

**INTERACTIONS BETWEEN THE INVASIVE
BROWN SPRUCE LONGHORN BEETLE, *TETROPIUM FUSCUM* (FABRICIUS)
(COLEOPTERA: CERAMBYCIDAE), AND ITS NATIVE CONGENER,
TETROPIUM CINNAMOPTERUM (KIRBY)**

by

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ABSTRACT

Tetropium fuscum (TF) (Coleoptera: Cerambycidae) is a European spruce borer established in Nova Scotia since at least 1990. I tested whether TF displaces a native congener, *T. cinnamopterum* (TC), in red spruce. Stressed trees, 24 girdled and 24 felled, were selected for natural colonization: 28 inside the invaded zone and 20 outside. Both *Tetropium* species and their parasitoid wasps emerged exclusively from felled trees. Combined *Tetropium* density (inside invaded zone = 0.34 ± 0.07 vs. outside = 0.63 ± 0.19 per m^2 ; $P = 0.070$) and overall parasitism rates (inside invaded zone = 31% vs. outside = 44%; $P = 0.111$) did not statistically differ inside vs. outside the invasion zone, but TC density was significantly greater outside the invasion zone (0.63 ± 0.19 compared to 0.18 ± 0.05 m^2 ; $P = 0.001$), suggesting TF may displace TC where they are sympatric.

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KENNETH DEARBORN

CHAPTER 1 – GENERAL INTRODUCTION

Invasions, whether military or biological, promote the idea of one entity, the exotic, entering a novel territory to establish populations aggressively in a new space. Charles Elton first popularized invasion ecology in the 1950s and biological invasions quickly became prominent in community ecology (Shea & Chesson 2002; Crooks 2005) as well as one of the most economically important pillars in biology (Patel 2012). Increased frequency of global trade has allowed for a consistent introduction pathway for a wide variety of organisms to cross geological barriers such as mountain ranges and oceans. Rapid expansion of the field of invasion ecology as well as in the number of invaders has resulted in a massive radiation in terminology related to exotic invasions and introduced species (Richardson *et al.* 2000). The diversity of vocabulary can be confusing when conveying the level of severity of species introductions both among scientists and the general public (Richardson *et al.* 2000; Falk-Petersen *et al.* 2006).

Introduced organisms are species that have overcome some significant geographical barrier to enter a new habitat. Exotic organisms are species that have been introduced to a new habitat through human activity, either accidentally or intentionally, and are synonymous with alien, non-native, and nonindigenous organisms (Richardson *et*

al. 2000). Exotic range expansions exclusively refer to populations of an exotic organism establishing in a novel geographical area. Range expansions may occur through host switches but are not exclusive to that method alone. Naturalization is the next step in the progression towards invasions, where the exotic population is sufficiently established that it will not be extirpated by biotic stochasticity (Shaffer 1981; Richardson *et al.* 2000). Invasive organisms, for the purpose of this thesis, are understood as nonindigenous species introduced to a novel biogeographical region causing harm or damage to the native economy or environment in which local populations have birth rates that exceed their death rates resulting in exotic range expansion (Richardson *et al.* 2000; Colautti & MacIsaac 2004). Many invasive organisms that rise to the forefront are large and charismatic such as European starlings (*Sturnus vulgaris*) (Elton 1958), cane toads (*Bufo marinus*) (Llewelyn *et al.* 2011), and feral cats (*Felis sylvestris*) (Courchamp *et al.* 2003). These examples are all macrofauna that were established through human negligence via intentional introductions (Elton 1958; Courchamp *et al.* 2003); even more astounding is that approximately one third of Britain's mammals were introduced by humans (Arnold 1993). Many introduced species are transported through seemingly innocuous methods such as ballast water, pet trade, soil transportation, and silvicultural products, due to the cryptic nature of a variety of plants and animals (Haack 2006; Wilson *et al.* 2009).

One of the most prevalent pathways of introducing wood boring species are wood packaging products such as crates or pallets, contributing at least 25 established exotic beetles to North America (Haack 2006). Canada's top ten ports averaged 11.78 million tons of unloaded forest-insect-associated materials per year (Yemshanov *et al.* 2012) and US ports have an even greater incidence of invasive interception (Haack 2006). Ongoing

importation and recurrent introductions ensure that there are ample opportunities for these insects to emerge as adults and for more than one population to establish in a novel environment (Liebhold *et al.* 2013). Three beetle families comprise the majority of established exotic wood-feeding insects posing significant threats to forest ecosystems: Buprestidae (jewel beetles), Cerambycidae (longhorn beetles), and Curculionidae (subfamily Scolytinae) (weevils, bark and ambrosia beetles) (Haack 2006; Aukema *et al.* 2010). All three families possess habits that allow them to excel at establishing in novel environments. First, with the exception of some species, e.g., the Asian longhorn beetle, *Anoplophora glabripennis* (Motschulsky), most species are relatively small and easily overlooked. Secondly, these families are cryptic in habit and are concealed beneath bark or in the wood, permitting transportation in firewood (Rhainds *et al.* 2011), saplings (Muirhead *et al.* 2006), and wood pallets (Haack 2006; Yemshanov *et al.* 2012). Third, an important trait for dispersal following immigration is flight capacity (Taylor *et al.* 2010; David *et al.* 2014). Many of these beetles fly in response to cues from host tree volatiles (Sweeney *et al.* 2004) and mating pheromones (Silk *et al.* 2007) to find mates and select oviposition sites. Pheromones and plant volatiles have been utilized for successfully sampling wood borer diversity (Sweeney *et al.* 2014). Some pest species are more apparent because of the substantial damage that they cause to forests; others need to be detected using pheromone traps. Regardless of how they are observed, integrated pest management intervention must be performed, such as in the forms of sanitation (Jones *et al.* 2013) and biological control (Brabbs *et al.* 2015).

One of the most prolific of invaders of North America, the emerald ash borer (EAB), *Agrilus planipennis* (Coleoptera: Buprestidae), was discovered in Detroit,

Michigan and nearby Windsor, Ontario in 2002, but dendrochronological analysis indicates it was likely present as early as 1993 (Siegert *et al.* 2014). Expansion of its exotic range was aided by the movement of firewood and nursery stock (Muirhead *et al.* 2006), consequently human-mediated transportation has allowed for many large jumps in the new range, including expansion and proliferation into Canada (Muirhead *et al.* 2006). Aside from the movement of firewood or planting of infected saplings, an asset to EAB invasive expansion seems to be the lack of any closely related species attacking the North American ash species (*Fraxinus*). Without a native *Agrilus* species attacking ash in North America, EAB could be taking advantage of ecological opportunities according to Darwin's naturalization hypothesis (1859), which proposes that exotic organisms with closely-related natives in the same genera less successfully invade a novel habitat. EAB can easily fly more than a kilometer (Taylor *et al.* 2010) aiding a successful spread of approximately 900 km since its introduction in 2002 (Muirhead *et al.* 2006; NRC 2015). Not all *Agrilus* without a congeneric native spread quickly: the nascent oak borer, *A. auroguttatus*, has spread approximately 50 km in 9 years (Coleman *et al.* 2012). Presence of a native congener and its associated predators, parasitoids, and diseases increases the probability of biotic resistance to an introduced species in the novel habitat, depending on how similar the niches are that the species occupy. This has been explored in fish (Ricciardi & Mottiar 2006), plants, and birds (Kolar & Lodge 2001) without a consensus on its importance for invasion success. Therefore, the invasive *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae) and its native congener *T. cinnamopterum* (Kirby) pose an interesting case due to the spread of introduced *T. fuscum* populations

being limited to approximately 125 km from the Halifax, NS introduction site (CFIA 2015) after over 20 years of establishment.

Tetropium fuscum is an exotic pest to North America (CFIA 2007) that infests the phloem of stressed Norway spruce, *Picea abies* (L.) Karst, in its native Europe (Juutinen 1955). It was discovered in 1999 infesting apparently healthy red spruce, *P. rubens* (Sarg.), within Point Pleasant Park (Halifax, Nova Scotia), located directly adjacent to one of the port city's shipping container facilities (Smith & Hurley 2000). This species went undetected for approximately a decade and was able to cryptically establish populations around Halifax (Rhains *et al.* 2010), occupying a similar niche to *T. cinnamopterum* and resembling the native congener at all life stages to the naked eye (Juutinen 1955, Linsley 1962; Smith & Humble 2000; Flaherty *et al.* 2012). Males of both *T. fuscum* and *T. cinnamopterum* emit the pheromone, (2*S*,5*E*)-6,10-dimethyl-5,9-undecadienol (fuscumol), which, together with host tree volatiles (Sweeney *et al.* 2004; Sweeney *et al.* 2006), synergizes attraction of both sexes (Silk *et al.* 2007; Sweeney *et al.* 2010). The fact that males and females of both *Tetropium* species can readily be sampled in the same semiochemical-baited traps has led to analyses of trap catch data from surveys and field experiments that show that *T. fuscum* adults flight starts 1–2 weeks earlier than that of *T. cinnamopterum* (Rhains *et al.* 2010), and that the relatively limited range expansion of *T. fuscum* may be due to mating failures in low density populations at the edge of its range (the Allee effect) (Rhains *et al.* 2011; 2015). Flaherty *et al.* (2011; 2013ab) investigated the effects of top-down and bottom-up influences on *T. fuscum* populations in a series of manipulative field experiments. A key finding by Flaherty *et al.* (2011) was that native parasitoid wasps were capable of using the exotic, *T. fuscum*, as a

host, suggesting that the community has a pre-adapted biological resistance to impede the invasion. Rates of range expansion for invasive species are not well understood, but one hypothesis is that invasion spread can be dampened for invaders that interact with competitors and enemies in their novel range. The slow exotic range expansion of *T. fuscum* compared to that of EAB could be partially attributed to its co-occurrence with *T. cinnamopterum*. This research evaluates interactions between *T. fuscum*, its primary host in Canada (red spruce), and native competitors and parasitoid wasps. The specific objectives addressed in chapter 2 are outlined below.

Chapter 2 investigated the rates of attack by *Tetropium* spp. on stressed (girdled) and felled red spruce trees within and outside of the exotic range of *T. fuscum*. Building upon this initial preference of tree vigour for oviposition, I compared red spruce associated insect communities and parasitism rates relative to *T. fuscum*'s exotic range. I also compared the within-tree distribution (that is, along the length of the tree's bole) of *Tetropium* spp., within and outside the exotic range of *T. fuscum*. These community evaluations provide the basis for indications of displacement of native beetles by *T. fuscum* entirely from red spruce.

Reference

Arnold, H. R. 1993. Atlas of Mammals in Britain. London, England: HMSO

Publications. 145 pp.

Aukema, J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton and S. J.

Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental US. *BioScience* 60: 886–897.

- Brabbs, T., D. Collins, F. Hérard, M. Maspero, and D. Eyre. 2015. Prospects for the use of biological control agents against *Anoplophora* in Europe. *Pest Management Science* 71: 7-14.
- (CFIA) Canadian Food Inspection Agency. 2007. Brown spruce longhorn beetle infested places order (second revision). <http://www.inspection.gc.ca/plants/plant-protection/insects/brown-spruce-longhorn-beetle/order/eng/1333085341951/1333085519708>
- (CFIA) Canadian Food Inspection Agency. 2015. 2014 brown spruce longhorn beetle survey.
- Colautti, R. I, and H. J. MacIsaac. 2004. A neutral terminology to define “invasive” species. *Diversity and Distributions* 10: 135-141.
- Coleman, T. W., A. D. Graves, M. Hoddle, Z. Heath, Y. Chen, M. L. Flint, and S. J. Seybold. 2012. Forest stand composition and impacts associated with *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) and *Agrilus coaxlis* Waterhouse in oak woodlands. *Forest Ecology and Management* 276: 104-117.
- Courchamp, F., J. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78: 347-383.
- Crooks, J. A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12: 316-329.
- Darwin C .1859. On the Origin of Species by Means of Natural Selection. London, England. John Murray. 502 pp.

- David, G., B. Giffard, D. Piou, and H. Jactel. 2014. Dispersal capacity of *Monochamus galloprovincialis*, the European vector of the pine wood nematode, on flight mills. *Journal of Applied Entomology* 138: 566-576.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Reprinted in 2000. Chicago, U.S.A.: The University of Chicago Press. 181 pp.
- Falk-Petersen, J., T. Bøhn, and O. T. Sandlund. 2006. On the numerous concepts in invasion biology. *Biological Invasions* 8:1409-1424.
- Flaherty, L., J. D. Sweeney, D. Pureswaran, and D.T. Quiring. 2011. Influence of the host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 40: 1200-1209.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. 2013a. Preference of an exotic wood borer for stressed trees is more attributable to pre-alighting than post-alighting behaviour. *Ecological Entomology* 38: 546-552.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. 2013b. Evaluating seasonal variation in bottom-up and top-down forces and their impact on an exotic wood borer, *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 42: 957-966.
- Haack, R. A. 2006. Exotic bark- and woodboring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* 36: 269-288.
- Jones, M. I., T. W. Coleman, A. D. Graves, M. L. Flint, and S. J. Seybold. 2013. Sanitation options for managing oak wood infested with the invasive goldspotted oak borer (Coleoptera: Buprestidae) in southern California. *Journal of Economical Entomology* 106: 235-246.

- Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199-204.
- Liebhold, A. M., D. G. McCullough, L. M. Blackburn, S. J. Frankel, B. Von Holle, and J. E. Aukema. 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and Distributions* 19: 1208-1216.
- Linsley, E. G. 1962. The Cerambycidae of North America part 2. Los Angeles. U.S.A.: University of California Press. 102 pp.
- Llewelyn, J., B. L. Phillips, G. P. Brown, L. Schwarzkopf, R.A. Alford, and R. Shine. 2011. Adaptation or preadaptation: why are keelback snakes (*Tropidonophis mairii*) less vulnerable to invasive cane toads (*Bufo marinus*) than are other Australian snakes? *Evolutionary Ecology* 25: 13-24.
- Muirhead, J. R., B. Leung, C. van Overdijk, D. W. Kelly, K. Nandakumar, K. R. Marchant, and H. J. MacIsaac. 2006. Modeling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions* 12: 71-79.
- (NRC) Natural Resources Canada. 2015. Emerald ash borer. <http://www.nrcan.gc.ca/forests/insects-diseases/13377> (Accessed June 2015)
- Patel, S. 2012. Threats, management and envisaged utilizations of aquatic weed *Eichhornia crassipes*: an overview. *Reviews in Environmental Science and Biotechnology* 11: 249-259.
- Rhainds, M., S. B. Heard, J. D. Sweeney, P. Silk, and L. Flaherty. 2010. Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 39: 1794-1800.

- Rhainds, M., W. C. MacKinnon, K. B. Porter, J. D. Sweeney, and P. J. Silk. 2011. Evidence for limited spatial spread in an exotic longhorn beetle *Tetropium fuscum* (Coleoptera: Cerambycidae). *Journal of Economic Entomology* 104: 1928-1933.
- Rhainds, M., S. B. Heard, C. Hughes, W. MacKinnon, K. Porter, J. Sweeney, P. Silk, I. DeMerchant, S. McLean and G. Brodersen. 2015. Evidence for mate-encounter Allee effect in an invasive longhorn beetle (Coleoptera: Cerambycidae). *Ecological Entomology* (published online 23 September 2015; DOI: 10.1111/een.12255).
- Ricciardi, A. and M. Mottiar. 2006. Does Darwin's naturalization hypothesis explain fish invasions? *Biological Invasions* 8: 1403-1407.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93-107.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131-134.
- Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170-176.
- Siegert, N. W., D. G. McCullough, A. M. Liebhold, and F. W. Telewski. 2014. Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. *Diversity and Distributions* 20: 847-858.
- Silk, P. J., J. Sweeney, J. Wu, J. Price, J. M. Gutowski, and E. G. Kettela. 2007. Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). *Naturwissenschaften* 94: 697-701.

- Smith, G. and L. M. Humble. 2000. The brown spruce longhorn beetle. Exotic Forestry Pest Advisory 5. Natural Resources Canada, Canadian Forest Service, Ottawa, Canada.
- Smith, G. and J. E. Hurley. 2000. First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin* 54: 540.
- Sweeney, J., P. de Groot, L. MacDonald, S. Smith, C. Cocquempot, M. Kenis, and J. Gutowski. 2004. Host volatile attractants for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* (L.) and other longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 33: 844-854.
- Sweeney, J., J. M. Gutowski, J. Price, and P. de Groot. 2006. Effect of semiochemical release rate, killing agent, and trap design on detection of *Tetropium fuscum* (F.) and other longhorn beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 35: 645-654.
- Sweeney, J. D., P. J. Silk, J. M. Gutowski, J. Wu, M. A. Lemay, P. D. Mayo, and D. I. Magee. 2010. Effect of chirality, release rate, and host volatiles on response of *Tetropium fuscum* (F.), *Tetropium cinnamopterum* (Kirby), and *Tetropium castaneum* (L.) (Coleoptera: Cerambycidae) to the aggregation pheromone, fuscumol. *Journal of Chemical Ecology* 36: 1309–1321.
- Sweeney, J. D., P. J. Silk, and V. Grebennikov. 2014. Efficacy of semiochemical-baited traps for detection of longhorn beetles (Coleoptera: Cerambycidae) in the Russian Far East. *European Journal of Entomology* 111: 397-406.

Taylor, R. A. J., L. S. Bauer, T. M. Poland, and K. N. Windell. 2010. Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight.

Journal of Insect Behavior 23: 128-148.

Wilson, J. R. U., E. E. Dormontt, P. J. Prentis, A. J. Lowe, and D. M. Richardson. 2009.

Something in the way you move: dispersal pathways affect invasion success. *Trend in Ecology and Evolution* 24: 136-144.

**CHAPTER 2 – DISPLACEMENT OF *TETROPIUM CINNAMOPTERUM*
(KIRBY) (COLEOPTERA: CERAMBYCIDAE) BY ITS INVASIVE CONGENER,
T. FUSCUM (FABRICIUS) FROM RED SPRUCE, *PICEA RUBENS* (SARG.) IN
ATLANTIC CANADA**

Introduction

Invasive pests are an important environmental topic due to the economic impact and ecological disruptions that follow their introduction (Elton 1958; Holzmüller & Jose 2011; Kolar & Lodge 2001; Shea & Chesson 2002). Invasive organisms have been defined as nonindigenous species introduced to a novel biogeographical region causing harm or damage to the native economy or environment in which they have established local populations and expanded their range (Richardson *et al.* 2000; Colautti & MacIsaac 2004). The vast majority of introduced organisms fail to establish in novel environments (Williamson & Fitter 1996). Species that become invasive have often been able to take advantage of open niche opportunities (Shea & Chesson 2002). However, not all invasive species fill previously open niches. Introduced pests can interact with community members and may alter the composition of established communities by consuming novel prey (Kipp & Ricciardi 2012), being consumed by native predators or parasitoids (Llewelyn *et al.* 2011; Flaherty *et al.* 2011), or by displacing competitors (Holzmüller & Jose 2011; Lessard *et al.* 2009; Patel 2012). These ecological interactions, and the way they depend on natural history traits of native and introduced species, can play vital roles in determining the extent to which an introduced species can become invasive. High reproductive potential of introduced species and their dispersal strategies can favour population growth (Levin 2000; Llewelyn *et al.* 2011) and range expansion of the invader

(Elton 1958; Holzmueller & Jose 2011) leading to a greater incidence of interactions with native species of the invaded community (Kipp & Ricciardi 2012).

Wood boring beetles have a variety of traits that favour their anthropogenic movement and introduction to novel environments and their potential to become invasive: their association with nursery stock, solid wood packaging of goods shipped internationally, and with firewood (Smith & Hurley 2000; Haack 2006; Muirhead *et al.* 2006) along with their cryptic nature with minimal visible signs of infestation (Juutinen 1955; Haavik *et al.* 2015) and high reproductive potential (Kenna 2002; Flaherty *et al.* 2011; Haavik *et al.* 2015). Small founder populations can easily proliferate if they remain unnoticed and are bolstered by conspecifics continuously being transported into the exotic environment (Elton 1958; Haack 2006).

Tetropium fuscum (Fabricius) (Coleoptera: Cerambycidae) is an exotic pest to North America (CFIA 2007) that infests the phloem of stressed Norway spruce, *Picea abies* (L.) Karst, in its native Europe (Juutinen 1955). In North America, *T. fuscum* was discovered in 1999 within Point Pleasant Park (Halifax, Nova Scotia), 1 km from the shipping port of Halifax attacking apparently healthy red spruce, *P. rubens* (Sarg.) (Smith & Hurley 2000). *Tetropium fuscum* has the ability to attack all spruce species that fall within its native and novel ranges: Norway, red, black (*P. mariana* (Mill.) BSP, white (*P. glauca* (Moench) Voss), and blue (*P. pungens*, Engelm.) (Juutinen 1955; Smith & Humble 2000; Eckenwalder 2009). *Tetropium fuscum* went undetected for at least 9 years due to presence of a native congener, *T. cinnamopterum* (Kirby), that occupies a similar niche throughout North America and is very similar to the naked eye at all life stages to *T. fuscum* (Juutinen 1955; Linsley 1962; Smith & Hurley 2000; Flaherty *et al.* 2012).

High reproductive rates coupled with cryptic life stages in wood materials including solid wood packaging and firewood have helped *T. fuscum* invade and expand its exotic range in North America (Smith & Hurley 2000; Haack 2006; Flaherty *et al.* 2011).

Invasive forest pests vary in their rate of geographic spread, with *T. fuscum* being relatively slow compared to some other species. *Tetropium fuscum* has populations established approximately 125 km from the introduction site (CFIA 2015) after over 20 years. In contrast, the emerald ash borer, *Agilus planipennis* (Fairmaire) (Coleoptera: Buprestidae) has spread approximately 900 km since its introduction in 2002 (Muirhead *et al.* 2006; NRC 2015). Not all *Agilus* spread quickly; the nascent oak borer, *A. auroguttatus* Schaeffer, has spread approximately 50 km in 9 years (Coleman *et al.* 2012), a rate comparable to *T. fuscum*. *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) have successfully spread globally, advancing upwards of 82 km per year within invaded regions (Lantschener *et al.* 2014) with evidence supporting interactions with native wood borers (Ryan *et al.* 2012) and parasitoids (Coyle & Gandhi 2012).

The ecological factors controlling rates of range expansion for invasive species are not well understood, but one possibility is that spread can be dampened for invaders that interact with competitors and enemies in their novel ranges. The slow exotic range expansion of *T. fuscum* 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 population growth and rate of spread of *T. fuscum* (Flaherty *et al.* 2011; Rhainds *et al.* 2011).

I investigated the role of community structure in the invasion ecology of *T. fuscum* by comparing the community of parasitoids and competitors in its established range in Nova Scotia with that in an area of New Brunswick, well outside of the known exotic range of *T. fuscum*, hereafter referred to as the invasion zone. This study involved documenting naturally colonized red spruce, without semiochemical-baited traps but artificially stressed trees, by *Tetropium* and the wood boring community. Previous studies of *T. fuscum* population biology in the North American exotic range have either used semiochemical lures (Rhainds *et al.* 2010; 2011) or artificially manipulated densities of *T. fuscum* adults or eggs (Flaherty *et al.* 2011; 2013ab).

My objectives were to: (1) compare rates of *Tetropium* attack on stressed (girdled) and felled red spruce trees; (2) compare the communities of wood boring insects, predators, and parasitoids of *Tetropium* spp. of red spruce inside and outside the established range of *T. fuscum* in Canada; (3) establish and compare the within-tree distribution (that is, along the length of the tree's bole) of *T. cinnamopterum* in red spruce with and without the presence of *T. fuscum*; (4) compare overall parasitism rates between New Brunswick and Nova Scotia; and (5) test for within-tree differences in parasitism rates of *Tetropium*.

Materials and Methods

Study Sites

I selected four mixed forest sites dominated by red spruce: two inside the exotic range of *T. fuscum* in Bedford, Nova Scotia (N44°44.27, W63°39.81) and two outside this range in the Acadian Research Forest near Minto, New Brunswick (N46°00.59, W66°21.82). Within each site I worked in a stand of approximately 300 m², selected so that stands at each site would be similar in topography, tree composition, and development stage. In each stand the canopy height was 12-18 m, with at least 60% red spruce and other common trees, including balsam fir (*Abies balsamea* (L.) Mill.), red maple (*Acer rubrum* L.), silver birch (*Betula papyrifera* Marsh.), and white pine (*Pinus strobus* L.). The Nova Scotia sites were approximately 20 km from the *T. fuscum* introduction epicentre (Smith & Hurley 2000; Rhainds *et al.* 2011). These pairs of stands were within a contiguous forest and separated by at least 1 km, divided by vehicle trails that are over 10 m wide with more than one kilometer between the nearest trees of each stand.

Red Spruce Selection

In each stand I selected 30 red spruce trees with diameters at breast height between 18-25 cm and heights between 10-17 m. Each selected spruce was at least 10 m from any other spruce meeting the minimum size criteria and from any gravel road. Five trees in each site were used for landing assessment (Appendix 1) and from the remaining 25 trees in each stand; I haphazardly selected 10 (New Brunswick) or 14 (Nova Scotia) trees per stand for a rearing study of the spruce-associated insect community. I allocated more sampling effort to the Nova Scotia sites in order to increase the power to detect interactions between *Tetropium* congeners within the exotic range.

Stressing and Felling Spruce

Trees were either felled or girdled (3-6 cm deep to the phloem and 3 cm wide) approximately 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.

The girdled trees were felled in late September 2013. I 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; I refer to these as base, base-middle, middle, middle-high, and apex bolts, respectively. The bolts were labeled and left on the forest floor until November 2013 to allow normal development and insect diapause. Two hundred and thirty nine bolts (one apex bolt could not be accounted for) were then collected and transported to the Atlantic Forestry Centre in Fredericton, New Brunswick and stored in a -2°C freezer pending insect rearing.

Rearing Insects

I focused on a red spruce-associated community (henceforth “focal community”) that I defined as including three feeding guilds: wood borers, parasitoids of wood borers, and predators. Wood borers include cerambycid beetles (longhorn beetles) and siricid wasps (woodwasps), and their corresponding solitary wasps of Ichneumonidae, Braconidae, and Ibaliidae make up the parasitoid guild. Predators consisted of clerid beetles. Other taxa present, but not considered in my analyses, included bark beetles and weevils (Curculionidae), fungivorous flies (Diptera), and flat bugs (Aradidae).

Spruce bolts were held for rearing in a controlled-environment quarantine facility (20-24°C, 16:8h photoperiod, with constant dehumidification) from January to May 2014

then transferred for three weeks to a 5°C fridge prior to being moved 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.

Each bolt was placed in an emergence cage made either from Lexan (cube shaped cage), or from a lidded plastic bucket attached to a funnel and collecting cup. Different cages were used to allow all 239 bolts to go through two emergence periods with simultaneous rearing. Lexan and bucket cages were mixed haphazardly with respect to province, site, and stress treatment, except that the widest bolts could not be accommodated in bucket cages. The rearing chambers were fitted with yellow sticky traps to catch escaping insects, but no target insects were trapped, suggesting that all organisms were collected within their rearing confines. Bolts were checked daily and emerging insects were collected every three days and placed in 70% ethanol in a -2°C freezer pending species identification. All emerged insects belonging to the focal guilds were identified to species and all *Tetropium* beetles and the parasitoid wasps, *Rhimphoctona macrocephala* (Provancher) (Hymenoptera: Ichneumonidae) and *Wroughtonia occidentalis* (Cresson) (Hymenoptera: Braconidae), were sexed. Identifications of insects were performed using Yanega (1996), Schiff *et al.* (2012), and reference collections at the Atlantic Forestry Centre of the Canadian Forest Service.

Data Analysis

Displacement for *T. cinnamopterum* was assessed using both abundance per tree section and density per m² (the latter was to ensure that within tree distributions were more precise, since bolts narrow toward the top of the tree). None of the *Tetropium*

records from the second emergence period were used in community data analysis, as all indications suggest they were the progeny of *Tetropium* that emerged and mated within the cages. All *Tetropium* that emerged in the second period exited bolts that had male(s) and female(s) that had overlapping time prior to collection and *Tetropium* readily mate upon exiting the tree (Juutinen 1955). All second-generation parasitoids were males, which suggest that an unfertilized female (Coyle & Gandhi 2012) had laid her eggs on these second-generation *Tetropium* larvae; these records were also ignored in further analyses. I used sites nested within provinces and interactions in all following comparisons; none proved to be significant and were subsequently removed to test main effects.

Insect Communities of Lab-Reared Red Spruce Bolts

I tested for the displacement of the native focal community in *T. fuscum*-attacked red spruce using a 2-way ANOVA, comparing insect abundance per tree inside and outside *T. fuscum*'s exotic range ("province" treatment) and between stress treatments. Species richness, Simpson's diversity, and abundances were tabulated, in each case excluding *T. fuscum*, as the intent was to test the effect of *T. fuscum* on the remaining community. Each metric was compared across provinces and stress treatments using 2-way ANOVAs. The collected focal community members were then placed in their feeding guilds of wood borers, parasitoids and predators.

Testing for *T. cinnamopterus* Displacement Within or From Red Spruce

I tested for the displacement of *T. cinnamopterus* by *T. fuscum* attack, in two ways. First, *T. cinnamopterus* might be displaced altogether from *T. fuscum*-attacked trees; I tested for such complete displacement by analyzing the number of *T.*

cinnamopterum per tree in a 1-way ANOVA to compare provinces (stress treatment is not included due to the fact that the girdled treatment did not yield any *T. cinnamopterum* or *T. fuscum*). Second, *T. cinnamopterum* might be displaced within an attacked tree to potentially sub-optimal larval habitat further up the tree's bole. I tested this hypothesis using ANCOVAs of *T. fuscum* and *T. cinnamopterum* abundance per bolt and density per m² as a function of province (discrete) and height (covariate) along with the nested effect of site. A significant "province" by "height" interaction effect for *T. cinnamopterum* would suggest within-tree displacement by *T. fuscum* in the region of their sympatry.

Tetropium Parasitism Rates

I tested for a difference in mean parasitism rates of *Tetropium* between provinces using a 1-way ANOVA. Parasitism tests were conducted on the combined attacks of *R. macrocephala* and *W. occidentalis*.

Results

Insect Communities of Lab-Reared Red Spruce Bolts

I 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 first rearing period a total of 85 adult *Tetropium* emerged, all from the felled treatment: 64 *T. cinnamopterum* and 21 *T. fuscum*. *Tetropium fuscum* were only collected from Nova Scotia trees, within the exotic range; *T. cinnamopterum* were collected from both inside (NS, 23 beetles) and outside (NB, 45 beetles) *T. fuscum*'s exotic range. 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).

Table 1 Presence and abundance of red spruce-associated insects that emerged from lab-reared bolts inside and outside of *Tetropium fuscum*'s exotic North American range. Family of species is denoted within the brackets (B) Braconidae, (Ce) Cerambycidae, (Cl) Cleridae, (Ib) Ibalidae, (Ic) Ichneumonidae, and (S) Siricidae.

*Denotes a single individual of collected species.

Organism grouping	Species	Outside exotic range (New Brunswick)	Inside exotic range (Nova Scotia)
Focal beetles	<i>Tetropium fuscum</i> (Ce)	X	21
	<i>Tetropium cinnamopterum</i> (Ce)	46	18
<i>Tetropium</i> parasitoids	<i>Rhimphoctona macrocephala</i> (Ic)	5	11
	<i>Wroughtonia occidentalis</i> (B)	16	21
Other woodborers	<i>Pogonocherus penicillatus</i> (Ce)	18	9
	<i>Monochamus scutellatus</i> (Ce)	2	2
	<i>Monochamus notatus</i> * (Ce)	0	1
	<i>Acanthocinus pusillus</i> * (Ce)	0	1
	<i>Xylotrechus undulatus</i> (Ce)	1	2
	<i>Urocerus albicornis</i> (S)	9	4
Woodwasp parasitoids	<i>Ibalia leucospoides</i> (Ib)	15	1
Clerid predators	<i>Thanasimus undatulus</i> (Cl)	8	10
	<i>Enoclerus nigripes</i> * (Cl)	0	1

Only two clerid beetles, and no individuals of either *T. fuscum* or its native congener *T. cinnamopterum*, emerged from any of the girdled trees (N = 24). Consequently, I focused solely on the felled spruce treatment (N = 24) in all subsequent analyses. Apical bolts yielded very few insects (0.08 ± 0.058 insects per tree; Figure 1) and never yielded *Tetropium* or its parasitoids. Therefore, I ignore the apical bolts in all analyses except for those of per-tree species richness and Simpson's diversity.

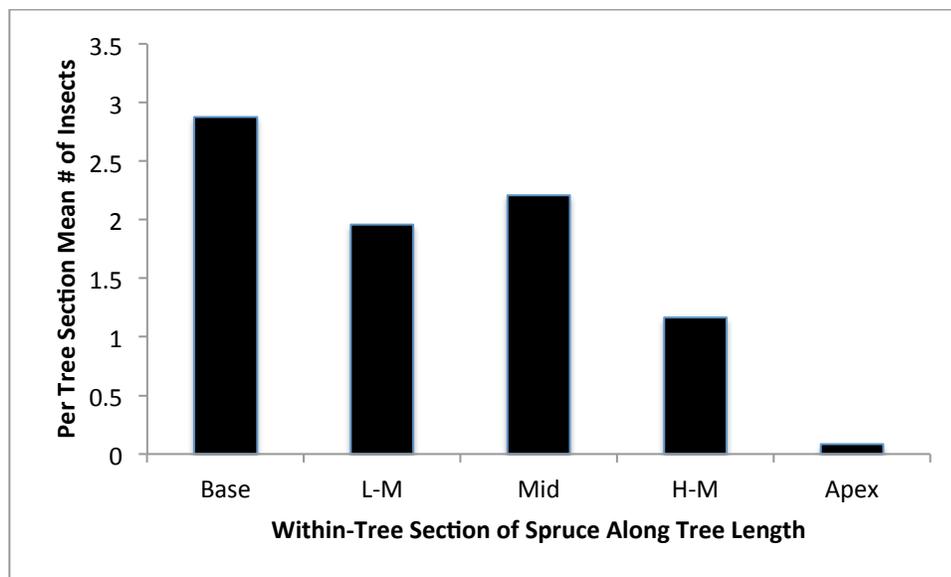


Figure 1. Mean abundance per tree section of felled red spruce focal community, excluding *Tetropium fuscum*, by tree section.

There was no significant difference between provinces in either total species richness (NB = 3.7 ± 0.54 ; NS = 3.1 ± 0.33 ; $P = 0.45$) or Simpson's diversity (NB = 0.41

± 0.09 ; NS = 0.64 ± 0.06 ; $P = 0.55$). However, total abundance (excluding *T. fuscum*) was higher outside the exotic zone of *T. fuscum* (NS) 12.0 ± 2.3 vs. 5.9 ± 0.876 (Table 2) and the effect was consistent when *T. fuscum* was included ($P < 0.01$). This effect remained for the difference in woodborer abundance outside (5.8 ± 1.6) vs. inside the exotic zone (2.0 ± 0.6); $P < 0.01$). There was no such difference for predators ($P = 0.82$) or parasitoids ($P = 0.27$).

Table 2. Abundance per tree of the red spruce associated insect community inside and outside the invasion zone, excluding *T. fuscum* and with the apical sections removed (analysis of deviance from generalized linear model).

	Df	Deviance	Residual df	Residual deviance	<i>P</i>
(Intercept)	--	--	95	116.30	--
Province	1	9.08	94	107.23	0.003
Section	3	5.95	91	101.28	0.114

Testing for *T. cinnamopterus* Displacement From Red Spruce

A total of 85 *Tetropium* beetles emerged from the felled spruce: 46 *Tetropium* from New Brunswick trees and 39 from Nova Scotia trees. The interaction between province and height was insignificant for *T. cinnamopterus*, suggesting its distribution along the length of the spruce bole was not affected by the presence of *T. fuscum* (Table 3). The native beetle, *T. cinnamopterus*, was much more abundant outside the exotic range of *T. fuscum* (4.6 ± 1.3 compared to 1.3 ± 0.3 per tree) and its density per m² of

bark was higher was well (Figure 2) but *T. cinnamopterum* density did not vary along the tree bole (below the apex) (Table 3; Figure 3).

Table 3. *Tetropium cinnamopterum* inside and outside the invasion zone, with the apical sections removed (analysis of deviance from generalized linear model). ^A is the abundance per felled tree and ^D is the density per m².

	Df	Deviance	Residual df	Residual deviance	<i>P</i>
^A (Intercept)	--	--	95	91.31	--
^A Province	1	11.03	94	80.28	<0.001
^A Section	3	5.59	91	74.68	0.133
^A Pro*Sec	3	6.07	88	68.62	0.108
^D (Intercept)	--	--	95	92.61	--
^D Province	1	10.48	94	82.12	0.001
^D Section	3	6.69	91	75.43	0.082
^D Pro*Sec	3	6.32	88	69.10	0.097

When both *T. fuscum* and *T. cinnamopterum* were combined to act as a single functional species, no statistical difference in abundance was detected between provinces (NB = 4.6 ± 1.3 vs. NS = 2.8 ± 0.5 per tree; $P = 0.15$ Table 4). A bimodal pattern in *Tetropium* abundance along the bole was marginally significant (Table 4; Figure 3) although no interaction between the province and section was present ($P = 0.20$). *Tetropium* congeners emerged from 36% of the NS trees; combined species attacks were 60% in NB and 86% in NS.

Table 4. *Tetropium* combined inside and outside the invasion zone, with the apical sections removed (analysis of deviance from generalized linear model).

^A is the abundance per felled tree and ^D is the density per m².

	Df	Deviance	Residual df	Residual deviance	<i>P</i>
^A (Intercept)	--	--	95	93.08	--
^A Province	1	2.07	94	91.01	0.150
^A Section	3	8.14	91	82.87	0.043
^D (Intercept)	--	--	95	97.76	--
^D Province	1	3.27	94	94.48	0.070
^D Section	3	7.46	91	87.03	0.059

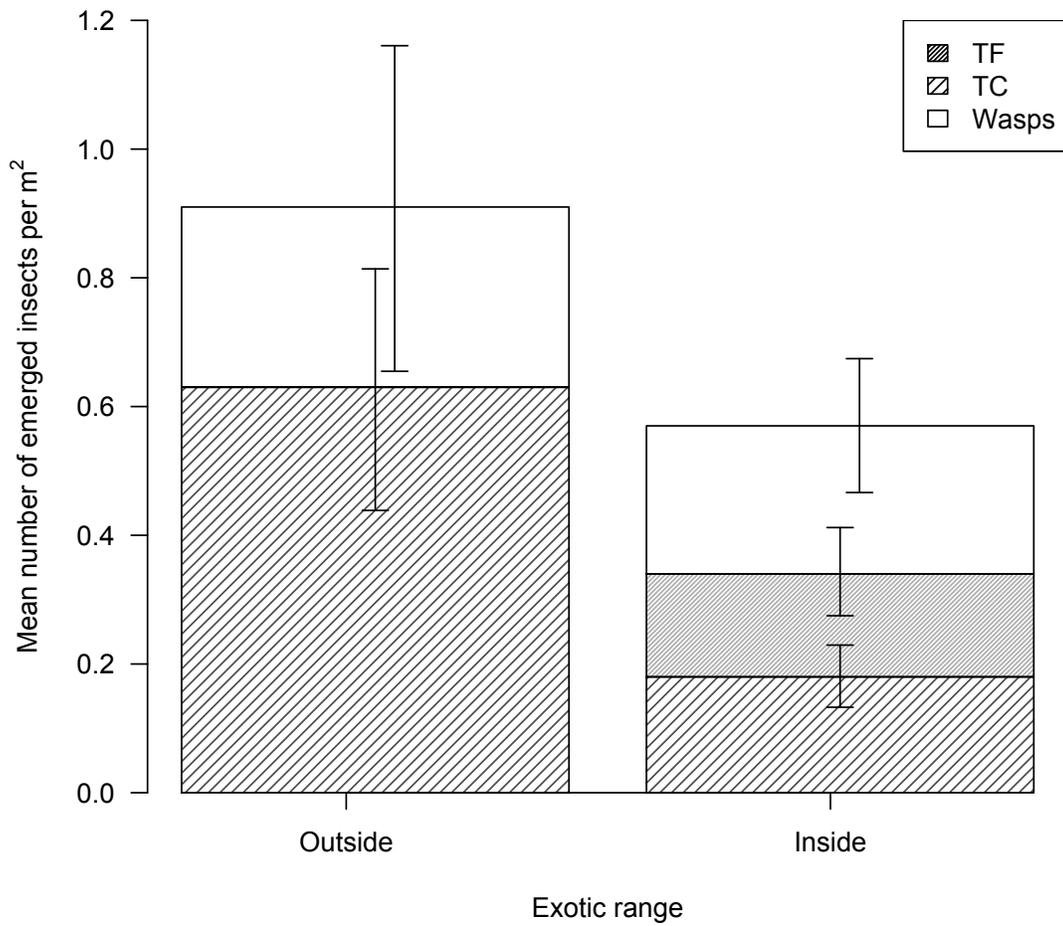


Figure 2. Mean \pm SE density per m² of adult *Tetropium cinnamopterum*, *T. fuscum*, and their parasitoid wasps that emerged from felled red spruce located outside or inside of *T. fuscum*'s exotic range in Canada.

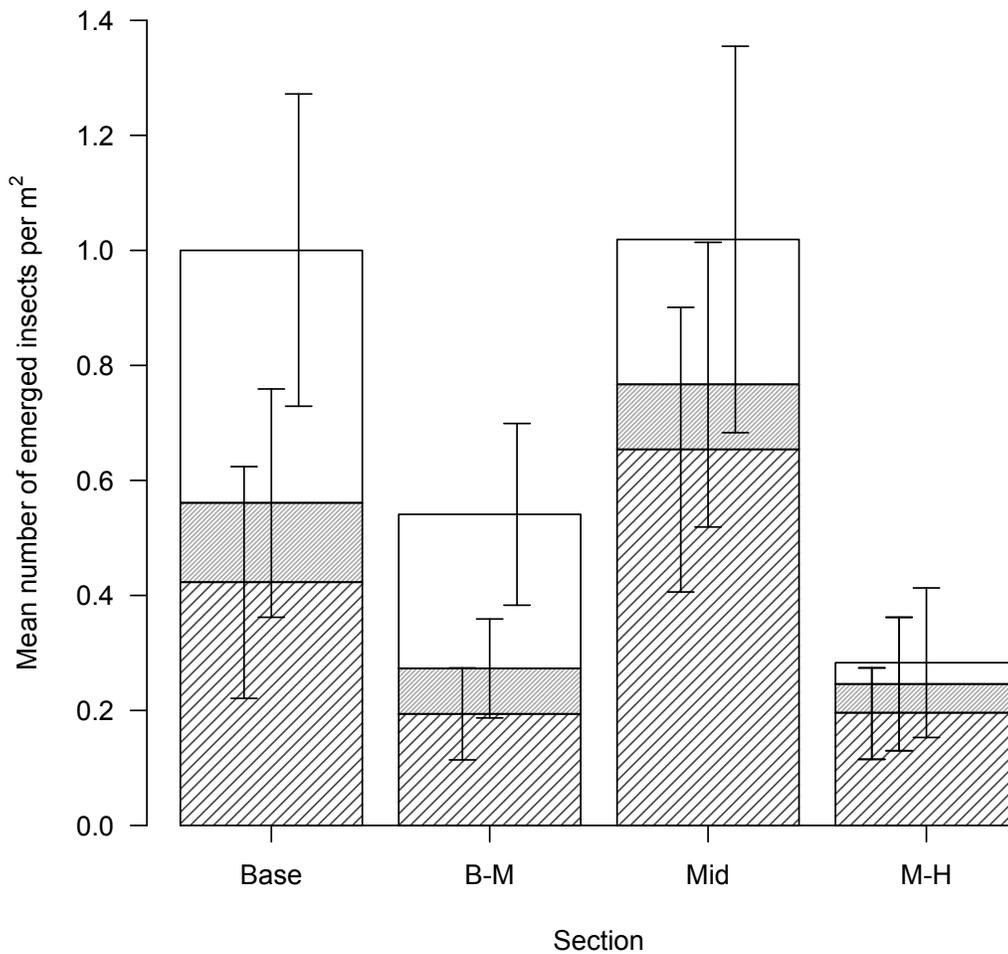


Figure 3. Mean \pm SE density per m² of adult *Tetropium cinnamopterum*, *T. fuscum*, and their parasitoid wasps that emerged from the base, base-middle (B-M), middle, and middle-high (M-H) sections along the bole of felled red spruce.

Tetropium Parasitism Rates

The overall parasitism rate of the native parasitoids, *R. macrocephala* and *W. occidentalis*, on both *Tetropium* species was 38%: 53 *Tetropium* of 138 were parasitized

(37 *W. occidentalis* and 16 *R. macrocephala*). Parasitism rates did not differ significantly between provinces (NB = 31% vs. NS = 44%; $P = 0.11$; Table 5). Parasitism was greatest lower on the bole with a range of 50% at the low-middle position to 11% at the middle-high position (Figure 4).

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

	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

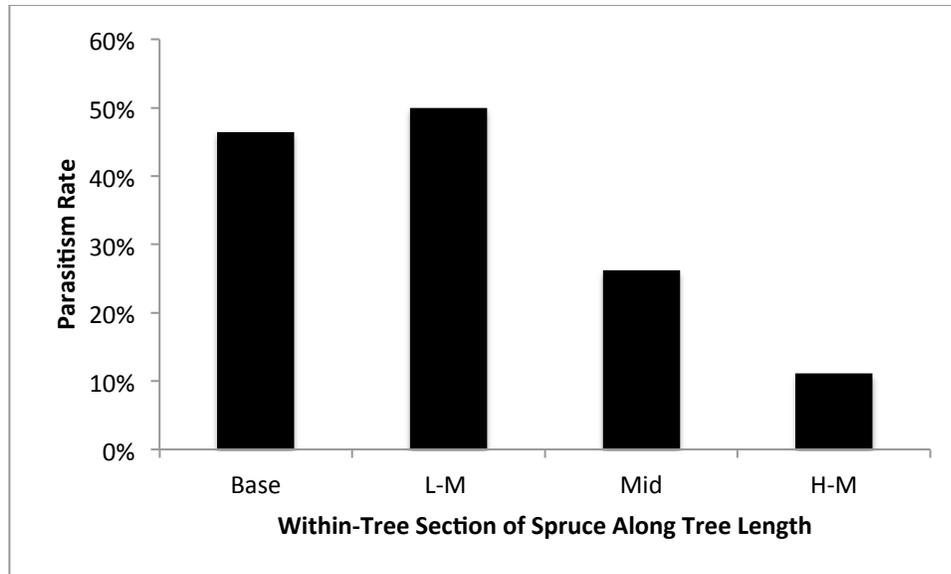


Figure 4. Parasitism rates by *Rhimphoctona macrocephala* and *Wroughtonia occidentalis* on *Tetropium* species that emerged from the base, base-middle (B-M), middle, and middle-high (M-H) sections along the bole of felled red spruce.

Discussion

Tetropium fuscum and *T. cinnamopterum* emerged exclusively from felled trees even though both species are able to develop on girdled and even apparently healthy red spruce (Flaherty *et al.* 2011) when they are lured there by semiochemical baits or introduced by caging adults. Although I never recovered emerging *Tetropium* from girdled trees, I know from sticky-band studies (Appendix 1) that beetles will land on such trees (we assume but cannot be certain that landing beetles were assessing the stressed spruce for oviposition sites as shown by Flaherty *et al.* (2013)). Developing in felled trees is congruent with the life history of *Tetropium* congeners in their native ranges: both are primarily univoltine, phloem-feeders of stressed or freshly felled spruce (*Picea*) (Juutinen

1955; Linsley 1962; Flaherty *et al.* 2013b). The focal communities, regardless of invasion zone, were similar for species richness and Simpson's diversity, and aside from singletons, *T. fuscum* was the only varying community member (Table 1). The similar communities of these felled spruce and documented life history traits of *Tetropium* allowed comparisons to examine for potential shifts or displacements of native insects by *T. fuscum*.

Tetropium fuscum has been slowly progressing westward from its introduction site in Halifax, Nova Scotia (Smith & Hurley 2000) and one of the factors assumed to aid this expansion is a slight phenological advantage of approximately two weeks earlier in adult emergence compared to the native congener (Rhains *et al.* 2010). Adult *Tetropium* are sexually reproductive and do not feed upon emergence from their natal trees (Juutinen 1955). The emergence of *T. fuscum* allows a two-week flight advantage and potential successive generations on the same tree (Juutinen 1955; Linsley 1962), and results in mate finding being a primary limitation for range expansion at the periphery (Rhains *et al.* 2011; 2015). Advantages in oviposition are crucial for overlapping wood borers; Schlyter and Anderbrant (1993) showed that congeneric *Ips* exhibit niche partitioning, resulting in the less competitive species being forced higher in the bole. *Ips typographus*, the larger congener, was more competitive at high densities and displaced the smaller, *I. duplicatus*. Despite *T. fuscum* and *T. cinnamopterum* having broadly overlapping body size ranges (Juutinen 1955; Linsley 1962; Yanega 1996; Flaherty *et al.* 2011), phenological advantages of *T. fuscum* (Rhains *et al.* 2010) and an ability to inhabit more vigorous spruce (Flaherty *et al.* 2011), could contribute to local displacement.

The total abundance of *Tetropium* emerging from my bolts (85 beetles) appears to be low compared to similar studies that have used semiochemical trapping (where individuals are overwhelmingly attracted to bait lures; Sweeney *et al.* 2004), and in which sites can yield tens of beetles per flight-intercept trap (i.e. Rhainds *et al.* 2010). Flaherty *et al.* (2013a) investigated pre-alighting host preferences on 20 unbaited red spruce; traps on the artificially girdled spruce captured significantly more *T. fuscum* and *T. cinnamopterum* than the healthy treatment. Unfortunately it is unknown whether the *Tetropium* developed successfully on any of the 20 unbaited (Flaherty *et al.* 2013a) trees with traps on the trunk because there was not a subsequent rearing period. Despite the choices to assess (Flaherty *et al.* 2013a) and capabilities to develop (Flaherty *et al.* 2011; Flaherty *et al.* 2013b) on healthy spruce, the *Tetropium* congeners are commonly found in the early spruce decay cycle stages, where needles remain present, in their native ranges (Linsley 1962; Juutinen 1955; Lee *et al.* 2014). *Tetropium* in my study were unlikely to be at the carrying capacity within the stressed spruce; *T. fuscum* can lay over 10 eggs per 10 cm² of bark on stressed red spruce (Flaherty *et al.* 2013a) and outbreak numbers of other cerambycids such as the red oak borer, *Enaphalodes rufulus* (Haldeman), can yield hundreds of individuals per tree (Fierke *et al.* 2005). Nevertheless, the significantly reduced number of *T. cinnamopterum* per tree in sympatry with *T. fuscum* (Figure 3) suggests that the congeners are competing within felled red spruce. Although I did not directly test which type of congeneric competition was occurring, the low overall emergence rate suggests that feeding does not limit the phloem resource enough to make any conclusive statements about the type of competition occurring. Competition between *Tetropium* species is not likely based on exhaustion of

available resources as shown in outbreaking *Ips* bark beetles (Schlyter & Anderbrant 1993). Interference competition may be taking place in the form of mistaken identity for conspecifics: allopatric congeners often have greater negative consequences related to reproductive interference than resource competition (Hochkirch *et al.* 2007). If congeners are able to mate and reproduce successfully, their young often have intermediate characters that are sub-optimally desirable for mating as adults (Höbel & Gerhardt 2003). However, no field surveys have been conducted for hybrid *Tetropium*.

Phloem is a highly competitive resource for developing wood boring larvae (Hanks *et al.* 1999) especially when the tree is felled and the vascular tissues can no longer fully circulate. Congener co-habitation has been shown for other wood boring insects (Davis & Hofstetter 2009; Ryan *et al.* 2011), although displacement has been difficult to determine unless there are epidemic levels of attacking insects (Schlyter & Anderbrant 1993). Vertical partitioning has been shown to occur for wood boring beetle communities at the forest level with respect to canopy height (Wermelinger *et al.* 2007) and at a smaller scale within trees (Schlyter & Anderbrant 1993; Abrahamsson & Lindbladh 2006; Ryan *et al.* 2012). With *Tetropium* species only emerging from felled trees, vertical partitioning is a misnomer, although the phloem resources do decrease in volume from the base to apex in the same fashion as in standing trees (Li & Weiskittel 2011). Combining *Tetropium* species to act as functionally one entity, there was no difference in abundance or density per m² between the provinces of origin (Table 4), suggesting there is some form of displacement by the invasive beetles. Although, it is unclear if this suggests complete eviction of the native, *T. cinnamopterum* or if it will

force partitioning of larvae developing regions to different levels along the bole in high density situations, similar to the findings of Schlyter and Anderbrant (1993).

Both *Tetropium* are known hosts for the native North America parasitoid wasps, *R. macrocephala* and *W. occidentalis* (Flaherty *et al.* 2011). My investigation of parasitism does not include any potential egg parasitoids. Oviposition occurs following the May-August adult emergence, and beetles were in larval stages prior to my lab rearing in the following Winter/Spring (Juutinen 1955; Rhainds *et al.* 2010). Parasitism rates of the combined congeners with *T. fuscum* present were slightly but not significantly higher at 44.44% compared to 31.82% with exclusively *T. cinnamopterum* (Figure 7). A limitation of this study was the inability to distinguish which *Tetropium* species either of the parasitoids used as a host. I was unable to retrieve even 5% of the pupal exuvia and furthermore, the remains were in such poor condition that *Tetropium* species determination could not be done.

The greater parasitism rate with the exotic *Tetropium* present may work in conjunction with an Allee effect, potentially lowering mate encounters at the periphery with low population densities (Rhainds *et al.* 2015). This could be a factor for the slow exotic spread of *T. fuscum* compared to prolific invasive expansions of wood borers like the emerald ash borer (Muirhead *et al.* 2006). Red spruce populations along the exotic range periphery may also have greater levels of overall health resulting in a more prolonged development of larval beetles. If the females select vigorous trees for oviposition sites (Flaherty *et al.* 2011), this biological pressure may extend development time; delaying adult emergence and increasing the potential for woodpecker predation and may result in a lag phase in *T. fuscum*'s invasion (Crooks 2005). Three other facets of

the insect community may also help dampen the westward expansion of *T. fuscum*. Both *Tetropium* species are capable of consecutive generations within the same stressed tree (Juutinen 1955; Flaherty *et al.* 2011), they also occur sympatrically in the same spruce relying on similar host tree volatile cues (Sweeney *et al.* 2004; Silk *et al.* 2007; Flaherty *et al.* 2011) providing a greater resource for the parasitoids, and finally unfertilized female wasps are capable of attacking and laying an egg of a haploid male on the subcortical larvae (Coyle & Gandhi 2012). Host chemical cues and haploid-wasp reproductive capabilities may help explain the significantly greater parasitism closer to the base of the felled red spruce. The two base sections had 46% and 50% parasitism, while the two sections closer to the apex that had emerging *Tetropium* had 26% and 11% parasitism (Figure 8). The long distance volatiles (Sweeney *et al.* 2004) and greater foraging area due to the base of the trunk having a greater diameter (Li & Weiskittel 2011) could allow the wasps a greater chance of finding a *Tetropium* host while a lower amount of flight time will reduce potential predation by spiders and insectivorous birds.

The competition for valuable phloem resources of felled red spruce is suggested between the native, *T. cinnamopterum*, and the exotic, *T. fuscum*, although with this sample size of 85 *Tetropium* it is not definitive that *T. fuscum* displaces any native wood borers to suboptimal habitat within the tree or if it could completely exclude them. The approximately two weeks advanced phenological window of the exotic may provide a competitive advantage when mate encounters are not a limiting factor (Rhains *et al.* 2010). This expansion of larval host resources appears to slightly benefit the native parasitoid wasps, although it is unclear what role these organisms play in the slow rate of expansion of the invasion. It is unclear if the rate of westward expansion has been a

consistent spread or if like many invasions experienced various lags in population growth (Crooks 2005). Disturbed ecosystems tend to lead to increased invasion over time (Crooks 2005) and in September 2003 Atlantic Canada was ravaged by a category 2 hurricane, Juan, which destroyed 90% of the mature growth within Point Pleasant Park, the *T. fuscum* introduction site (Environment Canada 2013). Potential reduction of red spruce vigour across the Atlantic Provinces may have relaxed the biotic pressures within the trees as Flaherty *et al.* (2011) showed that apparently healthy spruce slow larval development.

I found that *T. fuscum* and *T. cinnamopterum* in Atlantic Canada colonized felled spruce much more so than mechanically girdled red spruce, potentially providing the native parasitoids with a larger temporal window to attack their host beetles. The extensive overlap in biology of the *Tetropium* congeners suggests that within the invaded zone they act as a single functional species relative to other wood boring and parasitoid insects.

Reference

- (CFIA) Canadian Food Inspection Agency. 2007. Brown spruce longhorn beetle infested places order (second revision). <http://www.inspection.gc.ca/plants/plant-protection/insects/brown-spruce-longhorn-beetle/order/eng/1333085341951/1333085519708>
- (CFIA) Canadian Food Inspection Agency. 2015. 2014 Brown Spruce Longhorn Beetle Survey. 5 pp.

- Colautti, R. I, and H. J. MacIsaac. 2004. A neutral terminology to define “invasive” species. *Diversity and Distributions* 10: 135-141.
- Coleman, T. W., A. D. Graves, M. Hoddle, Z. Heath, Y. Chen, M. L. Flint, and S. J. Seybold. 2012. Forest stand composition and impacts associated with *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) and *Agrilus coaxlis* Waterhouse in oak woodlands. *Forest Ecology and Management* 276: 104-117.
- Coyle, D. R, and K. J. K. Gandhi. 2012. The ecology, behavior, and biological control potential of Hymenopteran parasitoids of woodwasps (Hymenoptera: Siricidae) in North America. *Environmental Entomology* 41: 731-749.
- Crooks, J. A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12: 316-329.
- Davis, T. S. and R. W. Hofstetter. 2009. Effects of gallery density and species ratio on the fitness and fecundity of two sympatric bark beetles (Coleoptera: Curculionidae). *Environmental Entomology* 38: 639-650.
- Eckenwalder, J. E. 2009. Conifers of the World: Complete Reference. Portland, U.S.A.: Timber Press Inc. 720 pp.
- Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Reprinted in 2000. Chicago, U.S.A.: The University of Chicago Press. 181 pp.
- Environment Canada. 2013. Hurricanes and tropical storms: Hazards and impacts. www.ec.gc.ca/ouragans-hurricanes/default.asp?lang=En&n=502E94BA-1 (Accessed May 2015).
- Fierke, M. K., D. L. Kinney, V.B. Salisbury, D.J. Crook, and F. M. Stephen. 2005. Development and comparison of intensive and extensive sampling methods and

- preliminary within-tree population estimates of red oak borer (Coleoptera: Cerambycidae) in the Ozark Mountains of Arkansas. *Environmental Entomology* 34: 184-192.
- Flaherty, L., J. Régnière, and J. Sweeney. 2012. Number of instars and sexual dimorphism of *Tetropium fuscum* (Coleoptera: Cerambycidae) larvae determined by maximum likelihood. *The Canadian Entomologist* 144: 720-726.
- Flaherty, L., J. D. Sweeney, D. Pureswaran, and D.T. Quiring. 2011. Influence of the host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 40: 1200-1209.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. 2013a. Preference of an exotic wood borer for stressed trees is more attributable to pre-alighting than post-alighting behaviour. *Ecological Entomology* 38: 546-552.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. 2013b. Evaluating seasonal variation in bottom-up and top-down forces and their impact on an exotic wood borer, *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 42: 957-966.
- Haack, R. A. 2006. Exotic bark- and woodboring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* 36: 269-288.
- Haavik L. J, M. L. Flint, T. W. Coleman, R. C. Venette, and S. J. Seybold. 2015. Goldspotted oak borer effects on tree health and colonization patterns at six newly-established sites. *Agricultural and Forest Entomology* 17: 146-157.
- Höbel, G. and H. C. Gerhardt. 2003. Reproductive character displacement in the acoustic communication system of green tree frogs (*Hyla cinerea*). *Evolution* 57: 894-904.

- Hochkirch, A., J. Gröning, and A. Bucker. 2007. Sympatry with the devil: reproductive interference could hamper species coexistence. *Journal of Animal Ecology* 76: 633-642.
- Holzmueller, E. J. and S. Jose. 2011. Invasion success of cogongrass, an alien C₄ perennial grass, in the southeastern United States: exploration of the ecological basis. *Biological Invasions* 13: 435-442.
- Juutinen, P. 1955. Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium Kirby*) in Finnland. *Acta Entologica Fennica* 11: 1-112. (English Translation via Translation Bureau of Public Works and Government Services Canada)
- Kenna, M. A. 2002. *Anoplophora glabripennis* (Coleoptera: Cerambycidae) fecundity and longevity under laboratory conditions: comparison of populations from New York and Illinois on *Acer saccharum*. *Environmental Entomology* 31: 490-498.
- Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199-204.
- Lantschner, M. V., J. M. Villacide, J. R. Garnas, P. Croft, A. J. Carnegie, A. M. Liebhold, and J. C. Corley. 2014. Temperature explains variable spread rates of the invasive woodwasp *Sirex noctilio* in the southern Hemisphere. *Biological Invasions* 16: 329-339.
- Lee, S., J. R. Spence, and D. W. Langor. 2014. Succession of saproxylic beetles associated with decomposition of boreal white spruce logs. *Agricultural and Forest Entomology* 16: 391-405.
- Lessard, J., J. A. Fordyce, N. J. Gotelli, and N. J. Sanders. 2009. Invasive ants alter the phylogenetic structure of ant communities. *Ecology* 90: 2664-2669.

- Levin, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852-854.
- Li, R. and A. R. Weiskittel. 2011. Estimating and predicting bark thickness for seven conifer species in the Acadian Region of North America using a mixed-effect modeling approach: comparison of model forms and subsampling strategies. *European Journal of Forest Research* 130: 219-233.
- Linsley, E. G. 1962. The Cerambycidae of North America part 2. Los Angeles. U.S.A.: University of California Press. 102 pp.
- Llewelyn, J., B. L. Phillips, G. P. Brown, L. Schwarzkopf, R.A. Alford, and R. Shine. 2011. Adaptation or preadaptation: why are keelback snakes (*Tropidonophis mairii*) less vulnerable to invasive cane toads (*Bufo marinus*) than are other Australian snakes? *Evolutionary Ecology* 25: 13-24.
- Muirhead, J. R., B. Leung, C. van Overdijk, D. W. Kelly, K. Nandakumar, K. R. Marchant, and H. J. MacIsaac. 2006. Modeling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions* 12: 71-79.
- (NRC) Natural Resources Canada. 2015. Emerald ash borer.
<http://www.nrcan.gc.ca/forests/insects-diseases/13377> (Accessed June 2015)
- Patel, S. 2012. Threats, management and envisaged utilizations of aquatic weed *Eichhornia crassipes*: an overview. *Reviews in Environmental Science and Biotechnology* 11: 249-259.
- Rhainds, M., S. B. Heard, C. Hughes, W. MacKinnon, K. Porter, J. Sweeney, P. Silk, I. Demerchant, S. McLean, and G. Brodersen. 2015. Evidence for mate-encounter Allee

- effect in an invasive longhorn beetle (Coleoptera: Cerambycidae). *Ecological Entomology* doi: 10.1111/een.12255.
- Rhains, M., S. B. Heard, J. D. Sweeney, P. Silk, and L. Flaherty. 2010. Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 39: 1794-1800.
- Rhains, M., W. C. MacKinnon, K. B. Porter, J. D. Sweeney, and P. J. Silk. 2011. Evidence for limited spatial spread in an exotic longhorn beetle *Tetropium fuscum* (Coleoptera: Cerambycidae). *Journal of Economic Entomology* 104: 1928-1933.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93-107.
- Ryan, K., P. de Groot, and S. M. Smith. 2012. Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. *Agricultural and Forest Entomology* 14: 187-195.
- Schiff, N. M., H. Goulet, D. R. Smith, C. Boudreault, A. D. Wilson, and B. E. Scheffler. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. *Canadian Journal of Arthropod Identification* 21: 1-305.
- Schlyter, F. and O. Anderbrant. 1993. Competition and niche separation between two bark beetles: existence and mechanism. *Oikos* 68: 437-447.
- Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170-176.
- Silk, P. J., J. Sweeney, J. Wu, J. Price, J. M. Gutowski, and E. G. Kettela. 2007. Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium*

- cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). *Naturwissenschaften* 94: 697-701.
- Smith, G. and L. M. Humble. 2000. The brown spruce longhorn beetle. Exotic Forestry Pest Advisory 5. Natural Resources Canada, Canadian Forest Service, Ottawa, Canada.
- Smith, G. and J. E. Hurley. 2000. First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin* 54: 540.
- Sweeney, J., P. de Groot, L. MacDonald, S. Smith, C. Cocquempot, M. Kenis, and J. Gutowski. 2004. Host volatile attractants for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* (L.) and other longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 33: 844-854.
- Williamson, M. and A. Fitter. 1996. The varying success of invaders. *Ecology* 77: 1661-1666.
- Yanega, D. 1996. Field Guide to Northeastern Longhorned Beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 6. Champaign, U.S.A: Illinois Department of Natural Resources. 184 pp.

CHAPTER 3 – GENERAL DISCUSSION

Using comparisons of wood boring communities within and outside the exotic range of *T. fuscum*, my research demonstrates that *T. fuscum* favoured felled over girdled spruce. I also establish the within tree distribution for *T. fuscum* and the native congener, *T. cinnamopterum* in felled red spruce, *Picea rubens* (Sarg.) in Atlantic Canada. I assessed species diversity and abundance to determine whether there were changes in colonizers of stressed spruce in the presence of *T. fuscum*.

My results show that both *Tetropium* species exclusively emerged from felled red spruce trees; this does not oppose their habits in their native ranges, where they attack stressed and freshly felled spruce (Linsley 1962; Juutinen 1955; Flaherty *et al.* 2013). *Tetropium* species are part of the early decay process of conifers, when the bark is still tight and fully intact (Saint-Germain *et al.* 2007; Lee *et al.* 2014), allowing multiple consecutive generations on the same tree (Linsley 1962; Juutinen 1955). These primarily univoltine phloem-feeders are early colonizers of stressed conifers and play a role in tree decay progression by consuming the vascular tissue. Saint-Germain *et al.* (2007) showed early decay stages of spruce are characteristically attacked by longhorn (Cerambycidae) and bark beetles (Scolytinae); consequently, the introduction of an exotic cerambycid poses the potential for niche overlap, competition, and displacement of native species. Congeneric representation by *T. cinnamopterum* in the native community increases the likelihood of species interactions.

In particular, my research findings are:

1. *Tetropium fuscum* disproportionately attacked felled compared to girdled red spruce.

2. *Tetropium cinnamopterum* had a significantly lower density and abundance in the presence of *T. fuscum*.
3. Total *Tetropium* density and abundances did not differ relative to *T. fuscum*'s exotic range.
4. The presence of *T. fuscum* did not result in a shift of within tree distribution of *T. cinnamopterum* in felled spruce.
5. Parasitism rates were slightly higher with the presence of *T. fuscum* although, statistically similar relative to *T. fuscum*'s exotic range.

Tetropium cinnamopterum is not a pest species in the coniferous forests of northern North America and due to its cryptic wood boring life history there is not a wealth of biological data for this species (Linsley 1962; Yanega 1996). Previous work by Schlyter and Anderbrant (1993) on bark beetle congener competition shows that there is clear partitioning in within tree distribution of bark beetles at high population densities. Elucidation of distributional patterns within red spruce for both the native and exotic are imperative to demonstrate if congener competition occurs. Both species of *Tetropium* emerged from felled trees, and their abundances per tree and within tree distribution were statistically similar, suggesting that niche overlap is even more synchronous than initially believed when *T. fuscum* was observed to be attacking healthy trees in Nova Scotia (Smith & Hurley 2000) and was shown to complete development on apparently healthy red spruce (Flaherty *et al.* 2011).

Niche overlap extends beyond host vigour and within tree distribution up the food chain where both *Tetropium* species are suitable hosts for parasitoid wasps, *Rhimphoctona macrocephala* (Provancher) (Hymenoptera: Ichneumonidae) and

Wroughtonia occidentalis (Cresson) (Hymenoptera: Braconidae) (Flaherty *et al.* 2011). Unfortunately this research was limited in the inability to determine the host *Tetropium* species for each individual parasitoid wasp. Within the exotic range with both *Tetropium* species there was a non-significant but higher parasitism rate compared to with exclusively *T. cinnamopterum*. Higher parasitism rates and possible increase in parasitoid densities with both *Tetropium* species present may take part in the relatively slow range expansion of *T. fuscum*. In addition, the presence of *T. fuscum* offers the parasitoids an expanded temporal reproductive window due to the two-week earlier adult emergence by *T. fuscum* (Rhainds 2010). It is unknown which larval instars parasitoid wasps specifically target or if there is a host size constraint, although other wood-boring parasitoid species partition primarily on bark thickness (Paine *et al.* 2000; Abell *et al.* 2012). It appears that the range expansion westward of *T. fuscum*, regardless of how fast or far they travel, will face biological resistance from the native community in the form of *R. macrocephala* and *W. occidentalis* that have host resources of native *T. cinnamopterum* in a variety of other trees in the mixed and coniferous forests of Canada.

While *T. cinnamopterum* may be displaced by the exotic *T. fuscum* from red spruce in Atlantic Canada, this species has a much broader host range, developing in tree species of *Abies* and *Pinus* not just *Picea* like its exotic relative (Craighead 1923; Linsley 1962; Yanega 1996). Regardless of the extent of *T. cinnamopterum* displacement locally from red spruce, they will not be extirpated from that environment with other viable hosts to develop on sympatrically. *Tetropium cinnamopterum* has a geographical range spanning northern North America and can develop on at least seven host conifer species (Craighead 1923; Gardiner 1957; Linsley 1962; Yanega 1996). Therefore *T. fuscum*

appears to have a successful invasion into North American red spruce, although it is unclear where in the invasion continuum other spruce species might fall as suitable hosts for *T. fuscum* to displace *T. cinnamopterum*.

Clarity in the language of invasion biology is somewhat obscure in the literature and terms get used haphazardly. Without a clearly defined sliding scale of intensity it can be confusing to have a reliable idea of how invasive an introduced species can be. For example, exotic species are synonymous with alien, non-native, and nonindigenous (Richardson *et al.* 2000), although I perceive implicit levels of positivity; nonindigenous and non-native being neutral, straddled by the negative alien and positive exotic. One would hope to go on an exotic vacation, as “exotic” is something originating from another country as well as having a strange or bizarre beauty (Collins 2004). Alien too is being foreign or unfamiliar with its environment although seventh on Collins English Dictionary’s (2004) list of definitions as repugnant. Richardson *et al.* (2000) suggest the invasion continuum of introduction, naturalization, and invasion. Invasion is overcoming a major geographical barrier, and naturalization is overcoming novel environmental barriers to achieve rates of reproduction high enough to result in population growth. Invasion is when the most prolific of these naturalized species achieve a greater overall survival rate that allows for expansion in the novel environment overcoming dispersal and biotic barriers. Naturalization appears to be a term primarily used in botany (Richardson *et al.* 2000; Gallagher *et al.* 2015) compared to zoological pests (Pyšek *et al.* 2010) for which a rapid progression is implied from pest to invasive (Reed *et al.* 2012). Richardson and colleagues’ (2000) continuum provides a basic framework although there are gaps translating to the animal kingdom and it is proposed that invasions are based on

biogeography and demographics without any connotation of their economical and environmental impacts, which unfortunately is often the reason for a particular organism's invasion ecology to be studied (Muirhead *et al.* 2006; Sweeney *et al.* 2006; Flaherty *et al.* 2011). I perceive *Tetropium fuscum* as being on the cusp of naturalized and invasive on the invasion continuum. *T. fuscum* has been able to advance westward but the combination of biological resistance and Allee effect limit the species at the periphery of the exotic range.

T. fuscum invasion biology has important implications for the future of global forestry pests, being the most successful non-native cerambycid in terms of exotic range in Canada (Grebennikov *et al.* 2010; CFIA 2015). Wood boring genera in Cerambycidae and other families, such as *Agrilus*, *Phoracantha*, and *Xyleborus*, have had multiple species become invasive pests in North America (Haack, 2006; Grebennikov *et al.* 2010; Coleman *et al.* 2012). *Tetropium*, as well, possesses characteristics to allow for more than *T. fuscum* and *T. gracilicorne* Reitter (EPPO 2005) to become problematic through the movement of wood-based goods. *Agrilus* shows stark differences in congener invasion rate (Muirhead *et al.* 2006; Coleman *et al.* 2012) and with so little information it is hard to estimate the range of intensity for *Tetropium* species in their role as forest pests. Fewer than half of the known *Tetropium* species even have host records (Appendix B) and all have drab colouration that ranges from a chestnut brown to black (Linsley 1962; Yanega 1996; pers. ob. Atlantic Forestry Centre Insect Collection). On bark, these impeccably camouflaged beetles oviposit in the furrows and under the scales of conifer bark where their first instar larvae burrow into the phloem to continue development (Linsley 1962). Without any signs from oviposition on trees of initial colonization and the cryptic

colourations of adults prevent detection even within areas of consistent forestry research (Smith & Hurley 2000). Thus, *Tetropium* species pose an interesting taxonomic case where the generic lack of charisma and obvious visual diversity allow for potential invasions.

The research I have conducted has contributed additional basic natural history knowledge of *Tetropium fuscum*, *T. cinnamopterum*, their parasitoids, and other wood borers of red spruce. Conservation is impossible without basic natural history knowledge of the target pests and organisms of concern (Dayton 2003). My research suggests that the native, *T. cinnamopterum*, is being displaced from red spruce trees in Atlantic Canada by the exotic, *T. fuscum*, although the type of competition causing this displacement was not resolved.

Reference

- Abell, K. J., J. J. Duan, L. Bauer, J. P. Lelito, and R. G. van Driesche. 2012. The effect of bark thickness on host partitioning between *Tetrastichus planipennisi* (Hymen: Eulophidae) and *Atanycolus* spp. (Hymen: Braconidae), two parasitoids of emerald ash borer (Coleop: Buprestidae). *Biological Control* 63: 320-325.
- (CFIA) Canadian Food Inspection Agency. 2015. 2014 Brown Spruce Longhorn Beetle Survey. 5 pp.
- Coleman, T. W., A. D. Graves, M. Hoddle, Z. Heath, Y. Chen, M. L. Flint, and S. J. Seybold. 2012. Forest stand composition and impacts associated with *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) and *Agrilus coaxlis* Waterhouse in oak woodlands. *Forest Ecology and Management* 276: 104-117.

- Collins. 2004. Collins English Dictionary: Canadian Edition. Glasgow, Scotland: Harper Collins Publishers. 1911 pp.
- Craighead, F. C. 1923. North American Cerambycid Larvae. Department of Agriculture Bulletin No. 27. Ottawa, Canada: Dominion of Canada. 150 pp.
- Dayton, P. K. 2003. The importance of the natural sciences to conservation. *The American Naturalist* 162: 1-13.
- (EPPO) European and Mediterranean Plant Protection Organization. 2005. *Tetropium gracilicorne*. *EPPO Bulletin* 35: 402–405.
- Flaherty, L., J. D. Sweeney, D. Pureswaran, and D.T. Quiring. 2011. Influence of the host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 40: 1200-1209.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. 2013. Evaluating seasonal variation in bottom-up and top-down forces and their impact on an exotic wood borer, *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 42: 957-966.
- Gallagher, R. V., R. P. Randall, and M. R. Leishman. 2015. Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. *Conservation Biology* 29: 360-369.
- Gardiner, L. M. 1957. Deterioration of fire-killed pine in Ontario and the casual wood-boring beetles. *The Canadian Entomologist* 89: 241-263.
- Grebennikov, V. V., B. D. Gill, and R. Vigneault. 2010. *Trichoferus campestris* (Faldermann) (Coleoptera: Cerambycidae), an Asian wood-boring beetle recorded in North America. *The Coleopterists Bulletin* 64: 13-20.

- Juutinen, P. 1955. Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium Kirby*) in Finnland. *Acta Entologica Fennica* 11: 1-112. (English Translation via Translation Bureau of Public Works and Government Services Canada)
- Lee, S., J. R. Spence, and D. W. Langor. 2014. Succession of saproxylic beetles associated with decomposition of boreal white spruce logs. *Agricultural and Forest Entomology* 16: 391-405.
- Linsley, E. G. 1962. The Cerambycidae of North America part 2. Los Angeles. U.S.A.: University of California Press. 102 pp.
- Muirhead, J. R., B. Leung, C. van Overdijk, D. W. Kelly, K. Nandakumar, K. R. Marchant, and H. J. MacIsaac. 2006. Modeling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions* 12: 71-79.
- Paine, T. D., E. O. Paine, L. M. Hanks, and J. G. Millar. 2000. Resource partitioning among parasitoids (Hymenoptera: Braconidae) of *Phoracantha semipunctata* in their native range. *Biological Control* 19: 223-231.
- Pyšek, P., S. Bacher, M. Chytrý, V. Jarošík, J. Wild, L. Celesti-Grappo, N. Gassó, M. Kenis, P. W. Lambdon, W. Nentwig, J. Pergl, A. Rogues, J. Sádlo, W. Solarz, M. Vilà, and P. E. Hulme. 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitat by alien plants, insects and vertebrates. *Global Ecology and Biogeography* 19: 317-331.
- Reed, N. R., J. D. Willson, G. H. Rodda, and M. E. Dorcas. 2012. Ecological correlates of invasion impact for Burmese pythons in Florida. *Integrative Zoology* 7:254-270.

- Rhainds, M., S. B. Heard, J. D. Sweeney, P. Silk, and L. Flaherty. 2010. Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 39: 1794-1800.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93-107.
- Saint-Germain, M., P. Drapeau, and C. M. Buddle. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography* 30: 737-748.
- Schlyter, F. and O. Anderbrant. 1993. Competition and niche separation between two bark beetles: existence and mechanism. *Oikos* 68: 437-447.
- Smith, G. and J. E. Hurley. 2000. First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin* 54: 540.
- Sweeney, J., J. M. Gutowski, J. Price, and P. de Groot. 2006. Effect of semiochemical release rate, killing agent, and trap design on detection of *Tetropium fuscum* (F.) and other longhorn beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 35: 645-654.
- Yanega, D. 1996. Field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 6. Champaign, U.S.A: Illinois Department of Natural Resources. 184 pp.

APPENDICES

APPENDIX A – METHODOLOGY FOR ASSESSING WOOD BORER LANDING DISTRIBUTIONS ON STRESSED RED SPRUCE WITH STICKY-BAND TRAPS

Introduction

Tetropium fuscum (Fabricius) (Coleoptera: Cerambycidae) is an exotic spruce (*Picea*) pest in North America (CFIA 2007) that infests the phloem of stressed Norway spruce, *Picea abies* (L.) Karst, in its native Europe (Juutinen 1955). *Tetropium cinnamopterum* (Kirby), a native congener that occupies a similar wood boring niche is not a pest throughout North America. *Tetropium fuscum* was discovered in 1999 attacking apparently healthy red spruce, *P. rubens* (Sarg.) (Smith & Hurley 2000), and established populations surrounding the Halifax epicentre were found to occur sympatrically with *T. cinnamopterum* (Rhainds *et al.* 2010). Flaherty *et al.* (2013) determined that sticky-band traps were more effective than quilt traps at capturing *Tetropium*, native and exotic that land on the trunk of spruce trees. I deployed sticky-band traps to measure *T. fuscum* and *T. cinnamopterum* landing distributions along the bole of stressed red spruce below the live crown.

Materials and Methods

Study Sites

The same four sites used in Chapter 2; four mixed forest sites dominated by red spruce, *Picea rubens* (Sarg.): two inside the exotic range of *Tetropium fuscum* (Fabr.) in Bedford, Nova Scotia (N44°44.27, W63°39.81) and two outside this range in the Acadian Research Forest near Minto, New Brunswick (N46°00.59, W66°21.82).

Red Spruce Selection

In each stand I selected 30 red spruce trees with diameters at breast height (dbh) between 18-25 cm and heights between 10-17 m. Each selected spruce was at least 10 m from any other spruce meeting the minimum size criteria and from gravel road. From the 30 trees in each stand, I studied 20 sticky-banded trees (5 trees x 4 stands), which were selected prior to the trees selected for Chapter 2.

Insect Vertical Distributions via Sticky-Band Traps

Stressing Spruce and Insect Trapping

Trees selected to receive sticky-bands were girdled (3-6 cm deep to the phloem and 3 cm wide approximately 15 cm from the ground) using a chainsaw in early May 2013, prior to flight of adult wood borers, to increase susceptibility to colonization by *Tetropium* spp. (Flaherty *et al.* 2011) and other phloem-feeding insects. In mid May 2013, all branches below half the tree's height were removed using a handsaw to allow a personal protection harness to move freely along the trunk. Swedish sectional ladders, 3 m long sections of ladders that can be assembled end-to-end parallel to the trunk, were used to access half the tree height below the live crown.

On May 14th, 2013 (NS) and May 21st, 2013 (NB), I placed sticky-bands on each selected tree at approximately 10, 23, 36, and 50% of tree height. Just below each sticky-band stratum, I hand-girdled the trunk with a U-shaped blade (3-6 cm deep to the phloem and 3 cm wide) to make traps as attractive as possible to beetles searching for suitable hosts (Zhang & Schlyter 2004). Heights for trees and sticky-bands were determined using a hypsometer (Haglöf, Sweden). I removed and replaced sticky-bands

every two weeks until the weeks of August 19th 2013 (NS) and August 26th 2013 (NB), providing seven sampling periods. Unfortunately, bands set up after the fourth sampling periods (June 24th and July 2nd) were lost, so the time series was truncated. Prior to removal, I covered each band with clinging plastic wrap to terminate sampling and to ensure no insects were transferred between bands during transport from the field. The sticky-bands were stored at 5°C pending insect removal and identification.

Insect Removal and Identification

I removed wood wasps (Siricidae), bark and wood boring beetles from the sticky-bands using limonene (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.) and stored them in 70% ethanol prior to identification to the lowest feasible taxonomic level. Most individuals were identified to genus or species, but identification was sometimes difficult because of body damage to insects that struggled on the sticky bands or were attacked by predators. Determinations of insects were performed using Bright 1976, Yanega 1996, Schiff *et al.* 2012, and the reference collections at the Atlantic Forestry Centre of the Canadian Forest Service.

Results

A total of 19 *Tetropium* were captured along the trunk of stressed red spruce, 4 from outside *T. fuscum*'s exotic range in New Brunswick and 15 in Nova Scotia within their range. Only *T. cinnamopterum* were captured on New Brunswick spruce. Along the trunk 12 were captured on the lowest traps, 5 on the low-middle, 2 on the middle-high, and none on the highest sticky-bands.

Reference

- Bright, D. E. 1976. The insects and arachnids of Canada Part 2: The bark beetles of Canada and Alaska, Coleoptera: Scolytidae. Canada Department of Agriculture, Research Branch, Biosystematics Research Institute, Publication 1576. 241pp.
- (CFIA) Canadian Food Inspection Agency. 2007. Brown spruce longhorn beetle infested places order (second revision). <http://www.inspection.gc.ca/plants/plant-protection/insects/brown-spruce-longhorn-beetle/order/eng/1333085341951/1333085519708>
- Flaherty, L., J. D. Sweeney, D. Pureswaran, and D.T. Quiring. 2011. Influence of the host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 40: 1200-1209.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. 2013. Preference of an exotic wood borer for stressed trees is more attributable to pre-alighting than post-alighting behaviour. *Ecological Entomology* 38: 546-552.
- Juutinen, P. 1955. Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium Kirby*) in Finnland. *Acta Entologica Fennica* 11: 1-112. (English Translation via Translation Bureau of Public Works and Government Services Canada)
- Rhains, M., S. B. Heard, J. D. Sweeney, P. Silk, and L. Flaherty. 2010. Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology* 39: 1794-1800.
- Schiff, N. M., H. Goulet, D. R. Smith, C. Boudreault, A. D. Wilson, and B. E. Scheffler. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. *Canadian Journal of Arthropod Identification* 21: 1-305.

- Smith, G. and J. E. Hurley. 2000. First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin* 54: 540.
- Yanega, D. 1996. Field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 6. Champaign, U.S.A: Illinois Department of Natural Resources. 184 pp.
- Zhang Q. and F. Schlyter. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology* 6: 1-19.

APPENDIX B – *TETROPIUM* GENERIC NATURAL HISTORY

Defending against degradation of biospheres is becoming more difficult due to declining research funding and consequently scientific interest for natural history and systematics (Dayton 2003). To understand the potential impacts of wood borers in introductions to novel environments it is not only imperative to be able to detect the presence of the exotic species (Haack 2006) but also know what other organisms in the biota they interact with (Hanks 1999; Shea & Chesson 2002). Wood boring insects can easily go undetected and establish populations quickly with high reproductive rates and migration due to flight or accidental human transportation (Smith & Hurley 2000; Muirhead *et al.* 2006). *Tetropium* are a prime example as they are not forest pests in their native ranges (Juutinen 1955; Linsley 1961) but have become pests in novel forests (EPPO 2005; CFIA 2007), although very little is known about their life history traits beyond host trees (Table B1).

The genus *Tetropium* belongs to the subfamily Spondylidinae of the longhorn beetles (Coleoptera: Cerambycidae). The larvae possess general longhorn biology where the individuals bore within and feed upon the tissues of plants (Yanega 1996; Hanks 1999). *Tetropium* species all seem to use conifers as their host plants, consuming the subcortical tissues similar to other relatives within the tribe Asemini. Adult beetles are known to attack the trunks of their host trees (Linsley 1961; Yanega 1996, Hanks 1999). On bark, impeccably camouflaged adults of various shades of brown and black oviposit in the furrows and under the scales of conifer bark where their first instar larvae burrow into the phloem to continue development (Linsley 1962).

Tetropium is most diverse in the northern hemisphere, being primarily a panarctic genus with a few species ranging into Central America as well as the Oriental region of south Asia (Linsley 1961; Yanega 1996; Löbl & Smetana 2010). The diversity of *Tetropium* begins to become depauperate toward the equator, due to the southern limits of Pinaceae (Linsley 1961; Eckenwalder 2009).

Table B1. *Tetropium* species, their distribution, and host trees.

<i>Tetropium</i> Species	Native Range	Host(s)	State of Native Host	Exotic Range	Exotic Host(s)	State of Exotic Host(s)
<i>T. abietis</i> (Fall)	Pacific Coast of North America: British Columbia south to ? ^{2,6,11}	<i>Abies</i> spp. ⁶ - <i>A. concolor</i> ² - <i>A. magnifica</i> ² <i>Juniperus</i> spp. ²	Living ²	N/A	N/A	N/A
<i>T. aquilonium</i> (Plavilstshikov)	Finland, Sweden, and Russia ¹⁰	<i>Picea</i> spp. - <i>P. abies</i> ¹⁷		N/A	N/A	N/A
<i>T. auripilis</i> (Bates)	South US and Mexico ^{2,16}			N/A	N/A	N/A
<i>T. beckeri</i> (Franz)	Guatemala			N/A	N/A	N/A
<i>T. castaneum</i> (Linnaeus)	Europe and Asia (Palearctic) ^{7,10}	<i>Picea</i> spp. - <i>P. excelsa</i> ⁷ <i>Pinus</i> spp. - <i>P. silvestris</i> ⁷		N/A	N/A	N/A
<i>T. cinnamopterum</i> (Kirby)	Northern North America ^{1,2,11}	<i>Abies</i> spp. ¹¹ - <i>A. balsamea</i> ^{6,1} <i>Larix</i> spp. ² <i>Picea</i> spp. ⁶ - <i>P. rubens</i> ^{3,24} - <i>P. mariana</i> ⁵ <i>Pinus</i> spp. ^{1,6} - <i>P. strobus</i> ⁹ - <i>P. resinosa</i> ⁹ - <i>P. banksiana</i> ⁹	Dead ^{1,2,3,6} Stressed ³ Living ^{1,2,3}	N/A	N/A	N/A
<i>T. confragosum</i> (Holzschuh)	Bhutan ¹⁰			N/A	N/A	N/A
<i>T. danilevskyi</i> (Sláma)* ^{10,21}	Tuva, southern Siberia (Russia) ^{10,21}			N/A	N/A	N/A
<i>T. fuscum</i> (Fabricius)	Spans Europe, Siberia, Kazakhstan,	<i>Picea</i> spp. - <i>P. abies</i> ⁷ - <i>P. pungens</i> ⁷	Dead ⁷ Stressed ⁷	Nova Scotia, Canada ^{10,11}	<i>Picea</i> spp. - <i>P. rubens</i> ^{3,4,24}	Dead ³ Stressed ³ Healthy ³

	and Xinjiang (NW China) ^{7,10}				<i>-P. glauca</i>	
<i>T. gabrieli</i> (Weise)	Spans Europe ¹⁰	<i>Larix</i> spp. ¹⁸ <i>-L. decidua</i> ¹⁹		Nearctic? ¹⁰	N/A	N/A
<i>T. gracilicorne</i> (Reitter)	Spans Russia to Japan south and Kazakhstan to South Korea ^{10,20}	<i>Abies</i> spp. <i>-A. nephrolepis</i> ²⁰ <i>Larix</i> spp. <i>-L. gmelinii</i> ²⁰ <i>-L. sibirica</i> ²⁰ <i>Picea</i> spp. <i>-P. ajanensis</i> ²⁰ <i>Pinus</i> spp. <i>-P. koraiensis</i> ²⁰ <i>-P. sibirica</i> ²⁰ <i>-P. sylvestris</i> ²⁰	Dead ²⁰ Stressed ²⁰ Living ²⁰	Control methods in eastern Europe ²⁰	Moving east, same genera as in the native range	Moving east, same stages as in the native range
<i>T. gracilicum</i> (Hayashi)	Heilongjiang (NE China), far east Russia, and Hokkaido (Japan) ^{10,22}			N/A	N/A	N/A
<i>T. guatemalanum</i> (Bates)	Guatemala			N/A	N/A	N/A
<i>T. morishimaorum</i> (Kusama & Takakuwa)	Japan and North Korea ¹⁰			N/A	N/A	N/A
<i>T. opacipenne</i> (Bates)	Vera Cruz (Mexico) ¹⁶			N/A	N/A	N/A
<i>T. opacum</i> (Franz)	Guatemala			N/A	N/A	N/A
<i>T. oreinum</i> (Gahan)	Spans India to Southern China and continues into the Oriental Region ¹⁰			N/A	N/A	N/A
<i>T. parallelum</i> (Casey)	East side of the Rocky Mountains: Alberta south to ? ^{2,11}			N/A	N/A	N/A
<i>T. parvulum</i> (Casey)	Alaska east to Quebec ^{1,11}	<i>Picea</i> spp. ¹ <i>-P. glauca</i> ⁸ <i>-P. engelmannii</i> ⁸		N/A	N/A	N/A
<i>T. pilosicorne</i> (Linsley)** ¹⁵	State of Mexico ¹⁵	Suspected <i>Picea</i> spp. <i>-P. pseudostrabus</i> ¹⁵		N/A	N/A	N/A

<i>T. scabriculum</i> (Holzschuh)** 10	Sichuan (central China) ¹⁰			N/A	N/A	N/A
<i>T. schwarzianum</i> (Casey)	Ontario east to Nova Scotia and NE USA ^{1,2,11}	<i>Pinus</i> spp. - <i>P. strobilus</i> ²⁴		N/A	N/A	N/A
<i>T. schwerdfegeri</i> (Franz)	Guatemala			N/A	N/A	N/A
<i>T. staudingeri</i> (Pic)	Kazakhstan south to Bhutan and Uzbekistan east to Xinjiang (NW China) ¹⁰			N/A	N/A	N/A
<i>T. tauricum</i> (Shapovalov) *** ¹⁰	Crimean Peninsula (Ukraine) ^{10,23}			N/A	N/A	N/A
<i>T. velutinum</i> (LeConte)	Pacific Coast and north Rocky Mountains ^{2,11} and Great Lakes Region ¹	<i>Abies</i> spp. ¹ <i>Larix</i> spp. ¹ <i>Pinus</i> spp. ⁶ <i>Pseudotsuga</i> spp. ⁶ - <i>P. taxifolia</i> ² <i>Tsuga</i> spp. ¹ - <i>T.</i> <i>heterophylla</i> ⁶	Living ²	N/A	N/A	N/A

* Represented by a single specimen

** Represented by two to nine specimen

*** Represented by ten to nineteen specimen

? Not sure if this is a real species

! Unlikely an accurate host tree (Raske 1973)

Reference

In Text

(CFIA) Canadian Food Inspection Agency. 2007. Brown spruce longhorn beetle infested places order (second revision). <http://www.inspection.gc.ca/plants/plant->

[protection/insects/brown-spruce-longhorn-beetle/order/eng/1333085341951/1333085519708](http://www.eppo.int/protected_species/pests_and_diseases/longhorn_beele/1333085341951/1333085519708)

- (EPPO) European and Mediterranean Plant Protection Organization. 2005. *Tetropium gracilicorne*. *EPPO Bulletin* 35: 402–405.
- Dayton, P. K. 2003. The importance of the natural sciences to conservation. *The American Naturalist* 162: 1-13.
- Eckenwalder, J. E. 2009. *Conifers of the World: Complete Reference*. Portland, U.S.A.: Timber Press Inc. 720 pp.
- Haack, R. A. 2006. Exotic bark- and woodboring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* 36: 269-288.
- Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of Cerambycid beetles. *Annual Review of Entomology* 44: 483-505.
- Juutinen, P. 1955. Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium Kirby*) in Finnland. *Acta Entologica Fennica* 11: 1-112. (English Translation via Translation Bureau of Public Works and Government Services Canada)
- Linsley, E. G. 1962. *The Cerambycidae of North America part 2*. Los Angeles. U.S.A.: University of California Press. 102 pp.
- Löbl, L. & A. Smetana. 2010. *Catalogue of Palaearctic Coleoptera Volume 6 Chrysoloidea*. Stenstrup, Denmark: Apollo Books. 924 pp.
- Muirhead, J. R., B. Leung, C. van Overdijk, D. W. Kelly, K. Nandakumar, K. R. Marchant, and H. J. MacIsaac. 2006. Modeling local and long-distance dispersal of

invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America.

Diversity and Distributions 12: 71-79.

Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170-176.

Smith, G. and J. E. Hurley. 2000. First North American record of the Palearctic species

Tetropium fuscum (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists*

Bulletin 54: 540.

Yanega, D. 1996. Field Guide to Northeastern Longhorned Beetles (Coleoptera:

Cerambycidae). Illinois Natural History Survey Manual 6. Champaign, U.S.A:

Illinois Department of Natural Resources. 184 pp.

In Table

1. Yanega, D. 1996. Field Guide to Northeastern Longhorned Beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 6. Champaign, U.S.A: Illinois Department of Natural Resources. 184 pp.
2. Linsley, E. G. 1962. The Cerambycidae of North America part 2. Los Angeles. U.S.A.: University of California Press. 102 pp.
3. Flaherty, L., J. D. Sweeney, D. Pureswaran, and D.T. Quiring. 2011. Influence of the host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environmental Entomology* 40: 1200-1209.
4. Smith, G. and J. E. Hurley. 2000. First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin* 54: 540.

5. Saint-Germain, M., P. Drapeau, and C. M. Buddle. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography* 30: 737-748.
6. Craighead, F. C. 1923. North American Cerambycid Larvae. Department of Agriculture Bulletin No. 27. Ottawa, Canada: Dominion of Canada. 150 pp.
7. Juutinen, P. 1955. Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium* Kirby) in Finnland. *Acta Entologica Fennica* 11: 1-112. (English Translation via Translation Bureau of Public Works and Government Services Canada)
8. Raske, A. 1973. *Tetropium parvulum* elevated to species rank and contrasted to *T. cinnamopterum* in morphology and host preference (Coleoptera: Cerambycidae). *The Canadian Entomologist* 105: 745-755.
9. Gardiner, L. M. 1957. Deterioration of fire-killed pine in Ontario and the casual wood-boring beetles. *The Canadian Entomologist* 89: 241-263.
10. Löbl, L. & A. Smetana. 2010. Catalogue of Palaeactic Coleoptera Volume 6 Chrysoeloidea. Stenstrup, Denmark: Apollo Books. 924 pp.
11. Bousquet, Y., P. Bouchard, A. E. Davies, and D. S. Sikes. 2013. Checklist of Beetles (Coleoptera) of Canada and Alaska. Sofia, Bulgaria: Pensoft Publishers. 402 pp.
12. Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of Cerambycid beetles. *Annual Review of Entomology* 44: 483-505.

13. Linsley, E. G. 1962. The Cerambycidae of North America part 1. Los Angeles. U.S.A.: University of California Press. 135 pp.
14. Eckenwalder, J. E. 2009. Conifers of the World: Complete Reference. Portland, U.S.A.: Timber Press Inc. 720 pp.
15. Linsley, E. G. 1935. Studies in the Longicornia of Mexico (Coleoptera: Cerambycidae). *Transactions of the American Entomological Society, Philadelphia* 61: 67-102.
16. Bates, H. W. and D. Sharp. 1879-1886. Insecta. Coleoptera. Longicornia and Bruchides. Volume V. London, England: Quaritch. 525 pp.
17. Lundberg, S. 1993. Långhorningen *Tetropium aquilonium* (Coleopteran, Cerambycidae) funnen i Sverige, med uppgifter om dess biologi. *Entomologisk Tidskrift* 114: 151-155.
18. Stover, W. 1973. Der Lärchenbock, ein Neufund für die westfälische Käferfauna. *Natur und Heimat* 33: 31-32.
19. Crawshay, G. A. 1907. Life History of *Tetropium gabrieli* Weise. *Transactions of the Entomological Society of London* 183-212.
20. (EPPO) European and Mediterranean Plant Protection Organization. 2005. *Tetropium gracilicorne*. *EPPO Bulletin* 35: 402-405.
21. Sláma, M. E. F. 2005. *Tetropium danilevskyi* sp. N. from Asia (Coleoptera, Cerambycidae). *Les Cahiers Magellanes* 48: 1-3.
22. Niisato, T. and K. Akita. 2001. Distributional records of the *Tetropium* species (Coleoptera, Cerambycidae) from the Russian far east. *Elytra, Tokyo* 29: 29-32.

- 23.** Shapovalov, A. M. 2007. A new *Tetropium* Kirby, 1837 from Crimean peninsula and a new *Doradion* Dalman, 1817 from south Kazakhstan (Coleoptera: Cerambycidae). *Russian Entomological Journal* 16: 71-74.
- 24.** Canadian Forestry Centre - Atlantic Forestry Centre. Fredericton, New Brunswick. Reference insect collection: host-plant rearings.

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- (2015) Displacement of a native woodborer by its invasive congener. Poster presentation delivered at the Acadian Entomological Society meeting, Montreal, QC, August 2015
- (2015) Displacement of a native woodborer by its invasive congener. Oral presentation delivered at the Canadian Entomological Society meeting, Montreal, QC, November 2015

