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ORIGINAL PAPER

Is cooperation relevant to ant invasiveness? Insights from cooperative food transport

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Abstract Cooperative behavior can enhance fitness and ecological success. However, its role in facilitating biological invasions remains underexplored. To assess the occurrence and importance of intraspecific cooperation in invasive species, we examine cooperative transport—working together to move large objects—across ant species. Specifically, we evaluate its prevalence in the world's top invasive ants and compare its occurrence between invasive and non-invasive species using a previously published dataset of ants from East Asia. Additionally, we conduct a field experiment comparing cooperative transport in the invasive Argentine ant (*Linepithema humile*) and a non-invasive, ecologically similar species (*Dorymyrmex tener*). Our literature review, complemented by experiments with the invasive *Wasmannia auropunctata*, confirms that cooperative transport is present in all five of the world's most invasive ant species. In the analyzed dataset, all invasive species exhibited cooperative transport, whereas only 60% of the non-invasive species did. In the field experiments, *L. humile* cooperatively transported more baits and showed greater accuracy toward its nests than *D. tener*. This cooperative ability may contribute to the invasion success of *L. humile* by enhancing resource acquisition and competitive dominance. Our findings suggest that cooperative transport is more prevalent among ants than previously reported and may be particularly common in invasive species. However, further research with a broader representation of global ant diversity and a larger sample size is needed to validate this pattern. Intraspecific cooperation could play a key role in invasion success, highlighting the need to incorporate cooperative behavioral traits into studies of species invasions and management strategies.

Keywords Collective behavior · Cooperative transport · *Dorymyrmex tener* · Intraspecific cooperation · Invasive species · *Linepithema humile*

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Introduction

Behavioral traits have been increasingly recognized as important factors influencing the establishment success following unintentional species introductions and species invasion (Chapple et al. 2012). Traits like boldness, aggression, and parental care are linked to successful invasions across various taxa, including birds (Sol et al. 2002), crustaceans (Weis 2010), and lizards (Damas-Moreira et al. 2019). Intraspecific cooperation— the collaboration of conspecifics for mutual benefits—is a key behavioral trait that enhances fitness and ecological success (Krebs and Davies 2009). Cooperation can improve resource acquisition, survival, and reproduction through collective behaviors like group foraging, collective defense, cooperative breeding, and communal nesting (Barker et al. 2017; Detrain and Deneubourg 2008; Kingma et al. 2010; Czaczkes and Ratnieks 2013). While it is clear that cooperation can enhance an individual's fitness and ability to dispersal, its impact on invasion success is less understood. Considering that species invasion is a major driver of global change (Ricciardi 2007), it is crucial to investigate the role of intraspecific cooperation in facilitating invasion success.

Several mechanisms and types of intraspecific cooperation can be identified across invasive species. The House mouse (*Mus musculus*) and Wild boar (*Sus scrofa*) are widespread invasive animals that display cooperation in foraging, breeding, or nesting (Manning et al. 1995; Focardi et al. 2015). Invasive birds, such as the European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*), engage in cooperative breeding, nest defense, and social foraging, which enhances their survival and adaptability in new environments (Toth et al. 2009; Liker and Bókonv 2009; Nichols and Arbuckle 2022; Lewis and Barber 2023). Intraspecific cooperation also contributes to trap and bait avoidance in the invasive Common Brushtail Possum (*Trichosurus vulpecula*; Godfrey et al. 2023). In aquatic environments, invasive Lionfish (*Pterois volitans*) often engage in cooperative hunting, which increases prey consumption (DeRoy et al. 2020). In plants, the invasive Diffuse Knapweed (*Centaurea diffusa*) demonstrates a form of intraspecific cooperation by forming large monocultures through the release of chemicals that suppress nearby plants, thereby creating a competition-free zone (Hierro and Callaway 2003; Kalisz et al. 2021). Thus, intraspecific cooperation is prevalent across invasive taxa and may provide introduced species with advantages over native species.

Ants are a unique model system for advancing our understanding of how intraspecific cooperation may influence species invasion because collective behaviors determine their success. As social insects, ants engage in cooperative behaviors including nest building, colony defense, brood care, foraging, and social learning (Zanola et al. 2024; Wagner and Czaczkes 2024). Some ant species, such as the invasive red imported fire ant (*Solenopsis invicta*), can form living structures through cooperation to survive floods (Adams et al. 2011). Importantly, nineteen ant species are listed as invasive, and five of them are among the 100 most invasive species on the planet (Lowe et al. 2000; GISD, http://www.issg.org/database), providing well-documented case studies for analyzing the role of cooperation in invasion success. Finally, invasive ants can have detrimental impacts on native communities and ecosystems, as well as on urban environments and production systems, resulting in substantial economic losses worldwide (Del Toro et al. 2012; Angulo et al. 2022). Therefore, studying the cooperative behaviors of invasive ants may be important for attenuating their negative impacts on natural communities and the global economy, and for developing new management strategies.

Ants have been a model system for examining cooperative behaviors because they are easy to observe and experimentally manipulate, both under field and laboratory conditions (Robson and Traniello 1998; Feinerman et al. 2018). Cooperative transport—working together to move large objects—is a type of intraspecific cooperative behavior that enhances the ecological success of ants (Czaczkes and Ratnieks 2013). It allows ants to move objects thousands of times heavier than they could individually (Wojtusiak et al. 1995), thereby increasing colony fitness by expanding the range of transportable food, reducing competition, clearing foraging trails of obstacles, and contributing to nest maintenance and construction (Czaczkes and Ratnieks 2013; Alma et al. 2019). Cooperative transport can even be superefficient, with groups of ants able to move more weight per unit ant weight than they could move individually (Franks 1986). Additionally, the size and mass of loads have been shown to influence cooperation during transport in ants, with larger loads causing delays in movement initiation and reduced transport velocities (McCreery et al. 2019). Cooperative transport therefore provides an opportunity to assess intraspecific cooperation as a behavioral trait that might impact invasion success.

We aim to investigate whether intraspecific cooperation, specifically cooperative transport, differs between invasive and non-invasive ant species and how these behaviors may contribute to invasive success. To address this, we combined three approaches: a literature review, analysis of experimental data from published work, and field experiments. Our literature search focused on whether top invasive ant species exhibit cooperative transport. We then used experimental data from Yamamoto et al. (2009) to assess the prevalence of cooperative transport across invasive and non-invasive species. In field experiments, we compared the cooperative transport abilities of the invasive Argentine ant (*L. humile*) and the non-invasive *D. tener*. The Argentine ant, native to South America, has invasive populations worldwide (Suarez et al. 2001), including in Los Angeles, CA, where we conducted our experiments. *D. tener*, native to Argentina and Chile, is similar in size to *L. humile* (Fig. 1a; *D. tener*, 3.82 mm and *L. humile*, 2.88 mm body size). Both species belong to the same ant subfamily (Formicidae: Dolichoderinae) and share numerous ecological and behavioral traits, including diet (preying on live and dead insects and tending aphids), aggressiveness, and competitive dominance respect to other ant species in the community (Devegili et al. 2020, 2021; Angulo et al. 2024). These similarities allow us to isolate differences in the cooperative transport abilities between the native *D. tener* and invasive *L. humile*.

We hypothesize that intraspecific cooperation is a behavioral trait that facilitates ant invasions, expecting the top invasive ant species to engage in cooperative transport and for this behavior to be more prevalent in invasive species than in non-invasive ones. Similarly, in our bait removal experiments, we predict that the invasive Argentine ant (*L. humile*) will display greater efficiency and accuracy in cooperative transport than the non-invasive *D. tener*.

Materials and methods

Cooperative transport in invasive ants

To examine the presence of cooperative transport in invasive ants, we searched the literature for evidence of this behavior in the most widespread, abundant, and harmful invasive species on the planet: *Anoplolepis gracilipes*, *L. humile*, *Pheidole megacephala*, *S. invicta*, and *W. auropunctata* (Lowe et al. 2000). We conducted a Google Scholar search for articles explicitly mentioning cooperative transport behaviors in these five species. If a research article included experiments in which cooperative transport could occur but was not reported, we contacted the authors asking for personal observations of cooperation in prey or bait transport.

For *W. auropunctata*, we did not find any literature documenting cooperative food retrieval. Therefore, we conducted our own experiment using three laboratory-reared nests of *W. auropunctata*. To encourage cooperative transport, we presented food baits of varying sizes and recorded videos to document the ants' behavior.

To compare cooperative transport behaviors between invasive and non-invasive ant species, we analyzed experimental data from Yamamoto et al. (2009), which includes food retrieval assays of 44 ant species from 34 genera across Indonesia, Japan, and Malaysia. Ant species represent eight ant subfamilies—Myrmicinae, Amblyoponinae, Formicinae, Cerapachyinae, Ponerinae, Dolichoderinae, Ectatomminae, and Leptanillinae—providing a robust foundation for comparing cooperative transport behaviors. Of the 44 species, we identified four as invasive and the remaining as non-invasive, with invasive status determined according to the Global Invasive Species Database (http://www.iucngisd.org/gisd/). Yamamoto classified food retrieval behaviors into three categories: (i) cooperative prey retrieval, where multiple workers transport prey without fragmenting it; (ii) prey fragmentation, where prey is divided and retrieved individually; and (iii) a mixed strategy, where prey is transported cooperatively to a hidden location before being fragmented for individual retrieval. For our analysis, we renamed the behavioral categories as: (i) cooperative transport, (ii) individual transport,

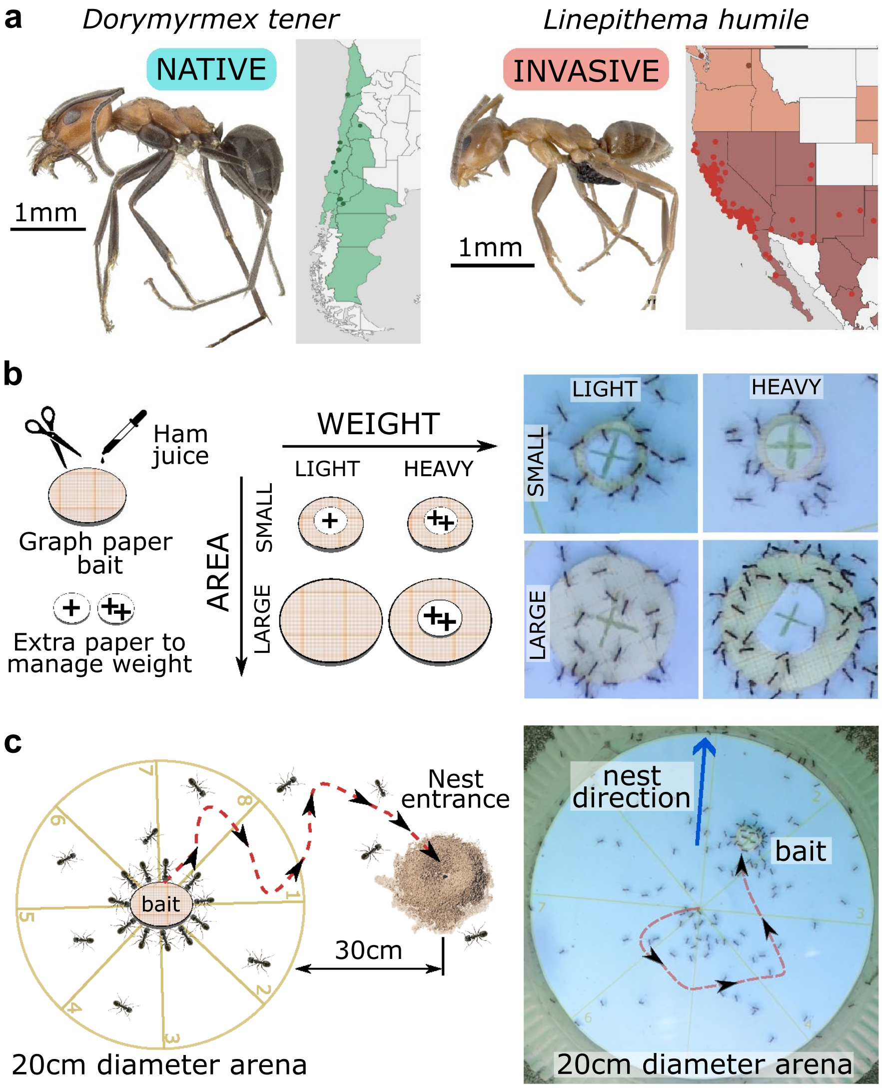


Fig. 1 Study species and experimental assay. **a** Photos of *D. tener* and *Linepithema humile*, modified from www.antwiki.com – both are on the same scale for comparison; and their distribution near the study sites is shown in the maps from www.antmaps.com, **b** different experimental protein bait designs, including changes to bait area and weight. Diagram on the left and photos on the right. We soaked the baits in ham juice because ants often collectively move protein, like large caterpillars and other dead arthropods. The + symbols indicate increased weight by adding paper to the bait **c** Experimental setup. A circular trial arena (20 cm diameter) was placed 30 cm from the nest entrance. Protein bait was placed at the center of the arena, and ant behavior was recorded with a video camera for 10 min. For easier video analysis and to determine the direction of the nest entrance, the arena was divided into numbered slices (e.g., in the diagram, Sect. "Introduction" points to the nest entrance). Photos on the right in B and C are video screenshots of experiments with *D. tener*

and (iii) both. For additional details, please refer to Table S1 in the Supplementary Material.

Field experiment: cooperative transport in native and invasive ants

We conducted cooperative transport experiments with the invasive *L. humile* in its invasive range in CA, USA and with the non-invasive *D. tener* in its native range in Northwest Patagonia, Argentina. Populations of *L. humile* introduced to California are thought to have originated in the humid subtropical environment of the southern Rio Paraná region in Northeast Argentina (Tsutsui et al. 2001). *L. humile* exhibits significant differences between its native and invaded ranges. In its native range, colonies are smaller, multicolonial, and exhibit intraspecific aggression. In contrast, invasive populations are unicolonial, larger, and lack intraspecific aggression (Tsutsui and Case 2001; Heller 2004). For this reason, we compared *L. humile* in its invaded range with *D. tener* in its native range, as this comparison provides an accurate context for examining whether cooperative behaviors contribute to invasion success.

Study sites

We conducted cooperative transport experiments with *L. humile* in the Mildred Mathias Botanical Garden (34°3′ 56.54″ N, 118°26′ 28.23″ W) at the University of California, Los Angeles, CA, USA. The UCLA Botanical Garden consists of 15 distinct areas featuring plants from diverse regions and functions as a documented collection for research, conservation, display, and education. It includes various walking paths and recreational areas. Ants were sampled from three locations within the garden, with an average distance of 50 m between sites. All samples were collected from walking paths, where *L. humile* is particularly abundant, and foraging trails are readily visible (AMD, personal observation). Although vegetation differed among the sampling sites, the walking paths themselves were consistently clear of vegetation and uniform across all locations.

For *D. tener*, we conducted cooperative transport experiments in Northwest Patagonia, Argentina, at two field sites near the city of San Carlos de Bariloche (41.12° S, 71.22° W). These sites are located three km apart and have similar vegetation cover, species composition, and weather conditions. This region consists predominantly of steppe ecosystems with cold and semiarid environment. However, *D. tener* exhibits significant environmental plasticity, thriving also in warmer and more humid areas, such as the transition zones between steppe and temperate forests in NW Patagonia and even warmer and more humid regions like central and northern Chile. Much like *L. humile*, *D. tener* is common in disturbed and periurban areas (Farji-Brener et al. 2002). Furthermore, within its native region, *D. tener* can be also found in city parks, house gardens, orchards, and within the houses (AMD personal observations).

Experimental design

We used the same experimental design to study cooperative transport by *D. tener* and *L. humile* (Fig. 1b, c). Both ant species engage in cooperative transport of protein foods such as dead arthropods (Fig. S1). In a preference trial for foods with different protein contents, ham was found to be the most preferred food item (Fig. S1). Consequently, we prepared the paper baits by soaking them in ham juices the night before the experiment. To examine how bait area and weight affect collective transport, we designed four different baits, resulting in a bifactorial design with four treatments: (1) Small-Light, (2) Small-Heavy, (3) Large-Light, and (4) Large-Heavy baits (Fig. 1b). Because *D. tener* is slightly larger than *L. humile* (Fig. 1a), we matched bait area and weight proportionally to ant size. For further details on the bait sizes and weights, refer to Table S2 in the Supplementary Material.

We recorded ant cooperative transport using GoPro Hero 8 camera (4 K resolution, 30fps) within a temporary structure for shading to create uniform lighting and prevent strong winds from moving the bait and arena (Fig. S2 in Supplementary material; Devegili et al. 2024). To standardize the trials, we offered the baits on a 20 cm-diameter circular white paper arena placed 30 cm from the ant nest entrance (Fig. 1c). Each paper arena was only used once because ants might have deposited pheromones on it during the experiment. We recorded ant behaviors for 10 min after placing the protein bait at the center of the arena. If the ants successfully removed the bait before the 10 min elapsed, we stopped recording. To ensure consistent ant recruitment to the arena, we placed a 1 cm square piece of ham in the center of the arena for 3 min before starting the protein bait trial. The ants were not able to move the ham.

We conducted the protein bait treatments at eight nest entrances each for *D. tener* and *L. humile*. For *D. tener*, we used a 30-m separation to identify distinct nests, as supported by previous research (Devegili et al. 2020). For *L. humile* we recorded videos from three distinct locations within the UCLA Botanical

Garden, each separated by more than 50 m. *L. humile* is often described as unicolonial in its introduced range, however, evidence suggests it forms mosaic colonies of smaller, interacting nests (Heller et al. 2008). These mosaics share resources within spatial networks of approximately 650m^2 (i.e., ~ 14 m radius, assuming a circular distribution) (Heller et al. 2008). The 50 m spacing between the sampling sites at the UCLA Botanical Garden ensured that we collected video recordings of *L. humile* cooperative behaviors from three distinct mosaic colonies. Unfortunately, due to logistical constraints, including funding and time limitations, we were unable to conduct additional sampling outside UCLA. We recognize this limitation and its potential impact on the generalizability of our findings.

We sampled both ant species during their respective summer seasons: *D. tener* in December–January and *L. humile* in July–August. To account for potential differences in collective transport performance across days, we sampled each nest entrance multiple times over one month. Ants are known to learn and habituate to recurring food stimuli over time, which may significantly influence outcomes in collective tasks (Dornhaus and Franks 2008). Such habituation and learning could introduce biases into our results by increasing efficiency over time. To address this concern, we analyzed the cooperative transport velocity of protein baits across all sampling days for both *D. tener* and *L. humile*. Specifically, we tested for patterns indicative of habituation or learning, such as a consistent increase in the transport velocity of bait removal across trials. If no such trend is observed, this would suggest that any variation in transport dynamics is more likely due to other ecological or behavioral factors rather than habituation or learning effects.

We tested all four experimental bait types at each nest. To account for the potential effect of bait type presentation order on our results, we randomized the bait type order and assigned each order to a specific nest before starting the sampling period. Across both species, we recorded 251 high-quality videos of ants performing cooperative transport attempts. Specifically, we recorded 63, 61, 64, and 63 videos for the Small-Light, Small-Heavy, Large-Light, and Large-Heavy protein baits, respectively. Of these, 31, 29, 32, and 31 videos correspond to *D. tener*, while 32 videos for each bait type correspond to *L. humile*.

Cooperative transport measurements

To quantify the cooperative transport behavior of *D. tener* and *L. humile*, we analyzed videos using the 'Tracker' software (Brown et al. 2022) and defined three measurements: (i) capacity, (ii) accuracy, and (iii) efficiency.

Capacity is the ability of the ants to cooperatively remove the protein bait from the arena within 10 min or less. Specifically, capacity was computed as a binary variable with success and failure of removing the bait from the arena. We also calculated the proportion and percentages of trials in which the baits were removed for each type of bait and each species. Accuracy is the direction in which the protein bait was cooperatively moved relative to the position of the nest (Fig. 1c). We defined accuracy as the angle between the direction in which the bait was moved and the direction of the nest. This angle ranged from 0° – bait moved directly towards the nest to 180° – bait was moved in the exact opposite direction of the nest. We defined efficiency as the cooperative transport velocity of the protein bait, i.e., the total distance that ants moved the bait divided by the transport time. Given that the number of ants transporting the baits varied across the trials, we adjusted the velocity based on ant number. Considering the slight difference in size between *D. tener* and *L. humile*, we adjusted the velocity for body size allowing a fair cross-species comparison. This adjustment was made by dividing the velocity by the body size.

For other commonly used efficiency measurements (consensus time, number of ants, and sinuosity) and a summary of the experimental design see Fig. S3 in the Supplementary material.

Cooperative transport index

To examine the global cooperative transport of both species, we created a composite measure by combining capacity, accuracy and efficiency into a "Cooperative transport index":

$$\textit{Cooperative transport index} = \textit{Capacity} \times \textit{Accuracy} \times \textit{Efficiency}$$

To ensure equal weighting of each measure in the index, we standardized Capacity, Accuracy, and

Efficiency to fall between 0 and 1. Capacity remained the proportion of removed baits (ranging from 0 to 1), as previously defined. To standardize accuracy to be between 0 (smallest accuracy) to 1 (largest accuracy), we used:

$$Accuracy = \frac{1}{Angle + 1}$$

To standardize efficiency, we used:

$$Efficiency = \frac{Measured\ velocity}{Max\ velocity}$$

In which max velocity is the maximum velocity measured in each ant species.

Statistical analyses

To compare cooperative transport across invasive and non-invasive species in the data set, we used a Chi-square test of independence. We considered species status (invasive, non-invasive) as the independent variable and food retrieval method as the response variable. Because we were specifically interested in comparing cooperative transport, we transformed the food retrieval data into a binary variable (1: cooperative transport, 0: no cooperative transport). For the data visualization, we calculated the percentages of ant species performing each food retrieval type for clarity.

To analyze the potential bias of learning and habituation on our cooperative transport measurements, we applied a general linear mixed model (GLMM) with a Gaussian distribution. We used cooperative transport velocity as the response variable, with date and bait treatments as fixed factors and trial order as a random factor. We constructed separate models for each species to capture species-specific dynamics effectively.

To compare the cooperative transport 'capacity' in our field experiments with *D. tener* and *L. humile*, we used a GLMM with a Binomial distribution. The response variable was the success or failure of cooperatively removing the bait from the trial arena. Fixed factors included bait area, bait weight, and species identity, while random factors were nest identity, sampling day, and trial order. For comparing cooperative transport 'accuracy','efficiency' and the 'cooperative transport index', we used three GLMMs with Gaussian distribution, constructing separate models for each response variable: using the direction of transport for 'accuracy', movement velocity for 'efficiency', and the product of capacity, accuracy and efficiency for the 'cooperative transport index'. The same fixed and random effects as detailed above for 'capacity' were used in these three models as well. In all the models, we assessed normality visually, using Q-Q plots, and statistically, using the Shapiro–Wilk test. We conducted post-hoc comparisons using Tukey tests with the *emmeans* package (Lenth and Lenth 2018).

We built the models and performed the statistical analyses in R, version 2024.09 (R Core Team 2023). We created the figures in R and added photographs and illustrations in Inkscape (Inkscape Project 2020).

Results

Cooperative transport in invasive ants

Cooperative transport was detected in all five of the most invasive ant species (Table 1). We also provide the first documented observation of the invasive *W. auropunctata* engaging in cooperative food transport behavior (Video S1 in the Supplementary Material).

In the experimental data of 44 ant species (Yamamoto et al. 2009), all invasive species (100%, 4/4) engaged in cooperative transport. In contrast, among the 40 non-invasive species, cooperative transport was observed in 50% (20/40), while 40% (16/40) relied on individual transport and the remaining 10% (4/40) employed a combination of both strategies (Fig. 2). When considering cooperative transport and mixed strategies, 60% of non-invasive species displayed some degree of cooperative transport. We found a significant association between cooperative transport and invasive ants ($\chi 2 = 5.18$, $p = 0.023$). Further details on the analyzed ant species can be found in Table S1, Supplementary Material.

Field experiment: comparing cooperative transport in native and invasive ants

Both the invasive *L. humile* and the native *D. tener* engage in cooperative transport of food baits. *L. humile* exhibits a greater capacity for cooperative

Table 1 Cooperative transport in the five most invasive ants on the planet

Common name (*Scientific name*)	Subfamily	Geographical range		Cooperative transport?
		Native	Introduced	
Long-legged ant, crazy ant (*A. gracilipes*)	Formicinae	South Asia	Africa (sub-Saharan), Asia, Australia, Caribbean, Indian Ocean (islands), Pacific Ocean (islands)	Yes[a]
Argentine ant (*L. humile*)	Dolichoderinae	South America (Argentina, Uruguay, Paraguay, Bolivia, and southern Brazil)	Africa (sub-Saharan), Atlantic Ocean (islands), Asia, Australia, Mediterranean, North America, Pacific Ocean (islands), rest of South America	Yes[a,b]
Big-headed ant (*P. megacephala*)	Myrmicinae	Africa (sub-Saharan)	Australia, North America, Caribbean, Indian Ocean (islands), Mediterranean, Pacific Ocean (islands), South America, rest of Africa	Yes[c]
Red imported fire ant (*S. invicta*)	Myrmicinae	South America	Caribbean, North America, Australia, New Zealand	Yes[d,e]
Little fire ant (*W. auropunctata*)	Myrmicinae	Central America, South America (from Colombia to northern Argentina)	Africa (sub-Saharan), Caribbean, Pacific Ocean (islands), rest of South America, North America	Yes[f]

[a] Yamamoto, A., Ishihara, S., and Ito, F. (2009). Fragmentation or transportation: mode of large-prey retrieval in arboreal and ground nesting ants. Journal of Insect Behavior, 22, 1–11

[b] Roulston, T. A. H., and Silverman, J. (2002). The effect of food size and dispersion pattern on retrieval rate by the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). Journal of insect behavior, 15, 633–648

[c] Dejean, A., Moreau, C. S., Uzac, P., Le Breton, J., and Kenne, M. (2007). The predatory behavior of *P. megacephala*. Comptes Rendus Biologies, 330(9), 701–709

[d] Qin, W., Lin, S., Chen, X., Chen, J., Wang, L., Xiong, H., … and Wang, C. (2019). Food transport of red imported fire ants (Hymenoptera: Formicidae) on vertical surfaces. *Scientific Reports*, *9*(1), 3283

[e] Wang, C., Chen, X., Strecker, R., Henderson, G., Wen, X., and Hooper-Bùi, L. M. (2016). Individual and cooperative food transport of the red imported fire ant (Hymenoptera: Formicidae): laboratory observations. *Journal of Insect Behavior*, *29*, 99–107

[f] Video S1 in the Supplementary Material. The video shows *W. auropunctata* engaging in cooperative food transport during experimental trials in the laboratory. Ants were offered protein baits of varying sizes presented on a circular plate connected to the nest. Recordings continued until the bait was removed from the plate, and the removal was categorized as individual or cooperative. Video credit: Tomer J. Czaczkes

transport compared to *D. tener*; *L. humile* cooperatively transported 91% of the baits, whereas *D. tener* transported 77% (GLMM: $\chi2 = 6.11$, $p = 0.04$; Fig. 3a). Consistently, across all area-weight treatments, *L. humile* moved more baits than *D. tener* (Fig. 3b). There was also an effect of bait weight and area on the percentage of baits moved (GLMM: weight, $\chi2 = 13.37$, $p = 0.001$, area, $\chi2 = 5.97$, $p = 0.01$; Fig. 3b and Table S3).

L. humile demonstrated significantly higher cooperative transport accuracy, measured as direction of transport, compared to *D. tener* (GLMM: $\chi2 = 18.74$, $p < 0.001$; Fig. 3c). This higher accuracy of *L. humile* was consistent regardless of bait area and weight (Fig. 3d). There was no significant difference in cooperative transport efficiency between *L. humile* and *D. tener*. This was consistent across the four efficiency measurements: velocity (Fig. 3e), consensus time, transporting ants, and sinuosity (Fig. S4). There was a strong effect of bait weight on transport velocity (GLMM: $\chi2 = 62.49$, $p < 0.001$; Fig. 3f), as well as an effect of bait weight and area on consensus time (GLMM: weight: $\chi2 = 4.47$, $p = 0.03$; area: $\chi2 = 4.63$, $p = 0.03$; Fig. S4b). Similarly, bait weight and area significantly affected the number of transporting ants (GLMM: weight: $\chi2 = 15.76$, $p < 0.001$;

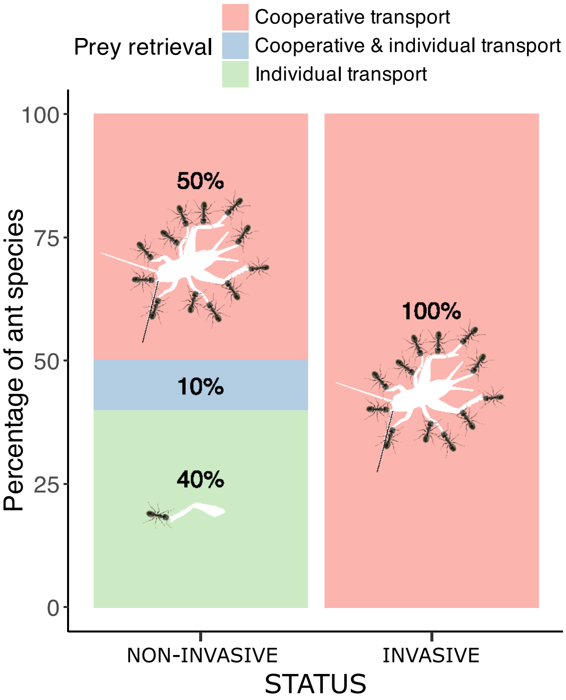


Fig. 2 Comparison of prey retrieval from published work on non-invasive and invasive ant species. Of the 44 ant species, four are invasive. For details on the species included, see Table S1 in the Supplementary Material. Invasive and non-invasive species significantly differ in their prey retrieval strategies following Chi-square comparison

area: $\chi2 = 23.46$, $p < 0.001$; Fig. S4d), and bait weight had a strong effect on sinuosity (GLMM: $\chi2 = 11.65$, $p < 0.001$). For interaction effects between bait weight, bait area, and species on the measured variables, refer to Table S3.

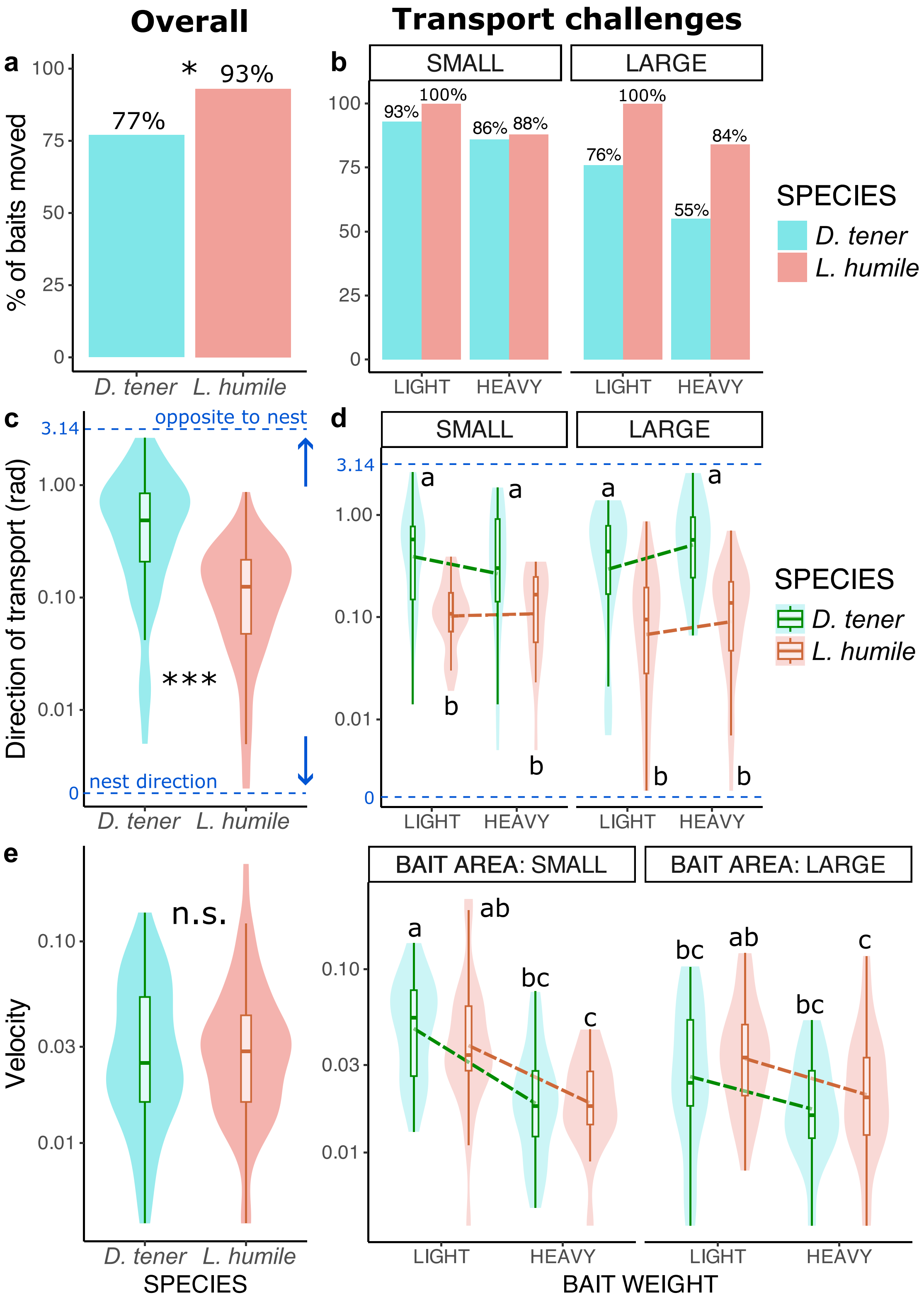
L. humile had a higher Cooperative transport index compared to *D. tener* (GLMM: $\chi2 = 14.48$, $p < 0.001$; Fig. 4a). This difference was consistent across area-weight treatments (Fig. 4b). There was also a significant effect of bait weight on the cooperative transport index (GLMM: $\chi2 = 22.30$, $p < 0.001$; Fig. 4b). For further results, refer to Table S3 in the Supplementary Material.

There was no increase in cooperative transport velocity over the sampling period for either species (GLMM: sampling date*bait treatment: *D. tener*: $\chi2 = 3.96$, $p = 0.26$; *L. humile:* $\chi2 = 0.82$, $p = 0.36$; Fig S5). These results suggest that no habituation and learning occurred over the experiment.

Discussion

This study shows that cooperative behavior may play an important role in the invasive success of ants. Our literature review, complemented by our experiments with the invasive *W. auropunctata*, confirms that cooperative transport is present in all five of the world's most invasive ant species. Analysis of the experimental dataset from Asia showed that cooperative transport is more prevalent in invasive species compared to non-invasive ones. However, given the high diversity of ants and the limited dataset, which includes only four invasive species, further validation with a broader sample is necessary to confirm this pattern. Our field experiment results suggest that the invasive *L. humile* displays more efficient cooperative transport than the non-invasive and ecologically similar *D. tener*. The suggested enhancement in cooperative transport abilities likely provide invasive species with a competitive edge in resource acquisition and territorial expansion, which are key factors in range expansion (Human and Gordon 1996; Holway and Case 2000). Our results thus build on previous research by highlighting the potential role of cooperative behaviors as important behavioral traits in facilitating biological invasions (Chapple et al. 2012).

Cooperative transport was more prevalent in the invasive ant species examined than in non-invasive species. In the analyzed dataset of 44 ant species from Asia, all invasive species (100%) exhibited cooperative transport, compared to 60% of non-invasive species. These findings suggest that, regardless of invasive status, cooperative transport may be more common among ants than previously thought. A previous report estimated its occurrence to be relatively rare, occurring in only 11.7% of all ant genera (i.e., 40 out of 343 valid genera; antcat.org) (Hölldobler and Wilson 1990). Additionally, our findings indicate that cooperative transport could be a common behavioral trait among invasive ants (Table 1, Fig. 2). Cooperative transport behaviors may provide invasive species with a competitive advantage. By efficiently retrieving and transporting large food items, invasive ants may outcompete native species, particularly in environments with high resource competition (Traniello 1983; Gil-Hoed et al. 2025). Rapid food removal minimizes the need for on-site dissection and


Overall
Transport challenges
a
b
% of baits moved
100
75
50
25
0
*
77%
93%
D. tener
L. humile
SMALL
LARGE
93%
100%
86%
88%
76%
100%
55%
84%
LIGHT
HEAVY
LIGHT
HEAVY
SPECIES
D. tener
L. humile
c
d
Direction of transport (rad)
3.14
1.00
0.10
0.01
0
opposite to nest
nest direction
***
a
b
e
Velocity
0.10
0.03
0.01
n.s.
BAIT AREA: SMALL
BAIT AREA: LARGE
a
ab
bc
c
bc
ab
bc
c
SPECIES
BAIT WEIGHT

◂**Fig. 3** Comparison of cooperative transport between the native *D. tener* (teal) and the invasive *L. humile* (red) based on field experiments. The visualizations combine violin plots with standard box plots. **a** Shows the overall cooperative transport capacity (% baits removed from arena) for both species, **b** cooperative transport capacity across bait area-weight treatments, **c** cooperative transport accuracy (direction of bait removal relative to the nest direction); blue dotted lines and text were added for clarity, **d** directional of bait removal across bait area-weight treatment, **e** cooperative transport efficiency (velocity of bait transport corrected for the number and size of ants). **f** Transport velocity across bait area-weight treatments. Additional efficiency measurements can be found in Fig. S4 in the Supplementary Material. Significance levels are indicated as $*p < 0.05$, $***p < 0.001$, and "n.s." for $p > 0.05$, based on GLMMs. In **d** and **f**, violin plots that do not share the same lowercase letters are statistically significantly different (p-value < 0.05) according to a post-hoc Tukey test of all eight treatment-species combinations

reduces the risk of losing resources to competitors, such as local ant colonies or scavengers (Traniello 1983; Wojtusiak et al. 1995). In contrast, less efficient native species may struggle with poor coordination, leading to transport deadlocks and delays (McCreery and Breed 2014). However, it is important to acknowledge the limitations of our analysis, which is based on a small subset of global ant diversity including only a few invasive species. While our findings suggest that cooperative transport may enhance resource acquisition and colony expansion in invasive ants, further research is necessary to determine how widespread and functionally significant this behavior is in invasion processes.

While cooperative food transport appears particularly advantageous in competitive environments, its relevance may be limited in scenarios characterized by high resource availability and low competition. In these contexts, other traits—such as reproduction, dispersion, or survival—may take precedence. However, it is important to emphasize that cooperative transport may not be confined to food foraging alone. It can play an important role in nest construction and maintenance, obstacle removal from foraging paths, and brood transport (Moffett 1987, 1992; Czaczkes and Ratnieks 2013). Therefore, cooperative transport may still contribute to colony-level efficiencies, even in resource-rich, low-competition environments. By enabling a broad range of collective activities, cooperative transport may enhance colony adaptability and resilience, traits often associated with invasive success.

The enhanced cooperative transport ability of *L. humile* compared to *D. tener* in our field experiments may be attributed to the ecological pressures that *L. humile* faces in its introduced range. Introduced species often encounter novel environments where efficient resource exploitation may be crucial for survival and successful establishment (Holway et al. 2002; Lockwood et al. 2013). The ability to rapidly and accurately transport food resources could reduce competition with native species, thereby allowing *L. humile* to dominate new territories. We found that *L. humile* successfully moved a greater proportion of baits of varying weights and areas than *D. tener*, demonstrating its robust cooperative behavior. However, based on our video analyses we found that *L. humile* still exhibits uncoordinated cooperative transport, characterized by frequent deadlocks, where ants pull in opposing directions (Czaczkes and Ratnieks 2013). Uncoordinated cooperative behaviors are frequent in invasive and non-invasive ant species, such as *Myrmica rubra* and *Ectatomma ruidum*, respectively (reviewed in Czaczkes and Ratnieks 2013). In contrast, highly efficient and invasive species like *Paratrechina longicornis* demonstrate highly coordinated transport, where groups of ants align their efforts, leading to faster and more successful movement of large items (McCreery et al. 2019).

Cooperative transport efficiency measures the resources employed by the ants to move food items into the nest, as the number of ants and time spent on the cooperative task. We found that cooperative transport efficiency was similar in L. *humile* and *D. tener*, suggesting that both species allocate comparable resources to retrieve food items cooperatively. While both species demonstrate high efficiency, the invasive *L. humile* may have fine-tuned its strategies to surpass native competitors in critical aspects such as cooperative transport capacity and accuracy. Our results suggest that not all facets of cooperation are equally critical for invasion success; instead, specific behaviors, like accurate resource transport, of most large resources encountered, may better distinguish invasive from non-invasive species. Despite this difference in specific measures, when capacity, accuracy, and efficiency were combined into a single cooperative transport index, *L. humile*

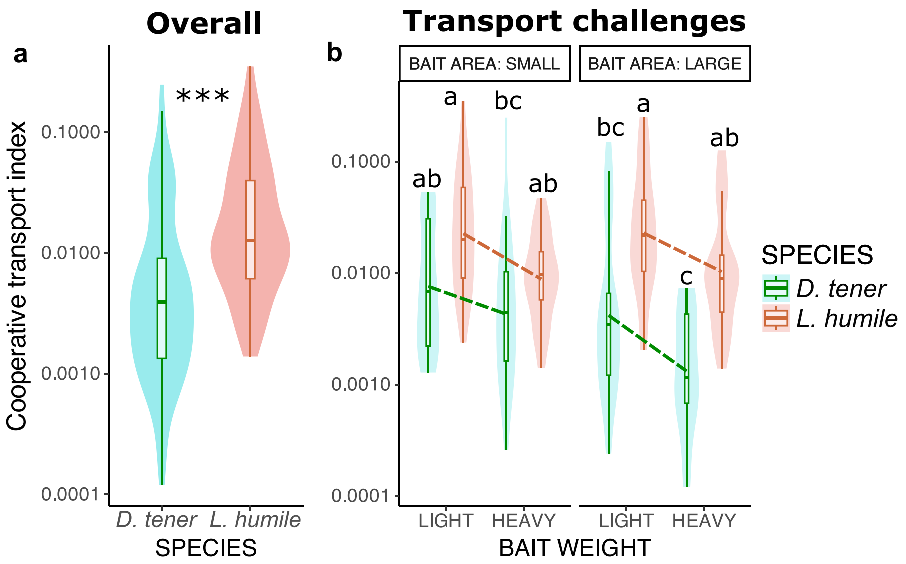


Fig. 4 Comparison of the cooperative transport index between the native *D. tener* (teal) and the invasive *L. humile* (red). The visualizations combine violin plots with standard box plots. **a** Cooperative transport index for both species. This index is the product of cooperative transport capacity, accuracy, and efficiency, **b** cooperative transport index across bait area-weight treatments. Significance levels are indicated as $^{***}p < 0.001$ based on GLMMs. Violin plots that do not share the same lowercase letters are statistically significantly different (p-value < 0.05) according to a post-hoc Tukey test of all eight treatment-species combinations

was found to be significantly better at cooperative transport than *D. tener*. Our findings emphasize the importance of assessing animal behavior using multiple and integrated measures, showing that while invasive species may outperform natives in some measures and not in others, the overall impact of behavior may still be significant.

While our findings highlight the cooperative transport abilities of *L. humile*, it is important to acknowledge that our sampling was restricted to three sites within the UCLA Botanical Garden, limiting broader geographic inference. Although we minimized the likelihood of sampling from a single colony based on spatial separation (Heller et al. 2008), we cannot rule out the possibility that sampled individuals belonged to the same unicolonial network. Future studies incorporating genetic analyses or multi-regional sampling would help assess potential variation in cooperative transport across distinct *L. humile* populations, further refining our understanding of its role in invasion success. Additionally, comparisons between sympatric invasive and non-invasive species would help isolate the effects of cooperative transport from other ecological and environmental factors influencing invasion success.

Beyond cooperative behaviors, other traits such as reproductive strategies, colony structure, and environmental adaptability can also contribute significantly to their invasive success. Polygyny (multiple queens), polydomy (colonies spanning multiple nests), and unicoloniality (large, cooperative networks) are factors that have been reported to enhance the success of invasive ants like the Argentine ant (*L. humile*) and the red imported fire ant (*S. invicta*) (Holway et al. 2002; Tsutsui and Suarez 2003). Similarly, life history plasticity—the ability to adjust reproductive and social behaviors in response to changing conditions—has been key for invasive species like the odorous house ant (*Tapinoma sessile*) (Buczkowski 2010). Understanding the interactions among these traits, processes, and cooperative behaviors, will be essential for advancing our knowledge of ant invasiveness and developing more effective management strategies.

An important aspect of our study was examining the impact of bait characteristics, specifically weight and size, on cooperative transport. We observed that bait weight had a strong effect on cooperative transport capacity, efficiency, and the overall cooperative transport index. Heavier baits required more ants, were transported with greater sinuosity, and resulted in slower transport velocities compared to lighter baits, underscoring the important role of weight in coordinating group efforts. These findings align with studies on other ant species, such as the longhorn crazy ant (*P. longicornis*), in which load mass, rather than size, was found to be more critical in determining cooperative transport success (McCreery et al. 2019). In our experiments, bait size had a relatively minor or non-significant effect, suggesting that while the physical dimensions of the bait may influence the number of ants involved, it is primarily the weight that dictates the coordination and success of the cooperative transport tasks. The differential impact of bait weight and area indicates that ants may prioritize adjustments to weight over adjustment to bait size when optimizing their cooperative transport strategies. These results emphasize the importance of considering load characteristics in behavioral studies of cooperative transport, particularly when comparing the capabilities of invasive and native species.

In conclusion, this study provides evidence suggesting that cooperative behaviors, particularly cooperative transport, may contribute to the success of invasive ant species. Expanding the scope of cooperative transport studies to include a broader range of both invasive and non-invasive ant species, as well as investigating other cooperative behaviors—such as communal nesting, cooperative foraging, and coordinated defense—will help clarify the ecological and evolutionary significance of intraspecific cooperation in biological invasions. Comparative studies examining sympatric invasive and non-invasive species could provide valuable insights into how cooperative behaviors influence invasion dynamics. Applying this growing body of knowledge to the development of management strategies may offer practical benefits. For instance, the use of synthetic pheromones to disrupt ant trail formation and recruitment (e.g., Suckling et al. 2008) could target cooperative behaviors that contribute to the competitive advantage of invasive species. Understanding intraspecific cooperation in animal invasions presents a promising research avenue, with the potential to reveal key mechanisms underlying invasion success and contribute to the development of more effective management strategies.

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Author contributions TC, AGFB, NPW, and AMD conceived the idea and contributed to the experimental design; NFC, DM, and AMD performed the experiments and collected the data; DM and AMD processed the data; AMD analyzed the data; AMD led the writing of the manuscript to which all authors contributed; all authors gave final approval for publication.

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Data availability The datasets and R scripts generated and analyzed during the current study will be made available in the Figshare Data Repository with an assigned DOI.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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