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RECEIVED 14 December 2023 ACCEPTED 22 January 2024 PUBLISHED 12 February 2024

CITATION

Venette RC, Ambourn A, Aukema BH, Jetton RM and Petrice TR (2024) Hosts and impacts of elongate hemlock scale (Hemiptera: Diaspididae): A critical review. *Front. Insect Sci.* 4:1356036. doi: 10.3389/finsc.2024.1356036

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Hosts and impacts of elongate hemlock scale (Hemiptera: Diaspididae): A critical review

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Fiorinia externa Ferris, elongate hemlock scale, was inadvertently introduced to North America from Japan. This insect is particularly problematic on hemlock, *Tsuga* spp., though it has been reported in association with several other conifers. The evidence that other conifers might be hosts, capable of supporting growing populations of the insect, has not been previously reviewed. Our review confirms that *F. externa* is an oligophagous pest of members of Pinaceae. Although species of Cupressaceae and Taxaceae have been reported as hosts of *F. externa*, they seem unable to support population growth of this pest. Evidence of the tree-killing potential of the insect, even on suitable hosts, is remarkably scant. The degree of pest risk posed by *F. externa* with respect to tree mortality in areas beyond the geographic range of hemlock seems modest, but uncertain.

KEYWORDS

invasive alien species, Tsuga, Abies, plant-insect interactions, forest health

Introduction

Fiorinia externa Ferris, elongate hemlock scale, is an alien armored scale (Hemiptera: Diaspididae) in North America. It is a primary threat to hemlock, *Tsuga* spp. (Figure 1A), that also are imperiled by the hemlock wooly adelgid, *Adelges tsugae* (Annand), another invasive alien insect (1). *Fiorinia externa* was first detected in 1908 in Queens and New York, NY, USA in association with an unspecified *Tsuga* sp. and Japanese hemlock, likely *Tsuga diversifolia* (Maxm.) Mast., respectively (2). By 1958, the insect had spread from New York state to Connecticut, Maryland, Massachusetts, New Jersey, Ohio, and Pennsylvania (3, 4), with no additional states reporting infestation through 1965 (5). By 1980, *F. externa* occurred as far south as Georgia (6). At about this time, the insect was spreading at 4.8 km/ year in Connecticut (7). The insect is now established also in Delaware, Kentucky, Maine, Michigan, New Hampshire, North Carolina, Rhode Island, South Carolina, Tennessee,



FIGURE 1

Elongate hemlock scale, *Fiorinia externa*, on the underside of eastern hemlock, *Tsuga canadensis*: (A) on the most current year of hemlock growth; and (B) closeup of adult females within tests. Both photographs by F.W. Ravlin, Department of Entomology, Michigan State University.

Vermont, Virginia, and West Virginia, states with significant acreages of Canadian/eastern hemlock, *Tsuga canadensis* (L.) Carrière (8). This insect has spread more slowly across the United States than many other invasive forest insects (9, 10).

At the time F. externa was first detected in the United States, the insect was recognized as having been accidentally imported from Japan (2). In his description of the species, Ferris (11) noted: "It is with regret that this species is described as new, since it would seem very probable that it has previously been named from some other part of the world." Yet, no earlier descriptions of the species have been found. Ironically, confirmed records of the species outside the United States were unknown until Takagi (12) first definitively recovered and reported F. externa from Honshu and Shikoku islands of Japan and characterized Japan as the "cradleland" for the species. Fiorinia externa also has been reported from Fujian, Guangdong, and Sichuan, China (13, 14). Whether the species is native or introduced there is unclear. Van Driesche et al. (15) speculated that reports of F. externa from China might be misidentifications, as infested trees were difficult to locate. Elsewhere globally, F. externa was reported from an "alpine house" in England (16) but was never considered to be established in the wild (17). Kosztarab (18) also listed this scale as being present in Canada without details on the basis for this report. Fiorinia externa has not established in Canada, but future spread from the United States into Canada is probable (D. Pureswaran, personal communication).

Continued spread of *F. externa* in the United States is a concern to regulatory agencies, Christmas tree growers, and foresters (19– 22). Human-mediated spread of this insect has been detected in California, Wisconsin, Minnesota, Oregon, and Florida on cut host material, e.g., Christmas trees, garlands, and wreaths, but the insect is not known to be established in these states (19, 21, 23, 24). The movement of infested nursery stock also may contribute to spread (25). Successful spread is contingent, in part, on the ability of the insect to locate and colonize hosts in its new environment(s) (9, 26). Herein, we briefly review the bionomics of *F. externa* that are relevant to interactions with conifers and summarize multiple studies on the diversity and quality of conifers as hosts. We conclude with a commentary on other taxa that might be hosts and the potential impacts this insect might have beyond the geographic range of hemlock.

Bionomics

The biology of F. externa has been reviewed extensively elsewhere (e.g., 5, 27-30). The species has one to two generations annually with extensive overlap between generations due to a prolonged period of egg hatch (6, 28, 31, 32). Eggs and adult females are generally considered to be the primary overwintering stages. Adult females are pupillarial, having developed within the exuvium of the second instar (Figure 1B); the enclosure also is known as the test (33). Adults are dimorphic. Only males possess functional wings. The species reproduces sexually. Females mate shortly after completion of the third instar and contract to about one-third of their previous size within the test. Eggs are laid in two rows along the central mid-line within the space of the test. Because only adult males can fly, first instars (i.e., crawlers) are the dispersal stage for females, with movement over short distances achieved by walking and intermediate distances facilitated by wind (34). Colonization of isolated trees is happenstance, affected by the speed and direction of wind, the densities of crawlers on infested trees, and the proximity of source trees to uninfested trees (10). Longer dispersal distances might occur if crawlers could hitchhike on birds and mammals, but phoretic movement of F. externa has not yet been demonstrated.

Fiorinia externa is a piercing-sucking insect. This insect feeds on host plants through a feeding tube made from fused mandibular and maxillary stylets. A crawler creates a feeding site, typically on the underside of the newest needles and occasionally on the surface of developing cones (18), by scraping away the host epidermis with its forelegs and inserting the stylets between epidermal cells or into a stomate (5). The stylets remain inserted once feeding commences (5). The stylets penetrate mesophyll cells and allow the insect to extract photosynthates and other cell contents from the needles and to inject of phytotoxic saliva (29). For adult females, the stylet is 6-7 times the body length (5).

Host range

In the first official U.S. report of the species, Sasscer (2) noted that the insect, then identified as *Fiorinia fiorinae japonica*, had been collected on *Tsuga* spp. He also shared anecdotal reports of the scale on other Pinaceae: Veitch fir, *Abies veitchi* Lindley; an unspecified *Pinus* sp.; a Japanese five-needled pine, *Pinus pentaphylla* Mayr [=*P. parviflora* var. *pentaphylla* (Mayr) Henry, currently]; Japanese black pine, *P. thunbergii* Parl.; and southern Japanese hemlock, *T. sieboldii* Carrière. He included additional hosts among Podocarpaceae: *Podocarpus elata* [=*P. elatus* R. Br. Ex Endl., currently], *P. chinensis* (Roxb.) Wall ex J. Forbes, and *P. nageia* R. Br. Ex Mirbel [=*Naegia nagi* (Thunb.) O. Kuntze, currently]. However, Sasscer (2) likely conflated potential hosts within Podocarpaceae, with hosts for *F. externa*, which has no confirmed hosts in that plant family (27).

The current list of hosts for F. externa was derived primarily from reported associations of the insect with different plants. Frequently, the reports summarized observations of plants growing near infested Tsuga spp. in ornamental plantings including arboreta. Some observations simply recorded the presence of F. externa on a plant. In other cases, observations included F. externa densities on different plants but often with no information about the size of the colonizing population or the time since infestation. If true, differences in densities of F. externa on different plants would reflect differences in host quality with respect to survivorship, developmental, or reproductive rates or chance variation in the number of crawlers that colonized a tree over time. In rare cases (e.g., 35), potential host trees were artificially infested to standardize initial colonization densities, so that differences in scale densities over time likely reflect differences in suitability among trees.

For this review, we assembled literature on potential hosts of F. externa published after Ferris' (1942) description of the species (Table 1). Ferris (11) considered *Tsuga* spp. to be the primary hosts for F. externa. Thus, when possible, we compare the performance of F. externa on a plant relative to its performance on eastern/ Canadian hemlock, Tsuga canadensis (L.) Carr. or Carolina hemlock, T. caroliniana Engelm. in the same study and location. 'Performance' is either the density of scales on individual trees (often expressed as scales/needle) or the proportion of trees that had been colonized. Qualitative ratings were assigned to facilitate comparisons among studies: '++++,' >80% performance as on a known host; '+++,' ~40-60% performance as on a known host; '+,' 1-20% performance as on a known host; and '-,' not likely to be a host. In cases where non-host status may reflect chance escape from colonization, we use '-(?)'. Intermediate categories were applied as needed. Wallner (5) characterized F. externa densities as "heaviest", "heavy", and "light," which we expressed as "+++++", "++++", and "+", respectively. All studies in our review observed *F. externa* directly.

Pinaceae

Fiorinia externa is an oligophagous pest of Pinaceae, though not all species within this plant family are equally suitable. The insect is regularly characterized as a serious pest of hemlocks, especially eastern/Canadian hemlock, Japanese hemlock, and Carolina hemlock, particularly in ornamental plantings (3, 6, 31, 39–41). In Japan, the primary host appears to be southern Japanese hemlock, *Tsuga sieboldii* Carrière (12). In addition, early reports of *F. externa* from North America casually note its association with fir, *Abies* spp., and spruce, *Picea* spp., typically without reference to species (3, 39–41). Murakami (42) listed Sakhlin fir, *Abies sachalinensis* (F. Schmidt) Masters var 'Mayriana' as a host. Stimmel (6) observed *F. externa* on Fraser fir, *Abies fraseri* (Pursh) Poir. Williams (16) reported *F. externa* as persisting and likely reproducing on Korean fir, *Abies koreana* E.H. Wilson.

The highest quality hosts for *F. externa* include many hemlocks and firs (Table 1). Other high-quality hosts are Atlas cedar, *Cedrus atlantica* (Endl.) Manetti ex Carrière, Norway spruce, *Picea abies* (L) Karsten, and Colorado blue spruce, *Picea pungens* Engelmann. However, other spruces and cedars seem to be of substantially lower quality. Deodar cedar, *Cedrus deodara* (Roxb. ex D.Don) G.Don, and Douglas fir, *Pseudotsuga menziesii* (Mirbel) Franco, may be quality hosts for *F. externa*, but the performance of the insect on these hosts was highly variable among studies (Table 1). Pines, *Pinus* spp., tend to be intermediate- to low-quality hosts or nonhosts (Table 1).

Cupressaceae

Members of this family are unlikely to be reproductive hosts (i.e., plant species that support population growth of a specified herbivore) for F. externa. Tao (14) lists the arborvitae Biota orientalis (L.) Endl [=Platycladus orientalis (L.) Franco, currently]; Chinese juniper, Juniperus chinensis L., and needle juniper, Juniperus rigida Siebold & Zucc. as hosts for F. externa without further information. No other sources independently corroborate these host associations. In earlier studies, false cypress, Chamaecyparis sp.; Japanese cedar, Cryptomeria japonica (L) Don, and junipers, Juniperus spp., growing next to infested hemlocks were not colonized by F. externa and therefore not considered to be hosts (35). Similarly, after being artificially infested on plants, F. externa failed to persist on the arborvitae Thuja x 'Green Giant' (a hybrid of Thuja plicata x Thuja standishii); Arizona cypress 'Blue Ice', Cupressus arizonica Greene; Atlantic whitecedar, Chamaecyparis thyoides (L.) B.S. P.; Leyland cypress, Cupressus x leylandii A. B. Jacks. & Dallim.; or southern eastern red cedar, Juniperus virginiana var silicicola (Small) E. Murray (37).

TABLE 1 Host status of conifers for Fiorinia externa.

Species	Common name	Host status	Source
Pinaceae			
Abies alba	Silver fir	+++	(35)
		++	(36)
Abies amabilis	Cascade fir	+++++	(35)
		+++++	(36)
Abies balsamea	Balsam fir	+	(35)
		Yes	(6)
Abies cephalonica	Greek fir	++++	(5)
		-(?)	(35)
Abies concolor	White fir	++++	(5)
		+++	(35)
		+	(36)
Abies fargesii	Farges fir	+++++	(35)
		+++++	(36)
Abies fraseri	Fraser fir	Yes	(6)
		++++*	(37)
Abies holophylla	Manchurian fir	+	(35)
Abies homolepis	Nikko fir	-(?)	(35)
Abies veitchii	Veitch fir	+++++	(35)
		+++++	(36)
Cedrus atlantica	Atlas cedar	+++++	(35)
		++++	(36)
Cedrus deodara	Deodar cedar	-(?)	(35)
		++++*	(37)
Cedrus libani	Cedar of Lebanon	-(?)	(35)
Picea abies	Norway spruce	++++	(5)
		+	(35)
		+++++	(36)
Picea asperata	Dragon spruce	+	(35)
Picea glauca	White spruce	+	(35)
Picea glehni	Saghalin spruce	+	(35)
Picea heterolepis	Red twig dragon spruce	+	(35)
Picea jezoensis	Yezo spruce	+	(35)
Picea koyamai	Koyama spruce	+	(35)
Picea mariana	Black spruce	+	(35)
Picea omorika	Serbian spruce	+++	(35)
		+++	(36)
Picea orientalis	Oriental spruce	+	(35)

TABLE 1 Continued

Species	Common name	Host status	Source
Picea pungens	Colorado blue spruce	++++	(5)
		+++++	(35)
		+++++	(36)
		++++*	(37)
Picea smithiana	Himalayan spruce	+	(35)
Pinus aristata	Rocky Mountain bristlecone pine	-(?)	(35)
Pinus bungeana	Lacebark pine	-(?)	(35)
Pinus cembra	Swiss stone pine	+	(35)
Pinus clausa	Sand pine	-	(37)
Pinus densiflora	Japanese red pine	-(?)	(35)
Pinus elliotti	Slash pine	+ ^{n.s.}	(37)
Pinus flexilis	Limber pine	-(?)	(35)
Pinus glabra	Spruce pine	+ ^{n.s.}	(37)
Pinus griffithi	Himalayan white pine	_	(35)
Pinus lambertiana	Sugar pine	-	(35)
Pinus mugo	Mugo pine	-(?)	(35)
Pinus parviflora	Japanese white pine	+	(35)
Pinus pumila	Dwarf stone pine	+	(35)
Pinus resinosa	Red pine	-(?)	(35)
Pinus rigida	Pitch pine	-(?)	(35)
Pinus strobus	Eastern white pine	+	(5)
		+	(35)
Pinus sylvestris	Scots pine	-(?)	(35)
Pinus taeda	Loblolly pine	++*	(37)
Pinus virginiana	Virginia pine	+++*	(37)
Pseudotsuga menziesii	Douglas fir	++++	(35)
		++	(36)
Tsuga canadensis	Eastern hemlock	+++++	(5)
		+++++	(35)
		+++++	(36)
		++++/+++	(38)
		++++*	(37)
Tsuga caroliniana		+++++	(5)
		+++++	(35)
		+++++	(36)
		Yes	(6)
		1	(Continued)

(Continued)

(Continued)

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TABLE 1 Continued

Species	Common name	Host status	Source
		++++/+++ ++°	(38)
Tsuga chinensis		+++/++++ +°	(38)
Tsuga diversifolia	Japanese hemlock	+++++	(5)
		+++++	(35)
		+++++	(36)
		n.a./++++ + °	(38)
Tsuga heterophylla		++/++++°	(38)
Tsuga mertensiana		n.a./++++ + °	(38)
Tsuga sieboldii	Siebold hemlock	+++++	(35)
		++++	(36)
		n.a./++++ + °	(38)
Cupressaceae			
Chamaecyparis thyoides	Atlantic white cypress	-	(37)
Cryptomeria japonica	Japanese cedar	-	(35)
Cupressus arizonica	Arizona cypress	-	(37)
Cupressus x leylandii	Leyland cypress	-	(37)
Juniperus virginiana var silicola	Southern red cedar	+ ^{n.s.}	(37)
<i>Thuja</i> x 'Green Giant'	Arborvitae 'Green Giant'	-	(37)
Тахасеае			
Taxus baccata	European yew	-(?)	(35)
Taxus cuspidata	Japanese yew	+	(5)
		-(?)	(35)
Taxus foridana	Florida yew	-	(37)
Torreya taxifolia	Florida torreya	+ ^{n.s.}	(37)

Qualitative rankings describe the performance of scales on a conifer species relative to hemlocks (*Tsuga* spp.) in the same study: +,1-20%; ++, 21-40%; +++, 41-60%, ++++, 61-80%; ++++++, >80% performance as on a known host; -, not likely to be host; and -(?), not likely to be a host or not colonized by chance.

*, significantly greater degree of infestation than a known non-host; ^{n.s.}, degree of infestation not significantly different from a known non-host. °, as reported in Weston and Harper (38) and as observed in 2020 (Richard Weston, personal communication); n.a., not available.

Fiorinia externa began to feed on all of these plants except *Thuja* x 'Green Giant' and *Cupressus* x *leylandii*; typically, <10% of trees in Cupressaceae - but 57% of *J. virginiana* var *silicicola* – had live scales at 19 weeks after infestation (37). By 50 weeks after infestation, no Cupressaceae had live scales, except *J. virginiana* var *silicicola* whose 3% frequency of infestation was equivalent to a known non-host (37). Members of Cupressaceae have been confirmed as hosts of the congeneric *Fiorinia japonica* in multiple studies (27).

Taxaceae

Members of this family are probably not reproductive hosts for *F. externa*. Yews, *Taxus* spp., were listed as (secondary) hosts in early publications about the species (3, 5, 30, 35, 39, 40). These reports typically noted the association of *F. externa* with the plant genus without mentioning species (3, 30, 39). Wallner (5) observed light densities of *F. externa* on Japanese yew, *Taxus cuspidata* Siebold et Zuccarini, compared to *Tsuga* spp. McClure and Fergione (35) documented that *F. externa* densities were less than one scale per 500 needles on European yew, *Taxus baccata* L, and Japanese yew. Dale et al. (37) recorded 90% of Florida torreya, *Torreya taxifolia* Arnott, and 80% of Florida yew, *Taxus floridana* Nuttall ex Chapman, were still infested at 19 weeks after artificial infestation; by 50 weeks, the frequency of infestation dropped to 3% and 0%, respectively, no different from known non-hosts.

Impact

Feeding by *F. externa* can cause decline-like symptoms such as needle yellowing, needle cast, branch dieback, stunted growth, and occasionally tree death (4, 5, 39, 41). Feeding likely reduces overall host vigor and may increase tree susceptibility to other abiotic and biotic stresses. Unlike hemlock woolly adelgid, feeding by *F. externa* has no measurable effect on the phytohormones abscisic acid or salicylic acid (43). The ability of the insect to vector plant pathogens is unknown. Dense infestations give foliage a "whitewashed appearance" from the waxy secretions from male scales (3, 6, 40).

The potential for F. externa to kill trees, even of highly suitable hemlocks, remains unclear. The progression of plant symptoms first was described for ornamental trees as no natural stands or plant nurseries were known to be infested at that time (reviewed in (5)). McClure (44) and McClure and Fergione (35) reaffirmed F. externa as a potential tree-killing insect and casually expanded the scope of potential impacts to include forest hemlocks. These anecdotal descriptions were sufficient for Miller et al. (45) to list F. externa as a "serious pest" of hemlock, arguably among the more threatening species of non-native scale insects in North America. However, the frequency of mortality among infested trees or the extent of mortality at stand scales had/has never been reported for this insect. (Note: Zahradnik (46) did not include F. externa among "the more important or interesting" scales that affect conifers.) More recently, Mech et al. (47) concluded that F. externa is capable, at worst, of killing "individual healthy plants" and, thus, did not consider it to be a high-impact species.

The severity of symptoms is partially related to the density of *F. externa*. Densities of *F. externa* are affected by soil texture and moisture (44) and are positively correlated with the nitrogen content of needles, both within and among host species (48). McClure and Fergione (35) posited that a density of >6 scales/100 needles was sufficient to cause substantial hemlock-needle discoloration and drop from the lower crown, but they did not provide the basis for this threshold. At low densities (<1 scale/ needle), *F. externa* did not affect growth or foliar nitrogen content of *T. canadensis*, but at similar densities, hemlock woolly adelgid

occasionally did (49). The intensity, beyond being "high", or duration of infestation that might be necessary for mortality has not been specified. McClure (50) argued that *F. externa* could kill hemlocks within 10 years if left uncontrolled but provided no data. Johnson and Lyon (51) suggested that infested hosts may begin to recover (i.e., flush new needles) if scale densities decline, for example, from intraspecific competition.

More recent research suggests that F. externa rarely kills trees and may prove modestly beneficial to hemlocks in the presence of hemlock woolly adelgid. During the late 1990s and early 2000s, the geographic range and density of F. externa substantially increased on Massachusetts and Connecticut (USA) hemlock with little apparent impact to tree health; hemlock mortality correlated more strongly with densities of hemlock woolly adelgid than F. externa (52). When hemlocks in this area were artificially infested with both insect species, densities of each insect were reduced by ~30%, but lateral growth was greater on trees infested with both species than with hemlock woolly adelgid alone (53). Fiorinia externa alone had no measurable impact on branch growth (53) or tree ring formation (54). Subsequent research has demonstrated that hemlocks with F. externa have similar foliar chemistry and growth rates as uninfested trees, unlike trees infested with hemlock woolly adelgid (49). The early presence of F. externa substantially lowered settlement rates for hemlock woolly adelgid crawlers (55); crawlers avoided settling at the base of needles where F. externa was already established (56). Ultimately, Miller-Pierce and Preisser (55) characterized F. externa as "relatively innocuous" to hemlock health in comparison to hemlock woolly adelgid. Preliminary observations from Michigan are consistent with these trends as no relationship was observed between current-year hemlock growth and F. externa densities (20).

Discussion

Fiorinia externa is an oligophagous pest of trees in the Pinaceae. The phylogeny and evolutionary history of genera within this family (57) and patterns of host utilization by *F. externa* (Table 1) suggest other genera within Pinaceae might be heretofore unreported hosts, particularly *Keteleeria*, *Nothotsuga*, and *Pseudolarix*, all native to portions of eastern Asia. Further research into these potential host associations is warranted and might provide insights into the coevolutionary history of *F. externa* with Pinaceae in Asia. Although the insect may attempt to feed on Cupressaceae or Taxaceae, *F. externa* appears unable to sustain populations on plants from these families.

Fiorinia externa, like other Diaspididae, is recognized as a parasite of its host plants (58). Females are incapable of directed long-distance movements, and directional movements are constrained by the walking capacity of crawlers, potentially <1 m (59). Further, once a crawler establishes a feeding site, it cannot retract its stylets to continue host searching (25). Thus, behavior plays little role in host choice for this species unlike many other oligophagous/polyphagous insects. The limited dispersal abilities of this insect put it under strong evolutionary pressure to attempt feeding on a potential host and not kill it until densities are high.

Similarly, limited dispersal has contributed to the rapid microevolution of *F. externa* to different host species (60) and potentially to environmental tolerances (61). Demic adaptations to hosts are not so strong as to preclude colonization of new hosts (59).

The risk that *F. externa* poses to regions beyond the range of *Tsuga* spp. is highly uncertain. Pest risk, in this context, is a function of the likelihood that *F. externa* might invade a new area and the extent of damages it might cause once there. If introduced to new areas on cut foliage, the insect may face significant challenges to locate live host material and withstand local climatic conditions. The arrival of *F. externa* on propagative hosts would thus seem to be the riskier pathway. Despite being present in the United States for >100 years, the circumstances that might lead *F. externa* to kill otherwise healthy trees are only coarsely characterized. Widespread tree mortality from *Fiorinia externa* has never been documented, even on preferred hosts. Evidence from prior pest activity and sentinel trees (62) indicates that although future host mortality from *F. externa* is possible, extensive host mortality is unlikely.

Author contributions

RV: Writing – original draft, Writing – review & editing. AA: Writing – review & editing. BA: Writing – review & editing. RJ: Writing – review & editing. TP: Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. Funding was provided by the Northern Research Station of the U.S. Department of Agriculture, Forest Service for the publication of this article.

Acknowledgments

We thank Pheylan Anderson, Marie Hallinen, Julia Leone, Clarissa Moore, Deepa Pureswaran, and Richard Weston for discussions about the ecology of *F. externa*. We thank Kevin T. Smith, Elizabeth Larry, and the reviewers for constructive comments on early drafts of this paper. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

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The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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