

Phenology and Spatial Distribution of Native and Exotic *Tetropium* Longhorned Beetles (Coleoptera: Cerambycidae)

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ABSTRACT The co-existence of two closely related *Tetropium* species in eastern Canada, invasive *T. fuscum* and native *T. cinnamopterum* (TF and TC, respectively), provides a model system to investigate seasonal and spatial demographic parameters of biological invasions at the interspecific level. In this study, we take advantage of the similar semiochemical communication of TF and TC to evaluate the abundance of adults of the two species concurrently using grids of traps baited with pheromone and host volatiles in stands of spruce. Adult TF emerged on average 2 wk before TC both in the field and under controlled laboratory conditions. This observation, combined with the early reproduction of emergent females, implies that the smaller (younger) larvae of native TC may be at increased risk of intra-guild predation by TF. The high spatial association between male and female TF in dense, aggregated populations suggests that the rate of mate encounter is depressed in sparse populations toward the edge of the invasive range. The higher level of spatial aggregation for TF than TC, particularly at high population density, suggests a higher propensity of adult TF to congregate at “landmarks.” Considering the broader range of host conditions, earlier seasonal emergence, and presumably more effective mate encounter for TF than TC, the exotic TF may be a superior competitor with the potential to displace or reduce the abundance of TC.

KEY WORDS aggregation, Allee effect, competitive displacement, SADIE analysis, spatial association

The growth in international trade and ubiquity of solid wood packaging material has led to repeated introductions of exotic wood borers (Haack 2006, Walters et al. 2009). In recent years, several species of longhorned beetles (Coleoptera: Cerambycidae) have become invasive pests because they kill trees in urban landscapes, spread to natural forests, threaten economic and ecological resources, and potentially displace native species (Smith and Hurley 2000, Buse et al. 2008, Haack et al. 2010). Documenting the spatial and temporal dynamics of longhorned beetles in natural habitats is difficult, owing to the cryptic nature of larval infestation within the phloem, difficulties in morphologically distinguishing larval species, as well as logistic constraints assessing the abundance of mobile adults. Despite recent advances in the development of semiochemical-baited traps for monitoring adults (Allison et al. 2004, Reddy 2007, Ibeas et al. 2007, Nehme et al. 2010), no study has yet compared the spatial distribution of exotic and native Cerambycidae during the process of biological invasion.

A recent example of an exotic–native pair of longhorned beetle species is *Tetropium fuscum* F.–*T. cinnamopterum* Kirby (TF and TC, respectively) in North America. The native TC has a broad distribution in Canada and predominantly infests spruce (*Picea* spp.) (Raske 1973). Larvae feed on phloem, usually on moribund or recently killed trees (fire killed or wind-blown) (Richmond and Lejeune 1945, Connola et al. 1956, Post and Werner 1988). The palearctic TF has become established on the Atlantic coast of Canada near Halifax, Nova Scotia (Smith and Hurley 2000). The two *Tetropium* species have similar univoltine life histories, primarily infesting weakened, dying spruce, except that TF occasionally infest live, apparently healthy spruce trees (Schimitschek 1944, Juutinen 1955, O’Leary et al. 2003).

Despite a presumably long separation on distinct continents, TF and TC use the same volatile cues to locate mates and host plants: individuals are attracted to the same host (spruce) volatiles, males of both species produce (*S*)-(*E*)-6,10-dimethyl-5,9-undecadien-2-ol as an aggregation pheromone that elicits a response from both males and females, and the simultaneous presence of the pheromone and host volatiles is essential for attraction (Sweeney et al. 2006, Silk et al. 2007, Lemay et al. 2010).

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The current study is part of a multi-year project aimed at developing semiochemical-based management strategies for TF. In this first installment, we document seasonal and spatial patterns of adult flight of TF and TC, using a protocol (matrix of traps) that allowed us to sample the two *Tetropium* species concurrently.

Materials and Methods

Laboratory Study. Data were obtained from daily emergence records from adults *Tetropium* from 80 red spruce (*Picea rubens*) Sarg. bolts (30–35 cm long \times 15–35 cm diameter) incubated at 20–22°C and 45–60% RH in the containment laboratory in Fredericton. The bolts were cut from 1.2 m long spruce bait in the winter months (30 November 2000 through 30 March 2001) after exposure to *Tetropium* infestation at Point Pleasant Park, Nova Scotia (44.62°N, 63.57°W) from 21 June through 30 August 2000 (35 bolts) or 6 June through 30 August 2001 (41 bolts) and at Morris Lake (44.65°N, 64.49°W) from 26 June through 30 August 2001 (four bolts). The bolts were stored at –2°C until set up in screen-vented Plexiglas cages (45 \times 45 \times 45 cm). Adult *Tetropium* were sexed and identified to species (Smith and Hurley 2000) and vouchers deposited in the Atlantic Forestry Centre collection.

Field Study Sites. The study was conducted in forested stands with documented infestations of TF in Halifax County, Nova Scotia, Canada. We selected three study sites in each of 2 yr [2008: Conrad one (44.72°N, 63.46°W), Devon (44.90°N, 63.43°W), and Lake (44.73°N, 63.46°W); 2009: Conrad two (44.70°N, 63.53°W, Devon, and Porto (44.76°N, 63.54°W)]; the sites were designed in reference to local landmarks. All sites had similar tree composition, with red spruce the most dominant (38 to 85% of stems >10 cm diameter at breast height, and balsam fir (*Abies balsamea* L.) and red maple (*Acer rubrum* L.) common (usually >10%). Each experimental site consisted of a 0.81-ha plot (90 \times 90 m plot) surrounded by forested stands, with the exception of Devon in 2009 where the immediate surrounding area (>20 ha) outside of the plot was clear cut in the winter of 2008–2009. All plots were within a 260 km² area; the closest plots were Conrad one and two (2.7 km apart) and the furthest were Conrad two and Devon (23 km apart). The plots closer to Halifax harbor (Conrad, Lake, Porto), where TF invasion was initially reported, generally had a greater percentage of trees with signs of TF infestation than did Devon, which lay \approx 20 km north.

Sampling Procedure. We evaluated the abundance of adult *Tetropium* species, using as a proxy captures in semiochemical-baited black intercept panel traps deployed in a regular grid of 100 evenly spaced traps (10 m apart in both directions). Most traps (>97%) were PT Intercept traps (AlphaScents, Bridgeport, NY), formerly known as the integrated pest management Intercept trap (Sweeney et al. 2006), which were suspended from ropes tied between two trees so that the trap was \approx 1 m from the nearest tree and the collecting cup was 10–20 cm above ground. Cross-vane pan traps (Sweeney et al. 2006) were used for

grid positions where it was not practical to suspend traps from ropes; these two trap designs do not differ in mean catches of *Tetropium* species (Sweeney et al. 2004). Each trap was baited with three lures: (1) a 0.2 ml thin wall, polymerase chain reaction sample tube (Axygen Scientific Inc., Union City, CA) with a 1 mm diameter hole drilled in the cap that emitted synthetic racemic fuscumol (sex/aggregation pheromone of TF and TC; Silk et al. 2007) at a rate of \approx 800 μ g/d; (2) an ultra high release “BSLB kairomone lure” that emitted a blend of five monoterpenes (44% racemic α -pinene, 19% (-)- β -pinene, 10% (+)-3-carene, 18% (+)-limonene and 9% α -terpinolene) at \approx 2,000 mg/d (Sweeney et al. 2006), and (3) an ultra high release ethanol lure (275 mg/d) (ConTech Inc., Delta, BC). All release rates were measured at 20°C. Captured beetles were killed and preserved in a 50:50 mixture of propylene glycol and deionized water plus 0.5 ml/L of Kodak Photo-Flo 200 to reduce surface tension, and 12.5 mg/L of Bitrex (denatonium benzoate [sigma-aldrich.com]) to deter consumption by mammals in the trap collecting bucket. It took 1–2 d per plot to set up the traps. Traps were baited 12–13 May and checked every 1–2 wk until 27 August in both years except at the Lake site where traps were out from 21 May to 20 August. The trapping period covered most of the interval of *Tetropium* adult activity between May and August of 2008 and 2009, as indicated by the very low captures for the earliest and latest sampling periods. Beetles were collected from traps every 1–2 wk, kept separate by individual trap and site, and stored in 70% ethanol until identified and sexed in the laboratory.

For each site and year, we estimated the local abundance of beetles by placing a 35 cm high black nylon emergence cage around the bole (at breast height) of five red spruce trees with signs of *Tetropium* infestation. Each trap was fitted with a 125 ml translucent Nalgene bottle, half-filled with propylene glycol to collect emerging beetles. Emergence traps were checked weekly to record in situ the number of emerged beetles (x_1 = number of beetles per tree for TF and TC). We evaluated the number of red spruce and white spruce (*Picea glauca* Moench Voss) in four to seven 11.3 m radius plots (400 m²) at each site; the variable number of plots at different sites was because of time constraints and also reflected an objective to examine \approx 100 trees per site. Spruce trees were classified as either infested with *Tetropium* (presence of emergence holes or resinous flow) or not, and the number of infested trees per ha (x_2) was calculated for each site. The local population of beetles (y) was estimated using the equation $y = x_1 * x_2$.

Spatial Analysis. We quantified spatial aggregation for beetle counts across traps, and spatial association between sexes and between species, using SADIEShell 1.22 (Kelvin F. Conrad and IACR-Rothamsted 2001). The SADIE (Spatial Analysis using Distance IndicEs) approach measures spatial aggregation (I_a) based on the number of individual movements needed to convert a given spatial distribution to regularity, expressed relative to the average number of movements needed for spatially randomized distribu-

Table 1. Parameters characterizing the abundance and seasonality of *Tetropium* species in stands of spruces (TF = *T. fuscum*; TC = *T. cinnemopterum*)

Parameter	Species	2008			2009			Mean \pm SE
		Conrad	Devon	Lake	Conrad	Devon	Porto	
Sampling based on host plant sampling								
Spruce trees per ha		358	92	255	700	92	370	235 \pm 77
Infested trees per ha		125	25	65	119	25	100	72 \pm 29
Emergent adults	TF	5.8	0.8	10.0	1.2	0	5.2	3.8 \pm 1.6
Per sentinel tree	TC	0	0.8	0.2	0.2	0	0.4	0.3 \pm 0.1
Relative density	TF	725	20	650	143	0	520	
Of adults per ha ^a	TC	0	20	13	24	0	40	
Sampling based on semiochemical trapping								
Total captures	TF	407	117	732	389	163	330	356 \pm 89
	TC	86	74	43	25	40	73	57 \pm 10
Sex-ratio (δ/φ)	TF	0.65	0.77	0.63	0.78	1.01	1.05	0.82 \pm 0.07
	TC	1.87	1.06	1.53	1.08	1.14	1.03	1.29 \pm 0.14
Median date of captures (Julian) ^b	TF	172	165	176	169	167	170	170 \pm 2
	TC	186	193	181	183	194	181	186 \pm 2
Level of protandry (Days) ^b	TF	6	2	10	8	1	12	5.4 \pm 1.7
	TC	9	9	7	17	6	6	9.6 \pm 1.9

^a Number of infested trees per ha * no. of emergent adults per sentinel tree.

^b Estimated using the logistic function of the no. of adults captured at a given time period in relation to the total no. of adults captured over the entire season.

tions. A distribution is aggregated when $I_a > 1.0$, and significance testing for I_a is provided by comparison with the randomized distributions (Perry 1998). Spatial association between sexes or species was estimated by χ , a statistic based on the spatial correlation between local clustering of each sex or species (Perry and Dixon 2002), with autocorrelation within each sex or species first removed using the method of Dutilleul (1993). Significance testing for χ , like that for I_a , is provided by spatial randomization of the data. We based all significance tests on 5,967 replicate randomizations, using two-tailed tests of significance.

Data Analysis. We conducted further statistical analyses with the SAS statistical package (version 9.1, SAS Institute, Cary, NC). We used paired t -tests to compare various demographic parameters (abundance, sex ratio, and timing of captures) between TF and TC across sites. At each site, we used logistic regression modeling to evaluate the cumulative proportion of individuals captured by a given date; the seasonality of emergence was then estimated as the ordinal date corresponding to the median point (50% of individuals) of captures. The level of protandry was calculated as the difference between the median date of captures for males minus that for females. Factorial analysis of variance (ANOVA) was used to evaluate the effect of species and sex on the timing of emergence of individuals reared in the laboratory. We used regression analysis to evaluate relationships between the number of beetles captured in baited traps or on sentinel trees and the indices of spatial aggregation (I_a) and association (χ).

Results

The number of trees with signs of infestation by *Tetropium* varied among sites from 25 to 125 ha⁻¹ (Table 1). Twelve times more TF than TC emerged from sentinel trees (3.8 vs. 0.3), although the differ-

ence was variable among sites and marginally insignificant ($t_5 = 2.22$; $P = 0.077$) (Table 1). The average number of adults captured per 100 traps at different sites was six times higher for TF ($N = 356$) than TC ($N = 57$) ($t_5 = 3.25$; $P = 0.023$) (Table 1). The sex ratio of trapped individuals was female-biased for TF (0.8

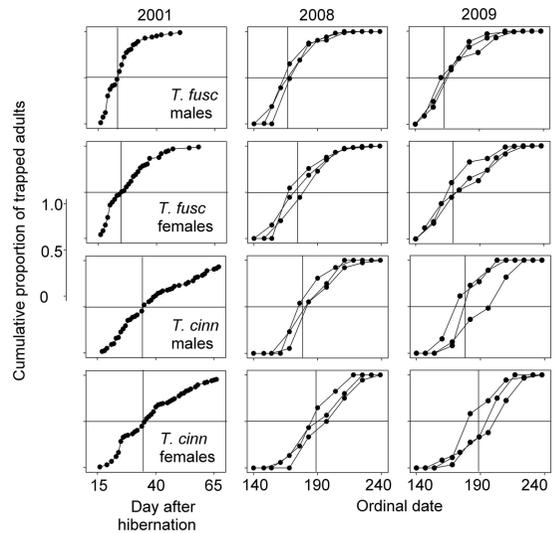


Fig. 1. Seasonal pattern of captures of exotic TF and native TC in intercept traps baited with fuscumol, spruce blend, and ethanol in spruce-dominated forest stands in Nova Scotia. For all sites, the cumulative proportion of trapped adults for a given time period t was obtained by dividing the number of adults captured up to time t by the total number of adults captured for the whole season. The vertical line for each plot indicates the average ordinal date corresponding to median level of captures. The study was conducted at three sites (corresponding to three lines per plot) in both 2008 and 2009. The demographic parameters for the different sites are listed in Table 1.

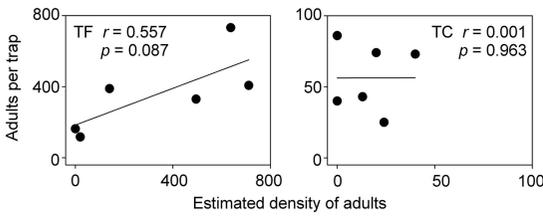


Fig. 2. Relationship between the estimated density of adults per ha and the number of individuals captured in intercept traps baited with fuscumol, spruce blend, and ethanol in spruce-dominated forest stands in Nova Scotia for exotic TF and native TC. Demographic parameters of populations of the two *Tetropium* species at different sites are listed in Table 1.

male per female) and male-biased for TC (1.3 male per female), but the difference between species was marginally insignificant ($t_5 = 2.39$; $P = 0.063$).

Adults were captured between late May and mid August (Fig. 1). The median date of captures, estimated using logistic regression models, varied between 14 and 25 June for TF and between 30 June and 14 July for TC (Table 1), which represents a significant interval of >2 wk between the two species ($t_5 = 4.42$; $P = 0.007$). Median capture dates occurred significantly earlier for males in each species (Table 1; Fig. 1; TF = 5.4 d, $t_5 = 3.64$, $P = 0.015$; TC: 9.6 d, $t_5 = 5.32$, $P = 0.003$); the degree of protandry did not differ between species ($t_5 = 1.05$; $P = 0.340$).

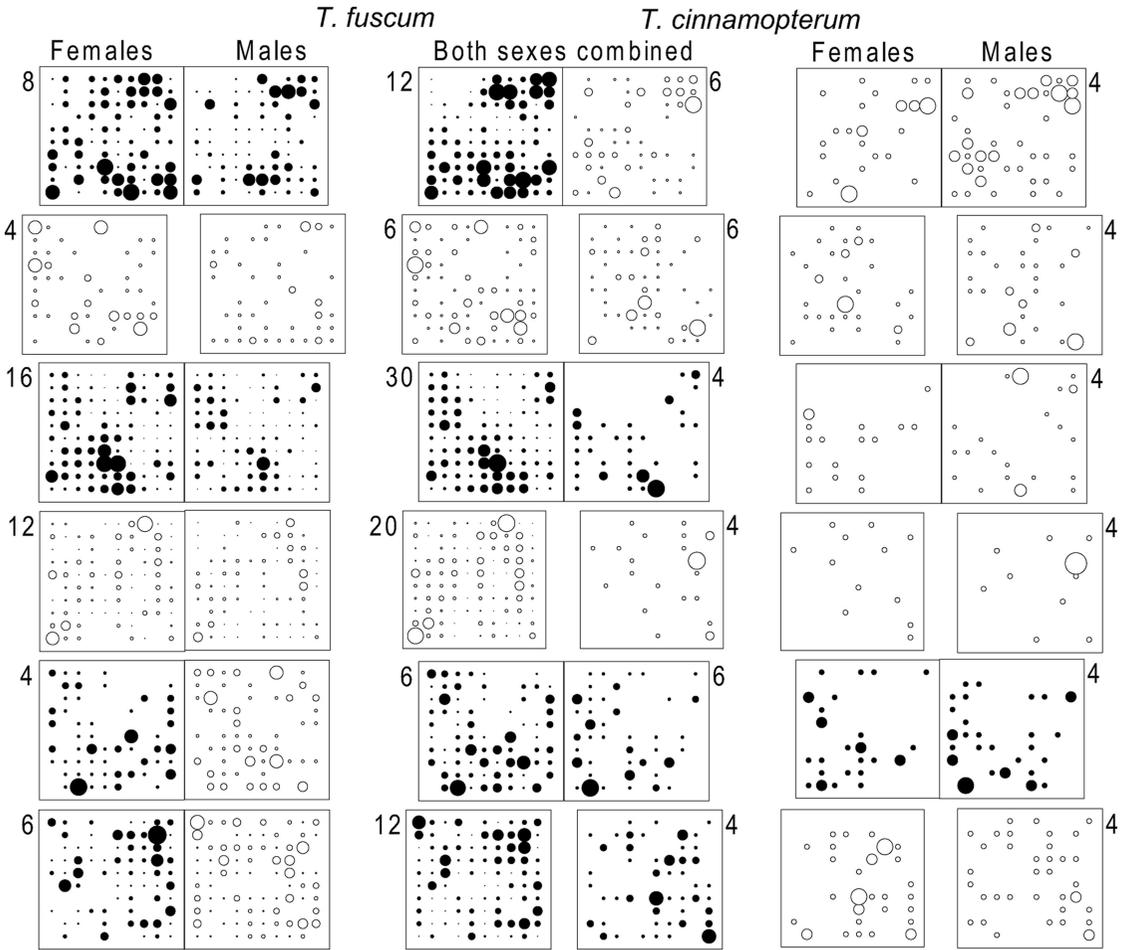


Fig. 3. Spatial distribution of males and females for exotic TF and native TC captured in intercept traps baited with fuscumol, spruce blend, and ethanol in spruce-dominated forest stands in Nova Scotia. Demographic parameters and descriptors of spatial distribution (SADIE analysis) of populations of the two *Tetropium* species at different sites are listed in Tables 1 and 2. The relative size (scale) of circles varied in different plots to ensure that the spatial distribution of beetles was visible; numbers beside the different plots represent the number of adults corresponding to the largest circles. The following sites are represented from top to bottom: (1) Conrad 2008, (2) Devon 2008, (3) Lake 2008, (4) Conrad 2009, (5) Devon 2009, (6) Porto 2009. The color of the circles indicates whether the distribution was significantly aggregated (black circles) or not significant (white circles) (index I_a in Table 2). The distance between plots indicates whether the spatial distribution was aggregated among species or sex (plots in contact with each other) or not aggregated (plots apart from each other) (index χ in Table 2).

Table 2. Parameters characterizing the spatial distribution of *Tetropium* species in stands of spruces (TF = *T. fuscum*; TC = *T. cinnamopterum*), as evaluated using the SADIE procedure

Parameter	Species	2008			2009			
		Conrad	Devon	Lake	Conrad	Devon	Porto	
Index of spatial aggregation (<i>I</i> _a)	TF ♀	1.95 ^b	1.08	2.03 ^b	1.14	1.39 ^a	1.70 ^b	
	TF ♂	1.75 ^b	1.14	1.49 ^a	1.19	1.20	1.15	
	TF all	2.09 ^b	1.15	1.95 ^b	1.22	1.53 ^a	1.59 ^a	
	TC ♀	1.09	0.99	1.33	1.08	1.57 ^a	1.23	
	TC ♂	1.22	0.86	1.36	1.05	1.37 ^a	0.97	
	TC all	1.30	1.01	1.40 ^a	1.22	1.73 ^b	1.22	
Level of spatial association (χ)								
	By sex	TF	0.564 ^b	0.168	0.454 ^b	0.343 ^a	0.331 ^a	0.249 ^a
By species		TC	0.292 ^a	0.137	0.226 ^a	0.075	0.176 ^a	0.107
			0.389 ^b	0.177	0.360 ^b	0.123	0.296 ^b	0.174

Significance level was determined using spatial randomization of the data, using 5,967 randomizations for each each test.

^a $P < 0.001$.

^b $P < 0.05$.

A total of 181 TF (84 males, 97 females) and 253 TC (119 males, 134 females) emerged from 80 bolts that were collected in winter and incubated at 20–22°C in the laboratory. The adults emerged from bolts after 16–98 d of incubation. On average, TF emerged ≈13 d before TC, a difference that was highly significant (Fig. 1). The timing of emergence was similar for males and females, as revealed by the nonsignificant effect of sex on emergence time, either alone ($F = 0.23$; $P = 0.633$) or in interaction with species ($F = 2.61$; $P = 0.107$).

The relationship between the numbers of adults per hectare and per trap was not significant for TC, and a marginally insignificant trend was observed for TF (Fig. 2). Trap captures were spatially aggregated (departure from random distribution) at four of six sites for TF and three sites for TC (Fig. 3; Table 2). The level of aggregation was density dependent for TF but not TC (Fig. 4). Captures of males and females were often spatially associated (local clustering) (TF: five of six sites; TC: three sites; Fig. 3; Table 2). The strength of spatial association between the sexes increased with spatial aggregation for TF but not TC (Fig. 5).

Discussion

Despite the recent development of semiochemical-baited traps to capture adult Cerambycidae (Allison et

al. 2004, Reddy 2007, Ibeas et al. 2007, Nehme et al. 2010), we are not aware of any study that has compared trapping data versus the local abundance of adults. The positive (yet marginally insignificant) relationship between the numbers of TF per hectare and per trap (Fig. 2) suggests that trapping reflects the local abundance of adults, which justifies the use of indices of spatial distribution based on pheromone traps to document demographic processes associated with biological invasion (Tobin et al. 2007). The absence of a density response for TC (Fig. 2), in contrast, suggests that some trapped individuals immigrated from outside the experimental sites, thus trap captures may not reflect the true population dispersal.

Earlier adult emergence for TF than TC (Fig. 1) may be of competitive advantage. Females of both *Tetropium* species readily mate and begin ovipositing soon thereafter (J.D.S, unpublished results) hence the 2 wk phenological offset between TF and TC suggests a priority effect favoring the exotic TF. Delayed oviposition and larval development for TC may lead to increased susceptibility to intraguild predation by TF larvae. Cannibalism and intraguild predation are common among insects that feed in concealed niches, including wood-boring cerambycid larvae, and early instars are most susceptible to predation by older larvae (Anbutsu and Togashi 1997, Ware and Stephen 2006, Richardson et al. 2010).

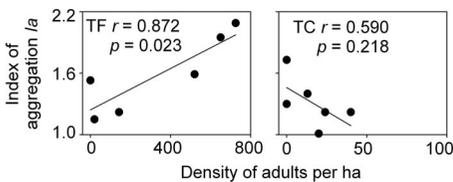


Fig. 4. Relationship between the estimated density of adults of exotic TF and native TC in spruce-dominated forested stands in Nova Scotia versus the level of spatial aggregation among individuals captured in intercept traps baited with fuscumol, spruce blend, and ethanol. Demographic parameters of populations of the two *Tetropium* species at different sites are listed in Tables 1 and 2.

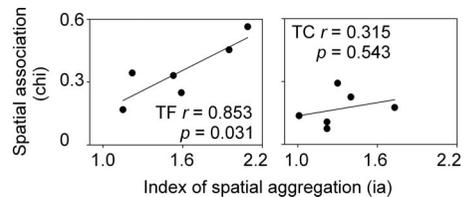


Fig. 5. Relationship between the spatial association between sexes and the level of spatial aggregation for exotic TF and native TC captured in intercept traps baited with fuscumol, spruce blend, and ethanol in spruce-dominated forested stands in Nova Scotia. Demographic parameters of populations of the two *Tetropium* species at different sites are listed in Tables 1 and 2.

Reduced mate encounters at low population density (Allee effect) sometimes preclude or retard the establishment and diffusion of invasive organisms (Liebhold and Tobin 2008, Rhainds 2010). The high spatial association between male and female TF in dense, aggregated populations (and conversely low association in low-density populations; Figs. 4 and 5) suggest that the rate of mate encounter is depressed in sparse populations toward the edge of the invasive range (Tobin et al. 2007). The overall low spatial association between males and females TC (Fig. 5) suggests a potentially higher risk of mating failure for the native species.

The level of spatial aggregation at the stand level was higher for TF than TC, particularly at high population density (Fig. 4), which suggests a higher propensity of adults to congregate at "landmarks" for TF. Because neither the distribution of resident adults or potential host plants was recorded, however, the mechanisms underlying spatial aggregation by TF remain unclear. The density dependence of aggregation for TF is potentially important because it suggests a mechanism for self-regulation of populations at high density (via increasing intraspecific competition, e.g., Ives and May 1985, Heard and Remer 1997).

In conclusion, the TF-TC exotic-native pair offers an interesting example of an invader that is phylogenetically related to and shares a similar ecological niche with a native species. A strong impact of the invader on the native species is expected in this system. The broader range of host conditions, earlier seasonal emergence, and presumably more effective mate encounter for TF than TC suggests that TF is a superior competitor. It remains to be determined if TC densities change in response to TF invasion or whether the long-term outcome of the interaction might result in species replacement.

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