

## Displacement of *Tetropium cinnamopterus* (Coleoptera: Cerambycidae) by Its Invasive Congener *Tetropium fuscum*

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### Abstract

We examined the native community of insects interacting with an invasive species, *Tetropium fuscum* (F.) (Coleoptera: Cerambycidae), in its new range to explore reasons for the invader's relatively slow spread. *Tetropium fuscum* is a European spruce borer established in Nova Scotia since at least 1990, but it has spread only about 125 km from its site of introduction. We compared the densities of *Tetropium* spp., their known parasitoids, and the community of wood-boring insects at sites located within the invasion zone in Nova Scotia versus well outside this zone, in New Brunswick, Canada. Using red spruce trees stressed by girdling or felling, we tested whether: 1) *T. fuscum* had altered the native wood-boring community; 2) *T. fuscum* displaced a native congener, *Tetropium cinnamopterus* (Kirby); and 3) parasitism rates of *Tetropium* spp. differed between the invaded and noninvaded zones. Both *Tetropium* spp. and their parasitoid wasps emerged exclusively from felled trees as opposed to girdled trees. We found no difference in community diversity inside versus outside the invasion zone. The combined densities of both *Tetropium* spp. and their overall parasitism rates also did not differ between zones, but *T. cinnamopterus* density was significantly greater outside the invasion zone, suggesting *T. fuscum* may displace the native congener where they are sympatric. Our results suggest that the native and invasive *Tetropium* spp. act as a single functional species in the invasion zone. We speculate that natural control agents (predators, parasitoids, and competitors) might be limiting the rate of spread of *T. fuscum*.

**Key words:** species invasion, range expansion, community structure, natural enemies, competition

Species invasions can have significant ecological and economic impacts (Elton 1958, Kolar and Lodge 2001, Shea and Chesson 2002, Holzmueller and Jose 2011). However, the vast majority of introduced organisms fail to successfully establish in their new environment and cause little or no damage (Williamson and Fitter 1996). Species that become invasive can take advantage of open niche opportunities that enable population growth and expansion from the point of introduction (Shea and Chesson 2002). Introduced species can interact with community members and may alter the composition of established communities by consuming novel prey (Kipp and Ricciardi 2012), being consumed by native predators and parasitoids (Flaherty et al. 2011, Llewelyn et al. 2011), or by displacing potential competitors (Lessard et al. 2009, Holzmueller and Jose 2011, Patel 2012). These ecological interactions depend on life-history traits of the native and introduced species and can play a vital role in determining the extent to which an introduced species becomes

invasive. High reproductive potential and dispersal strategies allowing long-distance movement can also favor population growth (Levin 2000, Llewelyn et al. 2011) and range expansion of the invader (Elton 1958, Holzmueller and Jose 2011), leading to a greater incidence of interactions with native species in the invaded community (Kipp and Ricciardi 2012).

Wood-boring beetles have a variety of traits that favor their anthropogenic movement, introduction into novel environments, and thereby their potential to become invasive. They are associated with nursery stock, solid wood packaging of goods shipped internationally, and firewood (Smith and Hurley 2000, Haack 2006, Muirhead et al. 2006). They are also cryptic in habit, with infested wood often exhibiting few or no visible signs (Juutinen 1955, Haavik et al. 2015), and can have high reproductive potential as well as high reproductive rates (Kenna 2002, Duan et al. 2010, Flaherty et al. 2011, Haavik et al. 2015). Small founder populations can therefore

easily proliferate if they remain unnoticed, especially when they are bolstered by continuous transport and release of conspecifics into the new environment (Elton 1958, Haack 2006).

*Tetropium fuscum* (F.) (Coleoptera: Cerambycidae) is an introduced pest in North America (Canadian Food Inspection Agency [CFIA] 2007) that in its native Europe infests the phloem of stressed and moribund Norway spruce, *Picea abies* (L.) Karst. (Juutinen 1955). In North America, *T. fuscum* was discovered in 1999 within Point Pleasant Park (Halifax, Nova Scotia), about a kilometer from the shipping port of Halifax, attacking apparently healthy red spruce, *Picea rubens* (Sarg.) (Smith and Hurley 2000). *Tetropium fuscum* has the ability to attack all spruce species that fall within its native and novel range: Norway, red, black (*Picea mariana* (Mill.) BSP), white (*Picea glauca* (Moench) Voss), and blue spruce (*Picea pungens* Engelm.) (Juutinen 1955, Smith and Humble 2000, Eckenwalder 2009). It went undetected in Nova Scotia for at least a decade due to the presence of a native congener, *Tetropium cinnamopterum* (Kirby), which is similar in morphology and occupies a similar ecological niche throughout North America (Juutinen 1955, Linsley 1962, Smith and Hurley 2000, Flaherty et al. 2012).

Invasive forest pests vary in their rate of geographic spread, with *T. fuscum* being relatively slow compared with some other species. *Tetropium fuscum* populations are currently established ~125 km from the site of introduction (CFIA 2015) after over 25 yr (about 5 km per year) of establishment in the region. In contrast, *Sirex noctilio* F. (Hymenoptera: Siricidae) has successfully spread globally, advancing at variable rates between 12 to 82 km per year in invaded regions in the southern hemisphere (Lantschner et al. 2014). *Sirex noctilio* is also interacting with native wood borers (Ryan et al. 2012) and parasitoids (Coyle and Gandhi 2012) in invaded regions in North America. Similarly, the emerald ash borer, *Agrilus planipennis* (Fairmaire) (Coleoptera: Buprestidae), has spread ~900 km since its introduction in 2002 (Muirhead et al. 2006, Natural Resources Canada [NRCAN] 2015). Insect dispersal accounts for a rate of 20 km per year (Prasad et al. 2010) and human-mediated movement of infested firewood increases the rate of spread (Herms and McCullough 2014). However, not all *Agrilus* spp. spread as quickly; the nascent oak borer, *Agrilus auroguttatus* Schaeffer, has spread ~50 km in a 9-yr period (Coleman et al. 2012), a rate comparable with *T. fuscum*'s.

The ecological factors controlling rates of range expansion for invasive species are not well understood, but one possibility is that the rate of spread can be dampened for invaders that interact with and are controlled by competitors and enemies in their novel range. The slow range expansion of *T. fuscum* in its introduced North American range could be partially attributed to its co-occurrence with *T. cinnamopterum*. Survival of *T. fuscum* is reduced by at least two species of Nearctic parasitic wasps that normally specialize on *T. cinnamopterum* but have accepted *T. fuscum* as a host (Flaherty et al. 2011): up to 56% parasitism of *T. fuscum* has been reported in Nova Scotia. It is possible that mortality caused by the native parasitoid complex has moderated the population growth and rate of spread of *T. fuscum* (Flaherty et al. 2011, Rhoads et al. 2011).

We examined the role of community structure on the invasion ecology of *T. fuscum* by comparing the community of parasitoids, competitors, and subcortical insects in its established range in Nova Scotia (hereafter referred to as the “invasion zone”) with that in an ecologically similar area of New Brunswick, well outside the known invasion zone. Previous studies of *T. fuscum* population biology in the North American range have either used semiochemical lures (Rhoads et al. 2010, 2011) or artificially manipulated densities of *T. fuscum* adults or eggs (Flaherty et al. 2011, 2013a,b). We used

naturally colonized red spruce, without semiochemical baiting, but we artificially stressed trees to induce attack by *Tetropium* spp. and the wood-boring community.

We tested the predictions that 1) the wood-boring community, including other phloem-feeding beetles, predators, and parasitoids of *Tetropium* spp., would differ on red spruce inside (Nova Scotia) versus outside (New Brunswick) the *T. fuscum* invasion zone; 2) there would be displacement of *T. cinnamopterum*: i) at the tree level (i.e., along the length of the tree's bole) to less optimal larval habitat higher up on the trunk, or ii) at the site level (i.e., away from trees infested by *T. fuscum* altogether); 3) overall parasitism rates of *Tetropium* spp. would differ inside and outside the “invasion zone” if, for instance, native parasitoids have switched to *T. fuscum* as a preferred host; and 4) parasitism rates would differ along the bole of the tree, being higher toward the base of the tree where phloem resources are abundant.

## Materials and Methods

### Study Sites

We selected four mixed forest stands dominated by red spruce, two inside the invasion zone of *T. fuscum* at a site in Bedford, Nova Scotia (44° 44.27' N, 63° 39.81' W) and two outside this zone at a site in the Acadian Research Forest near Minto, New Brunswick (46° 00.59' N, 66° 21.82' W). Within each site, we selected two stands of similar topography, tree composition, and development stage. Each stand was about 300 m<sup>2</sup> in area, and the two were separated by at least 1 km. Canopy height was 12–18 m, with at least 60% red spruce and with other common trees including balsam fir (*Abies balsamea* (L.) Mill.), red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh.), and white pine (*Pinus strobus* L.). The Nova Scotia sites were ~20 km from the *T. fuscum* introduction epicenter (Smith and Hurley 2000, Rhoads et al. 2011).

### Selection and Treatment of Trees

We haphazardly selected 10 (New Brunswick) and 14 (Nova Scotia) red spruce trees per stand from which to sample the insect community associated with *Tetropium* spp. Trees were 18–25 cm diameter at breast height, 10–17 m tall, and each tree was at least 10 m from any other spruce meeting the minimum size criteria. We sampled more trees from the Nova Scotia stands to increase our power to detect interactions between *Tetropium* congeners in the invasion zone. In each stand, we randomly assigned half the trees to each of two stress treatments: trees were either felled or girdled (3–6 cm deep to the phloem and 3 cm wide) ~15 cm from the ground using a chainsaw in early May 2013. Each treatment was imposed prior to adult beetle flight and was expected to increase susceptibility to colonization by *Tetropium* spp. (Flaherty et al. 2011) and other phloem-feeding insects.

Girdled trees were felled in late September 2013. We then measured the height of each tree and removed 35-cm sections of trunk (henceforth “bolts”) at 10, 30, 50, 70, and 90% of tree height; we refer to these as base, base-middle (B-M), middle, middle-high (M-H), and apex bolts, respectively. Bolts were labeled and left on the forest floor until November 2013 to allow normal insect development and diapause. We then collected 239 bolts [i.e., 5 bolts per tree × 48 trees (NB: 10 girdled + 10 felled; NS: 14 girdled + 14 felled – 1 apex bolt that could not be accounted for)] and transported them to the Atlantic Forestry Centre of the Canadian Forest Service in Fredericton, New Brunswick for storage in a –2°C freezer pending incubation of bolts to rear out insects.

## Rearing of Insects

We focused on the insect community associated with red spruce. We defined this as including three feeding guilds: wood borers, parasitoids of wood borers, and predators. Wood borers include cerambycid (longhorn) beetles and siricid wasps (woodwasps; Hymenoptera: Siricidae), whereas solitary wasps of the families Ichneumonidae, Braconidae, and Ibalidae make up the parasitoid guild. Predators consisted of clerid beetles. Other taxa present, but not considered in our analyses, included bark beetles and weevils (Coleoptera: Curculionidae), fungivorous flies (Diptera, various families), and flat bugs (Hemiptera: Aradidae).

We incubated the spruce bolts in a controlled-environment quarantine facility (20–24°C, and photoperiod of 16:8 [L:D] h, with constant dehumidification) from January to May 2014, transferred them for 3 wk to a 5°C refrigerator and then moved them to a freezer to simulate a (second) winter diapause. Bolts were kept between –2 and –5°C until September 2014, when they were returned to emergence cages for a second period of emergence. We placed each bolt in an emergence cage made either from Lexan (cube-shaped cage), or from a sealed plastic bucket attached to a funnel and collecting cup. We used different cages to allow all 239 bolts to go through two emergence periods with simultaneous rearing, and we mixed Lexan and bucket cages haphazardly with respect to province, site, and stress treatment (except the widest bolts, which could not be accommodated in bucket cages). We collected emerging insects every 3 d, placing them in 70% ethanol in a –2°C freezer pending species identification. We identified to species all emerged insects belonging to the focal guilds, and we sexed all *Tetropium* beetles and the parasitoid wasps, *Rhimphoctona macrocephala* (Provancher) (Hymenoptera: Ichneumonidae) and *Wroughtonia occidentalis* (Cresson) (Hymenoptera: Braconidae). We identified insects using descriptions and images in Yanega (1996) and Schiff et al. (2012), and reference collections at the Atlantic Forestry Centre.

## Data Analysis

We examined the subcortical insect community in experimentally stressed red spruce using analyses of variance (ANOVA; with sites nested within provinces; i.e., Nova Scotia in the invasion zone and New Brunswick, outside the invasion zone) of both beetle abundance per tree and density per m<sup>2</sup> of bark (the latter scales densities to resource abundance, as bolts narrow toward the top of the tree). No *Tetropium* records from the second emergence period were used in community data analysis, as there were indications that all of these were progeny of *Tetropium* that had emerged and mated within the cages. Interaction terms were not significant, and we removed them to better test main effects. Data were analyzed using the R statistical package (version 3.1.2; R Core Team 2013).

1) *Insect communities in red spruce inside versus outside the invasion range.* We compared insect abundance per tree and per m<sup>2</sup> of bark inside and outside the *T. fuscum* invasion zone (Nova Scotia versus New Brunswick) and between stress treatments (girdled versus felled trees). We calculated species richness, Simpson's diversity, and abundances, in each case excluding *T. fuscum* because our intent was to test the effect of *T. fuscum* on the remaining community. We compared each metric across provinces and stress treatments using two-way ANOVAs.

2) *Testing for displacement of T. cinnamopterus by T. fuscum within and away from red spruce.* We tested for displacement of *T. cinnamopterus* by *T. fuscum*, in two ways. First, we tested for displacement away from *T. fuscum*-attacked trees by analyzing the number of *T. cinnamopterus* per tree in a one-way ANOVA to compare zones with and without the invader (stress treatment was

not included because the girdled treatment yielded neither *T. cinnamopterus* nor *T. fuscum*). Second, we tested for displacement of *T. cinnamopterus* within attacked trees to potentially suboptimal larval habitat further up the bole, using analyses of covariance of *T. fuscum* and *T. cinnamopterus* abundance per bolt and density per m<sup>2</sup> as a function of zone (discrete) and height (covariate) along with the nested effect of site. A significant zone × height interaction for *T. cinnamopterus* would suggest within-tree displacement in the invasion zone.

3) *Parasitism rates of Tetropium spp.* We tested for differences in mean parasitism rates of *Tetropium* between zones and among tree sections from different heights using a generalized linear model. Parasitism tests were conducted on the combined attacks of *R. macrocephala* and *W. occidentalis*. Because we were unable to retrieve pupal exuviae in good enough condition for species identification, we were unfortunately unable to distinguish which *Tetropium* species, when both were present, was the host for an emerged parasitoid.

## Results

1) *Insect communities in red spruce inside versus outside the invasion zone.* We collected a total of 223 individual insects belonging to the focal insect community from the 239 bolts (Table 1). These belonged to 13 species, including cerambycid and clerid beetles, siricid wood wasps, and their hymenopteran parasitoids. From the felled treatment, 75% of trees were attacked. Outside the invasion zone in New Brunswick, six out of the 10 trees were attacked by *T. cinnamopterus*, all of which had parasitoids emerge as well. Inside the invasion zone in Nova Scotia, 12 out of the 14 trees were attacked by *Tetropium* spp. and seven of them had parasitoids emerge. Of these trees, five had both *T. fuscum* and *T. cinnamopterus* emerge. From the first rearing period, a total of 85 adult *Tetropium* emerged, all from the felled treatment: 64 *T. cinnamopterus* and 21 *T. fuscum*. *Tetropium fuscum* were collected only from trees in Nova Scotia, within the invasion zone. *Tetropium cinnamopterus* were collected from both inside (Nova Scotia, 23 beetles) and outside (New Brunswick, 45 beetles) the *T. fuscum* invasion zone. Five cerambycid and one siricid species constituted the wood-boring guild; three focal community members were singletons (two cerambycids and one clerid) all reared from Nova Scotia bolts (Table 1). Only two clerid beetles, and no individuals of either *T. fuscum* or *T. cinnamopterus*, emerged from any of the girdled trees ( $N=24$ ). Consequently, we focused solely on the felled spruce treatment ( $N=24$ ) in all subsequent analyses. Apical bolts yielded very few insects ( $0.08 \pm 0.058$  insects per tree) and never yielded *Tetropium* spp. or their parasitoids. Therefore, we ignored the apical bolts in all analyses except for those of per-tree species richness and Simpson's diversity.

There was no significant difference between zones in either total species richness (mean  $\pm$  1 SE: New Brunswick =  $3.7 \pm 0.54$ ; Nova Scotia =  $3.1 \pm 0.33$ ;  $P=0.45$ ) or Simpson's diversity (New Brunswick =  $0.41 \pm 0.09$ ; Nova Scotia =  $0.64 \pm 0.06$ ;  $P=0.55$ ). However, total insect abundance (excluding *T. fuscum*) was higher outside the invasion zone (Nova Scotia  $12.0 \pm 2.3$  versus  $5.9 \pm 0.876$  (Table 2), and the effect was consistent even when *T. fuscum* was included in the analysis ( $P < 0.01$ ). This effect remained for the difference in wood-borer abundance outside ( $5.8 \pm 1.6$ ) versus inside ( $2.0 \pm 0.6$ ;  $P < 0.01$ ) the invasion zone. There was no such difference for predators ( $P=0.82$ ) or parasitoids ( $P=0.27$ ) between zones.

2) *Testing for displacement of T. cinnamopterus by T. fuscum within and away from red spruce.* In total, 85 *Tetropium* beetles

**Table 1.** Total number of insects that emerged from lab-reared bolts outside and inside *T. fuscum*'s invasion zone

Feeding guild	Species	Outside invasion zone (New Brunswick)	Inside invasion zone (Nova Scotia)
Focal beetles	<i>Tetropium fuscum</i> (Cerambycidae)	0	21
	<i>Tetropium cinnamopterum</i> (Cerambycidae)	46	18
Parasitoids	<i>Rhimphoctona macrocephala</i> (Ichneumonidae)	5	11
	<i>Wroughtonia occidentalis</i> (Braconidae)	16	21
Other wood borers	<i>Pogonocherus penicillatus</i> (Cerambycidae)	18	9
	<i>Monochamus scutellatus</i> (Cerambycidae)	2	2
	<i>Monochamus notatus</i> <sup>a</sup> (Cerambycidae)	0	1
	<i>Acanthocinus pusillus</i> <sup>a</sup> (Cerambycidae)	0	1
	<i>Xylotrechus undulatus</i> (Cerambycidae)	1	2
	<i>Urocerus albicornis</i> (Siricidae)	9	4
Woodwasp parasitoids	<i>Ibalia leucospoides</i> (Ibaliidae)	15	1
Predators	<i>Thanasimus undatulus</i> (Cleridae)	8	10
	<i>Enoclerus nigripes</i> <sup>a</sup> (Cleridae)	0	1

<sup>a</sup> Denotes a single individual of collected species.

**Table 2.** Abundance per tree of the insect community associated with red spruce inside and outside the invasion zone, excluding *T. fuscum*

Effect	df	Deviance	Residual df	Residual deviance	P
(Intercept)	–	–	95	116.30	–
Zone	1	9.08	94	107.23	0.003
Tree section	3	5.95	91	101.28	0.114

Results of analysis of deviance from a generalized linear model.

emerged from felled spruce: 46 from New Brunswick trees and 39 from Nova Scotia trees. The interaction between zone and height was not significant for *T. cinnamopterum*, suggesting that its distribution along the length of the spruce bole was not affected by the presence of *T. fuscum* (Table 3). The native *T. cinnamopterum* was more abundant outside the invasion zone of *T. fuscum* ( $4.6 \pm 1.3$  compared with  $1.3 \pm 0.3$  per tree), and its density per m<sup>2</sup> of bark was also higher (Fig. 1; and this is true whether or not parasitized beetles are included in the count). However, *T. cinnamopterum* density did not vary along the tree bole (below the apex; Table 3; Fig. 2). When both *T. fuscum* and *T. cinnamopterum* were combined to act as a single functional species, there was no statistical difference in abundance between zones (New Brunswick  $4.6 \pm 1.3$  versus Nova Scotia  $2.8 \pm 0.5$  beetles per tree;  $P = 0.15$ ; Table 4). A bimodal pattern in *Tetropium* abundance along the bole was marginally significant (Table 4, Fig. 2), although there was no interaction between zone and section ( $P = 0.20$ ).

3) *Parasitism rates of Tetropium spp.* The overall parasitism rate for both *Tetropium* species was 38%: 53 *Tetropium* out of the 138 were parasitized ( $138 = 37$  *W. occidentalis* +  $16$  *R. macrocephala* +  $85$  uninfected *Tetropium*). Parasitism rates did not differ significantly within and outside the invasion zone (New Brunswick = 31% versus Nova Scotia = 44%;  $P = 0.11$ ; Table 5). Parasitism was greatest at the base of the bole (Table 5), with a range of 50% at the base-middle position to 11% at the middle-high position (Fig. 3).

## Discussion

The wood-boring insect communities inside and outside the invasion zone were similar in terms of species richness and Simpson's diversity. In fact, *T. fuscum* was the only community member that differed between the two zones (except for a few singletons; Table 1)

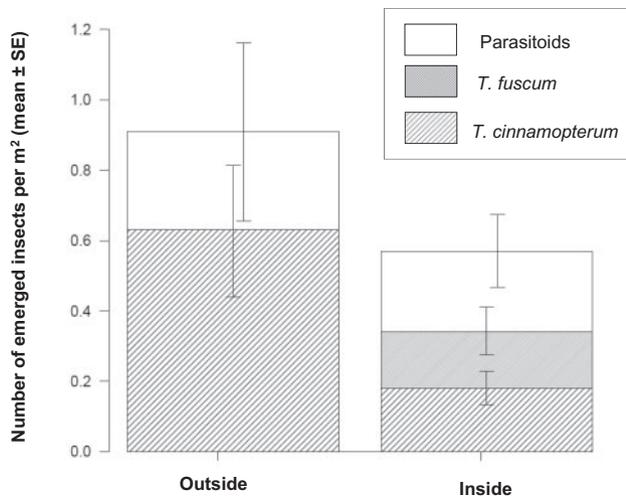
**Table 3.** Abundance of *T. cinnamopterum* inside versus outside the invasion zone

Effect	df	Deviance	Residual df	Residual deviance	P
<sup>a</sup> (Intercept)	–	–	95	91.31	–
<sup>a</sup> Zone	1	11.03	94	80.28	<0.001
<sup>a</sup> Section	3	5.59	91	74.68	0.133
<sup>a</sup> Zone × Sec	3	6.07	88	68.62	0.108
<sup>d</sup> (Intercept)	–	–	95	92.61	–
<sup>d</sup> Zone	1	10.48	94	82.12	0.001
<sup>d</sup> Section	3	6.69	91	75.43	0.082
<sup>d</sup> Zone × Sec	3	6.32	88	69.10	0.097

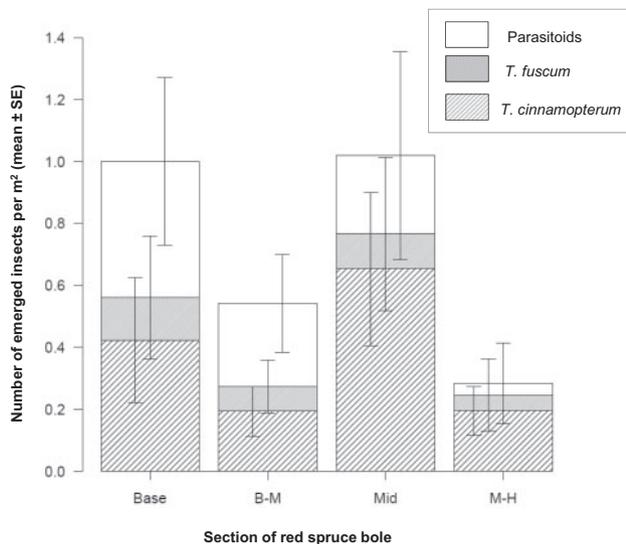
Results of analysis of deviance from a generalized linear model.

<sup>a</sup> is the abundance per felled tree and <sup>d</sup> is the density per m<sup>2</sup>.

allowing us to examine whether *T. fuscum* might have displaced *T. cinnamopterum* within this zone. When we combined both *Tetropium* species to act as one functional entity, there was no significant difference in abundance (density per m<sup>2</sup>) inside versus outside the invasion zone (Table 4), suggesting some form of displacement by the invasive beetle. The significantly lower number of *T. cinnamopterum* that emerged per tree in the invasion zone (Figs. 1 and 2) suggests a competitive interaction between the two species. Although we did not directly assess the mechanism for this interaction, emergence rates at least two orders of magnitude higher than ours have been recorded for individual spruce bolts (up to 661 beetles/m<sup>2</sup>, Wettstein 1951), suggesting that consumption did not exhaust the phloem resource in our bolts. There was also no displacement of *T. cinnamopterum* along the bole of the tree by *T. fuscum* (Table 3). Therefore, competition between *Tetropium* spp. is not likely based on exhaustion of available resources, as is the case (for instance) in outbreaking *Ips* bark beetles (Schlyter and Anderbrant 1993). Instead, it is possible that larval interactions may lead to interference competition, perhaps acting in concert with intraguild predation when older and larger larvae encounter smaller larvae as they feed on phloem (Rankin and Borden 1991). It is also possible that displacement is related to reproductive interference in adults rather than larval competition (Hochkirch et al. 2007). Although the two species will copulate in the laboratory (Silk et al. 2011), it is unknown whether such copulations prevent later within-species matings or whether hybrid individuals occur in the field.



**Fig. 1.** Mean density per  $m^2$  of *Tetropium* spp. and their parasitoids that emerged from felled red spruce inside versus outside *T. fuscum*'s invasion zone in Canada.



**Fig. 2.** Mean density per  $m^2$  of adult *T. cinnamopterus*, *T. fuscum*, and their parasitoids that emerged from felled red spruce inside the invasion zone. Differences among sections along the bole: base, base-middle (B-M), middle, and middle-high (M-H).

*Tetropium fuscum* and *T. cinnamopterus* emerged exclusively from felled trees in our study even though both species are able to develop on girdled and even apparently healthy red spruce (Flaherty et al. 2011) when they are introduced by releasing caged adults or lured there by semiochemical baits [*Tetropium* is attracted to such baits (Sweeney et al. 2004), and baited traps can capture many tens of adult beetles (Rhainds et al. 2010)]. The total abundance of *Tetropium* spp. emerging from our bolts (85 beetles total, or  $\sim 0.7$  beetles/ $m^2$  bark) was somewhat lower than previous rearings from unbaited trees and logs (average densities between 1 and 24 beetles/ $m^2$ , depending on *Tetropium* species and bolt source; J. Sweeney, unpublished data).

We reared *Tetropium* only from felled trees, but we know from sticky-band studies (K.W. Dearborn, unpublished data) that beetles will visit and land on girdled trees. Flaherty et al. (2013a) investigated prelighting host preferences on 20 unbaited red spruce trees

**Table 4.** Combined abundance of *Tetropium* spp. inside versus outside the invasion zone

Effect	df	Deviance	Residual df	Residual deviance	P
<sup>a</sup> (Intercept)	–	–	95	93.08	–
<sup>a</sup> Zone	1	2.07	94	91.01	0.150
<sup>a</sup> Section	3	8.14	91	82.87	0.043
<sup>d</sup> (Intercept)	–	–	95	97.76	–
<sup>d</sup> Zone	1	3.27	94	94.48	0.070
<sup>d</sup> Section	3	7.46	91	87.03	0.059

Results of analysis of deviance from generalized linear model.

<sup>a</sup> is the abundance per felled tree and <sup>d</sup> is the density per  $m^2$ .

**Table 5.** Parasitism rates by the native parasitoid wasps *R. macrocephala* and *W. occidentalis* on both *Tetropium* spp. inside and outside the invasion zone (analysis of deviance from generalized linear model)

Effect	df	Deviance	AIC	LRT	P (Chi)
(Intercept)	–	47.67	96.55	–	–
Province	1	50.21	97.09	2.55	0.111
Section	3	57.00	99.88	9.33	0.003

and found that traps on artificially girdled spruce captured significantly more *T. fuscum* and *T. cinnamopterus* than did traps on apparently healthy controls. We assume but cannot be certain that beetles landing on our girdled trees were assessing them for oviposition sites, as shown by Flaherty et al. (2013a), but we do not know whether they rejected them or whether larvae could not develop. Despite their ability to assess (Flaherty et al. 2013a) and capacity to develop (Flaherty et al. 2011, 2013b) on healthy spruce trees, *Tetropium* spp. in their native ranges are commonly found in moribund spruce trees that are at an early state of decay (Juutinen 1955, Linsley 1962, Lee et al. 2014). We suspect, therefore, that the absence of *Tetropium* spp. in our girdled trees and the relatively low emergence from felled trees are more indicative of their natural behavior than past studies that have introduced eggs on trees (e.g., Flaherty et al. 2011, 2013a,b). Populations on moribund, standing trees can build up for a few generations before population densities and emergence rates become high (Juutinen 1955). Developing in felled trees is therefore congruent with the life history of *Tetropium* spp. in their native range (Juutinen 1955, Linsley 1962, Flaherty et al. 2013b).

*Tetropium fuscum* has been expanding its range slowly westward from its introduction site in Halifax, Nova Scotia (Smith and Hurley 2000). One of the factors presumed to facilitate this expansion is the advantage of adult emergence 2 wk earlier compared with the native congener (Rhainds et al. 2010). Adult *Tetropium* are sexually reproductive upon emerging from their natal trees (Juutinen 1955). The earlier emergence phenology of *T. fuscum* is likely beneficial in terms of colonizing an as-yet unoccupied resource, resulting in a competitive advantage for successive generations that re-attack and emerge from the same tree (Juutinen 1955, Linsley 1962). It may also make *T. fuscum* the likely predator, and *T. cinnamopterus* the likely victim, in intraguild predation. Advantages in oviposition timing during the flight season are crucial for sympatric wood borers that share phloem resources on the same tree. Despite *T. fuscum* and *T. cinnamopterus* having broadly overlapping body size ranges (Juutinen 1955, Linsley 1962, Yanega 1996, Flaherty et al. 2011), the phenological advantage attributed to earlier emergence of

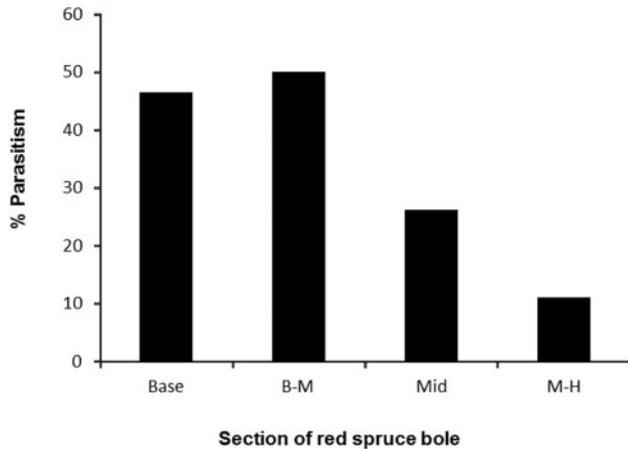


Fig. 3. Overall parasitism rates by *R. macrocephala* and *W. occidentalis* on *Tetropium* spp. that emerged from the base, base-middle (B-M), middle, and middle-high (M-H) sections along the bole of felled red spruce.

*T. fuscum* from diapause (Rhainds et al. 2010) and its ability to inhabit relatively more vigorous spruce (Flaherty et al. 2011) compared with *T. cinnamopterum* could contribute to its success in displacing the native congener. Nonetheless, the fact that there is a native congener present to be displaced could be one factor slowing *T. fuscum*'s rate of invasion.

*Tetropium fuscum* in North America is known to be attacked by two native parasitoid wasps, *R. macrocephala* and *W. occidentalis* (Flaherty et al. 2011), both of which frequently emerged from our bolts, both inside and outside the invasion zone. Parasitism rate was higher at the base of the tree (Table 5) where wasps would have a larger foraging area (Li and Weiskittel 2011) because of thicker phloem. Because the two *Tetropium* spp. rely on similar cues from host tree volatiles for host finding (Sweeney et al. 2004, Silk et al. 2007, Flaherty et al. 2011), they attack the same host species (red spruce) and often co-occur in the same individual tree. Although we were not able to conclusively identify the host species for emerging parasitoids in our study, it is overwhelmingly likely that both *Tetropium* spp. were parasitized. In fact, there is some reason to think that the presence of the invasive *T. fuscum* may increase vulnerability of both species to parasitoid attack. Because *T. fuscum* emerges and lays eggs earlier, but development times overlap, together they might provide native parasitoids with a larger window of host availability. In our study, parasitism rates of *Tetropium* spp. where both species are present were somewhat but not significantly higher (44 vs. 31%) than outside the zone. Future parasitoid-rearing studies with larger sample sizes would be valuable, because (if it is real) a higher parasitism rate in the invasion zone could further depress adult densities and thus rates of mate encounter at the zone's periphery, contributing to a mate-finding Allee effect (Rhainds et al. 2015).

Other aspects of the insect–host community may also help dampen the westward expansion of *T. fuscum*. First, life histories with obligate dispersal phases favor rapid range expansion, but both *Tetropium* spp. are capable of consecutive generations within the same stressed tree (Juutinen 1955, Flaherty et al. 2011) and so females need not undertake dispersal flights each year. Second, red spruce populations along the periphery of the invaded range may be relatively healthy, resulting in a more prolonged development of larvae. Forests at the origin of the invasion, in contrast, were ravaged in September 2003 by a Category 2 hurricane (Juan). The hurricane destroyed 90% of the mature growth in Point Pleasant Park, where *T. fuscum* was first introduced and detected (Environment Canada

2013). Reduction of tree vigor by hurricane damage may have relaxed tree defenses, allowing *Tetropium* populations to build up and begin spreading to healthier forests (Flaherty et al. 2011). If females are now accepting vigorous trees for oviposition (Flaherty et al. 2011), larval development times may be extended. This would delay adult emergence and increase the potential for parasitism and woodpecker predation. Under this scenario, *T. fuscum* may not have spread at a constant rate but instead (like many invasions) experienced a lag in population growth (Crooks 2005) broken by environmental factors favoring expansion.

Competition, parasitism, dispersal biology, and tree health may be acting together to retard the spread of *T. fuscum* compared with other more prolific expansions such as that of the emerald ash borer (Muirhead et al. 2006). Our data suggest important interactions between the native and exotic *Tetropium* congeners. In fact, their extensive overlap in biology and ecology suggests that within the invasion zone, they may act as a single functional species relative to other wood-boring and parasitoid insects.

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