

**IMPACTS OF THE BROWN SPRUCE LONGHORN BEETLE,  
*TETROPIUM FUSCUM* (FABRICIUS) (COLEOPTERA: CERAMBYCIDAE),  
ON INSECT COMMUNITY STRUCTURE IN ITS INVADED HABITAT OF  
NOVA SCOTIA, CANADA**

by

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## ABSTRACT

*Tetropium fuscum* (Coleoptera: Cerambycidae), a wood boring beetle native to Europe, was accidentally introduced to Halifax, Nova Scotia, likely in wood packaging in shipping containers. Non-indigenous species can change insect community diversity, or displace native species. I tested whether the invasive *Tetropium fuscum* or *Tetropium cinnamopterum* a native congener, had a significant impact on insect community structure (Simpson's Diversity, richness, and evenness) in spruce logs, and if impact was greater on closely related species by comparing emerged insects from red and Norway spruce bolts colonized with *Tetropium fuscum* and *Tetropium cinnamopterum* to control bolts. *Tetropium* egg treatments generally reduced community diversity, although the combination of significantly affected indices varied somewhat among *Tetropium* species and host. In Norway spruce, both *Tetropium* spp. significantly reduced Simpson's diversity and richness; evenness was significantly lower only for *T. fuscum*. In red spruce, both *Tetropium* spp. significantly reduced richness; only *T. fuscum* reduced Simpson's diversity and evenness. Impact of *Tetropium* on presumed competitors was not simply related to phylogenetic distance: the closest relative was not impacted, although the next closest relative, *Evodinus monticola*, was significantly reduced in both red and Norway spruce.

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## List of Abbreviations

+*TF-I*: With *Tetropium fuscum* – *invasive* egg treatments

+*TC-N*: With *Tetropium cinnamopterum* – *native* egg treatments



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**CHAPTER 1 – GENERAL INTRODUCTION**

Non-indigenous species are organisms not historically found in an area. These species are deemed exotic if they are accidentally or intentionally introduced to a new geographical area (Richardson et al. 2000). Not all introduced exotics establish populations in their newly introduced habitat (Williamson & Fitter 1996); however if successful in establishing a viable population in a novel range, they can have negative impacts on community members or the new ecosystem and are therefore deemed invasive (Colautti and MacIsaac 2004). Invasive species can have negative effects on native communities via effects on the surrounding community structure, including competitors, prey, natural enemies, and valuable resources and/or habitat (Gotelli & Arnett 2000, Sanders et al. 2002, Hedja et al. 2009, Lessard et al. 2009). This is true for a multitude of terrestrial, marine, and freshwater invasive species such as the zebra mussel (*Dreissena polymorpha*: Griffiths et al. 1991), purple loosestrife (*Lythrum salicaria*: Brown et al. 2002), green crab (*Carcinus maenas*: Cohen et al. 1995), emerald ash borer (*Agilus planipennis*: Poland et al. 2006), and European starlings (*Sturnus vulgaris*: Elton 1958).

Insect species in particular are often cryptic, meaning they are often hidden concealed or camouflaged in nature, and can have detrimental effects on the environment (Liebhold et al. 1995, Haack et al. 2006).

Introductions of non-indigenous species in marine, freshwater, and terrestrial habitats have increased near international ports over the last 500 years, and especially during the past two centuries (Mack et al. 2000, Kolar & Lodge 2001, Mooney & Cleland 2001, Bax et al. 2003, Colautti et al. 2006, Haack et al. 2006), and will most likely continue to intensify with the increase of global trade (Bradley et al. 2012, Brockerhoff et al. 2006, Hulme 2009). Common pathways for accidental species introductions include ballast water, soil transportation, pet trade, and silvicultural products and the potential invasive species are often cryptic in nature (Haack 2006, Wilson et al. 2009). Many insect invaders in North America have been accidentally introduced through solid wood packaging of cargo in ships and shipping containers, such as wood shipping pallets (Haack 2006), and these accidental introductions of species can lead to changes in native species community composition (Allen & Humble 2001). Wood boring beetles, such as the emerald ash borer and the Asian longhorn beetle, are cryptic in nature, meaning they are typically hidden, and are most commonly transported in infested wood that has not been heat-treated or fumigated. Some of these species can be very destructive and invasive in new habitats, e.g., the emerald ash borer has killed millions of ash trees in North America, and is changing the forest composition that invades (Pugh et al. 2011).

Aside from their potential economic impacts, invasives can also negatively alter native communities. Invasive ants, for example, have been known to displace and disrupt closely related native ant communities by significantly lowering densities of ants and other arthropods within the area (Porter & Savignano 1990, Gotelli & Arnett 2000, Sanders et al. 2003, Kenis et al. 2009, Lessard et al. 2009). Local biodiversity can be negatively affected by decreasing evenness (relative abundance of species), richness (number of species), or abundance (amount of species) of native species within the invaded community. Reduced biodiversity can facilitate other pest or exotic species introductions, and may increase ecosystem susceptibility to disease (Patrick 1988, Nijs & Roy 2000).

Invasive species that have closely related species with similar hosts and life histories, in their new range, may be subject to greater competition for resources than exotic species without such closely related native species; natural enemies may also be more likely to exploit exotic hosts that are more closely related to their native hosts, and both of these factors could slow the rate of spread of the invader (Darwin 1859, Cavender-Bares et al. 2009, Dearborn et al. 2016). An interesting model system in which to explore these ideas is the invasion into Nova Scotia of *Tetropium fuscum* (Fabricius), an invasive wood-boring cerambycid from Europe (Juutinen 1959). *Tetropium fuscum* was unintentionally introduced to Halifax, Nova Scotia circa 1990 (Smith & Hurley 2000). In Nova Scotia, *T. fuscum* is sympatric with a native congener, *Tetropium cinnamopterum* Kirby; both species have similar life history and developmental stages (Rhains et al. 2010; Drooz 1985). In their native habitats, both species colonize spruce

(*Picea* spp.) trees that are stressed, moribund, or recently felled (Juutinen 1955, Drooz 1985) and *T. fuscum* both prefers and performs better on stressed- than on healthy red spruce (*Picea rubens*) in Nova Scotia (Flaherty et al. 2013a, b). However, unlike *T. cinnamopterum*, *T. fuscum* may also successfully colonize “apparently healthy” red spruce with full, green crowns (Smith and Hurley 2000; Sweeney et al. 2001), although subsequent stem analysis of these trees revealed their very low radial growth rates indicative of low vigor (O’Leary et al. 2003). Hurricane Juan weakened trees in Point Pleasant Park near Halifax, Nova Scotia in 2003, and as a result *T. fuscum* populations increased as they can exploit a greater proportion of available host material than *T. cinnamopterum*. Also, *T. fuscum* adults emerge two weeks before *T. cinnamopterum*, giving them a developmental advantage in the phloem, leading to possible intraguild predation when the two species occur together. While Dearborn et al. (2016) argued that *T. fuscum* interacts with the native insect community, which is causing the rate of spread to slow, our hypothesis leads to an untested prediction: the same interactions should see *T. fuscum*, an invasive cerambycid beetle from Europe, suppress closely related native competitors in Nova Scotia.

Here I asked whether the brown spruce longhorn beetle (*Tetropium fuscum*) has had an impact on both abundance and diversity of the Nova Scotian wood-boring guild in the invasion zone *T. fuscum* is an interesting invasive species because, in its invasive range, it encounters both its European ancestral host Norway spruce (*Picea abies*), which is frequently planted in North America, and novel host red spruce. Here I ask if

community impact will differ in red spruce, the most common North American host for invading *T. fuscum* and Norway spruce (the most common host for *T. fuscum* in its native range, and a frequently planted tree in the North American range). Using insect community data collected from bolts exposed to natural colonization and to bolts artificially inoculated with eggs, I compared the effect of *T. fuscum* and *T. cinnamopterum* on diversity of the natural wood boring community attacking red and Norway spruce in Nova Scotia. We also tested for dependence of species-level impact on phylogenetic distance from *Tetropium* spp. This may have important implications for understanding invasive species introductions and their naturalization, the impact of invasive beetles on surrounding community structure, and it may improve methods of integrated pest management.

The general objective of my thesis is to examine the relationship between an invasive, *Tetropium fuscum*, and the surrounding community of insects within red and Norway spruce. In chapter 2 I will examine the impact of the invasive *T. fuscum* on the community as a whole. I predict that *T. fuscum* will negatively affect the insect community. In chapter 3 I will examine both the effect of *T. fuscum* on each species within the focal community, and the effect on closely related species for the entire community. I predict that *T. fuscum* will displace the most closely related species in both our samples and the community. In both chapters I examine the impact of *T. fuscum* as well as the native *T. cinnamopterum* as a control. Both *T. fuscum* and *T. cinnamopterum* are compared to control bolts without either *Tetropium* species.

The original experimental design for chapters 2 and 3 was conceived by Stephen Heard and Deepa Pureswaran. The *Tetropium* egg treatment used in both data chapters was designed by Rob Johns set up in the lab, and implemented in the field by Eric Moise, who also collected and identified most of the emerging insects from these bolts. I was responsible for organizing fieldwork, field setup, insect collection, analysis of the data, and writing of the manuscripts.

#### **REFERENCE:**

- Bax, N., Williamson, A., Agüero, M., Gonzalez, E., & Geeves, W. (2003). Marine invasive alien species: a threat to global biodiversity. *Marine Policy*, 27(4): 313–323.
- Bradley, B. A., Blumenthal, D. M., Early, R., Grosholz, E. D., Lawler, J. J., Miller, L. P., Sorte, C. J.B., Antonio, C. M. D., Diez, J. M., Dukes, J. S., Ibanez, I., Olden, J. D. (2012). Global change, global trade, and the next wave of plant invasions. *Front. Ecol. Environ*, 10(1): 20–28.
- Brockerhoff, E. G., Liebhold, A. M., & Jactel, H. (2006). The ecology of forest insect invasions and advances in their management. *Canadian Journal of Forest Research*, 36(2): 263–268.
- Brown, B. J., Mitchell, R. J., & Graham, S. A. (2002). Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology*, 83(8): 2328–2336.

- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology, *12*: 693–715.
- Cohen, A. N., Carlton, J. T., & Fountain, M. C. (1995). Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Marine Biology*, *122*(2): 225-237.
- Colautti, R. I., Bailey, S. A., Overdijk, C. D. A. van, Amundsen, K., & MacIsaac, H. J. (n.d.). Characterised and Projected Costs of Nonindigenous Species in Canada. *Biological Invasions*, *8*(1): 45–59.
- Colautti, R. I., and H. J. MacIsaac. (2004). A neutral terminology to define “invasive” species. *Diversity and Distributions*, *10*: 135-141.
- Darwin, C. (1859). *On the origin of species by means of natural election*. London, England: John Murray.
- Dearborn, K., Heard, S. B., Sweeney, J. D., & Pureswaran, D. (2016). Displacement of *Tetropium cinnamopterum* by its invasive congener *Tetropium fuscum*.
- Drooz, A. T. (1985). Insects of eastern forests, [USDA Forest Service, Miscellaneous Publication No. 1426].
- 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.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. (2013a). Evaluating seasonal variation in bottom-up and top-down forces and their impact on an exotic wood borer, *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environ. Entomol.* *42*: 957–966.
- Flaherty, L., D. Quiring, D. Pureswaran, and J. Sweeney. (2013b). Preference of an

- exotic wood borer for stressed trees is more attributable to pre-alighting than post-alighting behaviour. *Ecol. Entomol.* 38: 546–552.
- Gotelli, N. J., & Arnett, A. E. (2000). Biogeographic effects of red fire ant invasion. *Ecology Letters*, 3(4): 257-261.
- Griffiths, R. W., Schloesser, D. W., Leach, J. H., & Kovalak, W. P. (1991). Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(8): 1381-1388.
- Haack, Robert A. (2006). Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions, 36: 269–288.
- Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, 97(3): 393–403.
- Hulme, P. E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46(1): 10–18.
- Juutinen, P. (1955). Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium Kirby*) in Finland, 11: 1–112.
- Kolar, C. K., & Lodge, D. M. (2001). Progress in invasion biology: predicting invasions, 16(4): 199–204.
- Lessard, J., Fordyce, J A., Gotelli, N. J., & Sanders, N. J. (2009). Invasive ants alter the phylogenetic structure of ant communities. *Ecology*, 90(10): 2664–2669.
- Liebhold, A. M., MacDonald, W. L., Bergdahl, D., & Mastro, V. C. (n.d.). (1995). Invasion by exotic forest pests: A threat to forest ecosystems, 30: 1–49.
- Mack, R N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. (2000).



Biotic invasions: causes, epidemiology, global consequences and control. *Issues in Ecology*, 5.

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species.

*PNAS*, 98(10): 5446–5451.

Nijs, I., & Roy, J. (2000). How important are species richness, species evenness and interspecific differences to productivity? A mathematical model. *Oikos*, 88(1): 57–66.

Patrick, R. (1988). Importance of diversity in the functioning and structure of riverine communities. *Limnol. Oceanogr.*, 33(6): 1304–1307.

Poland, T. M., & McCullough, D. G. (2006). Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry*, 104(3): 118-124.

Porter, S. D., & Savignano, D. A. (1990). Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*, 71(6): 2095–2106.

Pugh, S. A., Liebhold, A. M., & Morin, R. S. (2011). Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. *Canadian Journal of Forest Research*, 41(11): 2165-2175.

Rhains, M., Heard, S. B., Sweeney, J. D., Silk, P., and Flaherty. (2010). Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environ. Entomol.*, 39(6): 1794–1800.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, & C. J. West. (2000). Naturalization and invasion of alien plants: concepts and definitions.

*Diversity and Distributions*, 6: 93-107.

Sanders, N. J., Gotelli, N. J., Heller, N. E., & Gordon, D. M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 100(5): 2474–2477.

Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G., & Savolainen, V. (2011). Testing Darwin's naturalization hypothesis in the Azores. *Ecology Letters*, 14, 389–396.

Smith, G., & Hurley, J. E. (2000). First North American record of the palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin.*, 54(4): 540.

Williamson, M., & Fitter, A. (1996). The varying success of invaders. *Ecology*, 77(6): 1661–1666.

Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: dispersal pathways affect invasion success. *Trend in Ecology and Evolution*, 24: 136-144.

**CHAPTER 2 - IMPACT OF THE INVASIVE BROWN SPRUCE  
LONGHORN BEETLE (*TETROPIUM FUSCUM FABRICIUS*) ON  
COMMUNITY STRUCTURE IN ITS INVADED RANGE**

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**ABSTRACT:**

Invasive species can significantly affect the community composition in the newly invaded range. *Tetropium fuscum* (Coleoptera: Cerambycidae) is an invasive wood-boring beetle that was accidentally introduced to Halifax, Nova Scotia from Europe. We tested whether *T. fuscum* and *Tetropium cinnamopterum*, a closely related native, had a significant effect on insect community structure (Simpson diversity, species richness, species evenness) in red and Norway spruce bolts. In red spruce, both *Tetropium* species significantly reduced richness, but only *T. fuscum* significantly reduced Simpson's diversity and evenness. In Norway spruce, both *Tetropium* reduced Simpson's diversity and richness, but only *T. fuscum* significantly lowered evenness. The impact of *T. fuscum* on community structure is comparable to that of the native *T. cinnamopterum*, but *T. fuscum* is more prevalent in red spruce meaning that the invasive *T. fuscum* is playing a similar role in the native community structure as the native *Tetropium* species.

## **INTRODUCTION:**

Invasive species may influence the composition of native communities via effects on competitors (Gotelli & Arnett 2000, Sanders et al. 2002, Hedja et al. 2009, Lessard et al. 2009), prey, and natural enemies (such as native parasitoids). Accidental introductions of non-indigenous species in marine, freshwater, and terrestrial habitats have increased near international ports over the last 500 years, and in particular during the past two centuries (Mack et al. 2000, Kolar & Lodge 2001, Mooney & Cleland 2001, Bax et al. 2003, Colautti et al. 2006, Haack et al. 2006), and will most likely continue to intensify with the increase of global trade (Bradley et al. 2012, Brockerhoff et al. 2006, Hulme 2009). With increasing rates of introduction, understanding interactions between an exotic/invasive species and native community members is important because some invasive species suppress and out-compete the native species present, and change the overall community structure in the newly invaded range (Porter & Savignano 1990, Gotelli & Arnett 2000, Sanders et al. 2002, Hejda et al. 2009), especially with regards to insect invaders (Liebhold et al. 1995, Haack et al. 2006). Many exotic species that are introduced do not successfully establish populations in their introduced range (Williamson & Fitter 1996), but when they are successful, the results can be catastrophic for the invaded community (Gotelli & Arnett 2000). It has been suggested that invaders with close relatives in their new range will spread more slowly and have lower population densities (Darwin 1859, Cavender-Bares et al. 2009, Dearborn et al. 2016) because they are expected to compete with ecologically similar congeners for niche space, and be attacked by their enemies (Darwin 1859, Schaefer et al. 2011). It is crucial to understand

how invasive species affect the surrounding community because maintaining diversity is key to reducing susceptibility to disease and future invaders (Patrick 1988, Nijis & Roy 2000).

*Tetropium fuscum* was unintentionally introduced to Halifax, Nova Scotia circa 1990 (Smith & Hurley 2000). In Nova Scotia, *T. fuscum* is sympatric with a congener, *Tetropium cinnamopterum* Kirby as they have similar life histories (Drooz 1985, Rhainds et al. 2010). *T. fuscum* appears to colonize both apparently healthy and damaged red spruce (*Picea rubens*) and Norway spruce (*Picea abies*) (Smith & Hurley 2000), whereas *T. cinnamopterum* is reported to colonize only weakened or stressed spruce (Sweeney et al. unpublished data). Because *T. fuscum* can more readily colonize healthier trees it is a species of higher concern than *T. cinnamopterum*. For example, after Hurricane Juan weakened trees in Point Pleasant Park near Halifax, Nova Scotia in 2003, a *T. fuscum* infestation was identified. Also, *T. fuscum* adults emerge two weeks before *T. cinnamopterum*, giving them a developmental advantage in the phloem, leading to possible intraguild predation when the two species occur together. While Dearborn et al. (2016) argued that the invasion of *T. fuscum* is being slowed by interactions with members of the native community, this hypothesis makes an untested prediction: that the same interactions should see *T. fuscum* suppress densities of native competitors in Nova Scotia

The objective of this study is to see whether the brown spruce longhorn beetle (*Tetropium fuscum* Fabricius), an invasive wood-boring cerambycid from Europe

(Juutinen 1959), has had an impact on abundance and diversity of the wood-boring guild in the invasion zone of Nova Scotia. *T. fuscum* is an interesting invasive species because, in its invasive range, it encounters both the novel and most common host red spruce (*Picea rubens*) and its ancestral host, Norway spruce (*Picea abies*), which is frequently planted in North America. Using insect community data collected from logs (bolts) freshly cut from red and Norway spruce, to which we added eggs of *T. fuscum* or *T. cinnamopterum* (and exposed to further natural colonization), we compared the diversity of the natural wood-boring insect community to that occurring in control bolts. We demonstrate significant impacts on species diversity, richness, and evenness. This may have important implications for understanding invasive species introductions and their naturalization, the impact of invasive beetles on surrounding community structure, and it may improve methods of integrated pest management by potentially allowing us to predict interactions between invasive and native species.

## **METHODS:**

### Experimental design:

In early May 2014, we felled 10 apparently healthy red spruce and 10 apparently healthy Norway spruce trees (24 – 26 cm diameter breast height) at the Acadia Research Forest (N45°99.876', W66°39.335') near Fredericton, New Brunswick (N.B.), Canada. This is an area with natural colonies of *T. cinnamopterum*, and without *T. fuscum*. From each tree we cut 10 bolts roughly 36 cm long. We coated bolt ends in paraffin wax to preserve moisture and stored the bolts in cold storage rooms (-2°C) until later use to reduce desiccation.

Adult *T. fuscum* and *T. cinnamopterum* were reared from bolts cut from infested red spruce trees in Nova Scotia and incubated at 20-22°C in the containment facilities at Canadian Forest Service – Atlantic Forestry Centre (CFS - AFC), Fredericton, N.B. We mated pairs of either *T. fuscum* or *T. cinnamopterum* in Petri dishes and collected eggs on black construction paper as described by Flaherty et al. (2013b). We placed 20 eggs on each experimental bolt by attaching pieces of black construction paper containing 1-5 eggs each as follows: we slit the bark using a scalpel so that the paper and attached eggs would directly contact the phloem, and secured it in place with pins. Eggs were distributed over  $\frac{3}{4}$  of each bolt, allowing for  $\frac{1}{4}$  of the bolt to make direct soil contact. The papers were removed after 2 weeks and egg hatch was quantified.

On 9 June 2014, we placed ten experimental blocks, each consisting of a red spruce and a Norway spruce bolt, at each of three sites in Nova Scotia, Canada: Westchester Valley (N45° 36.557' W63° 43.608'); Shubenacadie (N45° 10.079' W63° 34.274'); and Sandy Lake (N44° 44.162' W63° 40.585'). In Shubenacadie, four additional bolts were added to the block and had a manipulative treatment of either +*T. fuscum* eggs, or +*T. cinnamopterum* eggs; Sandy Lake and Westchester did not receive egg-treatment bolts because there were not enough eggs for these sites and Shubenacadie was the area most likely to have natural colonies of both *Tetropium* species. We placed bolts on flat ground in red spruce dominated stands and positioned them in a circle approximately 10 cm apart at the closest point.

From 8-9 October, we revisited the bolts and piled and covered them with heavy mosquito mesh to protect them from woodpeckers and other avian predators. We collected bolts in late November (24-28) 2014, and stored them at -2°C at CFS – AFC, Fredericton, New Brunswick, to simulate an overwintering period. In mid-January 2015 we incubated bolts at 20-22°C in rearing cages within containment facilities with day/night photoperiod lights (16L:8D) to mimic summer conditions.

#### Insect collection:

We checked bolts for emerging insects every 7 days. First, we swept bolts with brushes to dislodge any hiding insects. We sorted debris and insects then grouped them into micro vials and preserved them in 70% ethanol for later identification, with the exception of *Tetropium* spp., which we identified immediately and mounted on pins. We identified emerged insects to species (*Evodinus monticola*, *Polygraphus rufipennis*, *Urocerus albicornis*, and *Xylosandrus germanus*, *Hylobius congener*, *Pissodes nemorensis*), genus (*Dendroctonus*, prob. *rufipennis*, *Dryocoetes* (*affaber* and *autographus*), *Thanasimus* sp., *Xylophagus* sp.), or family (Histeridae, and Staphylinidae) using insect keys (Bright Jr. 1976) and a reference collection of wood-inhabiting insects from the AFC. All *Evodinus monticola* emerged as larvae, but were identifiable as Lepturinae by morphological features such as head, thorax, and the caudal spine. Previous incubations of such larvae have resulted in eclosion of *E. monticola* adults. We monitored emergence from our bolts for 15 weeks, ending 2 weeks after the last *Tetropium* spp. had emerged and the majority of wood-boring insects had also stopped emerging.



We disregarded small detritus-feeding flies that do not occupy the same niche space as *Tetropium* spp., and small parasitoids of scolytid beetles. We also disregarded the smallest scolytines as logistical difficulties prohibited their collection from the caged bolts. However, even for bolts in which they were very numerous, their small biomass was approximately 0.1% of the next-smallest species, making it likely that they had little community impact.

#### Analysis:

We pooled all of our data across sites, as preliminary analyses revealed no effect of site on emergence of *Tetropium* species. Out of the 60 control bolts *Tetropium* naturally colonized 3. We disregarded these 3, as they contained both *Tetropium* species, making it impossible to distinguish effects of *T. fuscum* or *T. cinnamopterum*. We compared Simpson diversity, richness, and evenness (of all species except *Tetropium* spp.) using 2-way ANOVAs with tree species and egg treatment as factors. Richness and evenness are important as these components of diversity could be affected differently by our treatments. We tested first for the interactions between the two main effects (tree species and egg-treatment), and as all interactions for Simpson diversity, richness, and evenness were non-significant we removed them before re-running the 2-way ANOVAs. All 2-way ANOVAs were based on Type II sum of squares, as the experimental design was unbalanced. We used Tukey post-hoc analyses to assess treatment effects on each tree species because there were three treatments on two tree species.

## **RESULTS:**

### Insect community from red and Norway spruce bolts

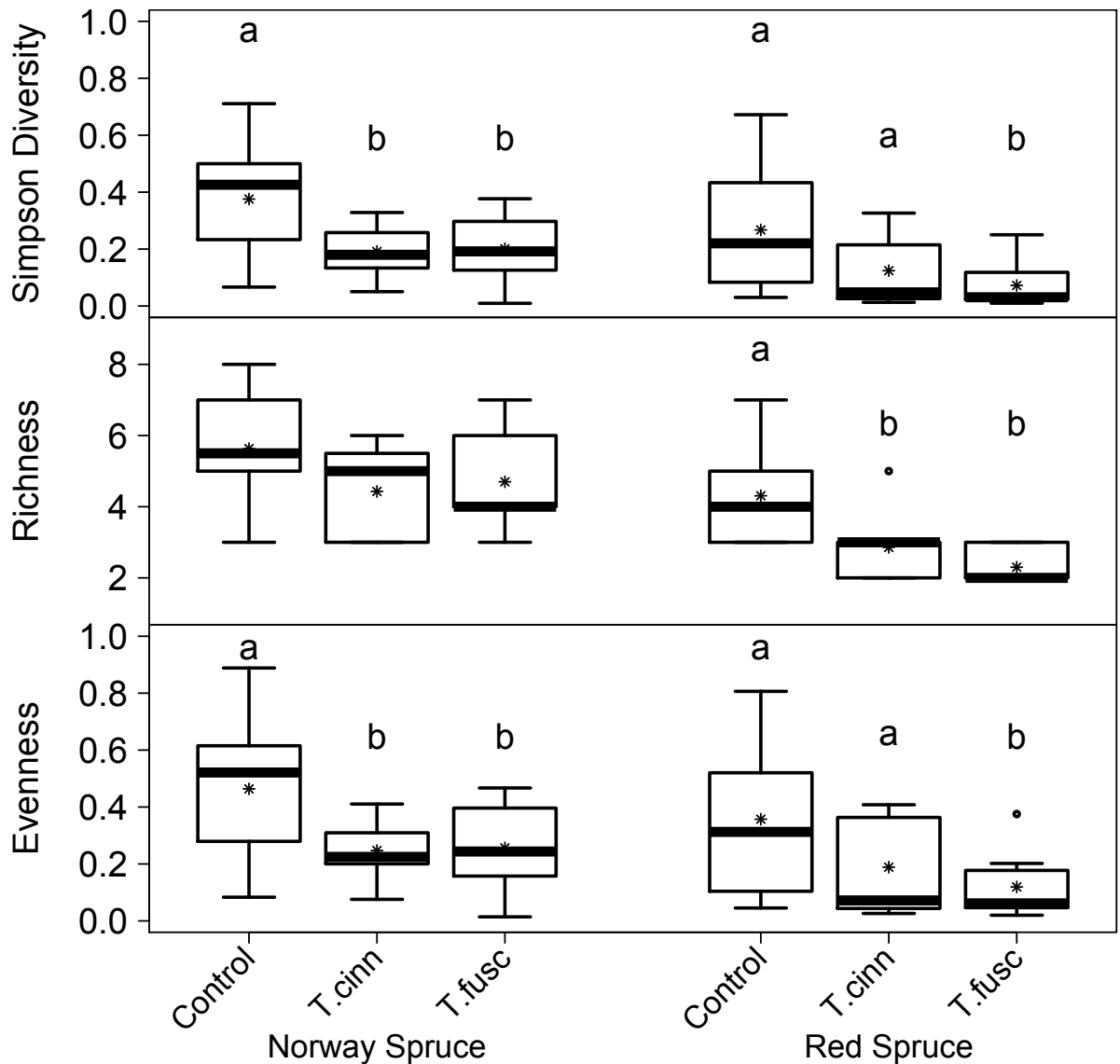
We collected a total of 32,118 individual insects within the focal insect group of study. The first insects emerged after less than a week of set up. The first *Tetropium* emerged after two weeks, and the last after 13 weeks, at which point few other insects were emerging. We collected a total of 15 species or morphospecies, three of which had total emergence of fewer than 10 individuals (Table 1). Average *T. fuscum* emergence from treatment bolts was ~1 beetle/bolt, and average *T. cinnamopterum* emergence from its respective treatment bolts was ~3 beetles/bolt. There were no significant differences in egg hatch between insect or on tree species,  $p = 0.99$ .

### Simpson diversity, richness, and evenness

Simpson diversity was significantly lower in + *T. fuscum* treatment bolts than control bolts in both red spruce ( $p = 0.006$ ) and Norway spruce ( $p = 0.0076$ ), and was significantly lower in *T. cinnamopterum* treatment bolts in Norway spruce only ( $p = 0.015$ )(Figure 1, Table 2). Richness was significantly lower in both red spruce bolts treated with either +*T. fuscum* or +*T. cinnamopterum* eggs compared to controls ( $p < 0.0001$ ,  $p = 0.0083$ , respectively) but did not differ among treatments in Norway spruce (Figure 1, Table 2). Evenness was significantly lower in + *T. fuscum* egg-treatment than in controls in both red ( $p = 0.014$ ) and Norway spruce ( $p = 0.011$ ) bolts, whereas it was lower in +*T. cinnamopterum* egg-treatments than in controls in Norway spruce bolts only ( $p = 0.023$ )(Figure 1, Table 2).

**Table 1:** Total emergence of the collected insect taxa from red and Norway spruce from control (n = 56), +*T. cinnamopterum* (+TC-N) (n = 14), and +*T. fuscum* (+TF-I) (n = 20) treatment bolts. Species in parentheses indicate any collected species with total emergence < 10 individuals.

| Order: Family             | Species   | Control    |               | Egg Treatment +TC-N |               | Egg Treatment +TF-I |               |
|---------------------------|---|------------|---------------|---------------------|---------------|---------------------|---------------|
|                           |   | Red Spruce | Norway Spruce | Red Spruce          | Norway Spruce | Red Spruce          | Norway Spruce |
| Coleoptera: Cerambycidae  | <i>Tetropium fuscum</i>                         | 0          | 0             | 0                   | 0             | 13                  | 13            |
|                           | <i>Tetropium cinnamopterum</i>                  | 0          | 0             | 32                  | 7             | 0                   | 0             |
|                           | <i>Evodinus monticola</i>                       | 37         | 107           | 0                   | 3             | 0                   | 5             |
| Coleoptera: Cleridae      | ( <i>Thanasimus</i> sp.)                        | 0          | 1             | 0                   | 0             | 0                   | 0             |
| Coleoptera: Curculionidae | ( <i>Dendroctonus rufipennis</i> )              | 5          | 0             | 0                   | 0             | 0                   | 0             |
|                           | <i>Dryocoetes affaber</i> or <i>autographus</i> | 8410       | 5747          | 3518                | 2057          | 5287                | 3106          |
|                           | <i>Polygraphus rufipennis</i>                   | 1316       | 643           | 128                 | 165           | 149                 | 211           |
|                           | <i>Xylosandrus germanus</i>                     | 12         | 201           | 0                   | 0             | 0                   | 0             |
|                           | <i>Hylobius congener</i>                        | 41         | 209           | 4                   | 32            | 1                   | 21            |
|                           | <i>Pissodes nemorensis</i>                      | 204        | 206           | 3                   | 32            | 12                  | 51            |
| Coleoptera: Staphylinidae | (Family: Staphylinidae)                         | 3          | 1             | 0                   | 0             | 1                   | 3             |
| Coleoptera: Histeridae    | Family: Histeridae                              | 17         | 17            | 5                   | 3             | 1                   | 9             |
| Diptera: Xylophagidae     | <i>Xylophagus</i> sp.                           | 5          | 46            | 0                   | 0             | 0                   | 1             |
| Hymenoptera: Siricidae    | <i>Urocerus albicornis</i>                      | 10         | 7             | 0                   | 0             | 0                   | 0             |



**Figure 1:** Effects of *T. cinnamopterum* (*T. cinn*) and *T. fuscum* (*T. fusc*) on Simpson diversity, richness, and evenness in red and Norway spruce. Average emergence values are indicated by asterisks (\*), and significant differences are indicated by letter differences. There was no significant difference in richness between control, *T. cinnamopterum* and *T. fuscum* in Norway spruce. The boxes represent the first (lower) and third (higher) quartiles, and the heavy line within each box represents the median. The highest and lowest lines represent the 90<sup>th</sup> percentiles.

**Table 2:** Simpson diversity, richness and evenness 2-way ANOVA main effects from red and Norway spruce emergence data.

|                   | Main effect   | Sum of Squares | Degrees of Freedom | F     | p value              |
|-------------------|---------------|----------------|--------------------|-------|----------------------|
| Simpson diversity | Tree Species  | 0.29           | 1                  | 12.02 | 0.00083              |
|                   | Egg Treatment | 0.66           | 2                  | 13.96 | 5.64e <sup>-06</sup> |
|                   | Residuals     | 2.03           | 86                 | -     | -                    |
| Richness          | Tree Species  | 57.7           | 1                  | 42.93 | 3.99e <sup>-09</sup> |
|                   | Egg Treatment | 41.7           | 2                  | 15.52 | 1.76e <sup>-06</sup> |
|                   | Residuals     | 115.5          | 86                 | -     | -                    |
| Evenness          | Tree Species  | 0.25           | 1                  | 6.31  | 0.014                |
|                   | Egg Treatment | 0.98           | 2                  | 12.27 | 2.05e <sup>-05</sup> |
|                   | Residuals     | 3.43           | 86                 | -     | -                    |

## **DISCUSSION:**

The invasive beetle *T. fuscum* has a significant negative impact on insect community structure in its invaded habitat in Nova Scotia. *T. fuscum* significantly decreased species richness in red spruce, and both Simpson's diversity index and evenness of our focal insect community in both Norway and red spruce. The native *T. cinnamopterum* significantly decreased species richness in red spruce and Simpson's diversity index and evenness in Norway spruce, but unlike *T. fuscum*, did not reduce Simpson's diversity or evenness in red spruce. This similarity in impact may not be surprising, because the two species are closely related and share a similar life history. However, *T. fuscum* also emerges two weeks before the native *T. cinnamopterum* (Juutinen 1955), which could allow for an advantage of *T. fuscum* preying on *T. cinnamopterum*. While our experiments did not test for intraguild predation, this suggests the possibility that community impacts of *Tetropium* in co-infested trees might be less than additive.

*T. fuscum* commonly attacks weakened Norway spruce in its native European range, and it performs better on weakened or stressed red spruce in its invaded range (Juutinen 1955, Flaherty et al. 2011, Dearborn et al. 2016). This has implications for invasion success, as organisms that utilize a range of food and habitat resources are more likely to be successful (Liebhold et al 1995). Gibbs and Wainhouse (1986) proposed that invasive species colonizing a new area within the same hemisphere are more likely to be successful invaders, as most hosts are common genera across most portions of the Northern Hemisphere.

Invasive species have been known to displace native species, often by outcompeting them, which has a negative effect on species diversity (Porter & Savignano 1990, Gotelli & Arnett 2000, Sanders et al. 2002, Sanders et al. 2003). Hejda et al. (2009) studied vascular plants in the Czech Republic in areas with and without an invasive plant and found that with the exception of two invaded areas, species richness, evenness, and diversity were all significantly lower in plots with the invasive species (Hejda et al. 2009). Another study by Gotelli & Arnett (2000) that found that native ant populations decreased significantly when the invasive fire ant *S. invicta* was present (Gotelli & Arnett 2000).

Understanding how invasive species affect the surrounding communities into which they are introduced is critical because the effect of each invasive species can differ immensely on the surrounding community (Hejda et al. 2009). In our experiments, both the invasive *T. fuscum*, and the native *T. cinnamopterum* affected the overall diversity of the bolts in which they colonize. This contrasts with recent work by Dearborn et al. (2016), who found no significant impact on Simpson diversity or species richness in focal communities. However, the two studies differed in that Dearborn et al. compared focal communities between the invaded area in Nova Scotia, and the non-invaded New Brunswick, whereas we compared individual bolt communities with or without *T. fuscum* and *T. cinnamopterum*. Furthermore, the focal communities differed in scope and total abundance between the two studies. Dearborn et al. tracked *T. fuscum* and *T. cinnamopterum*, their parasitoids, other woodborers, and clerid predators with a total

collection of 223 red spruce-associated individuals, whereas we collected over 32,000 individuals including many different wood-boring species, no parasitoids, and few beetle predators (Table 1). We presumably have much higher power in our experiment due to the immense increase in insect emergence compared to Dearborn et al's experiment, although this may be countered to some extent by the low emergence numbers of *T. fuscum* and *T. cinnamopterus* in our treatment bolts.

*T. fuscum* as an invasive species does have significant effects on the community structure of insects in red and Norway spruce. Normally this would be problematic; however, it seems that in this case it is only substituting in the invaded communities for the native *T. cinnamopterus*. This is congruent with Darwin's Naturalization Hypothesis because *T. fuscum* and *T. cinnamopterus* are extremely similar, and are therefore expected to compete for resources and overlap in ecological space. This was also suggested by Dearborn et al. (2016) and we believe that *T. fuscum* is having no broader effect on the community in Nova Scotia than the native *T. cinnamopterus* species already present. In red spruce, *T. fuscum* is consistently affecting diversity, richness, and evenness. This is interesting, as red spruce is the novel host to *T. fuscum*. What still makes *T. fuscum* a species of higher concern is that it can colonize healthier trees than *T. cinnamopterus*. *T. fuscum* should not fall between the cracks of the public and scientific eye. It seems as if the invasive *T. fuscum* has become dormant and is not as problematic at this time; however any opportunity of favourable conditions could lead to another rise of beetle populations.



## REFERENCES:

- Bax, N., Angela, W., Max, A., Exequiel, G., and Warren, G . (2003). Marine invasive alien species: A threat to global biodiversity. *Marine policy*, 27(4): 313–323.
- Bradley, B. A., Blumenthal, D. M., Early, R., Grosholz, E. D., Lawler, J. J., Miller, L. P., Sorte, C. J.B., Antonio, C. M. D., Diez, J. M., Dukes, J. S., Ibanez, I., Olden, J. D. (2012). Global change, global trade, and the next wave of plant invasions. *Front. Ecol. Environ.*, 10(1): 20–28.
- Bright Jr, D. E. (1976). The insects and arachnids of Canada. Part 2. The bark beetles of Canada and Alaska. Coleoptera: Scolytidae. *The insects and arachnids of Canada. Part 2. The bark beetles of Canada and Alaska. Coleoptera: Scolytidae.*
- Brockerhoff, E. G., Liebhold, A. M., and Jactel , H. (2006). The ecology of forest insect invasions and advances in their management. *Canadian Journal of Forest Research*, 36(2): 263–268.
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., and Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology letters*. 12: 693–715.
- Colautti, R. I., Bailey, S. A., VanOverdijk, C. D. A., Amundsen, K., and MacIsaac, H. J. (2006). Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, 8(1): 45–59.
- Darwin, C. (1859). On the origin of species by means of natural selection. London, England: John Murray.
- Dearborn, K., Heard, S. B., Sweeney, J. D., and Pureswaran, D. (2016). Displacement of

*Tetropium cinnamopterum* by its invasive congener *Tetropium fuscum*.

Drooz, A. T. (1985). Insects of Eastern forests, [USDA Forest Service, Miscellaneous Publication No. 1426].

Flaherty, L., Sweeney, J. D., Pureswaran, D., and Quiring, D. T. (2011). Influence of host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). *Environ. Entomol.*, 40(5): 1200–1209.

Gibbs, J. N., and Wainhouse, D. (1986). Spread of forest pests and pathogens in the Northern hemisphere. *Forestry.*, 59(2): 141–153.

Gotelli, N. J., and A. E. Arnett. (2000). Biogeographic effects of red fire ant invasion. *Ecology Letters.*, 3(4): 257-261.

Haack, R. A. (2006). Exotic bark- and wood-boring Coleoptera in the United States: Recent establishments and interceptions. *Can. J. For. Res.*, 36: 269–288.

Hejda, M., Pyšek, P., and Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology.*, 97(3): 393–403.

Hulme, P. E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology.*, 46(1): 10–18.

Juutinen, P. (1955). Zur biologie und forstlichen bedeutung der fichtenboche (*Tetropium kirby*) in Finnland. 11: 1–112.

Kolar, C. K., and Lodge, D. M. (2001). Progress in invasion biology: Predicting invasions. *Trends in Ecology and Evolution.*, 16(4): 199–204.

Lessard, J., Fordyce, J. A., Gotelli, N. J., and Sanders, N. J. (2009). Invasive ants alter the phylogenetic structure of ant communities. *Ecology.*, 90(10): 2664–2669.

- Liebhold, A. M., MacDonald, W. L., Bergdahl, D., and Mastro, V. C. N.d. (1995). Invasion by exotic forest pests: A threat to forest ecosystems. *For. Sci. Monogr.*, 30: 1–49.
- Mack, R. N., Simberloff, D., Lonsdale, W. M. (2000). Biotic invasions: Causes, epidemiology, global consequences and control. *Issues in Ecology*. 5.
- Mooney, H. A., and Cleland, E. E. (2001). The evolutionary impact of invasive species. *PNAS.*, 98(10): 5446–5451.
- Nijs, I., and Roy, J. (2000). How important are species richness, species evenness and interspecific differences to productivity? A mathematical model. *Oikos.*, 88(1): 57–66.
- Patrick, R. (1988). Importance of diversity in the functioning and structure of riverine communities. *Limnol. Oceanogr.*, 33(6): 1304–1307.
- Pearson, D. E., Ortega, Y. K., and Sears, S. J. (2012). Darwin’s naturalization hypothesis up=close: Intermountain grassland invaders differ morphologically and phenologically from native community dominants. *Biol. Invasions.*, 14: 901–913.
- Porter, S. D., and Savignano, D. A. (1990). Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology.*, 71(6): 2095–2106.
- Rhainds, M., Heard, S. B., Sweeney, J. D., Silk, P., and Flaherty, L. (2010). Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environ. Entomol.*, 39(6): 1794–1800.
- Sanders, N. J., Gotelli, N. J., Heller, N. E., and Gordon, D. M. (2003). Community disassembly by an invasive species. *PNAS.*, 100(5): 2474–2477.
- Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G., and Savolainen, V. (2011).

- Testing Darwin's naturalization hypothesis in the Azores. *Ecology Letters.*, 14: 389–396.
- Smith, G., and Hurley, J. E. (2000). First North American record of the palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *The Coleopterists Bulletin.*, 54(4): 540.
- Van Kleunen, M., Ewald, W., and Markus, F. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters.*, 13(2): 235–245.
- Williamson, M., and Fitter, A. (1996). The varying success of invaders. *Ecology.*, 77(6): 1661–1666.

**CHAPTER 3 – DOES *TETROPIUM FUSCUM* (FABRICIUS)  
PREDOMINANTLY AFFECT MORE CLOSELY RELATED  
SPECIES WITHIN ITS INVADED COMMUNITY?**

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**ABSTRACT:**

Invasive species can change the composition of native species in the invaded range, and it has been suggested that invasive species with close relatives in the invaded range will compete with those species for niche space and resources. We tested using lab tests whether *T. fuscum* and *T. cinnamopterum* had a significant effect on specific insects in our collected community, in particular species that are closely related, in red and Norway spruce. We used literature phylogenies to assemble a phylogenetic tree, and ran a regression to test whether impact of *T. fuscum* and *T. cinnamopterum* is correlated with phylogenetic relatedness. Although a few species' emergences were significantly lowered, there was no relationship between impact of *Tetropium* and phylogenetic relatedness. Neither *Tetropium* spp. have a significant impact on more closely related species; however there may be more complex interactions happening at a smaller scale.

## **INTRODUCTION:**

Invasive species can change the abundance of insect competitors in the invaded range and ultimately change insect community composition in the invaded range (Gotelli & Arnett 2000, Sanders et al. 2002, Hedja et al. 2009, Lessard et al. 2009). Studies have shown that invasive plant and insects can negatively influence local community assembly by outcompeting native species (Porter & Savignano 1990, Gotelli & Arnett 2000, Brown et al. 2002, Sanders et al. 2003, Kenis et al. 2009, Lessard et al. 2009). For example, native ant communities have been disrupted by significantly lowering the abundance of local arthropods within the area (Porter & Savignano 1990, Gotelli & Arnett 2000, Sanders et al. 2003, Kenis et al. 2009, Lessard et al. 2009). A decrease in the abundance of native species within the invaded community may have negative effects on local biodiversity, which may facilitate other pest introductions or susceptibility to disease (Patrick 1988, Nijs & Roy 2000). Understanding invasive species interactions with local flora and fauna is important because accidental introductions of non-indigenous species have increased with the increasing popularity of global trade within the last 500 years, particularly within the last two centuries (Mack et al. 2000, Kolar & Lodge 2001, Mooney & Cleland 2001, Bax et al. 2003, Colautti et al. 2006, Haack et al. 2006,). Rates of accidental species introduction will likely continue to intensify with increasing global trade (Brockerhoff et al. 2006).

Invasive species with ecologically similar congeners are likely to compete strongly with the species most closely related to them in the newly invaded habitat. (Darwin 1859), as these are the species most likely to have overlapping habitat, space

within that habitat, and food. Invasive species can impact native congeners by competing with them for resources such as nutrients or space (Brown & Mitchell 2001, Olsen et al. 2011, Wardle et al. 1994). Plants are commonly studied invasive species studied to quantify how invasive species are competing with native congeners (Brown & Mitchell 2001, Wardle et al. 1994, Brock 2004), however in this study we want to see if we can use phylogenetic analysis to predict the severity of our invasive species in question, brown spruce longhorn beetle (*Tetropium fuscum* Fabricius), and test the hypothesis that invasive species have more impact on closely related species.

*T. fuscum*, an invasive wood-boring cerambycid from Europe (Juutinen 1959), was accidentally introduced to Halifax, Nova Scotia via wood-shipping materials circa 1990. It established a population in the invaded range, and is known to displace its native congener *T. cinnamopterum* (Dearborn et al. 2016). We know that both *T. fuscum* and *T. cinnamopterum* negatively affect community structure (Simpson's diversity, richness, and evenness) of native insect species in red spruce and Norway spruce (Chapter 2), but we do not know how they affect individual insect species in the community. We used literature phylogenies and calculated relatedness of each species caught to *T. fuscum* and its native congener *T. cinnamopterum*. Using data from the insect community emerging from red and Norway spruce bolts exposed to natural insect colonization and *Tetropium*-addition treatments in Nova Scotia, Canada, we tested the hypothesis that the impact of *Tetropium* on native insect emergence was positively correlated with phylogenetic distance to *T. fuscum* and *T. cinnamopterum*. Although only *T. fuscum* is an invasive

species, it is important to test our hypotheses with the native beetle *T. cinnamopterum* as well to see the effects it as a native species has on the community as well.

## **METHODS:**

### Experimental Design:

Here we are describing the same experiment as in Chapter 2, however we are asking different questions of the data.

As in Chapter 2, 10 apparently healthy red spruce and 10 apparently healthy Norway spruce trees (24 – 26 cm diameter breast height) were cut and felled at the Acadia Research Forest (N45°99.876', W66°39.335') near Fredericton, N.B. We sectioned each felled tree into 10 bolts roughly 36 cm long. To preserve moisture, bolt ends were coated in paraffin wax and were stored in cold storage rooms (-2°C).

We collected adult *T. fuscum* and *T. cinnamopterum* emerging from bolts previously colonized by both *Tetropium* species at the Canadian Forest Service – Atlantic Forestry Complex in New Brunswick. We mated pairs of *T. fuscum* and *T. cinnamopterum* then collected their eggs that were laid on black construction paper (Flaherty et al. 2013b). We haphazardly placed 20 eggs over  $\frac{3}{4}$  of each bolt, allowing  $\frac{1}{4}$  to directly contact the soil, and fastened them by cutting slits into the bark using a scalpel so that the paper, i.e. eggs, could directly contact the phloem tissues, and used pins to secure them. The papers were removed after two weeks and egg hatch was quantified.



As in chapter 2, in early June of 2014, we set up ten experimental blocks, consisting of two bolts, one red and one Norway spruce, at three sites in Nova Scotia, Canada: Westchester Valley (N45° 36.557' W63° 43.608'); Shubenacadie (N45° 10.079' W63° 34.274'); and Sandy Lake (N44° 44.162' W63° 40.585'). We then added four manipulative egg *TF-I* or *TC-N* treatment bolts, two red two Norway spruce, to only Shubenacadie. We placed our blocks in red spruce dominated stands and positioned them in a spoke approximately 10 cm apart at the closest point. There were not enough eggs to place treatment bolts over all three sites; Shubenacadie received the treatment because it is most likely where both *T. fuscum* and *T. cinnamopterum* beetles are at the edge of the invasive front.

In early October, we returned to our sites to pile and cover bolts with heavy mosquito mesh to protect from avian predator damage, especially woodpeckers. In late November, (24-28) 2014, we collected bolts and overwintered them at -2°C at the Atlantic Forestry Centre of the Canadian Forest Service in Fredericton, New Brunswick. In mid-January 2015 we set up bolts in Plexiglas rearing cages in containment facilities at 20°C, with day/night photoperiod lights (16L:8D) to mimic summer conditions and facilitate insect emergence.

#### Insect Collection:

As in Chapter 2, we swept bolts with brushes every 7 days to dislodge any hiding insects. Debris was separated from insects, which were then grouped into micro vials, and preserved in 70% ethanol, with the exception of *Tetropium* spp., which we identified

immediately using a dissecting microscope. Emerged insects were identified to family, (Histeridae, and Staphylinidae), genus (*Dendroctonus*, prob. *rufipennis*, *Dryocoetes* (*affaber* and *autographus*), *Thanasimus* sp., *Xylophagus* sp.) or species (*Evodinus monticola*, *Hylobius congener*, *Pissodes nemorensis*, *Polygraphus rufipennis*, *Urocerus albicornis*, and *Xylosandrus germanus*) using insect keys (Bright Jr 1976) and a reference collection of wood-inhabiting insects from the Canadian Forest Service – Atlantic Forestry Centre. We stopped collections two weeks after the last *Tetropium* spp. had emerged, in total emergence lasted 15 weeks.

Small detritus-feeding flies that do not occupy the same niche as *Tetropium* spp. were disregarded, as were small parasitoids of scolytine beetles. We also disregarded the smallest scolytines as logistical difficulties prohibited their collection from the caged bolts. Their biomass was approximately 0.1% of the next-smallest species, even when extremely numerous, making it unlikely that they had large community impact.

#### Phylogenetic analysis:

##### (1) Estimating relatedness

We used literature phylogenies to assemble a backbone phylogenetic tree that included each collected species (Table A1) (Gaunt et al. 2002, Hedges et al. 2009, Parfrey et al. 2011, Ronquist et al. 2012, Vinther et al. 2012). Next we used a combination of literature phylogenies from Time Tree (timetree.org) to estimate phylogenetic distance of each species to *T. fuscum*; detailed justifications for our divergence-time estimates are provided in Appendix 1.

## (2) Estimating *Tetropium* impact

We calculated the impact of both *Tetropium* species on our focal insect community by running individual ANOVAs for each species to compare emergence between control and +*T. fuscum*, or +*T. cinnamopterum* egg-treatment bolts. Tukey's HSD was also used to see where our significant differences were. Once we knew which species were significantly affected by either *Tetropium* species, we calculated the % difference in emergence of each species between control and +*T. fuscum* or +*T. cinnamopterum* egg-treatment bolts separately in red and Norway spruce.

## (3) Correlating impact and relatedness

We ran a simple linear regression comparing the % difference in emergence of each species and average phylogenetic relatedness, regardless of whether their individual ANOVAs were significant; to test whether phylogenetic relatedness was a good indicator of *Tetropium* impact on species emergence in red and Norway spruce.

## **RESULTS:**

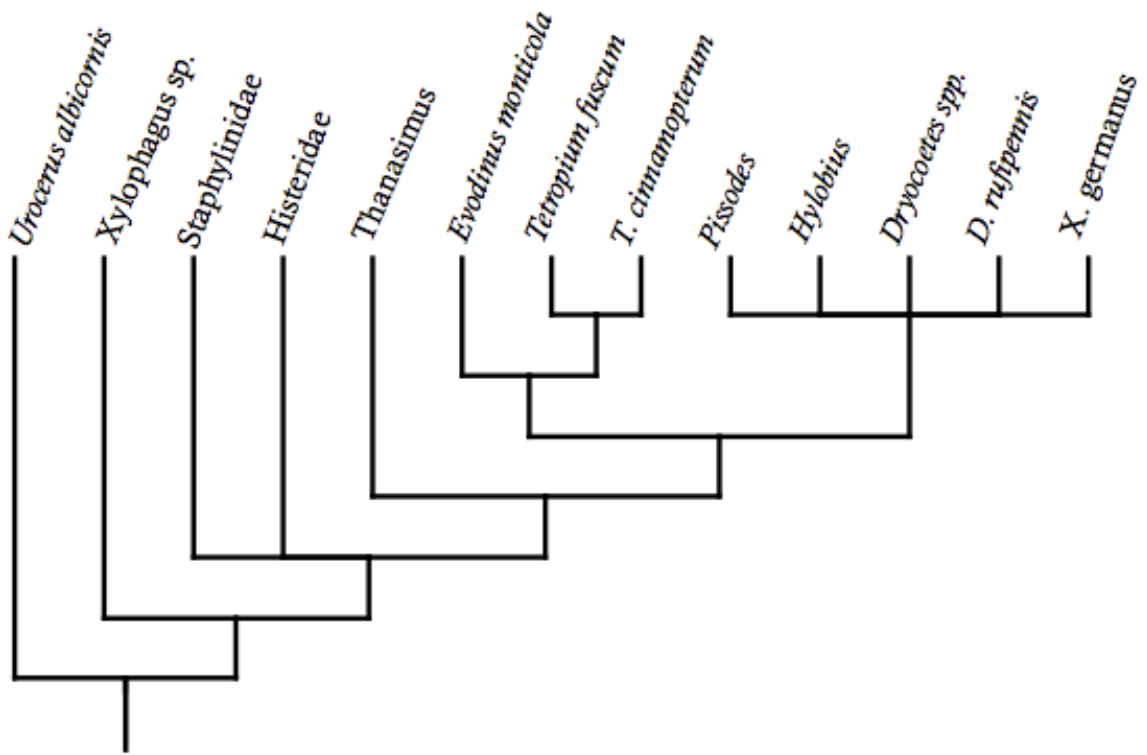
### Insect community from lab-reared red and Norway spruce bolts

The first insects emerged less than a week after set up, and in total we collected 32,118 individual insects within the focal insect group of study. The first *Tetropium* emerged after two weeks, and the last after 13 weeks, at which point most insects had stopped emerging. Out of 15 species collected, 3 had total emergence of fewer than 10 individuals (Table 3). Average *T. fuscum* emergence from +*T. fuscum* treatment bolts was ~1 beetle/bolt, and average *T. cinnamopterum* emergence from +*T. cinnamopterum*

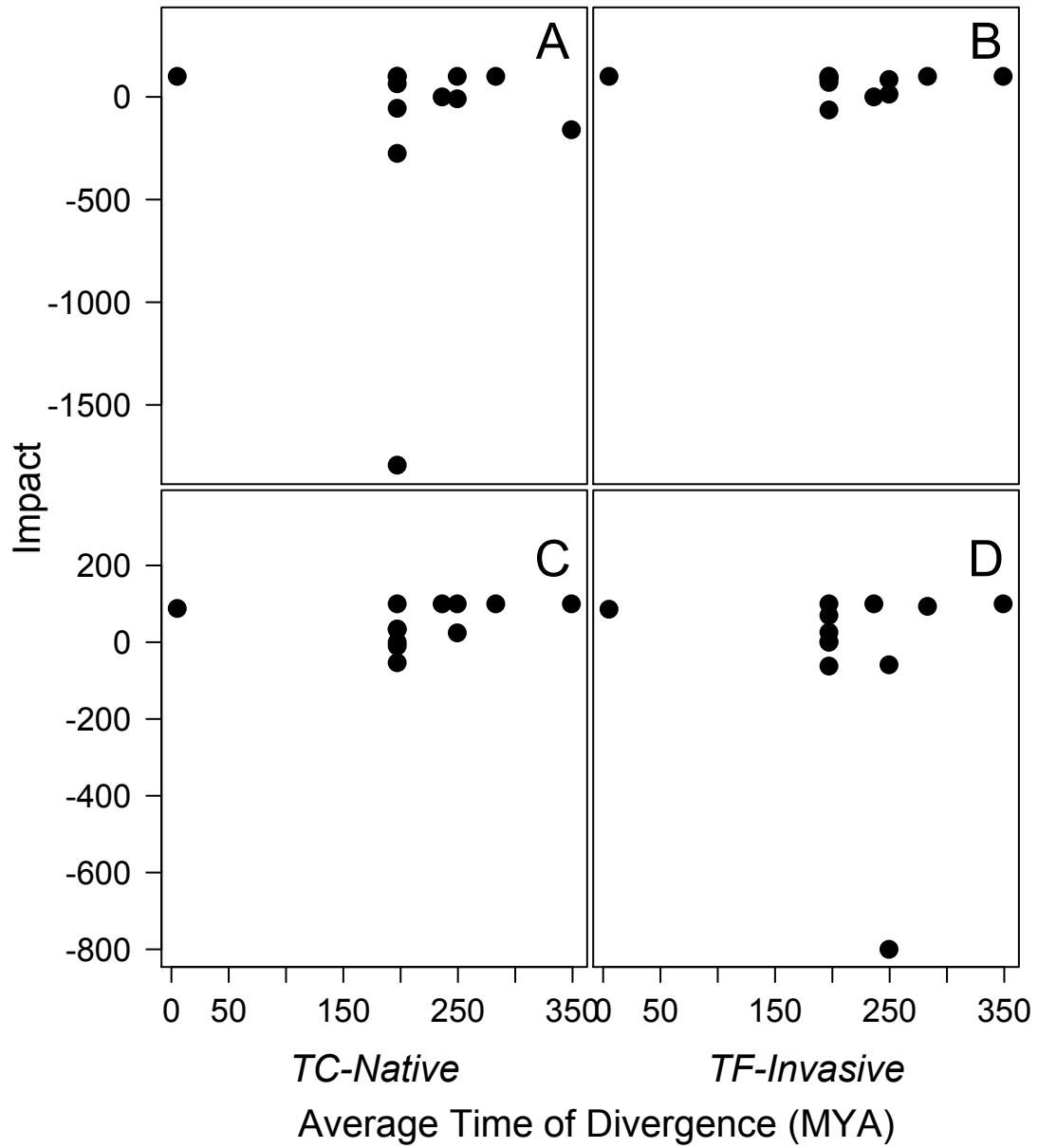
treatment bolts was ~3beetles/bolt. There were no significant differences in egg hatch between insect or on tree species,  $p = 0.99$ .

#### Displacement and phylogenetic relatedness

Emergence of individual species *Evodinus monticola* and *Hylobius congener* were significantly lower in +*T. fuscum* egg-treated bolts compared to controls in red spruce ( $p = 0.036$ ,  $p = 0.050$ , respectively). *Evodinus monticola* and *Xylophagus* sp. emergence were significantly lower in +*T. fuscum* ( $p = 0.008$ ,  $p = 0.001$ , respectively) and +*T. cinnamopterum* ( $p = 0.021$ ,  $p = 0.003$ , respectively) egg-treated bolts when compared to controls in Norway spruce (Table 4). Although only these species were significantly reduced, there was no relationship between the impact of *Tetropium* and phylogenetic distance to the impacted species for any of the *Tetropium* and host species combinations (Figure 3, Table 5). As some species were present in variable emergence numbers (Table 3) we weighted the regressions four ways accounting for emergence sample size and none of the four weighted regressions were significant.



**Figure 2:** Phylogenetic tree made using literature phylogenies for average time of divergence of each species from *Tetropium fuscum*.



**Figure 3:** Comparing impact native insect species that range in evolutionary time of divergence from either +TC (*T. cinnamopterum*) in red (panel A) and Norway spruce (panel C) or +TF (*T. fuscum*) in red (panel B) and Norway spruce (panel D). Both +TC and +TF treatments are compared to control bolts.

**Table 3:** Total emergence of the collected insect taxa from red and Norway spruce from control (n = 56), +TC-N (*T. cinnamopterum* – native) (n = 14), and +TF-I (*T. fuscum* – invasive) (n = 20) treatment bolts. Species in parentheses indicate any collected species with total emergence < 10 individuals. Data are from Heustis et al. (Chapter 2).

| Order: Family                | Species   | CTRL       |               | + TF-I     |               | + TC-N     |               |
|------------------------------|---|------------|---------------|------------|---------------|------------|---------------|
|                              |   | Red Spruce | Norway Spruce | Red Spruce | Norway Spruce | Red Spruce | Norway Spruce |
| Coleoptera:<br>Cerambycidae  | <i>Tetropium fuscum</i>                         | 0          | 0             | 0          | 0             | 13         | 13            |
|                              | <i>Tetropium cinnamopterum</i>                  | 0          | 0             | 32         | 7             | 0          | 0             |
|                              | <i>Evodinus monticola</i>                       | 37         | 107           | 0          | 3             | 0          | 5             |
| Coleoptera:<br>Cleridae      | ( <i>Thanasimus</i> sp.)                        | 0          | 1             | 0          | 0             | 0          | 0             |
| Coleoptera:<br>Curculonidae  | ( <i>Dendroctonus rufipennis</i> )              | 5          | 0             | 0          | 0             | 0          | 0             |
|                              | <i>Dryocoetes affaber</i> or <i>autographus</i> | 8410       | 5747          | 3518       | 2057          | 5287       | 3106          |
|                              | <i>Polygraphus rufipennis</i>                   | 1316       | 643           | 128        | 165           | 149        | 211           |
|                              | <i>Xylosandrus germanus</i>                     | 12         | 201           | 0          | 0             | 0          | 0             |
|                              | <i>Hylobius congener</i>                        | 41         | 209           | 4          | 32            | 1          | 21            |
|                              | <i>Pissodes nemorensis</i>                      | 204        | 206           | 3          | 32            | 12         | 51            |
| Coleoptera:<br>Staphylinidae | (Family: Staphylinidae)                         | 3          | 1             | 0          | 0             | 1          | 3             |
| Coleoptera:<br>Histeridae    | Family: Histeridae                              | 17         | 17            | 5          | 3             | 1          | 9             |
| Diptera:<br>Xylophagidae     | <i>Xylophagus</i> sp.                           | 5          | 46            | 0          | 0             | 0          | 1             |
| Hymenoptera:<br>Siricidae    | <i>Urocerus albicornis</i>                      | 10         | 7             | 0          | 0             | 0          | 0             |

**Table 4:** Comparing post-hoc p values (Tukey HSD) from various ANOVAs comparing species emergence between control, +*TF-I* (*T. fuscum* – invasive), and +*TC-N* (*T. cinnamopterum* – native) bolts in red and Norway spruce.

| Order: Family                | Species  | Norway spruce           |                        |                                  | Red spruce              |                         |                                  |
|------------------------------|--|-------------------------|------------------------|----------------------------------|-------------------------|-------------------------|----------------------------------|
|                              |  | CTRL –<br>+ <i>TF-I</i> | CTRL-<br>+ <i>TC-N</i> | + <i>TF-I</i> -<br>+ <i>TC-N</i> | CTRL –<br>+ <i>TF-I</i> | CTRL –<br>+ <i>TC-N</i> | + <i>TF-I</i> -<br>+ <i>TC-N</i> |
| Coleoptera:<br>Cerambycidae  | <i>Tetropium fuscum</i>                            | < 0.0001                | 1.000                  | 0.003                            | < 0.0001                | 1.000                   | 0.002                            |
|                              | <i>Tetropium cinnamopterum</i>                     | 1.000                   | 2.0e <sup>-07</sup>    | 5.5e <sup>-06</sup>              | 1.000                   | 0.000                   | 0.000                            |
|                              | <i>Evodinus monticola</i>                          | 0.008                   | 0.021                  | 0.998                            | 0.036                   | 0.075                   | 1.000                            |
| Coleoptera:<br>Cleridae      | <i>Thanasimus</i> sp.                              | 0.812                   | 0.854                  | 1.000                            | NA                      | NA                      | NA                               |
| Coleoptera:<br>Curculionidae | <i>Dendroctonus rufipennis</i>                     | NA                      | NA                     | NA                               | 0.784                   | 0.930                   | 1.000                            |
|                              | <i>Dryocoetes affaber</i><br>or <i>autographus</i> | 0.358                   | 0.559                  | 0.988                            | 0.289                   | 0.481                   | 0.988                            |
|                              | <i>Polygraphus rufipennis</i>                      | 0.999                   | 0.985                  | 0.985                            | 0.298                   | 0.465                   | 0.994                            |
|                              | <i>Xylosandrus germanus</i>                        | 0.493                   | 0.585                  | 1.000                            | 0.458                   | 0.549                   | 1.000                            |
|                              | <i>Hylobius congener</i>                           | 0.135                   | 0.681                  | 0.743                            | 0.050                   | 0.328                   | 0.829                            |
|                              | <i>Pissodes nemorensis</i>                         | 0.804                   | 0.758                  | 0.989                            | 0.173                   | 0.187                   | 0.985                            |
| Coleoptera:<br>Staphylinidae | Family:<br>Staphylinidae                           | 0.091                   | 0.970                  | 0.183                            | 0.993                   | 0.748                   | 0.849                            |
| Coleoptera:<br>Histeridae    | Family:<br>Histeridae                              | 0.670                   | 0.947                  | 0.645                            | 0.415                   | 0.992                   | 0.537                            |
| Diptera:<br>Xylophagidae     | <i>Xylophagus</i> sp.                              | 0.001                   | 0.0038                 | 0.980                            | 0.562                   | 0.643                   | 1.000                            |
| Hymenoptera:<br>Siricidae    | <i>Urocerus albicornis</i>                         | 0.698                   | 0.762                  | 1.000                            | 0.742                   | 0.795                   | 1.000                            |



**Table 5:** Comparing linear regression intercepts, standard error, and p values between control to *T. fuscum*, and control to *T. cinnamopterum* bolts in red and Norway spruce.

|                           |        | Intercept | Standard Error | P value |
|---------------------------|--------|-----------|----------------|---------|
| + <i>T. fuscum</i>        | Red    | 73.2      | 0.21           | 0.86    |
|                           | Norway | 57.5      | 0.97           | 0.69    |
| + <i>T. cinnamopterum</i> | Red    | -136      | 2.09           | 0.98    |
|                           | Norway | 28.8      | 0.21           | 0.62    |

## DISCUSSION:

*T. fuscum* is known to displace its native congener *T. cinnamopterum* in Nova Scotia, Canada (Dearborn et al. 2016) and to significantly alter wood-boring community structure (Chapter 2). We expected *T. fuscum* to have the strongest impact on its closest relatives, but we found only weak evidence for such a relationship. *Tetropium*'s closest relative, the cerambycid *Evodinus monticola*, was indeed strongly suppressed, but the next closest relatives were not and the only other species that was significantly reduced in density was *Hylobius congener*, one of two distantly related weevil species collected in our samples. The lesser of our two weevils was not significantly affected. This has implications for invasive species as Darwin's naturalization hypothesis predicts that an invasive species closely related to the newly invaded range will compete with closely related competitors and will ultimately blend itself into the natural community (Darwin 1859). Understanding species' autecology is important, and cannot necessarily be explained only from relatedness.

Although we found no significant pattern with phylogenetic relatedness and emergence, we found that both *Tetropium* species were reducing densities of their next closest relative, *E. monticola*. There are many examples of invasive species outcompeting native species for habitat, resources, and establishment especially with invasive insects (NRC 2002, Kenis et al. 2009). Some of the best insect examples are of invasive ants. Lessard et al. (2009) examined phylogenetic structure of invaded and intact ant communities by meta-analysis of 12 unpublished studies and found that intact communities were more phylogenetically evenly dispersed than invaded communities

(Lessard et al. 2009). Intraguild predation of insects could also be happening between *Tetropium* and the next closest relative. Intraguild predation can occur between insects, fish, amphibians and generalist predators if there is differential growth between them, especially when there is a limiting resource (Polis et al. 1989). In fire ants, intraguild predation is pervasive and often very intense. Eubanks et al. (2002) found that fire ant workers dramatically reduced abundance of competitors such as lady beetles and green lacewings, and important arthropods were higher in abundance where the invasive ant was suppressed. In another field and lab experiment *Tramea lacerata* and *Erythemis simplicicollis* dragonflies significantly reduced the amount of damselfly larvae (Wissinger & McGrady, 1993).

Although both *Tetropium* species significantly reduced emergence of some insect community members, results from the regression show that phylogeny is not correlated with impact. There was no relationship between the species most affected and phylogenetic relatedness to *T. fuscum* or *T. cinnamopterum*. This means another force is driving the interactions between affected species and their *Tetropium* affecters.

I conclude that neither *T. fuscum* nor *T. cinnamopterum* are having a significant impact on more closely related species; however, I believe that more experiments should be conducted to reinforce this conclusion. The most closely related wood-boring cerambicid was significantly affected by both *Tetropium* spp., so there may be more complex interactions happening at a smaller scale.

## REFERENCES:

- Bright Jr, D. E. (1976). The insects and arachnids of Canada. Part 2. The bark beetles of Canada and Alaska. Coleoptera: Scolytidae. *The insects and arachnids of Canada. Part 2. The bark beetles of Canada and Alaska., Coleoptera: Scolytidae*
- Brock, M.T. (2004). The potential for genetic assimilation of a native dandelion species, *Taraxacum ceratophorum* (Asteraceae), by the exotic congener *T. officinale*. *American Journal of Botany*. 91(5): 656-663.
- Brown, B. J., Mitchell, R. J., and Graham, S. A. (2002). Competition for pollination between an invasive species (purple Loosestrife) and a native congener. *Ecology*, 83(8), 2328–2336.
- Brown, B. J., and Mitchell, R. J. (2001). Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia*. 129(1): 43-49.
- Darwin, C. (1859). *On the origin of species by means of natural selection*. London, England.: John Murray.
- Eubanks, M. D., Blackwell, S. A., Parrish, C. J., Delamar, Z. D., and Hull-Sanders, H. (2002). Intraguild predation of beneficial arthropods by red imported fire ants in cotton. *Environmental Entomology*., 31(6), 1168–1174.
- Gaunt, M. W., and Miles, M. A. (2002). An insect molecular clock dates the origin of the insects and accords with palaeontological and biogeographic landmarks. *Molecular Biology and Evolution*., 19(5), 748–761.
- Gotelli, N. J., and Arnett, A. E. (2000). Biogeographic effects of red fire ant invasion. *Ecology Letters*., 3(4): 257-261.

- Flaherty, L., Sweeney, J.D., Pureswaran, D., and Quiring, D.T. (2011). Influence of host tree condition on the performance of *Tetropium fuscum* (Coleoptera: Cerambycidae). 40: 1200–1209.
- Hedges, S. B., and Kumar, S. (Eds.). (2009). *The timetree of life*. OUP Oxford.
- Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O. S., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gómez-Zurita, J., Riberta, I., Barraclough, T. G., Bocakova, M., Bocak, L., and Vogler, A. P. (2007). A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science (New York, N.Y.)*, 318(5858), 1913–1916.
- Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Péré, C., Cock, M. J. W., Settele, J., Augustin, S., and Lopez-Vaamonde, C. (2009). Ecological effects of invasive alien insects. In D. W. Langor & J. Sweeney (Eds.), *Ecological impacts of non-native invertebrates and fungi on terrestrial ecosystems.*, (pp. 21–45). Dordrecht: Springer Netherlands.
- Lessard, J-P., Fordyce, J. A., Gotelli, N. J., and Sanders, N. J. (2009). Invasive ants alter the phylogenetic structure of ant communities. *Ecology*, 90(10), 2664–2669.
- National Research Council. (2002). Predicting invasions of nonindigenous plants and plant pests.
- Nijs, I., and Roy, J. (2000). How important are species richness, species evenness and interspecific differences to productivity? A mathematical model. *Oikos*, 88(1), 57–66.
- Olsen, T. M., Lodge, D. M., Capelli, G. M., and Houlihan, R. J. (1991). Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners,

- snails, and macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences*. 48(10): 1853-1861.
- Papadopoulou, A. A. I., and Vogler, A. P. (2010). Revisiting the insect mitochondrial molecular clock: the mid-Aegean trench calibration. *Molecular Biology and Evolution*., 27(7), 1659-1672.
- Parfrey, L. W., Lahr, D. J. G., Knoll, A. H., and Katz, L. A. (2011). Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proceedings of the National Academy of Sciences of the United States of America*., 108(33), 13624–13629.
- Patrick, R. (1988). Importance of diversity in the functioning and structure of riverine communities. *Limnol. Oceanogr.*, 33(6), 1304–1307.
- Polis, G., Myers, C., and Holt, R. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*., 20, 297-330.
- Porter, S. D., and Savignano, D. A. (1990). Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*., 71(6), 2095–2106.
- Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D. L., and Rasnitsyn, A. P. (2012). A total-evidence approach to dating with fossils, applied to the early radiation of the hymenoptera. *Systematic Biology*., 61(6), 973–999.
- Sanders, N. J., Gotelli, N. J., Heller, N. E., and Gordon, D. M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*., 100(5), 2474–2477.
- Sweeney, J., Price, J., Price, S., Smith, G. S., Broad, G., Goulet, H., and Goulet, H.

- (2005). Parasitism of the brown spruce longhorn beetle, *Tetropium fuscum* (Fabr.) (Coleoptera: Cerambycidae) in Halifax, Nova Scotia (pp. 18–21).
- Vinther, J., Sperling, E. A., Briggs, D. E. G., and Peterson, K. J. (2012). A molecular palaeobiological hypothesis for the origin of aplacophoran molluscs and their derivation from chiton-like ancestors. *Proceedings. Biological Sciences / The Royal Society.*, 279(1732), 1259–1268.
- Wardle, D. A., Nicholson, K. S., Ahmed, M., Rahman, A. (1994). Interference effects of the invasive plant *Carduus nutans* L. against the nitrogen fixation ability of *Trifolium repens* L. *Plant and Soil*. **163**:287-297.
- Wissinger, S., and McGrady, J. (1993). Intraguild predation and competition between larval dragonflies: Direct and indirect effects on shared prey. *Ecology.*, 74(1), 207-218.

## CHAPTER 4 – GENERAL DISCUSSION

We hypothesized that the competition would be weak between *T. fuscum* and more distantly related species. We predicted that *T. fuscum* would negatively affect the surrounding insect community and results from my thesis show that both the invasive and the native *Tetropium* species affect our focal insect community in red and Norway spruce. Both *Tetropium* spp. significantly lowered a combination of Simpson diversity, richness, or evenness in red and Norway spruce, and they also negatively affected some individual species within our focal community. In chapter 1, I predicted that the invasive *T. fuscum* would negatively affect the insect community as a whole. I conclude that both *Tetropium* species negatively affect the evenness and richness, and therefore diversity, of the insect focal community. Although both *Tetropium* spp. negatively affect diversity, the effect is more consistent when looking at *T. fuscum* in red spruce. The second prediction from our main hypothesis was *T. fuscum* would displace the most closely related species. Although both *Tetropium* species significantly lowered the emergence of four species, I found that looking at the community as a whole, the relationship between phylogenetic relatedness and competitive impact was not significant.

Highly successful invasive species that establish populations and utilize resources in new ranges often have negative effects on native communities via effects on the surrounding competitors, prey, and valuable resources and/or habitat (Gotelli & Arnett 2000, Sanders et al. 2002, Hedja et al. 2009, Lessard et al. 2009). Invasive species may outcompete and displace native species, which negatively affects community diversity (Porter & Savignano 1990, Gotelli & Arnett 2000, Sanders et al. 2002, Sanders et al.



2003). Using our collected insect community data we were able to compare the effects of *T. fuscum* and *T. cinnamopterum* on native wood-boring insects in Nova Scotia, Canada. I established that although *T. fuscum* negatively affected diversity, richness, and evenness in part within red and Norway spruce, so did the native species *T. cinnamopterum*. Although *T. fuscum* appears to cause similar effects on the insect community in spruce logs as does the native *T. cinnamopterum* we should still be concerned about its probable effects on biodiversity in Nova Scotia because of its apparently greater ability to colonize red spruce of healthier condition than that colonized by *T. cinnamopterum*. Chapin III et al. (2000) found that changes to species diversity are important to study as number of species, species composition, and species evenness within an area affect direct organismal traits that contribute to ecosystem processes. Species diversity also heavily influences ecosystem resilience to environmental change. They also found that species evenness warrants attention as it has important consequences to ecosystems (Chapin III et al. 2000).

Negative effects of an invasive species on their invaded community are expected and should be more intense on more closely related species as competition with ecologically similar congeners is expected (Darwin 1859, Schaefer et al. 2011, Dearborn et al. 2016). We found significant negative effects of *T. fuscum* and *T. cinnamopterum* on some but not all of the most closely related community members and did not observe a significant negative relationship between percent emergence from bolts and phylogenetic relatedness. However my results support the idea that both *T. fuscum* and *T. cinnamopterum* compete for resources with some community members (e.g. *E.*

*monticola*). Although species abundances were not significantly different between the most closely related species in our samples I believe it is a good preliminary study for invasive species. We also do not know how our species of interest are competing, but we know that *T. fuscum* interacts with its most closely related congener *T. cinnamopterum* (Dearborn et al. 2016). Both *Tetropium* species compete with second closest relative *E. monticola*, which may be influenced by time lag of development between species, therefore potentially facilitating intraguild predation, which is common in the animal kingdom (Polis et al. 1989, Wissinger & McGrady 1993, Eubanks et al. 2002). It would be interesting to examine the competitive effects of *T. fuscum* and *T. cinnamopterum* on each other and on *E. monticola* to see if we can understand the competitive forces driving these interactions.

In favourable conditions, i.e. damaged tree stands, *T. fuscum* populations could grow and lead to more damage on both insects in the community and overall tree health. Any large-scale damage with potential to weaken our forest systems would increase susceptibility to other invasive pests, disease, or outbreaking species. *T. fuscum* should not fall between the cracks of the public or scientific eye as it has the potential to negatively affect species within its ecosystem and valuable resources such as red spruce trees. Although *T. fuscum* seems to be blending into the environment we know that it negatively affects species diversity and has the potential to outbreak in favourable conditions. If we do not focus on this seemingly cryptic species then we risk altering forests in negative ways.

## REFERENCES:

- Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Díaz, S. (2000). Consequences of changing biodiversity. *Nature.*, 405(6783), 234–242.
- Darwin, C. (1859). *On the origin of species by means of natural selection*. London, England.: John Murray.
- Dearborn, K., Heard, S. B., Sweeney, J. D., and Pureswaran, D. (2016). Displacement of *Tetropium cinnamopterum* by its invasive congener *Tetropium fuscum*.
- Eubanks, M. D., Blackwell, S. A., Parrish, C. J., Delamar, Z. D., and Hull-Sanders, H. (2002). Intraguild predation of beneficial arthropods by red imported fire ants in cotton. *Environmental Entomology.*, 31(6), 1168–1174.
- Gotelli, N. J., and Arnett, A. E. (2000). Biogeographic effects of red fire ant invasion. *Ecology Letters.*, 3(4): 257-261.
- Hejda, M., Pyšek, P., and Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology.*, 97(3), 393–403.
- Lessard, J-P., Fordyce, J. A., Gotelli, N. J., and Sanders, N. J. (2009). Invasive ants alter the phylogenetic structure of ant communities. *Ecology.*, 90(10), 2664–2669.
- Polis, G., Myers, C., and Holt, R. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics.*, 20, 297-330.
- Porter, S. D., & Savignano, D. A. (1990). Invasion of polygyne fire ants decimates native

- ants and disrupts arthropod community. *Ecology.*, 71(6), 2095–2106.
- Sanders, N. J., Gotelli, N. J., Heller, N. E., and Gordon, D. M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America.*, 100(5), 2474–2477.
- Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G., and Savolainen, V. (2011). Testing Darwin’s naturalization hypothesis in the Azores. *Ecology Letters.*, 14, 389–396.
- Wissinger, S., and McGrady, J. (1993). Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology.*, 74(1), 207-218.

**APPENDIX A: METHODOLOGY OF ASSIGNING  
PHYLOGENETIC DISTANCE FROM *TETROPIUM FUSCUM* TO  
EACH COMMUNITY MEMBER**

We began by assembling a phylogenetic tree for the 15 insect taxa emerging from our bolts. To do this, we used various literature phylogenies that have been constructed in recent and past years that portray the phylogenetic relatedness of many insect groups (Gaunt et al. 2002, Hedges et al. 2009, Parfrey et al. 2011, Ronquist et al. 2012, Vinther et al. 2012). We used the website Time Tree (timetree.org) to search through literature phylogenies for published times of divergence for pairs of taxa in our tree. We removed repeated literature phylogeny divergence times, as in a few instances Time Tree reported two literature phylogenies from the same source analysis. Table A1 gives a list of all comparisons used to produce average times of divergence for our given insect community (Table A1). After using these tools to calculate times of species divergence we used literature phylogenies to create our tree in Figure 1.

We know *Evodinus monticola* is *Tetropium*'s closest relative, however the exact time of evolutionary divergence of *Tetropium* spp. from *Evodinus* relatedness was not found. I calculated my regressions using a small value (5 million years) and a large value (190 million years) and neither changed the non-significant results of the regressions.

**Table A1:** Average times of divergence from multiple sources found on Time Tree.

Average times of divergence is in million of years.

| Comparisons                |                               | Average Time of Divergence (Million Years Ago) | Sources              |                      |
|----------------------------|-------------------------------|--|----------------------|----------------------|
| Species A                  | Species B                     |  |                      |                      |
| <i>Tetropium fuscum</i>    | <i>Urocerus albicornis</i>    | 349.0  | 346.1                | Ronquist et al. 2012 |
|                            |                               |  | 310.7                | Parfrey et al. 2011  |
|                            |                               |  | 352.0                | Hedges et al. 2009   |
|                            |                               |  | 378.0                | Gaunt et al. 2002    |
|                            | <i>Thanasimus sp.</i>         | 236.2  | 236.2                | Hedges et al. 2009   |
|                            | <i>Xylophagus sp.</i>         | 283.0  | 340.0                | Vinther et al. 2012  |
|                            |                               |  | 280.9                | Ronquist et al. 2012 |
|                            |                               |  | 283.0                | Hedges et al. 2009   |
|                            | <i>Staphylinidae</i>          | 249.4  | 249.4                | Hedges et al. 2009   |
|                            | <i>Histeridae</i>             | 249.4  | 249.4                | Hedges et al. 2009   |
|                            | <i>D. rufipennis</i>          | 197.3  | 197.3                | Hunt et al. 2007     |
|                            | <i>Dryocoetes affaber</i>     |  |                      |                      |
|                            | <i>Dryocoetes autographus</i> |  |                      |                      |
|                            | <i>Xylosandrus germanus</i>   |  |                      |                      |
|                            | <i>Polygraphus rufipennis</i> |  |                      |                      |
| <i>Pissodes nemorensis</i> |                               |  |                      |                      |
| <i>Hylobius congener</i>   |                               |  |                      |                      |
|                            |                               |  | Kergoat et al. 2014  |                      |
|                            |                               |  | Kölsch et al. 2008   |                      |
|                            |                               |  | Rainford et al. 2014 |                      |

## REFERENCES:

- Gaunt, M. W., and Miles, M. A. (2002). An insect molecular clock dates the origin of the insects and accords with palaeontological and biogeographic landmarks. *Molecular Biology and Evolution.*, 19(5), 748–761.
- Hedges, S. B., and Kumar, S. (Eds.). (2009). *The timetree of life*. OUP Oxford.
- Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O.S., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., and Gómez-Zurita, J. (2007). A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, 318(5858), 1913-1916.
- Kergoat, G.J., Bouchard, P., Clamens, A.L., Abbate, J.L., Jourdan, H., Jabbour-Zahab, R., Genson, G., Soldati, L., and Condamine, F.L. (2014). Cretaceous environmental changes led to high extinction rates in a hyperdiverse beetle family. *BMC evolutionary biology*, 14(1), 1.
- Kölsch, G., and Pedersen, B. V. (2008). Molecular phylogeny of reed beetles (Col., Chrysomelidae, Donaciinae): The signature of ecological specialization and geographical isolation. *Molecular phylogenetics and evolution*, 48(3), 936-952.
- Papadopoulou, A. A. I., and Vogler, A. P. (2010). Revisiting the insect mitochondrial molecular clock: the mid-Aegean trench calibration. *Molecular Biology and Evolution.*, 27(7), 1659-1672.
- Parfrey, L. W., Lahr, D. J. G., Knoll, A. H., and Katz, L. A. (2011). Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proceedings of the National Academy of Sciences of the United States of America.*, 108(33), 13624–13629.

- Rainford, J. L., Hofreiter, M., Nicholson, D. B., and Mayhew, P. J. (2014). Phylogenetic distribution of extant richness suggests metamorphosis is a key innovation driving diversification in insects. *PLoS One*, *9*(10),
- Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D. L., and Rasnitsyn, A. P. (2012). A total-evidence approach to dating with fossils, applied to the early radiation of the hymenoptera. *Systematic Biology*, *61*(6), 973–999.
- Vinther, J., Sperling, E. A., Briggs, D. E. G., and Peterson, K. J. (2012). A molecular palaeobiological hypothesis for the origin of aplacophoran molluscs and their derivation from chiton-like ancestors. *Proceedings. Biological Sciences / The Royal Society*, *279*(1732), 1259–12







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- (2016) Impacts of the brown spruce longhorn beetle, *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae), on insect community structure in its invaded habitat of Nova Scotia, Canada. Presented MSc data at the Acadian Entomological Society Annual Meeting, Moncton, New Brunswick.
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- (2015) Impacts of the brown spruce longhorn beetle, *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae), on insect community structure in its

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- (2015) Impacts of the brown spruce longhorn beetle, *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae), on insect community structure in its invaded habitat of Nova Scotia, Canada. Presenting my first year of MSc data at the Acadian Entomological Society Annual General Meeting, in Fredericton, New Brunswick.