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Research Article

Settlement and population competition assessments of invasive Argentine ants (*Linepithema humile*) in South Korea

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Abstract

This study assessed the effects of the Argentine ant (*Linepithema humile*), an invasive species, on the indigenous ant fauna in Busan, South Korea. Ant communities were sampled using pitfall traps placed along two transects in areas where *L. humile* was recently discovered (2019) in South Korea. Overall, we identified 14 ant species belonging to 12 genera and four subfamilies. We found that the species richness of the native ant community was significantly lower in areas invaded by *L. humile*, and most epigeic ants from the study area were not found co-existing with the Argentine ant. Five native epigeic species, namely *Nylanderia flavipes*, *Pristomyrmex punctatus*, *Tetramorium tsushimae*, *Formica japonica*, and *Lasius japonicus*, were strongly impacted by the invasion. In contrast, no effects were observed on two epigeic species (*Camponotus vitiosus* and *Monomorium chinense*) and one hypogeic species (*Brachyponera chinensis*). These results indicate that the successful settlement of Argentine ant has had a significant negative impact on native ant diversity in South Korea, confirming that *L. humile* is a very effective and competitive colonizer, despite its restricted dispersal capability. Management programs need to urgently implement control measures to ensure that *L. humile* does not spread further in South Korea.

Key words: Busan, diversity, epigeic, Formicidae, indigenous, introduced, native

Introduction

Invasion of alien species continues to increase due to human-mediated international trade and climate change, and these invasive species are known to reduce biodiversity or pose a threat to public health (Early et al. 2016; Hulme 2017; Seebens et al. 2017). The resulting economic effects globally are enormous, and have been estimated at approximately US$1.288 trillion over the last 50 years (Zenni et al. 2021).

Among them, the number of insect invasions is also increasing every year, as is the resulting economic, health, and ecological damage (Kenis et al. 2009; Venette and Hutchison 2021). In particular, social insects account for only approximately 2% of all insect species, but their negative impact is very serious, accounting for 57% of the most harmful invasive alien insects (IUCN 2020). Invasive alien social insects have stronger impacts than their solitary counterparts due to their large colonies, strong prey hunting ability, and high polygyny rates (Crowder and Snyder 2010; Beggs et al. 2011; Boulay et al. 2014; Wittman et al. 2018).

Linepithema humile (Mayr, 1868), which is native to South America, is one of the most successful invasive species in the world (Stone and Loope 1987; Williamson and Fitter 1996; Wetterer et al. 2009). It has been unintentionally introduced into several countries, including Brazil (e.g., Von Ihering 1894), Colombia (e.g., Forel 1912), Chile (e.g., Newell and Barber 1913), Mexico (e.g., Carpenter 1902), Peru (e.g., Dale 1974), Japan (e.g., Sugiyama 2000), New Zealand (e.g., Ward et al. 2010), South Africa (e.g., Mothapo and Wossler 2017), and South Korea (e.g., Lee et al. 2020). Based on its high invasiveness, *L. humile* is described as one of the 100 most competitive invasive species in the world, due to the serious consequences of its introduction on agricultural production, seed dispersal, and native arthropod communities (Erickson 1971; Bond and Slingsby 1984; Ward 1987; Human and Gordon 1996, 1997; Park et al. 2021).

In South Korea, *L. humile* was first detected in 2019 (Lee et al. 2020), and was found to consist of a single haplotype (named H3) (Park et al. 2021). Since the discovery of *L. humile*, chemical control has been implemented seven times to prevent its settlement and spread; however, it was not successfully eradicated (Yonhapnews 2020). On the contrary, its distribution has continued spreading.

Linepithema humile reproductives cannot disperse widely by themselves. One reason for this limitation is their behavior during the breeding period. In most ant species, virgin queens mate with males while flying during the breeding periods (i.e., the nuptial flight). Then, they form a new colony in new environments. Some researchers have reported that the annual expansion ranges of ants during nuptial flight can reach up to 5–16 km (Markin et al. 1971; Vogt et al. 2000). In contrast, *L. humile* does not exhibit nuptial flight behavior (Markin 1970), and the annual expansion range is on average 15–180 m (up to 340 m maximum) (Suarez et al. 2001; Tatsuki 2014; Kido et al. 2017). However, *L. humile* has been reported to spread over 100 km per year through the transportation of commodities (Suarez et al. 2001).

To reduce the ecological damage caused by this species and promote its management, it is essential to understand the introduction pathways and subsequent spread of this invasive species in new environments (Blackburn et al. 2011). Here, we investigated the distribution of *L. humile* based on its initial spread from the site where it was first discovered in 2019 (Lee et al. 2020), and documented its subsequent impact on native ant diversity.

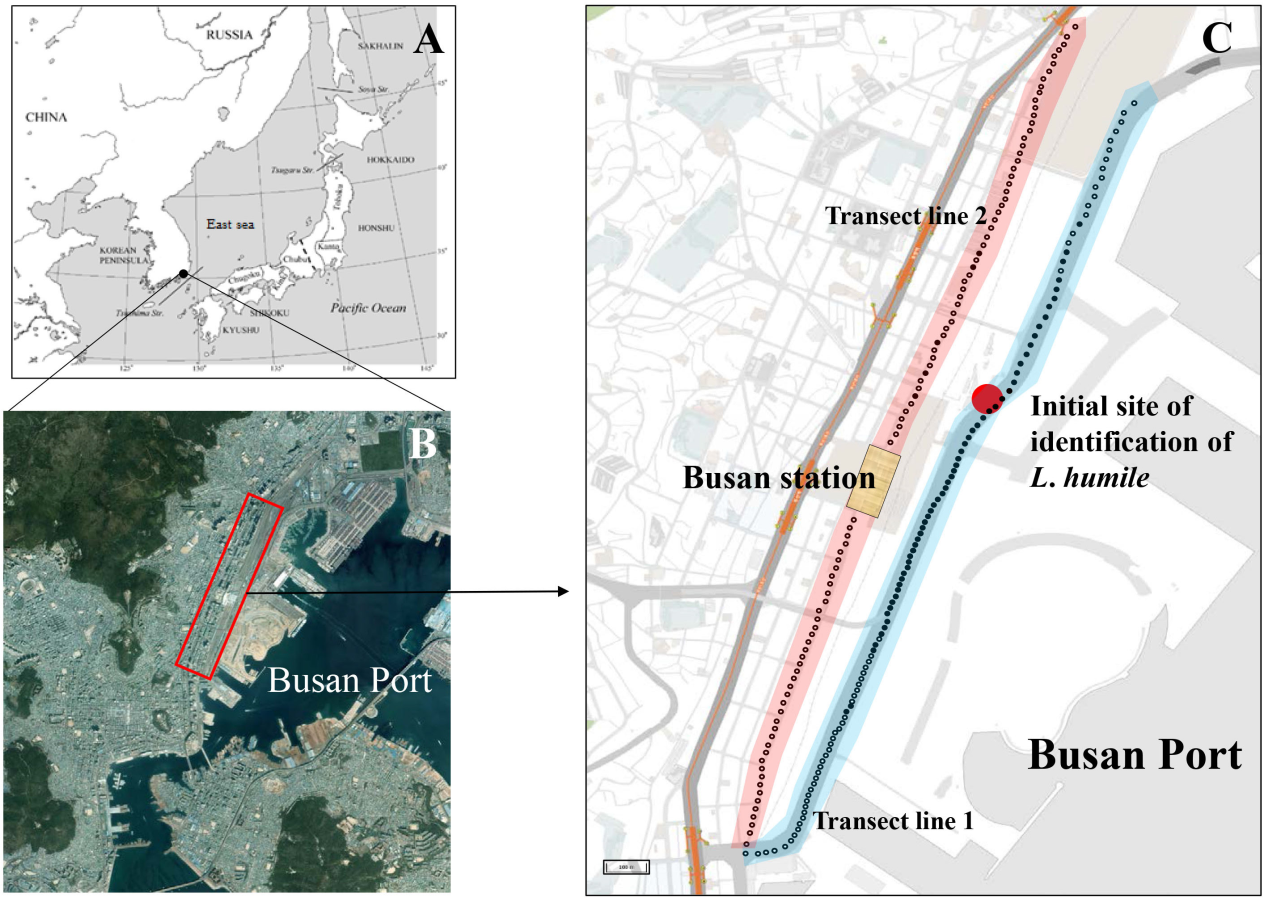


Figure 1. Invasion area of *Linepithema humile* in the study sites in Busan, South Korea (A, B). Black point: area invaded by *L. humile*, white point: uninvaded area (C).

Materials and methods

Study area and sampling of ant communities

Busan Port is the largest trade port in South Korea, located in the southeastern city of Busan (Figure 1). Busan handles 75% of all container cargo entering and leaving South Korea, representing more than 17 million twenty-foot equivalent units of goods annually. Therefore, it is a pathway through which a number of invasive alien species are introduced every year (Ryu et al. 2017). Our investigation was conducted in and around Busan train station, which is located near Busan port (Figure 1).

Sampling of the ant community was conducted using pitfall traps on the road connected to the point (N35°07′01,79″; E129°02′41.40″) where *L. humile* (Figure 2) was initially discovered by Lee et al. (2020).

Plastic containers (12 cm deep) with a mouth diameter of 5 cm were used as pitfall traps. A total of 230 traps were used, and each trap was filled with commercial car antifreeze fluid (RADI-Q, Korea) to a height of 4 cm and placed flush with the ground in a road verge, as described by Cole et al. (1992). All traps were set in two line transects on October 6, 8, and 10, 2021 and emptied every 48 h. Sampling was conducted in October (late summer/early Autumn), which is considered the ideal time period for sampling

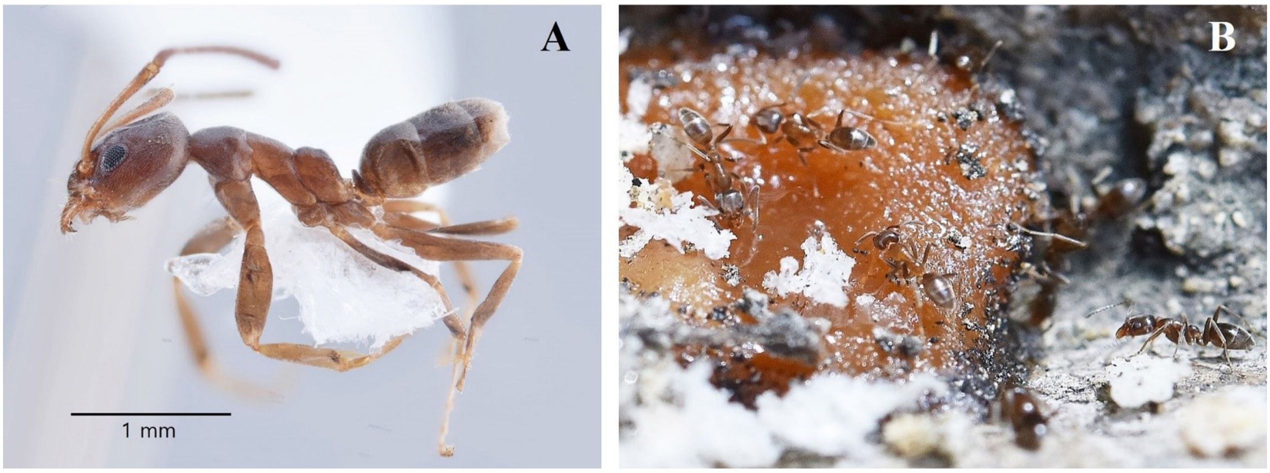


Figure 2. *Linepithema humile* worker, lateral view (A), and worker ants walking on food fragments dropped on the street (B). Photographs by Sang-Hyun Park.

ants. Pitfall traps and a 48-h trapping period were used, as these methods have been found to be effective for sampling ant communities (Andersen 1991). Both transects were approximately 2.5 km long, with 115 traps per transect installed at intervals of 20 m.

The contents of these traps were sorted and identified at the species level using the taxonomic keys of the Japanese Ant Database Group (2003). Ant specimens were identified using an Olympus SZ61 stereomicroscope (Tokyo, Japan) and stored in 95% ethanol. Sample specimens were deposited at the Laboratory of Medical Ecology, Department of Biomedical Sciences, Kosin University.

Data analysis

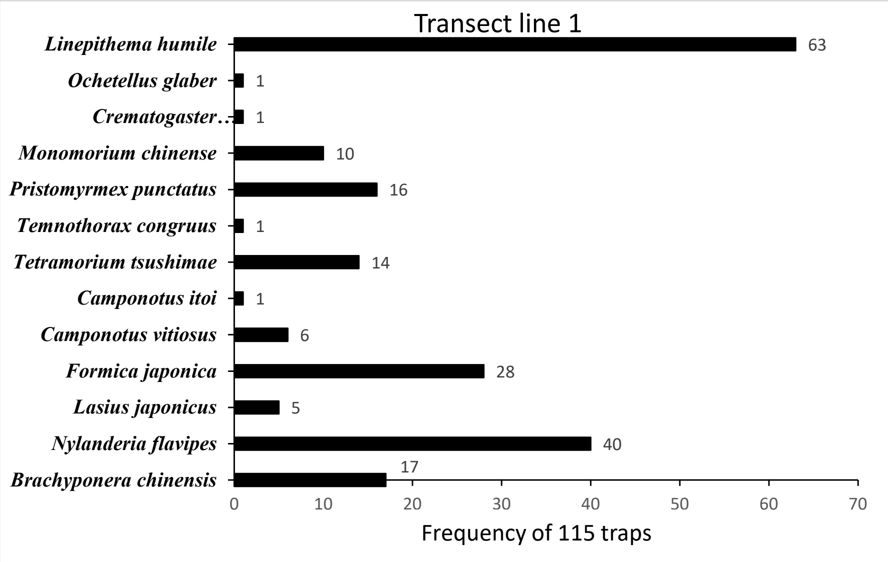
We classified each trap according to the presence or absence of native ants and exotic *L. humile*. Subsequently, chi-square analyses were used to determine whether the distribution of native ants was independent of the distribution of *L. humile*. Additionally, we used a two-sample t-test and the Shannon–Weiner index of diversity to determine whether the invasion of *L. humile* affects ant species richness and diversity. All statistical analyses were performed using the IBM SPSS 19 statistics package (IBM Corporation, Armonk, NY, USA).

Results

Overall, we identified 14 ant species belonging to 12 genera and four subfamilies (Table 1). We collected ants in 158 (69%) of the 230 traps. *Linepithema humile* was the single most abundant ant species at the study site, with a total of 2,766 workers (73.2% of the total) collected in 81 of the 158 traps, and was more broadly distributed along transect 1 (closer to the shoreline) than transect 2 (Figure 1). Moreover, a difference was observed in the frequency at which Argentine ants were found (Figure 3). A total of 1,011 individuals of indigenous ants representing 13 species were collected

Table 1. Species of ants and their abundance along the two sampled transects in Busan, South Korea (115 pitfall traps per transect).

No.	Ant Species	Transect 1		Transect 2		Total	
		Traps	N	Traps	N	Traps	N
	Dolichoderinae						
1	*Linepithema humile* (introduced)	63	2,726	18	40	81	2,766
2	*Ochetellus glaber*	1	5	0	0	1	5
	Myrmicinae						
3	*Crematogaster matsumurai*	1	8	0	0	1	8
4	*Monomorium chinense*	10	50	0	0	10	50
5	*Pristomyrmex punctatus*	16	46	4	4	20	50
6	*Temnothorax congruus*	1	1	1	1	2	2
7	*Tetramorium tsushimae*	14	137	8	19	22	156
	Formicinae						
8	*Camponotus itoi*	1	1	0	0	1	1
9	*Camponotus vitiosus*	6	12	2	2	8	14
10	*Formica japonica*	28	205	4	5	32	210
11	*Lasius japonicus*	5	9	6	7	11	16
12	*Nylanderia flavipes*	40	348	19	80	59	428
13	*Nylanderia sakurae*	0	0	1	1	1	1
	Ponerinae						
14	*Brachyponera chinensis*	17	24	9	46	26	70



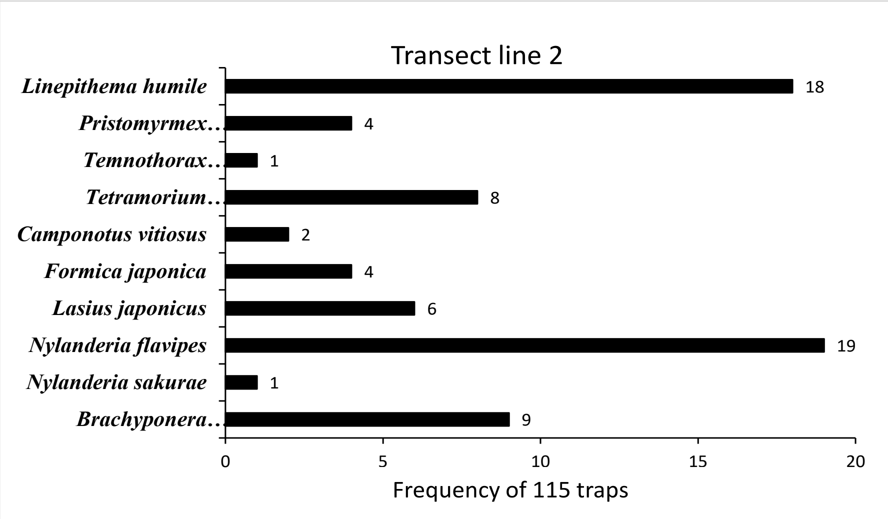


Figure 3. Ant species foraging in green spaces along two transects near Busan train station, South Korea.

Table 2. Chi-square test (expected frequencies in parentheses) for the presence of the Argentine ant (*Linepithema humile*) and native ants in Busan, South Korea. The results of this analysis were highly significant (Pearson $\chi^2 = 7.129$, df = 1, P < 0.01).

	L. humile present	*L. humile* absent	Total
Native ants present	27(36.6)	77(67.4)	104
Native ants absent	54(44.4)	72(81.6)	126
Total	81	149	230

Table 3. Number of invaded and uninvaded traps in which different native ant species were sampled in Busan, South Korea. Significance levels: ** P < 0.01, * P < 0.05, NS not significant.

		Invaded trap	Uninvaded trap	Fisher's Exact Test
Total number of traps		81	77	
	Arboreal ants			
1	*Crematogaster matsumurai*	0	1	–
2	*Ochetellus glaber*	0	1	–
3	*Temnothorax congruus*	1	1	–
	Epigeic ants			
4	*Camponotus itoi*	0	1	–
5	*Camponotus vitiosus*	1	7	NS
6	*Formica japonica*	0	24	*
7	*Lasius japonicus*	2	9	*
8	*Monomorium chinense*	6	4	NS
9	*Nylanderia flavipes*	11	48	**
10	*Paraparatrechina sakurae*	0	1	–
11	*Pristomyrmex punctatus*	2	18	**
12	*Tetramorium tsushimae*	1	21	**
	Hypogeic ants			
13	*Brachyponera chinensis*	10	16	NS

from 77 pitfall traps (Table 1; Figure 3). Eight of the native species had more than 10 individuals, whereas the other five were less abundant.

Native ants and *L. humile* occurred separately more frequently, and co-occurred less frequently, than expected by chance ($\chi^2 = 7.13$, df = 1, P < 0.01) (Table 2).

Ant species richness was significantly lower in areas invaded by *L. humile*. Traps with at least one *L. humile* worker had an average native species richness of 0.85, which was significantly less than 2.56, the average species richness for traps with native ants only (t = −7.56, df = 106, P < 0.01). This result was confirmed using the Shannon-Weiner diversity index. Areas with *L. humile* presence had a diversity index of 0.35, which was considerably lower than that of the uninvaded areas (diversity index of 1.60).

Of the 13 native ant species collected from traps in uninvaded areas, *Nylanderia flavipes* (Smith, 1874) (11.3%), *Formica japonica* Motschoulsky, 1866 (5.6%), and *Tetramorium tsushimae* Emery, 1925 (4.1%) were dominant (Table 3). Only eight native ant species were found in traps that also sampled *L. humile*. In the invaded areas, *Camponotus vitiosus* Smith, 1874; *Monomorium chinense* Santschi, 1925; and *Brachyponera chinensis* Emery, 1895, were able to feed together with *L. humile*. In contrast, *F. japonica*, *Lasius japonicus* Santschi, 1941, *N. flavipes*, *Pristomyrmex punctatus* (Smith, 1860), and *T. tsushimae* were not found in the invaded areas (Table 1).

Discussion

Our study provides the first fine-resolution analysis of the impact of *L. humile* on the native ant species of South Korea. The species richness of the native ant community was significantly lower in areas invaded by *L. humile*, and its presence had very contrasting impacts for different native ant species. Most epigeic ants at the study sites were not found co-existing with *L. humile*. The almost complete absence of *N. flavipes*, *P. punctatus*, *T. tsushimae*, *F. japonica*, and *L. japonicus*, in traps containing *L. humile* compared to them otherwise being the most commonly collected native species indicated they were strongly impacted by the invasion of *L. humile*. In contrast, three resident ant species, *C. vitiosus*, *M. chinense*, and *B. chinensis* did not differ in occurrence with or without *L. humile*. Similar results were reported in previous studies in Japan, which has a climate similar to that of Korea (Miyake et al. 2002; Touyama et al. 2003; Park et al. 2014). The distribution of *L. humile* at the study site varied depending on the transect line. In transect 1, *L. humile* individuals were found distributed along the road during initial site identification, but its distribution in transect 2 was limited (Park et al. 2021). Quantitatively, there was also a difference between transects 1 and 2 (Figure 3). Based on this observation, we concluded that transect 1 around the initial site is a focal point of the *L. humile* invasion in Busan.

Figure 3 and Table 2 suggest that *L. humile* is capable of completely displacing several native ants in the study area. Moreover, the range of *L. humile* here appears to have been carved out of the range of the native ant species. The quantitative evidence for the displacement of native ants by *L. humile* included the observation that only 16.1% of traps contained both native ants and exotic *L. humile*, and 19.1% only contained *L. humile*.

The results of this study agree with those of previous studies on *L. humile* invasions (Kennedy 1998; Miyake et al. 2002; Park et al. 2014). *Linepithema humile* successfully settled in an urban area in South Korea. Little co-occurrence between native ants and *L. humile* was observed, and native ant diversity was significantly lower in invaded areas.

A biological aspect of *L. humile* with enormous implications for their local-scale dispersal is their reproductive behavior (Holway et al. 2002; Silverman and Brightwell 2008). Unlike many ant species, the mated reproductive stages of *L. humile* do not disperse by flying. Local-scale dispersal occurs through budding, limiting the self-spread of *L. humile* to approximately 150 m per year (Suarez et al. 2001). Therefore, regional containment as well as local eradication of *L. humile* is technically feasible (Charles et al. 2002), provided that accidental dispersal within moved goods is prevented.

According to the report of the Ministry of Environment (2020), control measures for *L. humile* have been implemented seven times since it was first discovered in South Korea. Nevertheless, *L. humile* continues to spread around the infestation point despite early detection and the implementation of control measures (Lee et al. 2020; Park et al. 2021). As *L. humile* has settled in the main transport hub in South Korea, it has the potential to spread throughout the country through human-mediated transport if it is not effectively controlled (Suarez et al. 2001). *Linepithema humile* can spread over 100 km per year through the transportation of commodities (Suarez et al. 2001). Therefore, more aggressive management controls are required to prevent nationwide dispersal. We propose that the logical time to act to improve the management of *L. humile* is now, while there is still an opportunity to limit spread.

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Authors' contributions

Conceptualization: M.B.C., S.-H.P. and C.-J.K.; methodology: S.-H.P. and M.B.C.; formal analysis: S.-H.P. and M.B.C.; investigation: S.-H.P.; resources: M.B.C., S.-H.P. and C.-J.K.; supervision: M.B.C., I.-K.K. and C.-J.K.; visualization: S.-H.P. and M.B.C.; data curation: M.B.C. and S.-H.P.; writing – original draft preparation: M.B.C., S.-H.P. and C.-J.K.; writing – review and editing: M.B.C., S.-H.P., C.-J.K. and I.-K.K.; project administration: M.B.C., I.-K.K. and C.-J.K.; funding acquisition: C.-J.K. and I.-K.K. All authors have read and agreed to the published version of the manuscript.

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