Cross-Attraction between an Exotic and a Native Pine Bark Beetle: A Novel Invasion Mechanism?

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Background. Aside from the ecological impacts, invasive species fascinate ecologists because of the unique opportunities that invasives offer in the study of community ecology. Some hypotheses have been proposed to illustrate the mechanisms that allow exotics to become invasive. However, positive interactions between exotic and native insects are rarely utilized to explain invasiveness of pests. Methodology/Principal Findings. Here, we present information on a recently formed association between a native and an exotic bark beetle on their shared host, Pinus tabuliformis, in China. In field examinations, we found that 35–40% of P. tabuliformis attacked by an exotic bark beetle, Dendroctonus valens, were also attacked by a native pine bark beetle, Hylastes parallelus. In the laboratory, we found that the antennal and walking responses of H. parallelus to host- and beetle-produced compounds were similar to those of the exotic D. valens in China. In addition, D. valens was attracted to volatiles produced by the native H. parallelus. Conclusions/Significance. We report, for the first time, facilitation between an exotic and a native bark beetle seems to involve overlap in the use of host attractants and pheromones, which is cross-attraction. The concept of this interspecific facilitation could be explored as a novel invasive mechanism which helps explain invasiveness of not only exotic bark beetles but also other introduced pests in principle. The results reported here also have particularly important implications for risk assessments and management strategies for invasive species.

INTRODUCTION

Invasive species have long fascinated ecologists and invasive biologists, not only because they can cause tremendous destruction, but also because we do not yet understand fully how they can successfully invade novel communities [1–3]. To curb the future economic and environmental impacts of invasive exotic species, we need to understand the invasion mechanisms behind invasive species. Understanding such mechanisms also might be crucial for the successful management of biological invasions.

Attempts to determine the mechanisms of invasiveness by exotic species have focused primarily on ecological (such as empty niche [4] and enemy release [5]) and evolutionary hypotheses (such as evolution of increased competitive ability [6] and founder events) [7]. In contrast, facilitation between exotic and native invertebrates has received much less attention although the relevance of facilitation may be important, especially when several invasion mechanisms work in synergy [7–9]. This may be particularly true for bark beetles (Coleoptera: Scolytidae) that breed in the phloem tissue of coniferous trees, often in multiple-species associations [10].

Competition and facilitation are arguably two of the most important forces in the community ecology of bark beetles. Typically, bark beetles tunnel within phloem tissue, laying eggs along the way [10]. The larvae hatch and feed through the phloem tissue, creating fan or star-shaped galleries. Competition has likely separated different species by host species as well as by host requirements within the same species, resulting in unique niches based on such characters as phloem thickness, tree defense chemistry, nutritional quality and water content [11]. Separation of species within a tree can occur through preference for specific part of a tree (cones, twigs and small branches, large branches, upper and lower trunk, root collar and roots) [10].

Facilitation in bark beetles is evident from concurrent within-tree attacks by secondary species (such as species in the genera Ips DeGeer, Hylastes Erichson, Pityogenes Bedel and Pityophthorus Eichhoff) following the activities of aggressive tree-killing bark beetles (such as Dendroctonus species) [10], [12]. Attacks by tree-killing species are generally restricted to the main trunks of trees thereby leaving other portions of the same trees (such as upper holes, large branches and twigs) available for other species with little risk of beetle mortality from tree defenses [10]; the trees have already been killed by the aggressive species [12]. These types of facilitated associations may be important in understanding the invasiveness of exotic bark beetles in areas with few competing species of bark beetles and on hosts with little evolutionary experience with aggressive bark beetles.

The most destructive terrestrial invertebrate species to pine forests in China is the exotic red turpentine beetle, Dendroctonus valens LeConte [13]. Dendroctonus valens was likely introduced into China through the importation of unprocessed logs from the Pacific-Northwest region of the United States [14–15]. In 1999, the first major epidemic of D. valens began in Shanxi province in northern China, spreading to three adjacent provinces and killing...
more than 6 million *P. tabuliformis* over an area of 0.5 million hectares in a period of three years [13], [16–18].

The aggressive ability of *D. valens* to kill healthy pine trees in China is in distinct contrast to its biology in its native range of North America where *D. valens* favors weakened, dying or fire-scorched trees, rarely killing trees outright but at times weakening them enough for successful attacks by other species of bark beetles [10]. During the course of field studies on *D. valens* in China, the authors noted an unusual prevalence of another bark beetle species, *Hylastes parallelus* Chapuis, in pine forests under attack by *D. valens*. Historically, *H. parallelus* is a secondary bark beetle, common in spruce and pine forests of China, Korea, Russia and Japan, and generally breeding in roots and stems of stressed trees [19–20]; *H. parallelus* is not found in North America [21]. It is possible that initial attacks by the exotic *D. valens* are followed closely by infestations by the native *H. parallelus*, leading to facilitation between the two species. Stress in the root system of a pine tree, such as one caused by an infestation by a phloem-feeding species (*H. parallelus*), could increase the attack success of a primary species such as *D. valens*. Elevated levels of stress caused by an increase in *D. valens* attack success could also enhance the breeding opportunities for *H. parallelus*. Instances of tree mortality involving *D. valens* in North America have involved attacks by both primary and secondary bark beetles [10].

Cross-attraction of bark beetle species is fairly common in North America and Europe, particularly with respect to compounds produced by host trees, such as ethanol and monoterpenes, and pheromones, such as ipsenol and ipsdienol [22–23]. Pre-adaptations in chemical communication may facilitate mutualistic associations with exotic species [24]. Therefore, we evaluated facilitation of an exotic and a native bark beetle based on field study and antennal and behavioral experiments in the laboratory.

**RESULTS**

**Field Association between *D. valens* and *H. parallelus***

We found *H. parallelus* on roots of *P. tabuliformis* at both locations in China, with a significant association with attacks by *D. valens* (ANOVA, *F*~2, 27~ = 68.71, *P* < 0.001 at the Tunlanchuan Forest Station; *F*~2, 27~ = 57.41 at Yaopin Forest Station, *P* < 0.001). At both locations, healthy pines with no evidence of attacks by *D. valens* had low numbers of roots infested by *H. parallelus* (<0.05%), with approximately one adult beetle on each attacked root (Fig. 1A–B). Pines with recent and old attacks by *D. valens* had significantly more roots with *H. parallelus* than pines unattacked by *D. valens*, with the highest percentage of infested roots on trees with old attacks by *D. valens* (35–40%) (Fig. 1B). The infestation rate of roots in trees with recent attacks by *D. valens* was approximately 20% at both sites (Fig. 1B). The same relationship was found with the number of adult *H. parallelus* on infested roots, with significantly more beetles on roots of trees with either recent or old attacks by *D. valens* than on infested roots on unattacked trees (Fig. 1A). The
number of beetles on infested roots was lower on trees with recent attacks by *D. valens* than on trees with old attacks. There were no significant differences in total numbers of roots/tree among uninfested, newly-attacked and old-attacked trees at the Tunlanchuan and Yaopin Forest Stations (ANOVA, $F_{2, 27} = 2.134$, $P = 0.34$ and $F_{2, 27} = 1.765$, $P = 0.41$, respectively). The total numbers (±SD, $n = 10$) of roots/tree at the Tunlanchuan Forest Station were 5.12 (±3.01), 6.17 (±2.31) and 5.71 (±2.91) for unattacked, new-attacked and old-attacked trees, respectively. At the Yaopin Forest Station, the total numbers (±SD, $n = 10$) of roots/tree were 4.98 (±2.51), 6.57 (±3.04) and 5.89 (±2.77), respectively. We found some evidence of successful brood production by *H. parallelus* in roots of old-attacked trees, from attacks that occurred in the previous year. However, brood establishment was not quantified. Recurring attacks by *D. valens* were also evident in old-attacked trees.

### Volatiles Produced by *H. parallelus*

In experiment 2, the most prominent volatile in the hindguts of male and female *H. parallelus* was $\alpha$-pinene, with mean (±SE) percentages of 58.4 (±1.0) and 58.4 (±1.2), respectively ($n = 4$) (Fig. 2). The next most common terpenes were $\beta$-pinene and limonene, with mean (±SE, $n = 4$) percentages of 15.5 (±1.0) and 10.7 (±1.3), respectively, in extracts from male hindguts, and 13.8 (±1.0) and 13.8 (±0.8), respectively, in extracts from female hindguts. Myrtenol, myrtenal and norinone accounted for 6.4 (±0.2), 3.4 (±0.2) and 2.6 (±0.3) percent, respectively, of volatiles in male extracts and 6.5 (±0.3), 3.2 (±0.3) and 1.9 (±0.1) percent, respectively, of volatiles in female extracts. In male and female extracts, $\alpha$-trans-verbenol, cryptone, $\alpha$-cis-verbenol and isoborneol were each present at ≤1%. 3-Carene was not detected in hindgut extracts. We found no evidence of any sex-specific production of compounds.

### Antennal and Walking Responses of *H. parallelus*

The electroantennographic detector (EAD) responses of *H. parallelus* in experiment 3 were comparable among all ten male and ten female antennae that we tested. Typically terpinolene, ($\pm$)-myrtenal and ($\pm$)-myrtenol elicited responses by male and female antennae of *H. parallelus* (Fig. 3A, compounds 5, 6 and 7, respectively), with little, if any, response to ($+$)-$\alpha$-pinene, ($\pm$)-$\beta$-pinene, myrcene or ($\pm$)-limonene. Similarly, ($+$)-3-carene elicited responses in both male and female antennae (Fig. 3B, compound 8), with little, if any, EAD response to ($+$)-trans-verbenol, ($+$)-cis-verbenol and verbenone. There were no significant differences between sexes in antennal responses to ($+$)-3-carene, terpinolene, ($\pm$)-myrtenal and ($\pm$)-myrtenol (Mann-Whitney test, $P = 0.728$, $P = 0.376$, $P = 0.459$, and $P = 0.241$, $n = 10$, respectively).

The walking responses of *H. parallelus* in experiment 4 were similar to the EAD responses in experiment 3. Male and female *H. parallelus* were attracted to ($+$)-3-carene, terpinolene, ($\pm$)-myrtenal, and ($\pm$)-myrtenol (Fig. 4). Walking responses were unaffected by the common monoterpenes, ($+$)-$\alpha$-pinene, ($\pm$)-$\beta$-pinene, myrcene and ($\pm$)-limonene, and the terpene-derived compounds, ($+$)-$\alpha$-trans-verbenol, ($+$)-$\alpha$-cis-verbenol and verbenone.

![Figure 2. Typical gas chromatograms of male (A) and female (B) *H. parallelus* hindgut extracts. Each extract contains contents from 20 individuals. 1 $\alpha$-pinene, 2 $\beta$-pinene, 3 limonene, 4 norinone, 5 myrtenal, 6 trans-verbenol, 7 cryptone, 8 cis-verbenol, 9 myrtenol, 10 isoborneol. doi:10.1371/journal.pone.0001302.g002](image-url)
Interspecific Responses of \textit{D. valens}

The EAD responses of antennae from \textit{D. valens} in experiment 5 were consistent among all antennae that we tested. Typically, trans-verbenol, myrtenol, cis-verbenol and myrtenal in hindgut extracts from \textit{H. parallelus} elicited EAD responses from \textit{D. valens} (Fig. 5), with no significant differences between the sexes (Mann-Whitney test, \(P = 0.479, P = 0.598, P = 0.794, \) and \(P = 0.198, n = 10,\) respectively). In experiment 6, male and female \textit{D. valens} were significantly attracted to male and female \textit{H. parallelus} hindgut extracts in the Y-tube olfactometer (Fig. 6).

\textbf{DISCUSSION}

Various factors have likely led to facilitation among bark beetles. Natural selection should favor bark beetles that can locate and occupy breeding niches in a timely manner since the nutrient quality of phloem tissue can desiccate and degrade quickly [26]. The selective advantage for utilizing these nutrient-rich opportunities seem clear as breeding opportunities for bark beetles tend to be patchy and unpredictable [27]. Chemical ecology is an important part of the facilitation between bark beetle species, allowing individuals to quickly locate breeding opportunities yet
D. valens seems to prefer the lower trunk and upper roots of P. tabuliformis. Leptographium terebrantis Barras & Perry, a fungal associate of D. valens and other bark beetles in North America, is associated with decline and mortality of various species of pines and bark beetles [35–38].

Further work is required to determine the role of facilitation and other invasion mechanisms for D. valens in China. The reproductive success of both species, together and separate in P. tabuliformis needs to be determined. The availability of natural breeding opportunities for H. parallelus in the absence of D. valens needs to be determined as well. It is possible that the activities of D. valens in China provide H. parallelus with greater opportunities than normal for breeding purposes.

Our results also suggest that the risk from exotic species may not be limited to those species that are aggressive in their native ranges. With the use of semiochemicals, two relatively benign species (the exotic D. valens and the native H. parallelus) may act in concert to overcome tree defenses. Recently, an exotic ambrosia beetle from Asia, Xyleborus glabratus Eichhoff, was introduced into the coastal region of southeastern United States. In a fashion similar to Dutch elm disease, the association of X. glabratus with a wilt disease has caused extensive mortality of redbay, Persea borbonia (L.) Spreng, from Jacksonville, Florida, to Charleston, South Carolina, within a span of only five years [39]. Neither species had previously been known to cause damage in any other country. So

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**Figure 4. Walking responses of H. parallelus compounds in Y-tube olfactometer trials.** **,** significant differences at P < 0.01. n = 40 (20 male: 20 female) responding beetles for each treatment. doi:10.1371/journal.pone.0001302.g004

| Solvent blank | Treatment | Sig | N_{mean±SD}   |
|--------------|-----------|-----|---------------|
|              | (+)-cis-verbenol | NS | 40±20        |
|              | (+)-trans-verbenol | NS | 40±20        |
|              | verbenone | NS | 40±20        |
|              | (±)-myrtenol | ** | 40±20        |
|              | (±)-myrtenal | ** | 40±20        |
|              | terpinolene | NS | 40±20        |
|              | (-)-limonene | NS | 40±20        |
|              | myrcene | NS | 40±20        |
|              | (+)-3-carene | ** | 40±20        |
|              | (-)-β-pinene | NS | 40±20        |
|              | (+)-α-pinene | NS | 40±20        |
Figure 5. Typical EAD responses of *D. valens* antennae to male and female *H. parallelus* hindgut extracts. 1 α-pinene, 2 β-pinene, 3 limonene, 4 norinone, 5 myrtenal, 6 trans-verbenol, 7 cryptone, 8 cis-verbenol, 9 myrtenol, 10 isoborneol. doi:10.1371/journal.pone.0001302.g005
risk assessments for invasive species need to consider diverse potential scenarios and not simply focus on species that are detrimental in their native ranges. Similarly, management programs for invasive species will have to be highly innovative and adaptable in reducing such threats.

Some reported invasive mechanisms, such as invasional meltdown, focus on the interspecific facilitation between introduced species [8, 40]. However, our results report, for the first time, facilitative relationship between an exotic and a native bark beetle seems to involve overlap in the use of host attractants and pheromones. Mondor and Addicott also showed that cross-species communication exists between the invasive Argentine ant, Linepithema humile Mayr and native poplar aphid, Chaitophorus populicola Thomas [24]. In addition, such interactions, which may well be possible for many other secondary pest groups, may be of great benefit in predicting invasiveness of these heretofore low-visibility pests. As the further step, more examples on facilitation between exotic and native insects should be investigated, which could be explored as a novel invasive mechanism for not only exotic bark beetles but also other introduced pests.

MATERIALS AND METHODS

Field Association between D. valens and H. parallelus

In experiment 1, we assessed the association between D. valens and H. parallelus in plantations of P. tabuliformis at two locations in China: (1) the Tunlanchuan Forest Station (N37°48', E111°44'; average, elevation 1400 m), west of the city of Gujiao, Shanxi Province; and (2) the Yaopin Forest Station (N35°46', E109°16'; average, elevation 1000 m), Shaanxi Province. The plantations were 35 and 40 years in age, respectively, with mean tree diameters at breast height of 23.2 cm and 24.4 cm, respectively.

At each location, we randomly selected ten pine trees (at least 20 m apart) with no attacks by D. valens, ten pine trees with new attacks by D. valens in 2006 and 10 pine trees with old attacks by D. valens from 2005. Trees attacked in 2005 had fading foliage, yellow in color, whereas unattacked and recently-attacked trees had green foliage. In October 2006, each tree was excavated from the stem base along the roots for a length of about 1.5 m. For each tree, we recorded the total number of main roots and the number of roots under current attack by H. parallelus as well as the total number of adult H. parallelus on each infested root. The term “infested” is used simply to differentiate attack activities of H. parallelus from those of D. valens and is not meant to imply successful establishment of brood galleries. Successful brood establishment was not assessed for either species in this study.

Volatile Produced by H. parallelus

In all laboratory experiments, we used D. valens and H. parallelus that emerged from naturally-infested P. tabuliformis collected at the Tunlanchuan Forest Station. Beetles were sexed and maintained in an incubator at 25°C and 55% RH, under a light regime of 14L:10D prior to use in experiments. Semiochemical compounds used for all experiments were purchased from Pherotech International Inc. (Delta, British Columbia, Canada) and included the following compounds which were known to be associated with pine hosts or D. valens [25]: (+)-α-pinene, (−)-β-pinene, myrcene, (−)-limonene, (+)-3-carene, terpinolene, (±)-myrtenol, (+)-trans-verbenol, (+)-cis-verbenol, (±)-myrtenol and verbene (chemical purities, 85, 86, 84, 87, 86, 95, 84, 87, 95 and 98%, respectively). The enantiomeric composition of verbenone was 66% (+) and 34% (−).

In experiment 2, we determined the composition of volatiles in the hindguts of H. parallelus. The hindguts of 20 male and 20 female H. parallelus were transferred to separate glass vials containing 4 ml hexane. The extracts were filtered through glass wool and stored in a freezer (−10°C) until analyzed. This extraction procedure was repeated three times, resulting in four extracts representing 80 beetles for both male and female H. parallelus (n = 4). Prior to analysis, hindgut extracts for each sex were diluted to 200 μl. Aliquots of extracts (2.5 μl) were injected splitless into a gas chromatograph-mass spectrometer (GC-MS) (Hewlett Packard 6890N GC model coupled with 5973 MSD), equipped with a DB-WAX column (60 m length×0.25 mm i.d.×0.25 μm film) (J&W Scientific, Folsom, CA, USA). The GC oven temperature program was set at 50°C for 2 min; increased to 220°C at 5°C/min; increased to 230°C at 4°C/min; and set at 230°C for 5 min. The on-column injector temperature was 220°C and helium was the carrier gas (flow rate, 1ml/min). The mass spectrometer (MS) electron impact source was operated in scan mode (30-300 amu) with the MS source temperature at 230°C and the MS Quad at 150°C. Identifications of chromatogram peaks were based on comparisons with retention times and mass spectra of known standards and those in the NIST02 library (Scientific Instrument Services, Inc., Ringoes, NJ, USA). Enantiomeric compositions of volatiles were not determined.

Antennal Responses of H. parallelus

In experiment 3, we examined the coupled gas chromatography-electroantennographic detector (GC-EAD) [41] responses of H. parallelus antennae to various semiochemicals associated with H. parallelus (experiment 2) and D. valens [25]. The procedure allows separation of individual compounds in blends prior to simulta-
neous exposure of individual compounds to a flame ionization detector (FID) and an electroantennographic detector (EAD). Each EAD was made by cutting off the tip of an excised antenna and then mounting the antenna between two glass micropipette electrodes, filled with Kaissling saline. The recording electrode was positioned at the distal edge of the antennal club whereas the reference electrode was positioned near the scape. The electrodes were held with micromanipulators (Syntech MP15; Syntech, Hilversum, the Netherlands) and connected to a high impedance input AC/DC amplifier model UN-06 (Syntech) through Ag/AgCl junctions. Amplified GC-EAD responses were digitized using a Nelson 900 Series Interface, and displayed and processed using AutoSpike software (Syntech).

In order to minimize overlap in GC retention times, two blends of compounds were used in GC-EAD determinations. Blend A consisted of (+)-x-pinene, (-)-β-pinene, myrcene, (-)-limonene, terpinolene, (±)-myrtenol, and (±)-myrtenal (1 mg of each), and diluted to 5 ml hexane. Blend B consisted of (+)-5-carene, (+)-cis-verbenol, (+)-trans-verbenol and verbenone (10 mg of each), and diluted to 10 ml hexane. For each EAD, an aliquot (1 µl) of one of the two blends was injected, splitless into a HP 6890 gas chromatograph, equipped with a DB-WAX column (30 m x 0.25 mm x 0.25 µm film thickness) (J&W Scientific, Folsom, CA, USA) using the following temperature program: initially set at 80 °C; increased to 200 °C at 5 °C/min; increased to 230 °C at 6 °C/min. The carrier gas was helium (flow rate, 1.5 ml/min). The injector and detector temperatures were 220 °C and 240 °C, respectively. At the end of the column, a GC effluent splitter (press-fit connection; split ratio 1:1) was used to supply the FID and an EAD. For the EAD, effluent from the GC column was added to a purified and humidified air stream, passed over the excised antenna. Each blend was tested separately on antennae from ten male and ten female H. parallelus.

Walking Responses of H. parallelus

In experiment 4, we assessed the walking responses of H. parallelus to the same compounds tested on antennae in experiment 3, with each tested separately. Walking responses were assessed in a glass Y-tube olfactometer (35-mm diameter by 40 cm long, with a 120° inside angle) with airflow at 200 ml/min through each branch. Incoming air was filtered through activated charcoal and humidified with double distilled, de-ionized water. The filtered air was split between two holding chambers: one chamber served as a control (solvent blank) and the other chamber held the test material. Test chemicals (100 µg in 10 µl hexane) were applied to a paper filter strip (5 by 50 mm) that was placed in one of the two holding chambers after the solvent had been allowed to evaporate for 20 sec. Air passed from each holding chamber into the respective branches of the Y-tube. A smoke test verified laminar airflow in both branches and throughout the olfactometer. Approximately 30 min before trials were initiated, adult H. parallelus were placed into individual holding/release tubes and isolated from possible semiochemical sources. At the beginning of each trial, a single beetle was placed at the down-wind end of the Y-tube. Each beetle was given 10 min to respond, with the choice of left or right branches of the olfactometer noted when the beetle walked 5 cm past the Y-tube junction. The olfactometer was maintained at 25 °C and 70% RH during trials. Treatments associated with the right and left branches of the olfactometer were exchanged after every fifth beetle. Y-tubes replaced with clean ones when treatments were changed or positions exchanged. Individual bark beetles were tested only once.

Interspecific Responses of D. valens

In experiment 5, we determined the interspecific EAD responses of D. valens to hindgut extracts from H. parallelus. One aliquot of extract (2.5 µl), derived from one male H. parallelus hindgut, was injected into the GC using the same protocol noted above in experiment 3, with D. valens antennae used for the EAD. Each extract was presented to ten male and ten female D. valens. The procedure was repeated with hindgut extracts from individual female H. parallelus.

In experiment 6, we assessed the walking responses of D. valens to volatiles produced by H. parallelus using the same protocol noted in experiment 4. The test chemicals were extracts of male and female H. parallelus hindguts. In each trial, one aliquot (2.5 µl) of either male or female hindgut extracts (equivalent to the hindgut contents of a single beetle) was applied to a paper filter strip and deposited into one of the two holding chambers of the Y-tube olfactometer.

Statistical analyses

All data were analyzed with SPSS 11 for Windows [42]. One-way ANOVA was used to compare the differences among roots of different attack categories and average number of H. parallelus on each attacked root in experiment 1. Differences between the sexes in amplitude of EAD responses in experiments 3 and 5 were analyzed using Mann-Whitney tests. In experiments 3 and 6, the null hypothesis that beetles showed no preference for either olfactometer arm (and thus showed no response to test compound) was tested using a table of cumulative binomial probabilities with a p-value of 0.05. We used Chi² tests to compare differences between sexes in walking responses in olfactometer.

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Author Contributions

Conceived and designed the experiments: ML JS. Performed the experiments: ML. Analyzed the data: ML DM. Wrote the paper: ML JS DM.

REFERENCES

1. Mack RN, Simberlof D, Lonsdale WM, Evans H, Clout M, et al. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10: 689–710.
2. Rejmánek M, Reichard S (2001) Predicting invaders. Trends Ecol Evol 16: 545–546.
3. Drake JM, Lodge DM (2004) Global hot spots of biological invasions: evaluating options for ballistic-water management. Proc R Soc Lond B 271: 575–580.
4. MacArthur RH (1970) Species packing and competitive equilibrium for many species. Theor Popul Biol 1: 1–11.
5. DeBach P, Rosen D (1993) Biological Control by Natural Enemies, 2nd edition. Cambridge: Cambridge University Press.
6. Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive non-indigenous plants—a hypothesis. J Ecol 83: 887–889.
7. Hufbauer RA, Torchin ME (2007) Integrating ecological and evolutionary theory of biological invasions. In: Neutregn W, ed (2007) Biological Invasions. Ecological Studies. New York: Springer-Verlag Berlin Heidelberg. pp 79–96.
8. Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1: 21–32.
9. Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18: 119–123.
10. Furriss RL, Carolin VM (1980) Western Forest Insects. U.S. Dept. Agric. Forest Service Misc. Publ. 1339, Washington, D.C. USA, pp 654.
11. Byers JA (1989) Behavioral mechanisms involved in reducing competition in bark beetles. Holartic Ecol 12: 466–476.
12. Lieteteor F (2002) Mechanisms of resistance in conifers and bark beetle attack strategies. In: Wagner MR, Clancy KM, Lieteteor F, Paine TD, eds (2002) Mechanisms and Deployment of Resistance in Trees to Insects, The Netherlands: Kluwer Academic Publishers. pp 51–77.
13. Yan ZL, Sun JH, Owen D, Zhang ZN (2005) The red turpentine beetle, Dendroctonus valens LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodiver Conserv 14: 1735–1760.
14. Sun J, Miao Z, Zhang Z, Zhang Z, Gilette N (2004) Red turpentine beetle, Dendroctonus valens LeConte (Coleoptera: Scolytidae), response to host semi-chemicals in China. Envir Entomol 33: 206–214.
15. Cognato AI, Sun JH, Anducho-Reyes MA, Owen DR (2003) Genetic variation and origin of red turpentine beetle (Dendroctonus valens LeConte) introduced to the People’s Republic of China. Agric. For Entomol 7: 87–94.
16. Li JS, Chang GB, Song YS, Wang YW, Chang BS (2001) Control project on red turpentine beetle (Dendroctonus valens). For Pest Dis 4: 41–44 (in Chinese).
17. Miao ZW, Chou WM, Hao FY, Wang XL, Fang JX, et al. (2001) Biology of Dendroctonus valens in Shanxi Province. Shanxi For Sci Tech 23: 34–37 (in Chinese).
18. Zhang LY, Chen QC, Zhang XB (2002) Studies on the morphological characters and biromics of Dendroctonus valens LeConte. Scientia Silvae Sinicae 28(4): 95–99 (in Chinese).
19. Yin HF, Huang FS (1984) Scolytidae. In: Editorial Committee of Fauna Sinica Economic Insect Fauna of China. Beijing: Science Press, (in Chinese).
20. Ko JH, Morimoto K (1985) Loss of tree vigor and role of boring insects in red pine stands heavily infested by the pine needle gill mite. Ensaikai 23: 151–158.
21. Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae). A taxonomic monograph. Great Basin Natur Memoirs. pp 6, 1359.
22. Borden JH (1982) Aggregation pheromones. In: Mitton JB, Sturgeon KB, eds (1982) Bark beetles in North American Conifers. A System for the Study of Evolutionary Biology, Texas: University of Texas Press. pp 74–139.
23. Blum MS (1996) Semiochemical disparity in the Aphidoidea. Annu Rev Entomol 41: 353–374.
24. Monder EB, Addicott JF (2007) Do exaptations facilitate mutualistic associations between invasive and native species? Biol Invasions 9: 623–628.
25. Zhang LW, Sun JH (2006) Electrophysiological and behavioral responses of Dendroctonus valens (Coleoptera: Curculionidae: Scolytinae) to candidate pheromone components identified in hindgut extracts. Environ Entomol 35: 1232–1237.
26. Redmer JJ, Wallin KF, Raffa NF (2004) Effect of host tree seasonal phenology on substrate suitability for the pine engraver, Ips pini. J Econ Entomol 97: 844–849.
27. Aikino MD (1966) Behavioural variation among scolytids in relation to their habitat. Can Entomol 98: 283–288.
28. Paine TD, Birch MC, Svhira P (1981) Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia 48: 1–6.
29. Birch MC, Svihira P, Paine TD, Müller JC (1980) Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. J Chem Ecol 6: 395–414.
30. Svhira P, Paine TD, Birch MC (1989) Interspecific olfactory communication in southern pine beetles. Naturwiss 67: 518–529.
31. Smith MT, Payne TL, Birch MC (1990) Olfactory-based behavioral interactions among five species in the southern pine bark beetle group. J Chem Ecol 16: 3317–3332.
32. Wood DL (1982) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annu Rev Rev Entomol 27: 411–446.
33. Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17: 164–170.
34. Wu JG, Zhao MM, Zhang CM, Guo BP, Li JZ, et al. (2002) Damage of Dendroctonus valens on Pinus tabuliformis and its distribution on trunk and root before and after overwinterning period. For Pest Dis 3: 30–41 (in Chinese).
35. Owen DR, Lindahl KQ Jr, Wood DL, Parmeter JR Jr (1987) Pathogenicity of fungi isolated from Dendroctonus valens, D. brevicomis and D. ponderosae when inoculated into ponderosa pine seedlings. Phytopath 77: 631–636.
36. Parmeter JR, Slaughter GW, Chen MM, Wood DL, Stubbs HA (1989) Single and mixed inoculations of ponderosa pine with fungal associates of Dendroctonus spp. Phytopath 79: 796–772.
37. Klepzig KD, Raffa NF, Smalley EB (1991) Association of an insect-fungal complex with red pine decline in Wisconsin. For Sci 37: 1119–1139.
38. Paine TD, Raffa NF, Harrington TC (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annu Rev Entomol 42: 179–206.
39. Faedrich SW, Harrington TC, Rahagila RJ, Ulyshen MD, Hamula JL, et al. (2008) A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern USA. Plant Dis in press.
40. Simberloff D (2006) Invasive meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecol Let 9: 912–919.
41. Arn H, Stadler E, Rauscher S (1975) The electroantennographic detector—a sensitive and selective tool in the gas chromatographic analysis of insect pheromones. Z Naturforsch 30c: 722–725.
42. SPSS Inc (2001) SPSS 11 for Windows. Chicago, IL: SPSS Inc.