

Interspecific competition between *Coptotermes gestroi* and *Odontotermes formosanus* in a forest ecosystem

by

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Abstract

Coptotermes gestroi (Wasmann) is an invasive termite species, and *Odontotermes formosanus* (Shiraki) a species endemic to Taiwan. Both are found in the Xiaping Tropical Botanical Garden, Nantou, Taiwan. Among 581 termite-monitoring wood stakes in Xiaping Tropical Botanical Garden, 280 were not consumed by termites, while 384 were exclusively occupied by *O. formosanus*, 5 by *C. gestroi*, and 12 stakes were fed upon by both species. The later 12 stakes were assumed to represent their interspecific territory. In the interspecific territory, succession between *O. formosanus* and *C. gestroi* on wood stakes was observed, and these two species rarely co-occurred on a wood stake at the same time. Both species have different seasonal activity patterns and responded to climatic factors in the intraspecific territories which indicates that seasonality maybe the main factor affecting succession. Only *C. gestroi* displayed seasonal activity in the interspecific territory, and the seasonal activity pattern of *O. formosanus* was different in interspecific and intraspecific territories. Thus, termite succession was not fully explained by seasonal activity. A control strategy of *C. gestroi* was conducted with Recruit HD termite baits starting in October 2014, and *O. formosanus* rapidly foraged on the wood stakes in the intraspecific territory of *C. gestroi*. It supports that once *C. gestroi* populations are weakened, *O. formosanus* may quickly invade its territory. The interspecific competition between endemic *O. formosanus* and invasive *C. gestroi* was documented in this study.

Keywords: invasive species, endemic species, interspecific competition, interspecific territoriality, multi-genera termite fauna, species succession

Introduction

Coptotermes gestroi (Wasmann) is a widespread termite pest in the world. *C. gestroi* is invasive to Taiwan (Li et al. 2009), and has become one of the major structural pests in southwestern Taiwan (Yang and Li 2012, Termite Identification Service 2015). In addition, *C. gestroi* was recently reported in Taiwanese forests and infesting living trees (Li et al. 2011, Li et al. 2015), including some native and economically valuable tree species, such as *Fraxinus formosana* Hayata and *Calocedrus formosana* (Florin) making *C. gestroi* a potential forest pest in Taiwan. In February 2013 four long-term monitoring plots were set up in a forest of Nantou, Taiwan to conduct a risk assessment of *C. gestroi* damage in the forest. The fungus-growing termite *Odontotermes formosanus* (Shiraki), a common, endemic species in Taiwan (Chiu et al. 2010,

Yang and Li 2012), also occurred in the monitoring plots. *C. gestroi* and *O. formosanus* both fed on wood stakes in the monitoring plots, and their succession on wood stakes was recorded. Since October 2014, Recruit HD termite baits were placed near *C. gestroi* colonies within the monitoring plots to control their populations. The assumption was that elimination of a *C. gestroi* colony would open the niche previously occupied by *C. gestroi* for *O. formosanus*. The invasion of other termite genera during the baiting process has been reported in previous studies (Sornnuwat et al., 1996; Messenger et al., 2005; Lee et al., 2007). The succession of *C. gestroi* and *O. formosanus* on wood stakes provided a chance to study the interactions between an invasive termite and an endemic termite in a natural environment. Two possible mechanisms of termite succession, seasonal activity and interspecific competition, were examined in this study.

Material and Methods

A total of 581 wood stakes (143–148 stakes per plot) were installed in four long-term monitoring plots in the Xiaping Tropical Botanical Garden, the Experimental Forest, National Taiwan University, Nantou, Taiwan, in February 2013. The wood stakes were inspected monthly until October 2015, and the termite species infesting each wood stakes was identified.

Wood stakes occupied by only one termite species in the observed period were defined as intraspecific territory, and the stakes previously occupied by both termite species were defined as interspecific territory.

Seasonal activity

The monthly number of wood stakes occupied by termites in the intraspecific territory were used for analysis of seasonal activity from February 2013 to September 2014. Stepwise regression was used to find potential climatic factors affecting seasonal activity of the termites. Six climatic factors, humidity, rainfall, mean temperature, number of rainy days, evaporation, and range of temperature were included in the full model.

To test whether termites displayed general seasonal activity in the interspecific territory, the seasonal activities in intraspecific and interspecific territory were compared using Pearson correlation analysis.

Post effects of *C. gestroi* elimination

Three colonies of *C. gestroi* were marked in the monitoring plots, and treated with Recruit HD termite baits beginning in October 2014. To test the post effects of *C. gestroi* elimination on foraging of *O. formosanus*, the foraging pattern of *O. formosanus* in four area types, including non-termite-occupied areas, the intraspecific territory of *C. gestroi*, the intraspecific territory of *O. formosanus* and the interspecific area, were compared with a Kolmogorov-Smirnov test. The monthly cumulative number of wood stakes infested by *O. formosanus* from October 2014 to October 2015 was used for analyzing the foraging pattern of *O. formosanus*.

Results and Discussion

The intraspecific territories of *O. formosanus* and *C. gestroi* contained 387 and 5 wood stakes, respectively, showing that *O. formosanus* was the dominant species in this area. The interspecific area contained 12 stakes.

Eleven species succession events occurred in the interspecific territory during February 2013 – September 2014, 6 events involved *C. gestroi*, replacing *O. formosanus* and 5 events were when *O. formosanus* replaced *C. gestroi*. In the interspecific territory, wood stakes were mostly occupied by one species (28 observations) and rarely occupied by two species at the same time (2 observations), which indicates that these two species are not likely to share a wood stake. Agonistic behavior between *C. gestroi* and *O. formosanus* was observed in the laboratory, supporting the contention that these two species are competitors.

In the intraspecific territory, seasonal activity of *O. formosanus* responded negatively to mean temperature, and activity of *C. gestroi* provided a positive response to mean temperature, range of temperature, but negatively to number of rainy days (Table 1). The two species provided different responses to the climatic factors we examined, and their distribution in a habitat may therefore separate naturally. However, we found that the seasonal activity of *O. formosanus* in the interspecific territory was different to that in intraspecific territory (Fig. 1A), and the seasonal activity of *C. gestroi* in intraspecific and interspecific territories were similar (Fig. 1B). Thus, termite succession in the interspecific territory was not fully explained by the seasonal activity data. We propose that, in the interspecific territory, agonistic interactions between *O. formosanus* and *C. gestroi* affect the seasonal activity of *O. formosanus*.

Table 1. Testing the effects of climatic factors on termite seasonal activity with stepwise regression. Six climatic factors, humidity, rainfall, mean temperature, number of rainy day, evaporation, and range of temperature were included in the full model.

Dependent variable	Independent variable	Slope	t value	P
No. of stake occupied by <i>O. formosanus</i>	Rainfall	-0.02	-1.64	0.12
	Mean temperature	-1.91	-2.88	<0.05
No. of stake occupied by <i>C. gestroi</i>	Mean temperature	0.28	5.26	<0.001
	No. of rainy day	-0.06	-2.41	<0.05
	Range of temperature	0.24	4.89	<0.001

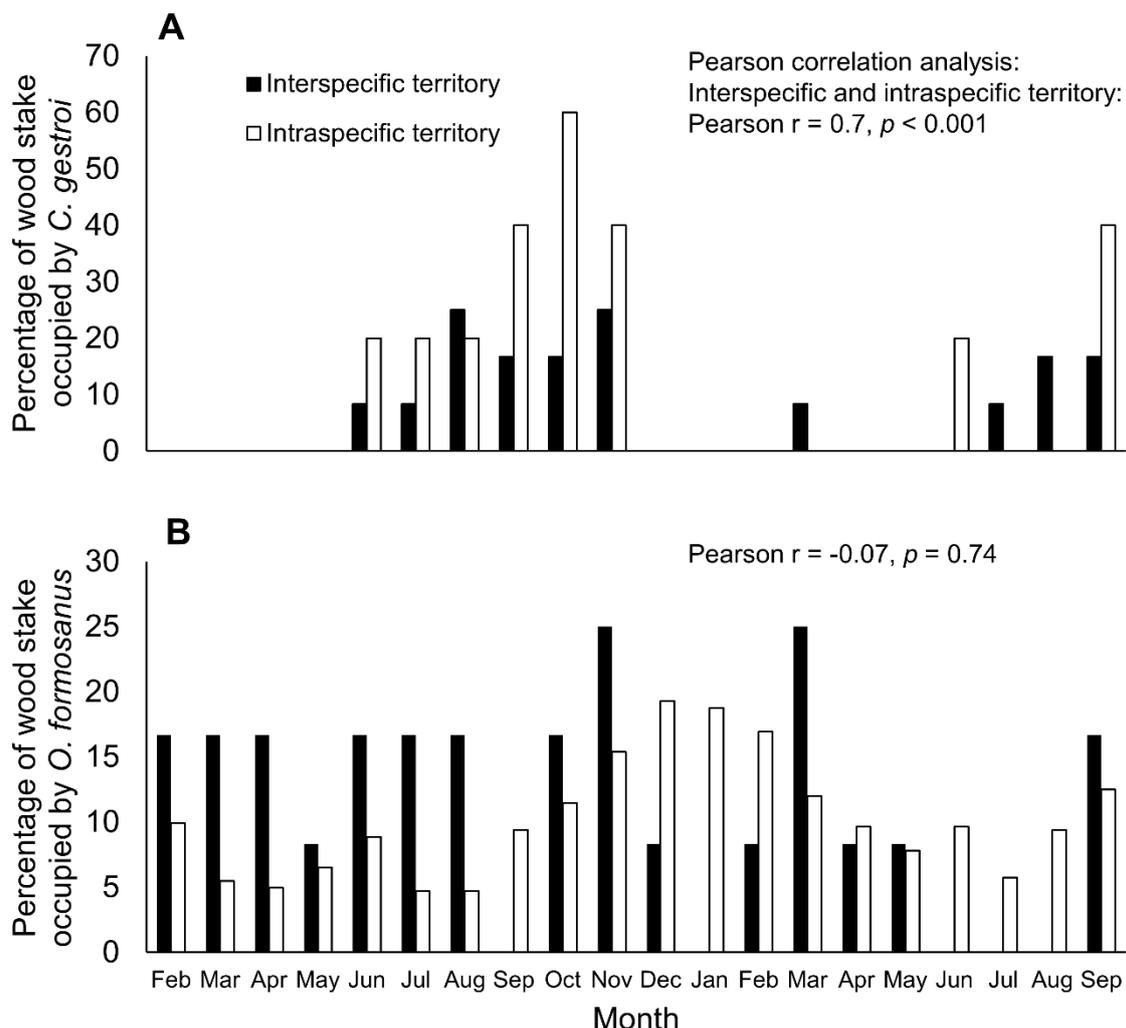


Fig. 1. Comparing seasonal activity at wood stakes in interspecific and intraspecific territories of *O. formosanus* (A) and *C. gestroi* (B). Seasonal activity of *O. formosanus* in the intraspecific territory was different in the interspecific territory, and seasonal activity of *C. gestroi* in the interspecific and intraspecific territories were similar.

After the *C. gestroi* colonies were baited, *O. formosanus* rapidly took over stakes in the intraspecific territory previously occupied by *C. gestroi* (Fig. 2). The foraging territory replacement rate of *O. formosanus* in the intraspecific territory of *C. gestroi* was significantly higher than in the non-termite-occupied area, the intraspecific territory of *O. formosanus*, and the interspecific territory (Fig. 2; Kolmogorov-Smirnov test: non-termite-occupied area: $D = 0.89$, $p < 0.001$; intraspecific territory of *O. formosanus*: $D = 0.89$, $p < 0.001$; interspecific territory: $D = 0.67$, $p < 0.05$). We propose that, foraging of *O. formosanus* in the intraspecific territory was inhibited by *C. gestroi*'s activity, and once *C. gestroi* was baited and being weakened, *O. formosanus* quickly invaded the abandoned *C. gestroi*'s territory through the empty subterranean gallery system.

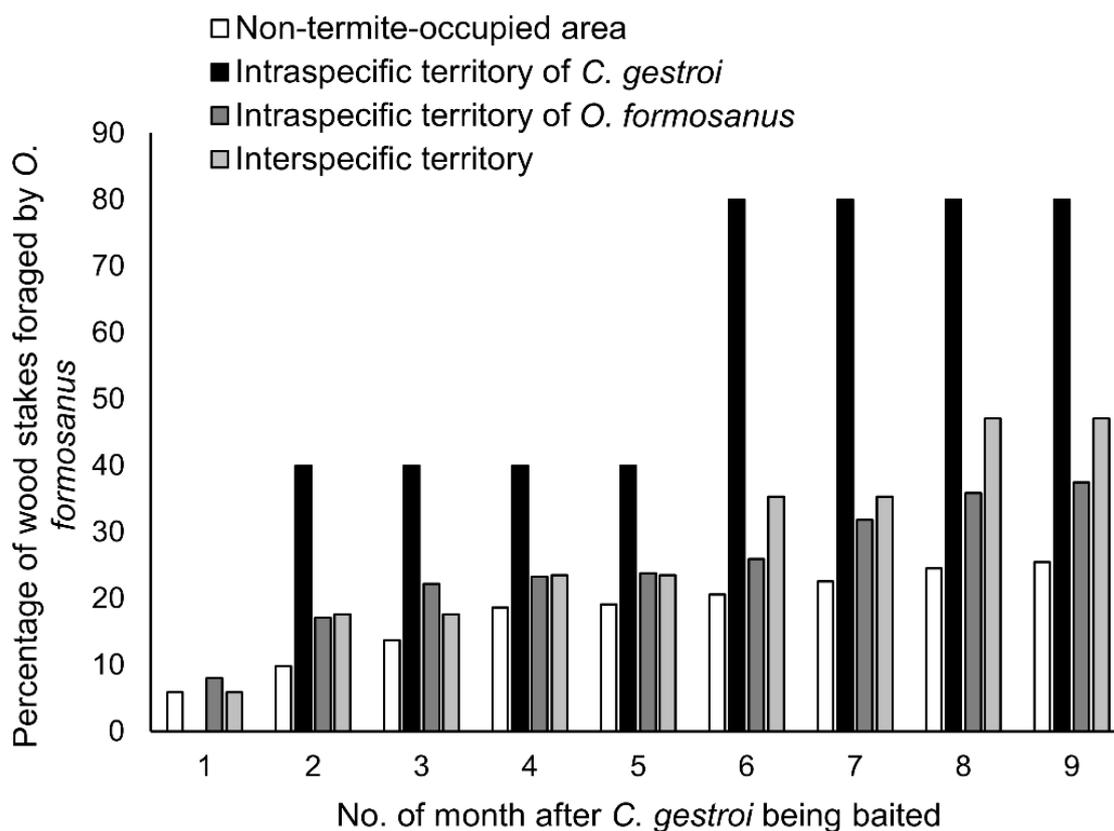


Fig. 2. Monthly cumulative number of wood stakes occupied by *O. formosanus* in non-termite-occupied area, the intraspecific territory of *C. gestroi*, the intraspecific territory of *O. formosanus* and the interspecific area after *C. gestroi* being baited. The foraging speed of *O. formosanus* in intraspecific territory is higher than that in the other three area types.

Conclusions

The current study documented the foraging interaction between invasive and endemic termites in a natural environment. In the forest study site, the territory of *O. formosanus* was larger than that of *C. gestroi*. In the overlapping intraspecific territory, the seasonal activity of *O. formosanus* was significantly affected by *C. gestroi* but not vice versa. The foraging behavior of the endemic higher termite, *O. formosanus*, was inhibited by the invasive subterranean *C. gestroi*. Once *C. gestroi* was baited, *O. formosanus* quickly occupied the territory left by *C. gestroi*. Further study is needed to more clearly understand the ecological effects of invasive termites on native fauna and flora.

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