarix* branches (Figure 4B). Furthermore, compared with *Tamarix* branches in the LDB group, the number of eggs oviposited on *Tamarix* branches in the SDB group was significantly higher (39.3 ± 3.8 ind./branch for SDB vs. 3.1 ± 1.1 ind./branch for LDB, Mann-Whitney $U = 472.5$, $n_1 = n_2 = 60$, $P < 0.001$; Figure 4C).

The results of the host-selection experiment showed that *Zeuzera* larvae preferentially selected small-diameter-branches of *Tamarix* (i.e., SDB) as food resources rather than large-diameter-branches (i.e., LDB; 75.0% ± 4.3% for SDB vs. 23.3% ± 4.9% for LDB [mean ± SE], $t = 7.9$, $n = 6$, $df = 10$, $P < 0.001$; Figure 5A). In the laboratory feeding preference trial, the dry weight of excreta produced by *Zeuzera* larvae that fed on SDB was significantly higher than that by those that fed on LDB (1.99 ± 0.06 g/branch for SDB vs. 0.68 ± 0.28 g/branch for LDB, Mann-Whitney $U = 4.5$, $n_1 = n_2 = 10$, $P < 0.001$; Figure 5B). Similarly, the mean tunnel length excavated by *Zeuzera* larvae inside branches in the SDB group was significantly longer compared with branches in the LDB group (4.47 ± 0.32 cm/branch for SDB vs. 1.38 ± 0.57

cm/branch for LDB, Mann-Whitney $U = 6.5$, $n_1 = n_2 = 10$, $P < 0.001$; Figure 5B). Furthermore, the excreta dry weight and tunnel length were both negatively correlated with the *Tamarix* branch diameter, where $R^2 = 0.72$ (n = 20, $P < 0.001$, Figure 5C) and $R^2 = 0.73$ (n = 20, $P < 0.001$, Figure 5D), respectively.

In the common garden experiment, the damage intensity of the *Tamarix* saplings in “with larvae” treatment was significantly higher than that in “without larvae” treatment (70.1% ± 6.1% vs. 0.0% ± 0.0%, Mann-Whitney $U = 0.0$, $n_1 = n_2 = 12$, $P < 0.001$; Figure 5E). Analogously, the survival of *Tamarix* saplings was also strongly affected by herbivory of *Zeuzera* larvae (16.7% ± 11.2% “with larvae” vs. 91.6% ± 8.3% “without larvae”, Mann-Whitney $U = 18.0$, $n_1 = n_2 = 12$, $P = 0.001$; Figure 5F).

3.5 Systematic literature review on testing the MKB or PPH across global ecosystems

Our systematic literature review included 135 peer-reviewed studies. The full list of studies included in the review and associated database are given in Supporting information: Text S3 and Table S4. Previous tests of the MKB or PPH in phytophagous insects were mainly conducted in terrestrial ecosystems (e.g., farmland, forest, grassland, and freshwater regions; Figure 6B), and they targeted insects with different feeding modes (e.g., leaf-eater, leaf-miner, stem/bark borer, etc.; Figure 6C) and host-plant types (e.g., herbaceous plants and woody plants; Figure 6D). Some studies did not support the MKB hypothesis, but positive relationships between the female oviposition preference and the performance of their offspring are potentially common in various phytophagous insects across global ecosystems (almost 77% of the studies identified in our literature review supported the MKB; Figure 6A).

4. Discussion

Whereas it is well recognized that the range expansion of insect herbivores under global change can affect the health of newly reached ecosystems (Jepsen et al., 2008; Carrasco et al., 2018), little is known about the oviposition behaviour of such herbivorous insects and what role maternal oviposition effects play in impacting the receiving ecosystem. Using a terrestrial range-expanding insect that affects woody plants in salt marshes, we demonstrated that maternal effects could strongly influence the receiving ecosystem. According to the field survey and behaviour experiment, we found that most *Tamarix* populations were heavily infested by *Zeuzera* larvae along the coastal region of northern China. The adult females preferred to oviposit on the top-forked sections of young branches over old ones. The damage intensity of *Tamarix* by caterpillars strongly increased with decreasing size of plants. The survival of *Tamarix* saplings decreased dramatically when they were bored by caterpillars, which generated profound negative impacts on the recruitment and succession of *Tamarix* populations. These results suggest that the terrestrial wood-borer insect could expand its range and pose a new threat to the populations of a coastal foundation woody plant species, leading to severe degradation of coastal salt marshes.

4.1 Evaluating the "Mother knows best" hypothesis

The performance of the larval stages of insects depends greatly on the maternal oviposition preference, where females should prefer to select an ideal position on host plants to support the development of their offspring, which is so-called MKB or PPH hypothesis (Jaenike, 1978; Kohandani et al., 2017). In this study, we found that adult females mostly selected the top-forked sections of young branches for oviposition in both the field survey and laboratory experiment. The following two explanations might account for the oviposition behaviour of this wood-borer insect. *First*, the quality of young branches is often higher, especially in terms of the reduced toughness and higher nutrient contents. By ovipositing on younger branches, caterpillars can readily access the most nutritional branches of host plants to support their optimal development. Previous studies also showed that insect herbivores such as leaf eaters and miners preferred to consume young leaves, which were softer, and their nutrient contents were often higher (Coley, 1983; Caldwell et al., 2016). *Second*, this oviposition preference might allow a herbivorous caterpillar to feed from the top stem to roots belowground throughout the larval stages. Most importantly, both explanations support the MKB principle that adult females can make an appropriate choice to maximize the performance of caterpillars, even on a novel host plant. Importantly, the systematic literature review demonstrated that the present study is the first to test the MKB or PPH in a coastal ecosystem, using a terrestrial range-expanding phytophagous insect that feeds inside of a coastal foundation woody plant species. Our findings enrich the MKB theory and suggest that the mother knows best principle might still apply to the range-expanding phytophagous insects when they extend into new habitats/ecosystems.

4.2 Phenological synchronization drives sapling damage

Synchronization of the phenology between insect development and plant growth is critical for establishing populations of range-expanding insect herbivores (Posledovich et al., 2018; Chorbadjian et al., 2019). We found that the larval stage of the wood-borer matched with the growing season of the woody plant, thereby indicating that the range-expanding insect herbivore could potentially be adapted to the developmental phenology of its new host plant.

Furthermore, small woody plants (saplings) were more likely to be attacked by the wood-borer insect, thereby disrupting the population dynamics of the host plant species. In addition, caterpillars that fed on saplings often performed better than those that fed on old trees, and thus they benefited from the oviposition preference of their mother. Interestingly, adult females often oviposited a cluster of eggs on a single branch where only one hatched larva survived and consumed the young branch (C. Chen, *personal observations*). Therefore, the possibility of intraspecific competition should be investigated in future research.

4.3 Insect species range-expansion and global change

Previous studies have shown that the frequency and intensity of insect outbreaks and range expansions have increased dramatically due to rapid climate change and human disturbance (Johnson et al., 2010; Nelson et al., 2013). Several potential factors could drive the range-expanding insect outbreak that affects the ecosystem's functioning and sustainability in their range. *First*, global warming and associated drought may have beneficial effects on the physiology of range-expansion insects, including rapid growth, increased reproduction, and high winter survival rates (Bale et al., 2002; Ju et al., 2017), as well as decoupling the trophic interactions between the insect herbivore and its natural enemies (Carrasco et al., 2018; Stephenson et al., 2019). Concurrently, the warming climate could have weakened the plant defences against insect herbivores that facilitate its range expansion to new habitats/ecosystems (Raffa et al., 2013). *Second*, another key factor - winds may also influence the insect outbreak in coastal ecosystems, which are expected to occur more frequently under windy conditions than in terrestrial ecosystems, because they can reduce predation risk and even create an enemy-free space for insect herbivores (Chen et al., 2018). *Third*, the presence of various types of intense human disturbances in terrestrial ecosystems (e.g., land-use change and pesticide abuse) may have made the habitat unsuitable for population development by the insect, thereby forcing them to expand into protected areas of coastal wetlands (neighbouring ecosystems) with relatively low environmental stress. In the present study, we found that the herbivorous wood-borer insect is shifting its range from inland to the coastal ecosystem and making the coastal foundation species its new host plant. The observed range expansion might be strongly related to the environmental changes (e.g., drought, wind, and human disturbance) that we discussed above, and future studies should take these environmental changes triggered by climate changes and anthropogenic activities into account for an understanding of the insect outbreak and expansion mechanisms.

4.4 Outlook

Species range expansions caused by climate change and human activities are predicted to be increasingly frequent in the future (Raffa et al., 2013; Dainese et al., 2017; Carrasco et al., 2018). The present study is the first to quantify the ecological impact of a terrestrial range-expanding phytophagous wood-borer insect on a woody plant in coastal salt marshes. It is essential for future studies to disentangle how and under which conditions insects can expand their range and how this affects native plants and other associated communities. In addition, future studies should measure insect colonization time, distribution and frequency of range expansions, to systematically evaluate the differences in damage intensity of range-expanding insects among different plant populations on the large-scale of coastal salt marshes. Furthermore, it is essential to conduct research aimed at identifying natural enemies in the new habitats where the pests spread. Only by obtaining an in-depth mechanistic understanding of the questions mentioned above, the negative effects of range expansion may be mitigated. Given that coastal ecosystems like salt marshes have a relatively limited plant diversity compared to terrestrial ecosystems, they may be especially vulnerable to species loss due to range-expanding insects stresses induced by environmental changes. Therefore, long-term dynamic monitoring and assessment of the ecological effects of range-expanding species on native communities under intensifying global changes are necessary to ensure the health and sustainability of coastal ecosystems.

5. Conclusions

The present study provided the first evidence that maternal oviposition effects of a terrestrial range-expanding wood-borer moth (i.e., *Zeuzera*) strongly affected a foundation plant species (i.e., *Tamarix*) in coastal salt marshes of northern China. The preference of adult females to oviposit eggs on the top-forked sections of young branches over old ones was of benefit to their offspring's development and performance, which supports the "mother knows best" hypothesis. As a result, the health and survival of *Tamarix* saplings, which consist of young plant branches, were negatively affected by the caterpillars. Our results suggest that the terrestrial wood-borer moth could expand its range and pose a new threat to *Tamarix* population dynamics, potentially leading to salt marsh degradation. As the species range expansions induced by climate change and anthropogenic disturbance are likely to occur more frequently, long-term monitoring and risk assessment of their effects on native communities in the context of intensifying global changes should be in-depth considered for ecosystem health and sustainability.

Acknowledgements

This research was supported by the Key Project of the National Science Foundation of China (No. U2243208 & U1901212), the National Science Foundation for Young Scientists of China (No. 32001177), the General Program of China Postdoctoral Science Foundation (No. 2019M660518). We appreciate the handing editor and two anonymous reviewers for their help in improving this manuscript.

Conflict of interest

The authors declared that they have no conflict of interest.

Data availability statement

Data supporting the study findings are available from the corresponding author upon request.

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Figure legends

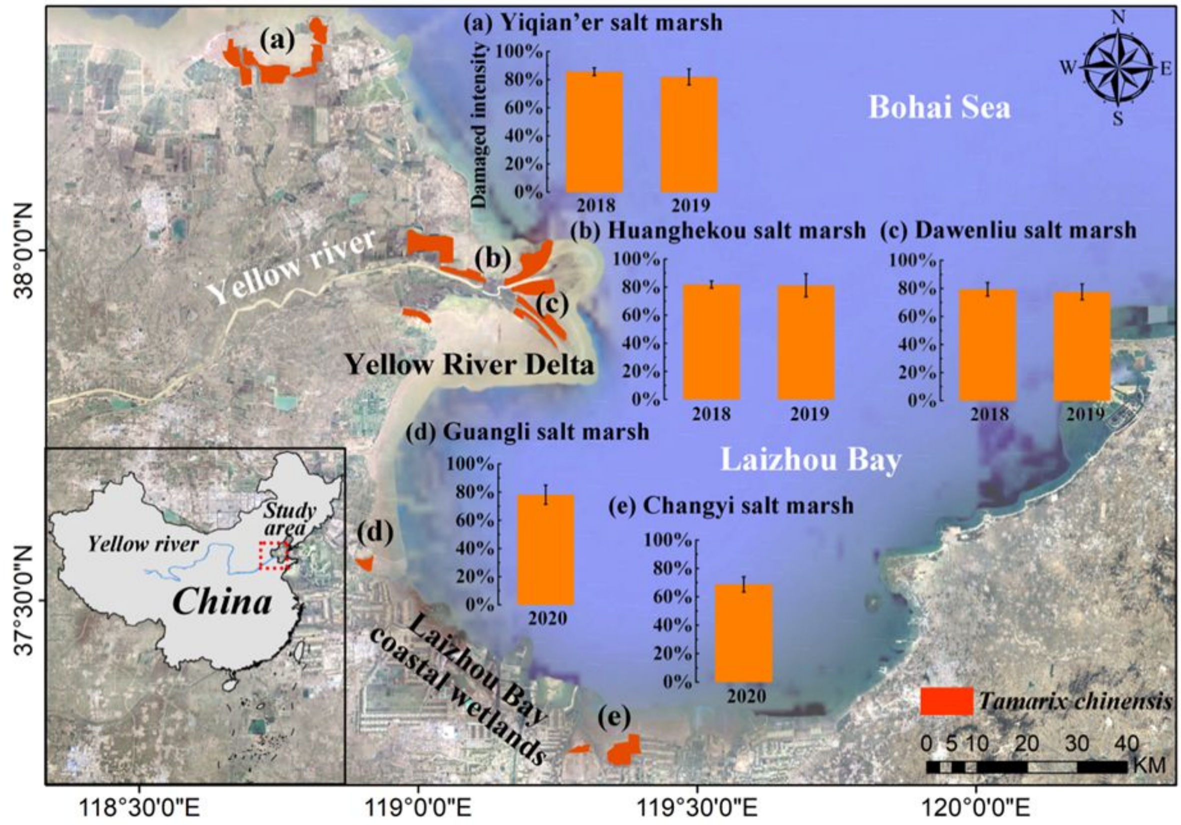


Figure 1. Massive damage intensity observed on woody plant - *Tamarix chinensis* in various major salt marshes of northern China, which proved to be induced by the novel wood-borer insect (*Zeuzera leuconotum* Butler). Observations in 2018 & 2019 covered the Yellow River Delta (a, b, c), and observations in 2020 covered the Laizhou Bay coastal wetlands (d, e).

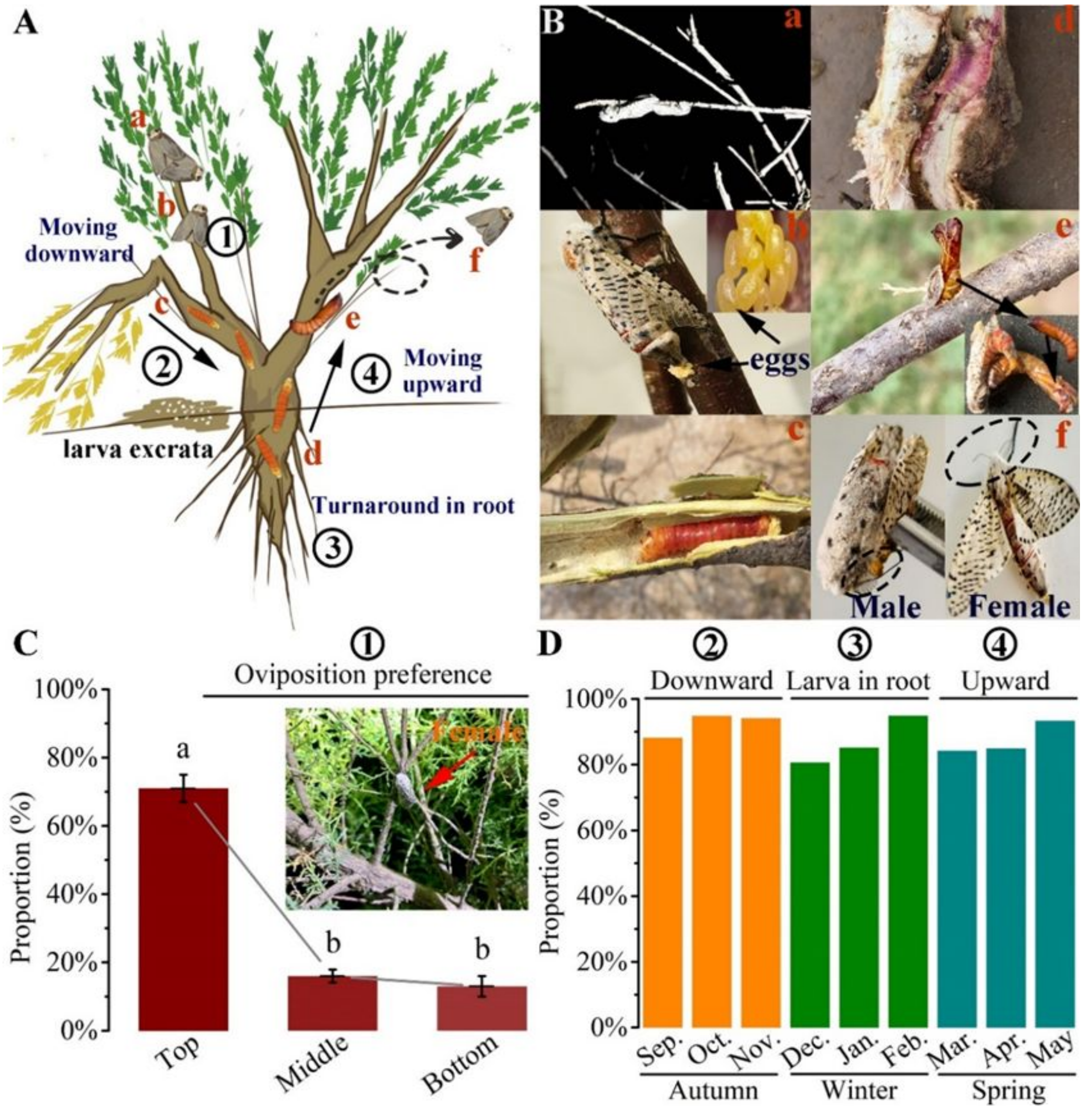


Figure 2. Schematic diagram (A) showing the life history of *Zeuzera* and how *Zeuzera* larvae move from the *Tamarix* stem to its root, and then back to the stem as part of its feeding trajectory. The small letters in figure A refer to photos taken in the field (in panel B) depicting the different developmental stages of this herbivorous insect: a) adult stages, b) female oviposition stage starting the infection, c) larva in the stem, d) larva in the root, e) eclosion of pupa, and f) adult stage leaving the plant. The encircle number in figure A refers to histograms (in panel C) showing the: 1) oviposition preferences of the *Zeuzera* females in the field (means ± SE with n = 20 per night; different letters indicate significant differences based on One-way ANOVA with Tukey's HSD test, $P < 0.001$), and to histograms (in panel D) showing during which months between September to May, the caterpillar inside the plant feeds on the 2) stem while moving downward, 3) the roots while turning around, and 4) the stem while moving upward. Photo credits: Z. Ning.

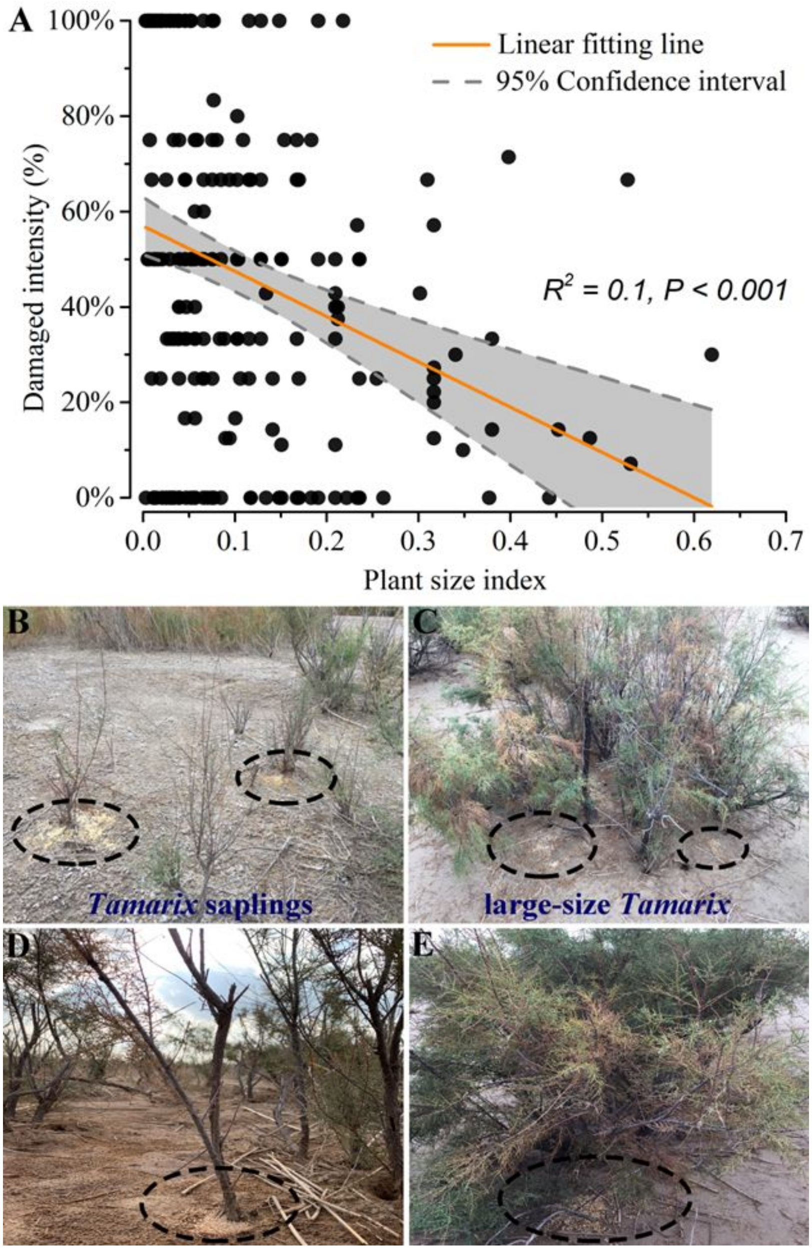


Figure 3. Intensity of damage caused by *Zeuzera* strongly depends on the plant sizes of *Tamarix* infested. The damage intensity was estimated as the proportion of larva-infested branches to all branches of the *Tamarix* tree. The plant size index was determined by the volume of *Tamarix* by measuring the maximum length of stem and crown axes of each plant, treating the *Tamarix* tree as an upside-down cone. The grey shading area indicates the 95% confidence interval around the linear-regression model. Young *Tamarix* saplings infected by *Zeuzera* were typically damaged in all parts (see field photos B & D), whereas the damage in older *Tamarix* plants typically comprised completely dead branches exploited by the wood-borer *Zeuzera* (the branches with yellow leaves in field photos C & E). The cluster in dotted circles of the photos comprises the excreta of the wood-borer produced by its tunnelling activity. Photo credits: Z. Ning.

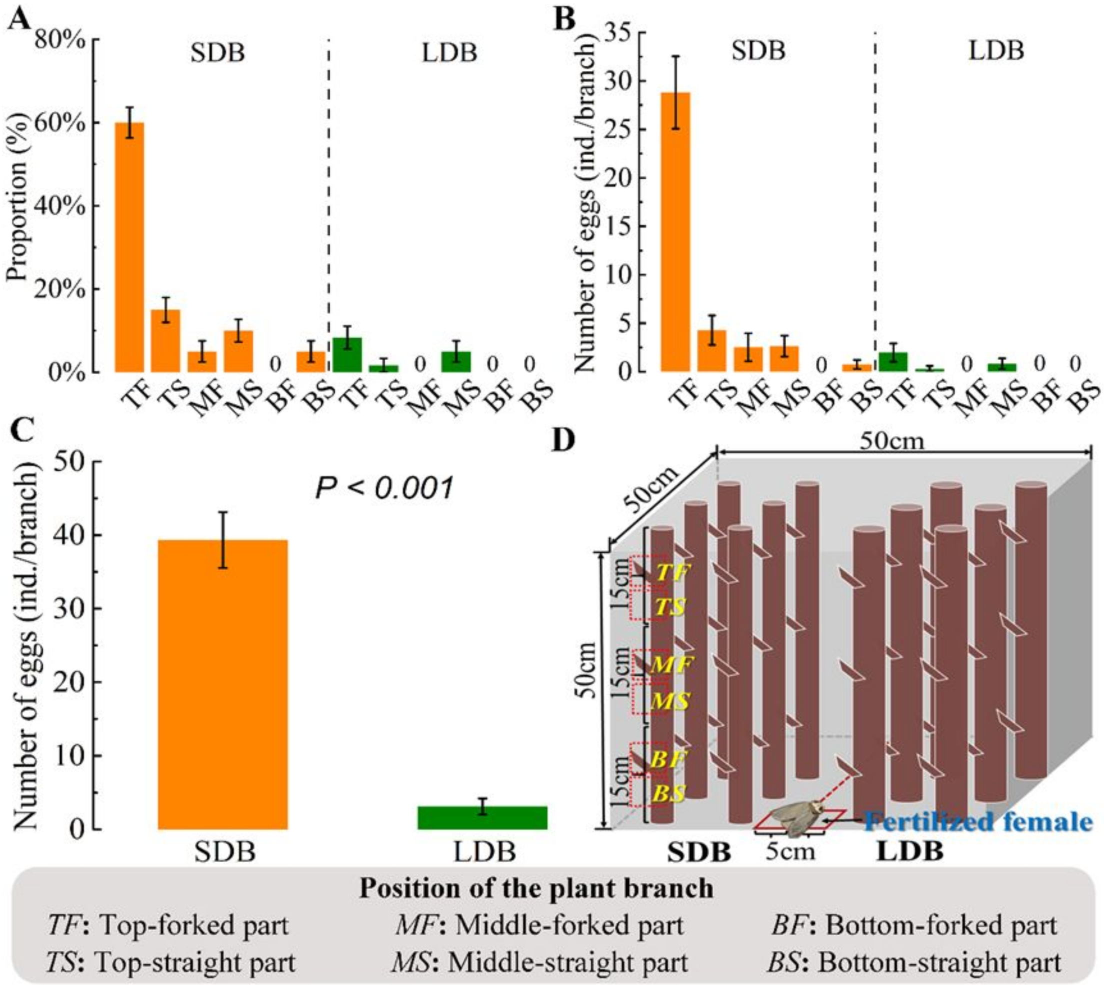


Figure 4. Oviposition preference of *Zeuzera* females in mesocosm experiment. Subfigures (A) and (B) show the selection proportion and the number of eggs on different oviposition positions from *TF* to *BS* successively (see bottom shadow part of this figure for details), respectively, in two *Tamarix* branch groups, i.e., small diameter branches group with diameter < 1 cm (SDB) and large diameter branches group with diameter > 1 cm (LDB). The difference in the overall number of oviposited eggs (C) was significant between the two branch groups (means ± SE with 10 replicates; Mann-Whitney *U* test, $P < 0.001$). Subfigure (D) shows the design of the oviposition preference mesocosm experiment.

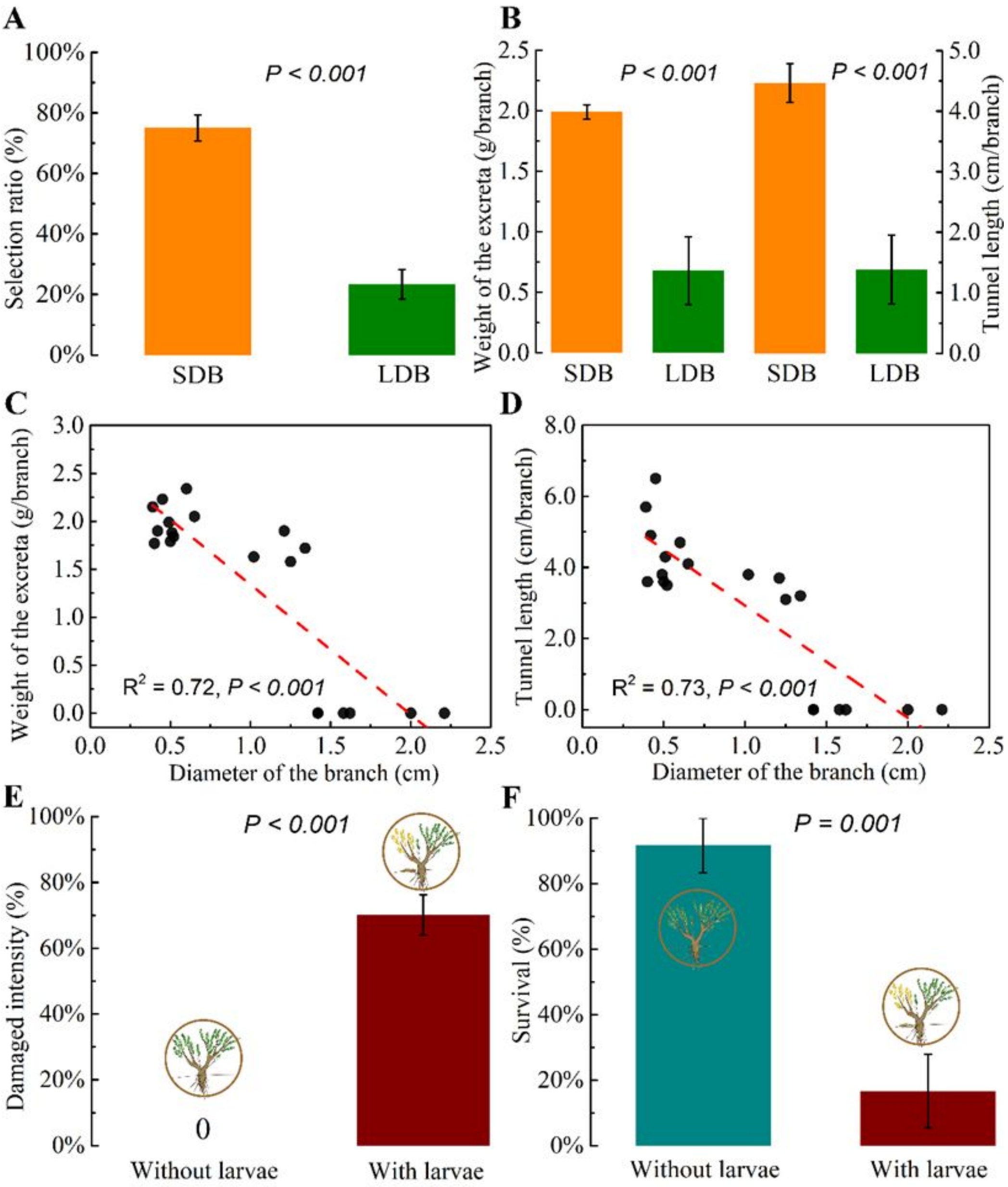


Figure 5. Feeding preference of *Zeuzera* caterpillars in the mesocosm experiment (A, B, C & D), and performances of *Tamarix* saplings in response to *Zeuzera* larvae infestation in the common garden experiment (E & F). The larvae selection ratio (A) between small-diameter-branches group (SDB, diameter < 1cm) and large-diameter-branches group (LDB, diameter > 1cm) shows a significant preference of *Zeuzera* larvae for young *Tamarix* branches (means ± SE with 6 replicates; *T*-test, $P < 0.001$). The dry weight of excreta and tunnel length grazed by the caterpillar (B) is significantly higher in SDB (means ± SE with 10 replicates; Mann-Whitney *U* test, $P < 0.001$). The dry weight of larval excreta (C) and tunnel length (D) were negatively correlated with the diameter of the feeding branches ($P < 0.001$). The damage intensity per plant (E) and final survival proportion of *Tamarix* (F) responded significantly to *Zeuzera* herbivory (means ± SE with 12 replicates; Mann-Whitney *U* test, $P < 0.001$).

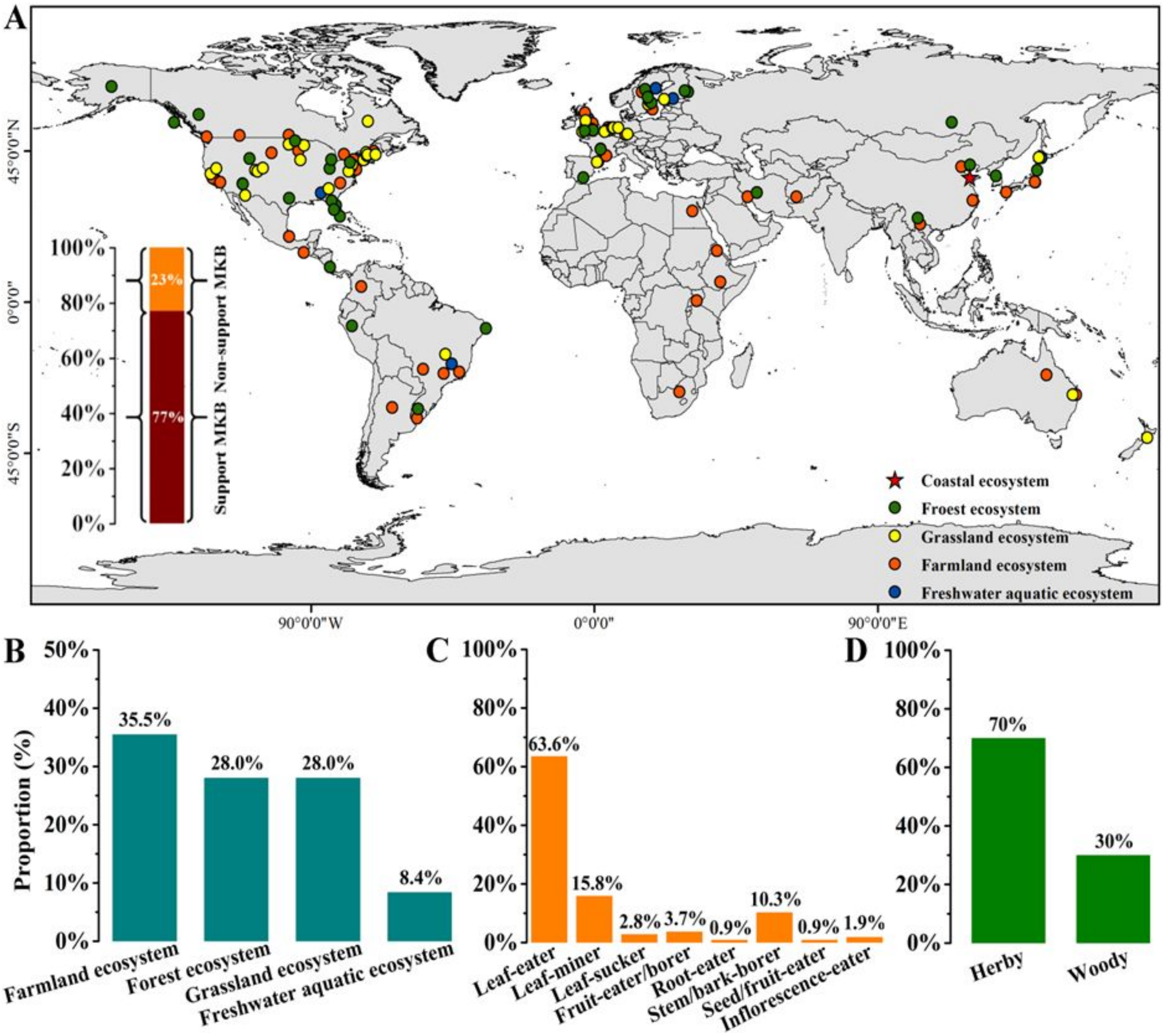


Figure 6. Testing the "Mother Knows Best (MKB)" hypothesis or "Preference-Performance Hypothesis (PPH)" in phytophagous insects across global ecosystems reported in the literature. Subfigure (A) shows the distribution of previously reported studies in different ecosystems. The red star in northeast Asia indicates our study sites that test the MKB hypothesis in coastal ecosystems. Subfigures (B) to (D) show the proportions of global studies conducted for different ecosystems, insect feeding modes, and the relevant host plant types, respectively. The literature searching methods are given in the main text, and the publication list and associated database are given in Supporting information: Text S3 and Table S4.

Figure S1. Field photos showing larvae of the wood-borer moth feeding on several native woody plants in terrestrial ecosystems.

As shown below in the photographs, the caterpillars (Lepidoptera: Cossidae) burrow into and feed on trunks or stems of woody plants in terrestrial ecosystems, such as *Fraxinus chinensis* Roxb., *Populus tomentosa* Carr., and *Salix babylonica* Linn.). Photo (a) to (d) shows the wood-borer damaging the main stem of several woody plant species. Photo (e) to (f) shows the die-offs of the wood-plants after being severely damaged by the caterpillars. Photos credit: Z. Ning and C. Chen.

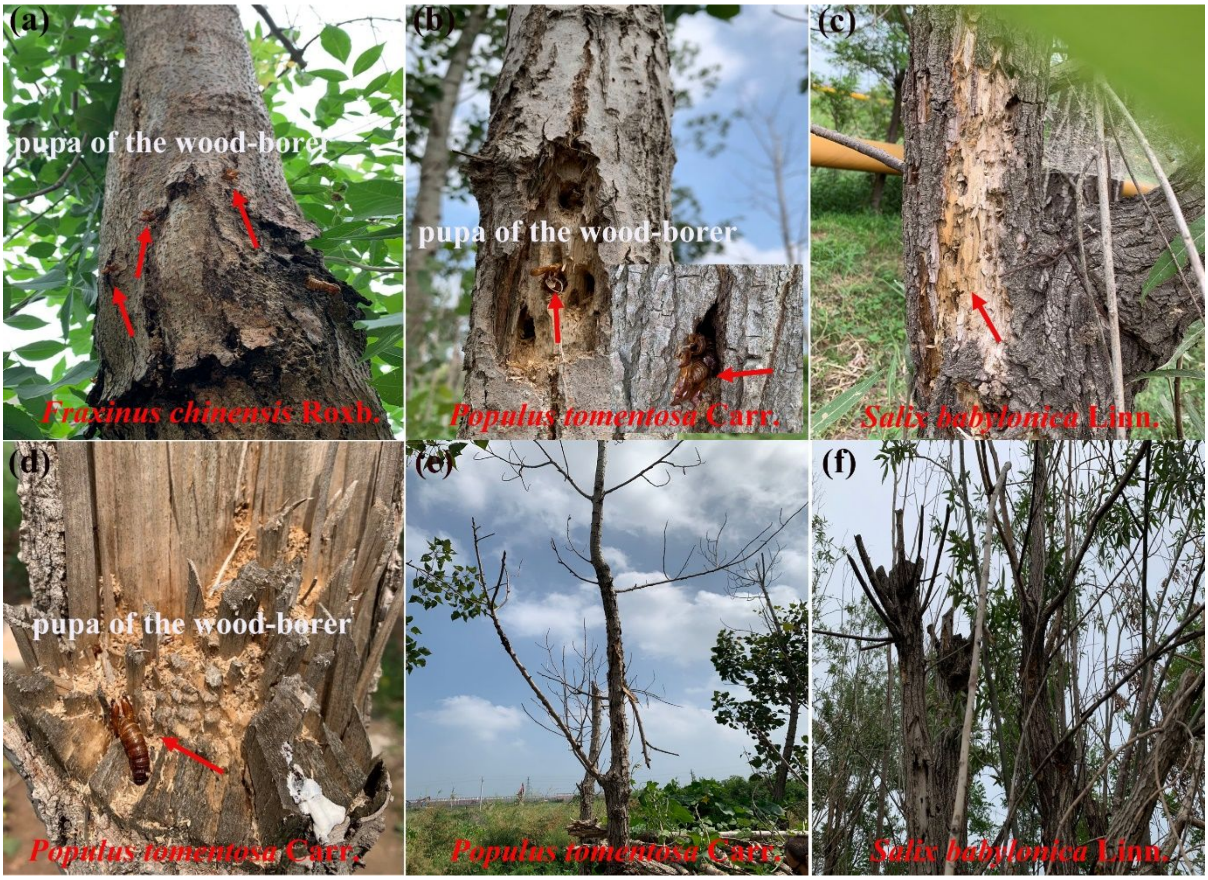
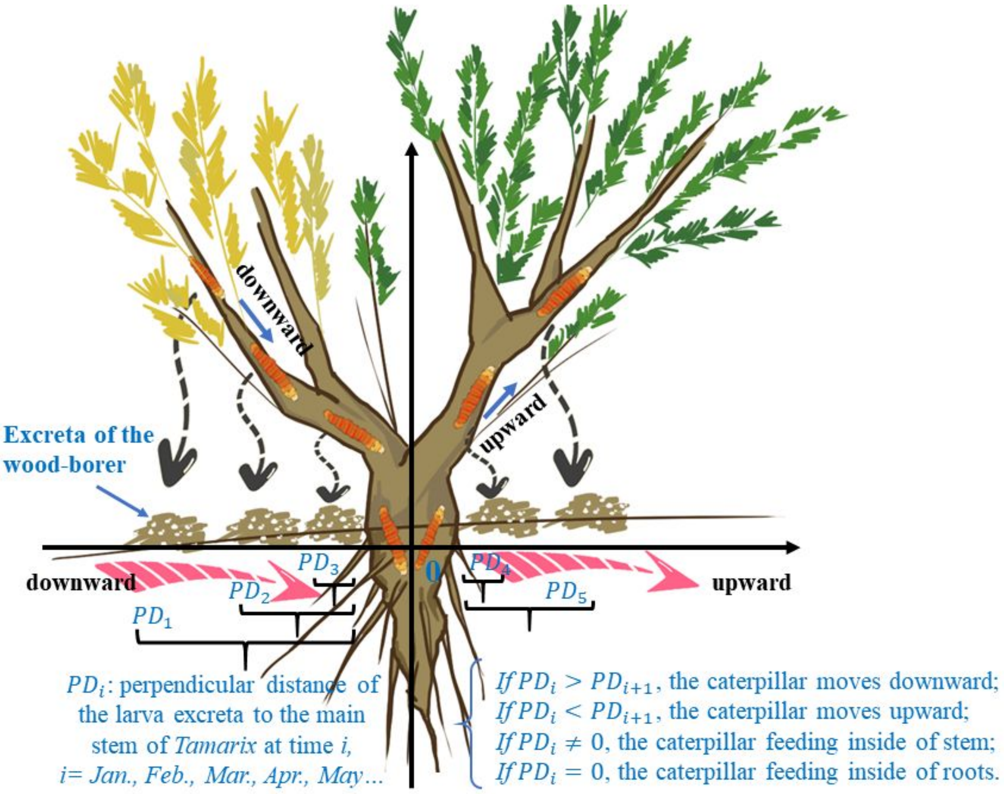


Figure S2. Methods for identifying the larval feeding position (i.e., within stem or roots) and direction of movement (i.e., downward or upward) of the caterpillar (i.e., *Zeuzera leuconotum* Butler).

As shown below in the diagram, the feeding position (i.e., within stem or roots) and movement direction (i.e., downward or upward) of the caterpillar were estimated by the perpendicular distance of the larva excreta to the main stem of *Tamarix chinensis* (i.e., PD_i, *i = Jan., Feb., Mar., Apr., May., Jun., Jul., Aug., Sep., Oct., Nov., Dec.*). We randomly selected 10 *Tamarix* plants in the observation plots during the larval development stage and monthly recorded the PD_i. Thus, the two variables were identified by the equation as follows:

$$\begin{cases} if\ PD_i > PD_{i+1}, \text{the caterpillar moves downward;} \\ if\ PD_i < PD_{i+1}, \text{the caterpillar moves upward;} \\ if\ PD_i \neq 0, \text{ the caterpillar feeding inside of stem;} \\ if\ PD_i = 0, \text{ the caterpillar feeding inside of stem;} \end{cases}$$



Text S3. The list of the literature-reported case studies testing the “Mother Knows Best (MKB)” hypothesis or “Preference-Performance Hypothesis (PPH)” in the present study.

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2. Courtney, S.P. (1981) Coevolution of Pierid butterflies and their cruciferous foodplants III. *Anthocharis cardamines* (L.) survival, development and oviposition on different hostplants. Oecologia, 51, 91-96.
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5. Leather, S. R. (1985). Oviposition preferences in relation to larval growth rates and survival in the pine beauty moth, *Panolis flammea*. Ecological Entomology, 10, 213-217.
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7. Forsberg, J. (1987). Size discrimination among conspecific hostplants in two pierid butterflies; *Pieris napi L.* and *Pontia daplidice L.* Oecologia, 72, 52-57.
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Table S4. The database of the systematic literature review includes the information extracted from each study (i. e., authors, location, latitude and longitude of study site, ecosystem type, preferred and less preferred host-plant for insect, type of the host plant (i.e., woody or herby), insect name and its order, feeding mode of insect, and whether the insect supports the MKB hypothesis).

Author	**Location**	**Lat.**	**Lon.**	**Ecosystem**	**Prefered host**	**Less prefered host**	**Plant type**	**Insect**	**Order**	**Feeding mode**	**Support MKB?**
Cherry, 1980	Southern Florida, USA	28.86	-82.03	Forest Ecosystem	Black olive	Sweet orange	Woody	*Aleurodicus dispersus*	*Homoptera*	leaf-eater	Yes
Courtney 1981	County Durham, North East of England	54.72	-1.88	Freshwater Aquatic Ecosystem	*Hesperis matrionalis*	*Alliaria petiolata*	Herby	*Anthocharis cardamine*	*Lepidoptera*	seed/flower-eater	No
Åhman 1984	Central Sweden	63.4	16.18	Forest Ecosystem	*Salix alba*	*Salix fragilis*	Woody	*Rabdophaga terminalis*	*Diptera*	leaf-eater	Yes
Åhman 1985	Central Sweden	62.64	15.08	Farmland Ecosystem	*Brassica napus*	*Brassica juncea*	Herby	*Dasineura brassicae*	*Diptera*	fruit/seed-eater	Yes
Leather 1985	Alaskan of USA	64.27	-153.4	Forest Ecosystem	*Lodgepole pine (CI)*	*Lodgepole pine (KLP)*	Woody	*Panolis flammea*	*Lepidoptera*	leaf-eater	Yes
Myers 1985	Vancouver of Canada	49.25	-123.1	Farmland Ecosystem	*Brassica oleracea L.(KPN)*	Control	Herby	*Pieris rapae*	*Lepidoptera*	leaf-eater	Yes
Forsberg 1987	Stockholm of Sweden	59.33	18.07	Farmland Ecosystem	*Thlaspi arvense* (low plants)	Thlaspi arvense (tall plants)	Herby	*Pieris napi*	*Lepidoptera*	leaf-eater	Yes
Forsberg 1988	Gotland Island of Sweden	57.46	18.47	Farmland Ecosystem	*R lutea* (low plants)	*R lutea* (tall plants)	Herby	*Pontia daplidice*	*Lepidoptera*	leaf-eater	Yes

Papaj & Rausher 1987	Texas of USA	30.96	-96.99	Forest Ecosystem	*Aristolochia reticulate* (Young leaves)	*Aristolochia reticulate* (Old leaves)	Herby	*Battus philenor*	*Lepidoptera*	leaf-eater	Yes
Quiring & McNeil 1987	Quebec of Canada	53.83	-71.91	Grassland Ecosystem	unexploited alfalfa plants	alfalfa plants with nutrition holes	Herby	*Agromyza frontella*	*Diptera*	leaf-miner	Yes
Taylor & Forno 1987	Brisbane of Australia	-27.5	153	Freshwater Aquatic Ecosystem	*Salvinia molesta* with high N	*Salvinia molesta* with high N damaged	Herby	*Samea multiplicalis*	*Lepidoptera*	stem-borer	Yes
Moore et al., 1988	British Columbia of Canada	55.91	-125.7	Forest Ecosystem	Sun leaves of tree	Shade leaves of tree	Woody	*Malacosoma californicum*	*Lepidoptera*	leaf-eater	Yes
Minkenberg & Fredrix 1989	Wageningen of Netherlands	51.97	5.64	Farmland Ecosystem	*Lycopersicon esculentum Mill*e with 5,6% N	*Lycopersicon esculentum Mille* with 4,2% N	Herby	*Liriomyza trifolii*	*Diptera*	leaf-miner	Yes
Roininen & Tahvanainen 198	Joensuu, Eastern Finland	62.6	29.75	Forest Ecosystem	*S.aq.* of willow	*S.fr.* of willow	Woody	*Nematus pavidus*	*Hymenoptera*	leaf-eater	Yes
Minkenberg & Ottenheim 1990	Wageningen of Netherlands	51.97	5.64	Farmland Ecosystem	*Lycopersicon esculentum* with N4,9%	*Lycopersicon esculentu*m with N4,6%	Herby	*Liriomyza trifolii*	*Diptera*	leaf-eater	Yes
Auerbach & Alberts 1992	North-central Minnesota, USA	48.1	-95.07	Forest Ecosystem	*Populus balsamifera*	*Populus grandidentata*	Woody	*Phyllonorycter salicifoliella*	*Lepidoptera*	leaf-miner	Yes
Fox & Eisenbach 1992	California, USA	36.58	-120.4	Farmland Ecosystem	*Collard low*	*Collard high*	Herby	*Plutella xylostella*	*Lepidoptera*	leaf-eater	Yes

Larsson & Strong 1992	Uppsala, Sweden	59.86	17.56	Forest Ecosystem	*Susceptible clones*	*Resistant clones*	Woody	*Dasineura*	*Diptera*	leaf-eater	Yes
Lederhouse et al., 1992	Paramedes, Southern Floradia, USA	25.54	-80.79	Forest Ecosystem	*Persea borbonia*	*Sassafras albidum*	Herby	*Papilio palamedes*	*Lepidoptera*	leaf-eater	Yes
Hamilton & Zalucki 1993ab	Brisbane, Australia	-27.57	152.33	Farmland Ecosystem	M1 of cotton	C6 of cotton	Herby	*Crocidosema plebeja*	*Lepidoptera*	stem-borer	Yes
Kouki 1993	Lake Ridasjairvi, southern Finland	60.67	25	Freshwater Aquatic Ecosystem	Young leaves	Old leaves	Herby	*Galerucella nymphaeae*	*Coleoptera*	leaf-eater	Yes
Leddy et al., 1993	California, USA	37.62	-121.4	Farmland Ecosystem	*Peach*	*Toyon*	Woody	*Siphoninus phillyreae*	*Homoptera*	leaf-eater	Yes
Marino et al., 1993	Delaware, USA	39.5	-75.62	Farmland Ecosystem	Fertlized plants	Unfertilized plants	Woody	*Phytomyza ilicola*	*Diptera*	leaf-miner	Yes
Nylin & Janz 1993	Stockholm, Sweden	59.33	18.12	Forest Ecosystem	*Urtica dioica*	*Salix caprea*	Woody	*Polygonia c-album*	*Lepidoptera*	leaf-eater	Yes
Shishehbor & Brennan 1996	Ahwaz, Iran	31.35	48.66	Farmland Ecosystem	Cotton	Potato	Herby	*Trialeurodes ricini*	*Homoptera*	leaf-eater	Yes
Bigger & Fox 1997	California, USA	38.43	-121.1	Farmland Ecosystem	*Brassica oleracea*	*Iberis umbellata*	Herby	*Plutella xylostella*	*Lepidoptera*	leaf-eater	Yes
Björkman et al., 1997	Trekanten, Sweden	61	17	Forest Ecosystem	*High density trees*	*Low density trees*	Woody	*Neodiprion sertifer*	*Hymenoptera*	leaf-eater	Yes
Berdegue et al., 1998	California, USA	36.96	-121.3	Farmland Ecosystem	*Chenopodium murale*	*Apium graviolens*	Herby	*Spodoptera exigua*	*Lepidoptera*	leaf-eater	Yes

Carr et al., 1998	Northern Arizona, USA	35.17	-111.6	Forest Ecosystem	vigorous shoots	medium shoots	Woody	*Nematus oligospilus*	*Hymenoptera*	leaf-eater	Yes
Gratton & Welter 1998	California Delta, Northern California, USA	38.26	-121.9	Grassland Ecosystem	*Helianthus annuus (cultivated)*	*Xanthium strumarium*	Herby	*Liriomyza helianthi*	*Diptera*	leaf-miner	Yes
Mayhew 1998	Berkshire, UK	51.55	-0.83	Grassland Ecosystem	*Sonchus oleraceus*	*Sonchus arvensis*	Herby	*Chromatomyia syngenesiae*	*Diptera*	leaf-miner	Yes
Olson 1998	Minnesota, USA	45.12	-93.97	Farmland Ecosystem	embryo of corn	far from the enbryo of corn	Herby	*Trichogramma nubilale*	*Hymenoptera*	core-borer	Yes
Rank et al., 1998	Joensuu, Finland	62.67	29.75	Forest Ecosystem	*S. myrsinifolia*	*S. myrsinifolia*	Woody	*Phratora vitellinae*	*Coleoptera*	leaf-eater	No
Tinney et al., 1998	Lancaster, UK	54.04	-2.81	Grassland Ecosystem	*Senecio jacobaea*	*Senecio vulgaris*	Herby	*Tyria jacobaeae*	*Lepidoptera*	leaf-eater	Yes
Barros & Zucoloto 1999	Ribeirao Preto, Brazil	-21.18	-47.87	Farmland Ecosystem	*Kale*	*Mustard*	Herby	*Ascia monuste*	*Lepidoptera*	leaf-eater	Yes
Sato et al., 1999	Matsudo, Japan	35.77	139.89	Farmland Ecosystem	*Lentinula edodes*-growing	*Lentinula edodes*-decaying	Herby	*Dacne picta Crotch*	*Coleoptera*	leaf-eater	Yes
Yamaga & Ohgushi 1999	Northwest of Sapporo, Hokkaido, Japan	43.08	141.17	Grassland Ecosystem	*Blue cohosh*	*Thistle*	Herby	*Epilachna pustulosa*	*Coleoptera*	leaf-eater	Yes
Craig et al., 2000	Lewisburg, Pennsylvania, USA	40.97	-76.9	Grassland Ecosystem	*Solidago altissima*	*Solidago altissima*	Hervy	*Eurosta solidaginis*	*Diptera*	leaf-miner	No

Fritz et al., 2000	Otsego County, New York, USA	42.59	-75.19	Freshwater Aquatic Ecosystem	longer shoots of *Salix discolor*	shorter shoots of *Salix discolor*	Woody	*Phyllocolpa leavitii*	*Hymenoptera*	leaf-miner	Yes
Leyva et al., 2000	San Francisco Peaks, USA	35.33	-111.7	Forest Ecosystem	*Douglas fir*	*Engelmann spruce*	Woody	*Choristoneura occidentalis*	*Lepidoptera*	leaf-eater	No
Pires et al., 2000	Federal District, Brazil	-15.52	-47.35	Grassland Ecosystem	near host plant-*Brachiaria ruziziensis*	far from host plant	Herby	*Deois flavopicta*	*Homoptera*	remets/roots-eater	No
Scheirs et al., 2000	Hoboken, Belgium	51.18	4.3	Grassland Ecosystem	*Poa trivialis*	*Dactylis glomerata*	Herby	*Chromatomyia nigra*	*Diptera*	leaf-miner	Yes
Harris et al., 2001	Palmerston North, New Zealand	-40.35	175.6	Grassland Ecosystem	7 of 10 grasses	3 of 10 grasses	Herby	*Mayetiola destructor*	*Diptera*	leaf/stem-eater	Yes
Jallow et al., 2001	Kumamoto, Japan	32.77	130.77	Farmland Ecosystem	Tomato, eggplant, pepper	Maize and okra	Herby	*Helicoverpa armigera*	*Lepidoptera*	leaf-eater	No
Kagata & Ohgushi 2001	Ishikari Rive, Ishikari City, Hokkaido, Japan	43.19	141.4	Freshwater Aquatic Ecosystem	*Populus sieboldii*	*Salix miyabeana*	Woody	*Paraleucoptera sinuella*	*Lepidoptera*	leaf-miner	Yes
Haile & Hofsvang 2002	Halhale and HalhalBegos, Asmara, Eritrea	15.28	38.91	Farmland Ecosystem	Sudan grass	Pearl millet, finger millet, setaria and wheat	Herby	*Busseola fusca*	*Lepidoptera*	stem-borer	Yes
Hodar et al., 2002	National Park of Sierra	37.09	-3.47	Forest Ecosystem	*Scots pine*	*Cluster pine*	Woody	*Thaumetopoea pityocampa*	*Lepidoptera*	leaf-eater	Yes

	Nevada, Granada, Spain										
Pappers et al., 2002	Nijmegen, Netherlands	51.87	5.83	Grassland Ecosystem	Nymphaeaceae	Polygonaceae	Herby	*Galerucella nymphaeae*	*Coleoptera*	leaf-eater	Yes
Scheirs et al., 2002	Antwerp, Belgium	51.15	4.35	Grassland Ecosystem	*Medium-aged leaves*	Old leaves	Herby	*Chromatomyia milii*	*Diptera*	leaf-miner	Yes
Steinbauer 2002	Mildura, Victoria, Australia	34.28	142.8	Forest Ecosystem	Juvenile foliage of *Eucalypyus dunnii*	Adult foliage of *Eucalypyus dunnii*	Woody	*Mnesampela privata*	*Lepidoptera*	leaf-eater	Yes
Wise & Weinberg 2002	Boyce, Virginia, USA	39	-78	Grassland Ecosystem	Undamaged plant	Flea beetle damaged plant	Herby	*Leptinotarsa juncta*	*Coleoptera*	leaf-eater	Yes
Catta-Preta & Zucoloto 2003	Bandeirantes, Brazil	-19.96	-54.35	Farmland Ecosystem	apical and medium parts of kale leaves	basal part of Kale leaves	Herby	*Ascia monuste*	*Lepidoptera*	leaf-eater	Yes
Fritz et al., 2003	Otsego County, New York, USA	42.62	-75.05	Freshwater Aquatic Ecosystem	damaged *Salix discolor*	undamaged *Salix discolor*	Woody	*Phyllocolpa leavitti*	*Hymenoptera*	leaf-eater	Yes
Mustapha & Zalucki 2003	Gatton, South-Queensland, Australia	-27.56	152.27	Farmland Ecosystem	na	na	Herby	*Helicoverpa armigera*	*Lepidoptera*	leaf-eater	No
Koo et al., 2003	Mt. Kwanak, Korea	37.6	127.5	Forest Ecosystem	large acorns	egg-free acorns	Woody	*Mechoris ursulus*	*Coleoptera*	fruit-eater	Yes
Lamb et al., 2003	Winnipeg, Canada	49.79	-97.1	Farmland Ecosystem	wheat-Robin	wheat-superb, Key 97-10	Herby	*Sitodiplosis mosellana*	*Diptera*	leaf-eater	Yes
Morewood et al., 2003	Pennsylvania, USA	41.61	-77.58	Forest Ecosystem	sugar maple, Acer	red maple, Acer rubrum L., green	Woody	*Anoplophora glabripennis*	*Coleoptera*	stem-borer	Yes

					saccharum Marshall	ash, Fraxinus pennsylvanicaMarshall, or red oak, Quercus rubra L.					
Nomikou et al., 2003	RijkZwaan, De Lier, The Netherlands	51.97	4.26	Farmland Ecosystem	host plant without predator	host plant with predator	Herby	*Bemisia tabaci*	*Hemiptera*	leaf-sucker	Yes
Scheirs et al., 2003	Marke, Belgium	50.8	3.23	Grassland Ecosystem	*Poa trivialis*	*Lolium perenne*	Herby	*Chromatomyia milii*	*Diptera*	leaf-miner	Yes
Smyth et al., 2003	Cornell, Ithaca, New York, USA	42.45	-76.45	Farmland Ecosystem	cabbage at 7-8 wk from planting	cabbage at 9-11 wk from planting	Herby	*Crocidolomia pavonana*	*Lepidoptera*	leaf-eater	Yes
Ferrier & Price 2004	Flagstaff, Northern Arizona, USA	35.17	-111.7	Forest Ecosystem	Longest shoot-length classes	Short shoot-length classes of Salix scouleriana	Woody	*Euura mucronata*	*Hymenoptera*	leaf-eater	No
Balagawi et al., 2004	Queensland, Australia	-21.6	143.58	Farmland Ecosystem	Grosse Lisse and Roma tomato cultivars	Cherry tomato cultivar	Herby	*Bactrocera tryoni*	*Diptera*	leaf-eater	Yes
Harvey et al., 2005	Wageningen, Netherlands	51.96	5.66	Grassland Ecosystem	*High iridoid*	*Low iridoid*	Herby	*Melitaea cinxia*	*Lepidoptera*	leaf-eater	Yes
Harvey et al., 2006	Wageningen, Netherlands	51.98	5.7	Grassland Ecosystem	*High iridoid*	*Low iridoid*	Herby	*Spodoptera exigua*	*Lepidoptera*	leaf-eater	Yes
Heisswolf et al., 2005	Northern Bavaria, Germany	50.05	10.58	Grassland Ecosystem	Large plants	Small plants	Herby	*Cassida canaliculata*	*Coleoptera*	leaf-eater	Yes

Janz 2005	Catalonia, Spain	41.8	1.23	Farmland Ecosystem	*Cirsium arvense*	*Urtica dioica*	Herby	*Vanessa cardui*	*Lepidoptera*	leaf-eater	Yes
Ladner & Altizer 2005	Atlanta, USA	33.79	-84.36	Grassland Ecosystem	*Asclepiadaceae incarnata*	*Asclepiadaceae fasciculari*	Herby	*Danaus plexippus*	*Lepidoptera*	leaf-eater	Yes
Martin et al., 2005	Kettleby, Canada	44.01	-79.58	Farmland Ecosystem	Pea	Potato, lettuce, gai lan, celery, cucumber, and onion	Herby	*Liriomyza huidobrensis*	*Diptera*	leaf-miner	No
Prudic et al., 2005	Colorado, USA	39.31	-107.8	Grassland Ecosystem	*Unfertilized Plantago lanceolata*	*Fertilized Plantago lanceolata*	Herby	*Junonia coenia*	*Lepidoptera*	leaf-eater	Yes
Digweed 2006	Edmonton, Alberta, Canada	53.52	113.52	Forest Ecosystem	Leaves already bearing eggs from other females	Damaged leaves	Woody	*Profenusa thomsoni*	*Hymenoptera*	leaf-miner	No
Johnson et al., 2006	Devon, UK	50.77	-3.82	Grassland Ecosystem	Plants with root nodules	Plants without root nodules	Herby	*Sitona lepidus*	*Coleoptera*	root-eater	Yes
Van der Berg 2006	Potchefstroom, South Africa	-26.72	27.05	Farmland Ecosystem	Napier grass-*Pennisetum purpureum*	Maize	Herby	*Chilo partellus*	*Lepidoptera*	stem-borer	No
Videla et al., 2006	Córdoba City, in central Argentina	31.33	64.17	Farmland Ecosystem	*Phaseolus vulgaris*	*Cucurbita maxima var. Zapallito*	Herby	*Liriomyza huidobrensis*	*Diptera*	leaf-miner	Yes
Brodbeck et al., 2007	North Florida, USA	30.27	-83.48	Forest Ecosystem	*Lagerstroemia indica* and *Citrus sinensi*	*V. vinifera, and G. max.*	Woody	*Homalodisca vitripennis*	*Hemiptera*	leaf-eater	No

Müller & Arand 2007	Würzburg, Germany	49.81	9.95	Farmland Ecosystem	*Sinapis alba L., Brassica nigra (L.) Koch, and Barbarea stricta Andrz.*	*Sinapis alba L., Brassica nigra (L.) Koch, and Barbarea stricta Andrz.*	Herby	*Athalia rosae* L.	*Hymenoptera*	leaf-eater	Yes
Ishihara & Ohgushi 2008	Ishikari River, Hokkaido, Japan	43	142	Freshwater Aquatic Ecosystem	*S. sachalinensis*	*S. miyabeana* and *S. integra*.	Woody	*Plagiodera versicolora*	*Coleoptera*	leaf-eater	No
Keeler & Chew 2008	Massachusetts, USA	42.35	-73.28	Grassland Ecosystem	*Garlic mustard*	*Normal host*	Herby	*Pieris oleracea*	*Coleoptera*	leaf-eater	Yes
Keeler & Chew 2008	Vermont, USA	43.63	-72.28	Grassland Ecosystem	*Garlic mustard*	*Normal host*	Herby	*Pieris oleracea*	*Coleoptera*	leaf-eater	Yes
Keeler & Chew 2008	Wolcott, USA	44.55	-72.47	Grassland Ecosystem	*Garlic mustard*	*Normal host*	Herby	*Pieris oleracea*	*Coleoptera*	leaf-eater	Yes
Keeler & Chew 2008	Texas Falls, USA	43.93	-72.08	Grassland Ecosystem	*Garlic mustard*	*Normal host*	Herby	*Pieris oleracea*	*Coleoptera*	leaf-eater	Yes
Bertheau et al., 2009	Chamboux, France	45.67	2	Forest Ecosystem	*Picea abies and P. sitchensis*	*Pinus spp.*	Woody	*Pityogenes chalcographus*	*Coleoptera*	bark/stem-borer	Yes
Bertheau et al., 2009	Larfeuil, France	45.5	1.95	Forest Ecosystem	*Picea abies and P. sitchensis*	*Pinus spp.*	Woody	*Pityogenes chalcographus*	*Coleoptera*	bark/stem-borer	Yes
Forister et al., 2009	California, USA	39.78	-120.1	Grassland Ecosystem	*Astragalus canadensis*	*Medicago sativa*	Herby	*Lycaeides melissa*	*Lepidoptera*	leaf-eater	Yes
Azerefegne & Solbreck 2010	Awassa, Sweden	6	40	Farmland Ecosystem	*Ipomoea tenuirostris* and	remaining three species	Herby	*Acraea acerata*	*Lepidoptera*	leaf-eater	Yes

					Ipomoea cairica						
Bonebrake et al., 2010	Colorado, USA	38.95	-107	Grassland Ecosystem	*L. involucrata*	*L. involucrata*	Herby	*Euphydryas gillettii*	*Lepidoptera*	leaf-eater	Yes & No
Jazorek et al., 2010	Fort DeSoto Park, Pinellas County, Florida, USA	27.63	-82.72	Forest Ecosystem	*O. engelmannii*	*C. acanthocarp*a, *O. streptacantha*, *C. spinosior*, etc.	Herby	*Cactoblastis cactorum*	*Lepidoptera*	leaf-eater	No
Karungi et al., 2010	Kabanyolo, Uganda	0.47	32.45	Farmland Ecosystem	Chinese cabbage and broccoli	Other cabbage	Herby	*Crocidolomia pavonana*	*Lepidoptera*	leaf-eater	Yes
Liu et al., 2010	Toowoomba, southeastern Queensland, Australia	-27.56	151.88	Grassland Ecosystem	Flowering tobacco and sunflower plants	Withot flowering	Herby	*Helicoverpa armigera*	*Lepidoptera*	inflorescences/leaf-eater	Yes
Maboko & Stephen 2010	Lowa, USA	42.33	-93.39	Grassland Ecosystem	Sunflower pre-breeding lines	Sunflower pre-breeding lines	Herby	*Homoeosoma electellum*	*Lepidoptera*	inflorescences/leaf-eater	Yes
Santos et al., 2010	Minas Gerais, southeastern Brazil	-18.38	-45.33	Freshwater Aquatic Ecosystem	Longer shoots of *Bauhinia brevipes*	Medium shoots of *Bauhinia brevipes*	Herby	*Asphondylia microcapillata*	*Diptera*	leaf-eater	Yes
Shikano et al., 2010	British Columbia, Vancouver, Canada	49.23	-123.1	Farmland Ecosystem	Cabbage, green bush bean, tomato, anise hyssop, geranium hybrid	Cabbage, green bush bean, tomato, anise hyssop, geranium hybrid	Herby	*Trichoplusia ni*	*Lepidoptera*	leaf-eater	No

Videla et al., 2010	Córdoba City, central Argentina	-31.33	-64.17	Farmland Ecosystem	*V. faba*	*B. vulgaris var. cicla*	Herby	*Liriomyza huidobrensis*	*Diptera*	leaf-miner	Yes
Wennström et al., 2010	Hummelholm, Sweden	63.72	19.52	Freshwater Aquatic Ecosystem	*Salix triandra L.* without secondly chemical compounds	*Salix triandra L* with secondly chemical compounds	Woody	*Gonioctena linnaeana Schrank*	*Coleoptera*	leaf-eater	Yes
Blake et al., 2011	Lethbridge, Alberta, Canada	49.68	-112.7	Farmland Ecosystem	Higher supply of nitrogen on cabbage	Lower supply of nitrogen on cabbage	Herby	*Ceutorhynchus obstrictus*	*Coleoptera*	leaf-eater	No
Clark et al., 2011	Dundee, UK	56.43	-3	Farmland Ecosystem	Root of *Rubus idaeus*	Root of *Rubus idaeus*	Herby	*Otiorhynchus sulcatus*	*Coleoptera*	root-eater	No
De-silva et al., 2011	San Martin, Peru	-7.06	-76.95	Forest Ecosystem	*Solanum mite* Ruiz & Pav with lower predation	*Solanum mite* Ruiz & Pav with higher predation	Herby	*Oleria onega* Hewitson	*Lepidoptera*	leaf-eater	Yes
Ero et al., 2011	Brisbane, Qld, Australia	-27.49	152.97	Farmland Ecosystem	Guava and peach	Apple, pear and orange	Woody	*Diachasmimorpha kraussii*	*Hymenoptera*	fruit-eater	Yes
Inoda 2011	Fallow wetlands, Chiba Prefecture, Japan	35.68	140.01	Freshwater Aquatic Ecosystem	Stems of *O. javanica*	Acorus calamus, Cardamine flexuosa, Azolla japonica, Persicaria thunbergii,Alisma canaliculatum	Herby	*Dytiscus sharpi*	*Coleoptera*	stem-borer	Yes

Mazaheri et al., 2011	Isfahan, Iran	32.64	51.59	Forest Ecosystem	*U. carpinifolia* and *U. carpinifolia var. umbraculifera*	*Platanus orientali*s, *P. alb*a, and F. rotundifolia subsp. persica	Woody	*Aeolesthes sarta*	*Coleoptera*	stem-borer	Yes
Nyman et al., 2011	Luikonlahti,eastern Finland	62.9	28.66	Forest Ecosystem	*Salix myrsinifolia* Salisb and hybridised *S* . *myrsinifolia* × *phylicifoliaL*. Clones	*Salix myrsinifolia* Salisb and hybridised *S* . *myrsinifolia* × *phylicifoliaL*. Clones	Woody	*Rabdophaga rosaria*	*Diptera*	leaf-eater	No
Sadek 2011	Assiut, Egypt	27.17	31.16	Farmland Ecosystem	Yong leaves of *Gossypium hirsutum*	Mature leaves of *Gossypium hirsutum*	Herby	*Spodoptera littoralis*	*Lepidoptera*	leaf-eater	Yes
Santos et al., 2011	Igarassu, Pernambuco, northeastern Brazil	-7.8	-34.45	Forest Ecosystem	Yong leaves of *Miconia prasin*a	Long leaves of *Miconia prasin*a	Herby	*Prospoliata bicolorata*	*Coleoptera*	leaf-eater	Yes
Seagraves et al., 2011	State of South Dakota, USA	44.51	-102.5	Farmland Ecosystem	Stressed plants	Unstressed plants	Herby	*Orius insidiosus*	*Hemiptera*	leaf-eater	Yes
Clark et al., 2012	Lincoln, UK	53.23	-0.58	Farmland Ecosystem	Glen Rosa and Glen Ample	Glen Rosa and Glen Ample	Herby	*Otiorhynchus sulcatus*	*Coleoptera*	leaf-eater	No
Garc´ıa-Robledo & Horvitz 2012	Costa Rica, Central America	10.43	-83.98	Forest Ecosystem	Native host plants	Novel host plants	Herby	*Cephaloleia belti, Cephaloleia*	*Cephaloleia*	leaf-eater	Yes

								dilaticollis, Cephaloleia placida, Cephaloleia dorsalis			
Potter et al., 2012	Southeastern Arizona, USA	31.8	-110.9	Grassland Ecosystem	Larger leaves of *D. wrightii*	Small leaves of *D. wrightii*	Herby	*Manduca sexta* L.	*Lepidoptera*	leaf-eater	No
Soler et al., 2012	Wageningen, Netherlands	51.97	5.63	Farmland Ecosystem	*Brassica oleracea* with aphid-infested	*Brassica oleracea* without aphid-infested	Herby	*Pieris brassicae*	*Lepidoptera*	leaf-eater	Yes
Videla et al., 2012	Córdoba City, Central Argentina	31.33	-64.17	Farmland Ecosystem	*Vicia faba* (Fabaceae)	*Beta vulgaris var.cicla* (Chenopodiaceae)	Herby	*Liriomyza huidobrensis*	*Diptera*	leaf-miner	Yes
Zhang et al., 2012	Hangzhou, China	30.32	120.11	Farmland Ecosystem	Chinese cabbage (*Brassica campestris L. ssp. pekinensis*)	Chinese cabbage (*Brassica campestris L. ssp. pekinensis*)	Herby	*Plutella xylostella*	*Lepidoptera*	leaf-eater	Yes
D'coata et al., 2013	Surrey, UK	51.18	-0.48	Forest Ecosystem	*A. hipppocastanum, A. turbinata, etc.*	*A. indica*, *A. syivatica*, etc.	Woody	*Cameraria ohridella*	*Lepidoptera*	leaf-miner	Yes
Fortuna et al., 2013	Gelderland, Netherlands	52	6.15	Grassland Ecosystem	Native host plant-*Sinapis arvensis*	Exotic host plant-*Bunias orientalis*	Herby	*Pieris brassicae*	*Lepidoptera*	leaf-eater	Yes

Chirumamilla et al., 2014	Prosper, southeastern North Dakota, USA	46.96	-97.02	Grassland Ecosystem	Sunflower-PI 494859	Sunflower-Par 1673-2	Herby	*Cochylis hospes*	*Lepidoptera*	seed-eater	No
D'coata et al., 2014	Taunton, UK	51.01	-3.1	Forest Ecosystem	*A. hippocastanum*	*A.turbinata*	Woody	*Cameraria ohridella*	*Cameraria ohridella*	leaf-miner	No
Gómez Jiménez et al., 2014	Marengo, Colombia	4.67	-74.02	Farmland Ecosystem	Cabbage, broccoli, alstroemeria, potato, red clover (*Trifolium repens L.*), hot pepper, onion, and cape gooseberry	Cabbage, broccoli, alstroemeria, potato, red clover (*Trifolium repens L.*), hot pepper, onion, and cape gooseberry	Herby	*Copitarsia decolora,Peridroma saucia*	*Lepidoptera*	leaf-eater	No
Kutyniok et al., 2014	Münster, Germany	51.94	7.57	Grassland Ecosystem	*Arabidopsis thaliana* with nematode-free	Arabidopsis thaliana with nematode-infested	Herby	*Myzus persicae*	*Hemiptera*	leaf-sucker	Yes
Rigsby et al., 2014	Wright, USA	39.8	-84.1	Forest Ecosystem	Ash species native to North America	Manchurian ash	Woody	*Agrilus planipennis*	*Coleoptera*	stem-borer	Yes
Rigsby et al., 2014	Novi, USA	42.5	-83.5	Forest Ecosystem	Ash species native to North America	Manchurian ash	Woody	*Agrilus planipennis*	*Coleoptera*	stem-borer	Yes

Wang et al., 2015	Kunming, China	25.02	102.68	Forest Ecosystem	Branches with fewer acorns and larger acorns of *Cyclobalanopsis glaucoides* Schottky and *Quercus franchetii* Skan	Branches with smaller acorns of *Cyclobalanopsis glaucoides* Schottky and *Quercus franchetii* Skan	Woody	*Mechoris ursulus*	*Coleoptera*	stem/fruit-borer	Yes
Du et al., 2016	Beijing, China	40.4	116.5	Farmland Ecosystem	Huaijiu	Other three chestnut cultivars-Huaihuang, Yanhong, and Shisheng	Woody	*Conogethes punctiferalis*	*Lepidoptera*	fruit-borer	Yes
Helmberger et al., 2016	Duluth, Minnesota, USA	46.71	-92.23	Grassland Ecosystem	Low-water treatment plants	High-water treatment plants	Herby	*Corythucha marmorata*	*Hemiptera*	leaf-eater	Yes
Kelly & Bowers 2016	Longmont, Colorado, USA	39.92	-105.3	Grassland Ecosystem	More chemically defended host plant of genus *Penstemon*	Less well defended host plant of genus *Penstemon*	Herby	*Euphydryas anicia, Estigmene acrea*	*Lepidoptera*	leaf-eater	No
König et al., 2016	Ludgo, Sweden	58.92	17.13	Grassland Ecosystem	*Cardamine pratensis*	*Cardamine pratensis*	Herby	*Anthocharis cardamines*	*Lepidoptera*	leaf-eater	No

Schäpers et al., 2016	Catalonia, Spain	41.71	0.83	Grassland Ecosystem	High quality host plant	Poor quality host plant	Herby	*Five nymphalid butterfly species*	*Lepidoptera*	leaf-eater	Yes
Wist & Evenden 2016	Edmonton, Alberta, Canada	53.53	-133.5	Forest Ecosystem	Green ash *of Fraxinus* spp.	Black ash *of Fraxinus* spp.	Woody	*Caloptilia fraxinella*	*Lepidoptera*	leaf-miner	Yes
Arce et al., 2017	Viçosa, Brazil	-20.75	-42.89	Farmland Ecosystem	*Solanum lycopersicu*m without root-infested	*Solanum lycopersicum* with root-infested	Herby	*Tuta absoluta*	*Lepidoptera*	leaf-miner	Yes
Brown et al., 2017	Harvard, MA, USA	42.82	-109.5	Forest Ecosystem	Introduced host plant-Plantago lanceolata	Native host Chelone glabra	Woody	*Euphydryas phaeton*	*Lepidoptera*	leaf-eater	Yes
Fei et al., 2017	Wageningen, Netherlands	52	5.61	Farmland Ecosystem	Younger and smaller of cabbage-*B. nigr*a and *S. arvensi*s	Mature and pre-senescinh of cabbage-*B. nigr*a and *S. arvensi*s	Herby	*Pieris brassicae*	*Lepidoptera*	leaf-eater	No
Martín et al., 2017	INIA Experimental Station	-31.73	-55.97	Forest Ecosystem	*Eucalyptus grandis W. Hill ex Maiden* and *E. tereticornis* adult leaves that had been previously damaged by	*E. grandis*	Woody	*Thaumastocoris peregrinus*	*Heteroptera*	leaf-sucker	Yes

					female conspecifics						
Morse 2017	Lincoln County, Maine, USA	43.95	-69.55	Grassland Ecosystem	Shelters that provide enemy-free space	Exposed pinnae	Herby	*Herpetograma theseusalis*	*Lepidoptera*	leaf-eater	Yes
Vankosky & Van Laehoven	California, USA	35.7	-118.8	Farmland Ecosystem	Higher-nitrogen fertilized host plant-tomato	Lower-nitrogen fertilized host plant-tomato	Herby	*Dicyphus hesperus*	*Hemiptera*	leaf-eater	No
Altersor & González 2018	Canelones, Uruguay	-34.53	-56.3	Farmland Ecosystem	*S. commersonii*	*S. tuberosum* var	Herby	*Tequus schrottkyi*	*Hymenoptera*	leaf-eater	Yes
Birke et al., 2018	Xalapa, Veracruz, Maxico	19.52	-96.93	Farmland Ecosystem	Mango and grapefruit	Guava, pepper, peach, and white sapote	Herby	*Anastrepha ludens*	*Diptera*	fruit-eater	No
Coapio et al., 2018	Tapachula, Chiapas, Mexico	14.84	-92.28	Farmland Ecosystem	Cabbage and tomato	Soybean and wormseed	Herby	*Trichoplusiani* (Hubner)	*Lepidoptera*	leaf-eater	Yes
Hou et al., 2018	Lingyuan of Liaoning, China	40.93	119.29	Forest Ecosystem	Chinese pine-One year generation	Chinese pine-Two year generation	Woody	Dendrolimus punctatus tabulaeformis	*Lepidoptera*	leaf-eater	Yes
Rojas et al., 2018	Carlisle, Pennsylvania, USA	40.2	-77.22	Farmland Ecosystem	Maize	Maize	Herby	*Spodoptera frugiperda*	*Lepidoptera*	leaf-eater	No
He et al., 2019	Mengzi, Yunnan, China	23.27	103.42	Farmland Ecosystem	Six host plants, i.e., pumpkin, cucumber,	Six host plants, i.e., pumpkin, cucumber,jiangbin	Herby	*Bactrocera tau and Bactrocera cucurbitae*	*Diptera*	fruit-eater	No

					jiangbing melon, zucchini, towel gourd and balsam pear	g melon, zucchini, towel gourd and balsam pear					
Jones & Agrawal 2019	Maine, USA	44.93	-70.02	Farmland Ecosystem	*Asclepias incarnata* subspecies *pulchra*	*Asclepias incarnata* subspecies *pulchra*	Herby	*Danaus plexippus*	*Lepidoptera*	leaf-eater	No
Krug & Sosa 2019	Hurlingham, Buenos Aires Province, USA	35.59	-58.64	Freshwater Aquatic Ecosystem	*Alternanthera philoxeroides* (Martius) *Grisebach*-hexaploids	*Alternanthera philoxeroides* (Martius) *Grisebach*-tetraploids	Herby	*Agasicles hygrophila*	*Coleoptera*	leaf-eater	Yes
Olazucaga et al., 2019	Montpellier, France	43.6	3.83	Farmland Ecosystem	Cherry, Blackberry, Blackcurrant	Rose hips, Tomato, Strawberry, etc.	Herby	*Drosophila suzukii*	*Diptera*	fruit-eater	No
Laihonen et al., 2020	Ruissalo Botanical Garden, Finland	60.43	22.17	Grassland Ecosystem	*Festuca rubra*, *Festuca arundinaces*	*Festuca rubra*, *Festuca arundinaces*	Herby	*Coenonympha hero*	*Lepidoptera*	leaf-eater	No