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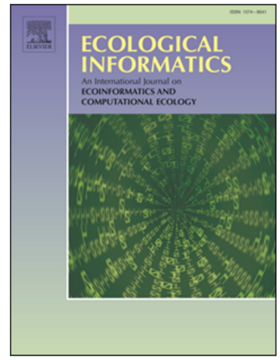

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Transfer entropy analysis reveals interaction dynamics between termite castes

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Abstract

Termites exhibit complex social structures characterized by distinct castes, each playing specialized roles within the colony. This study explores the interaction dynamics between the worker and soldier castes of *Reticulitermes lucifugus* using a transfer entropy framework. Inter-individual interactions were investigated across three caste pairings (worker with worker, soldier with soldier, and worker with soldier), enabling direct comparison of interaction dynamics. A computer-vision pipeline tracked movements, and two variables—occupied area and speed—were analyzed as proxies of interaction. Transfer entropy quantified the amount, direction, and timing of information transfer; sampling resolution and time lags were systematically varied to map temporal scales of influence. The working assumption was that higher transfer entropy values reflect higher levels of interaction between individuals. First, in the temporal-resolution analysis of speed, worker–worker pairs showed the highest total transfer entropy, and mixed pairs exhibited directional asymmetry, with higher information flow from soldiers to workers than vice versa. Second, in the time-lag analysis, total transfer entropy for occupied area was higher in worker–worker pairs (1.04 bits), compared with soldier–soldier (0.67 bits) and mixed (0.68 bits) pairs. The same pattern held for speed, with worker–worker pairs reaching 0.25 bits, whereas soldier–soldier and mixed pairs reached 0.20 bits. Overall, results indicate caste-specific interaction dynamics, with workers exhibiting higher interaction and faster responsiveness. These insights advance understanding of termite social organization and suggest applications in pest management, with broader implications for swarm robotics and bio-inspired engineered systems.

Key words – Termites; Interaction dynamics; Information theory; Collective behavior; Swarm intelligence; Complex systems;

Introduction

Termites, recognized for their complex social organization and cooperative behaviors, establish colonies that are defined by a highly specialized division of labor among distinct castes (Traniello & Rosengaus, 1997). Recent advancements in research have deepened our understanding of information exchange within these colonies, with a growing emphasis on characterizing the interaction processes occurring between various termite castes (Korb & Thorne, 2017; Turner, 2011).

Termites (Blattodea, Termitoidae) play a crucial role in soil ecosystems of warm climates, contributing to soil structure and fertility through their wood-degrading activities. However, they also pose a substantial threat to human wooden structures. The economic impact of termite-related damage is significant, with estimated losses ranging from $3–5 billion annually in the United States and around €1 million each year in the European Union (Luchetti et al., 2013).

The termite order Isoptera boasts societies ranging from a few hundred to millions of individuals. Termite colonies are composed of distinct castes that fulfill specialized roles crucial for colony survival and success. This study focuses on the mediterranean termite *Reticulitermes lucifugus* (Rossi) (Blattodea: Rhinotermitidae). In *R. lucifugus*, the primary castes include workers, soldiers, and reproductive individuals (Hare 1934; Ivanova et al. 2020; Roisin & Korb, 2011; Snyder 1925; Snyder, 1926). Workers are responsible for foraging, brood care, and nest maintenance, while soldiers are endowed with enlarged mandibles and defend the colony against intruders. Reproductive individuals, including the king and queen, ensure the continuation of the colony. These castes do not function in isolation; instead, their survival depends on frequent and coordinated interactions. Communication among castes is predominantly mediated through chemical signals (pheromones), vibrational cues, and tactile contacts, which facilitate efficient task allocation, defense responses, and social cohesion (Costa-Leonardo & Haifig, 2010; Howard & Thorne, 2011). Understanding how these interactions are structured and maintained is important to understand the mechanisms of collective behavior in termites.

Several computational ecology approaches and behavioral interdisciplinary techniques have been explored for termites (Lee & Lee, 2020; Nanda et al., 2021; Seo et al, 2018; Wang et al., 2025). Information theory is increasingly used in contemporary scientific research, offering a rigorous framework for quantifying information and complexity across a wide range of systems. From the structure of neural networks (Avantaggio et al., 2023; Mazzoni et al., 2011; Valentini et al., 2020) to the dynamics of ecological communities (Margalef, 1973; Ulanowicz 2001), it provides a unified framework for exploring the principles that govern complex behaviors. The development of dedicated software tools has further expanded its use, providing researchers with efficient algorithms to compute measures from information theory and analyze large, multidimensional datasets (Ince et al. 2010; Lindner et al., 2011; Montalto et al., 2014).

The application of information theory, specifically transfer entropy, which was first introduced by Schreiber (2000), has found extensive use in various scientific fields. Transfer entropy is a powerful tool from information theory since it allows to quantify the directional flow of information between two systems or variables. Unlike traditional correlation measures, which only assess the strength of relationships, transfer entropy captures the dynamic and causal influence one variable has over another by considering the history of their states (Zhou et al., 2022). This makes it especially useful in complex systems where interactions are not merely simultaneous but have a temporal aspect, such as in social dynamics, or communication between agents in biological systems (Das & Porfiri, 2023). By assessing how the state of one system influences the future state of another, transfer entropy helps reveal the mechanisms behind their interactions, making it a valuable tool for investigating causality across a range of scientific fields. In neuroscience, it has been utilized to explore causal relationships between different regions of the brain (Vicente et al., 2011) and to reconstruct connectivity within simulated neuronal networks composed of both excitatory and inhibitory neurons (Orlandi et al., 2014). However, its relevance extends beyond neuroscience. For instance, transfer entropy has also been applied to examine the processes underlying the dynamics of collective social phenomena, helping to characterize the complex behaviors that emerge in group settings (Borge-Holthoefer et al., 2016). Transfer entropy was first applied to model data of collective behavior by Wang et al. (2012). It has since been studied in in both vertebrates (Orange et al, 2015; Porfiri, 2018) and invertebrates (Tomaru et al., 2016), including termites (Mizumoto et al., 2021). However, it is still little explored in animal interaction, although it is a particularly promising approach for inferring interaction dynamics in animal groups with potential applications in complex systems physics, ethology and autonomous systems.

This study applies transfer entropy to examine the interaction dynamics within colonies of the termite *R. lucifugus*, focusing on interactions between and within the worker and soldier castes. A computational framework based on information theory was used to quantify the amount, direction, and timing of information transfer between individuals. Two variables—occupied area and speed—were selected as proxies for interaction, as they reflect spatial coordination and activity levels during social encounters. By analyzing how these variables contribute to information transfer, the study identifies caste-specific differences in interaction dynamics, including directionality of influence and variations in response timing. The results provide insights into the mechanisms supporting coordinated behavior in termite societies and contribute to a broader understanding of social insect organization. These findings may support the development of behaviorally informed pest control strategies. In addition, the observed interaction dynamics may inform the design of distributed systems in fields such as robotics and swarm-based technologies.

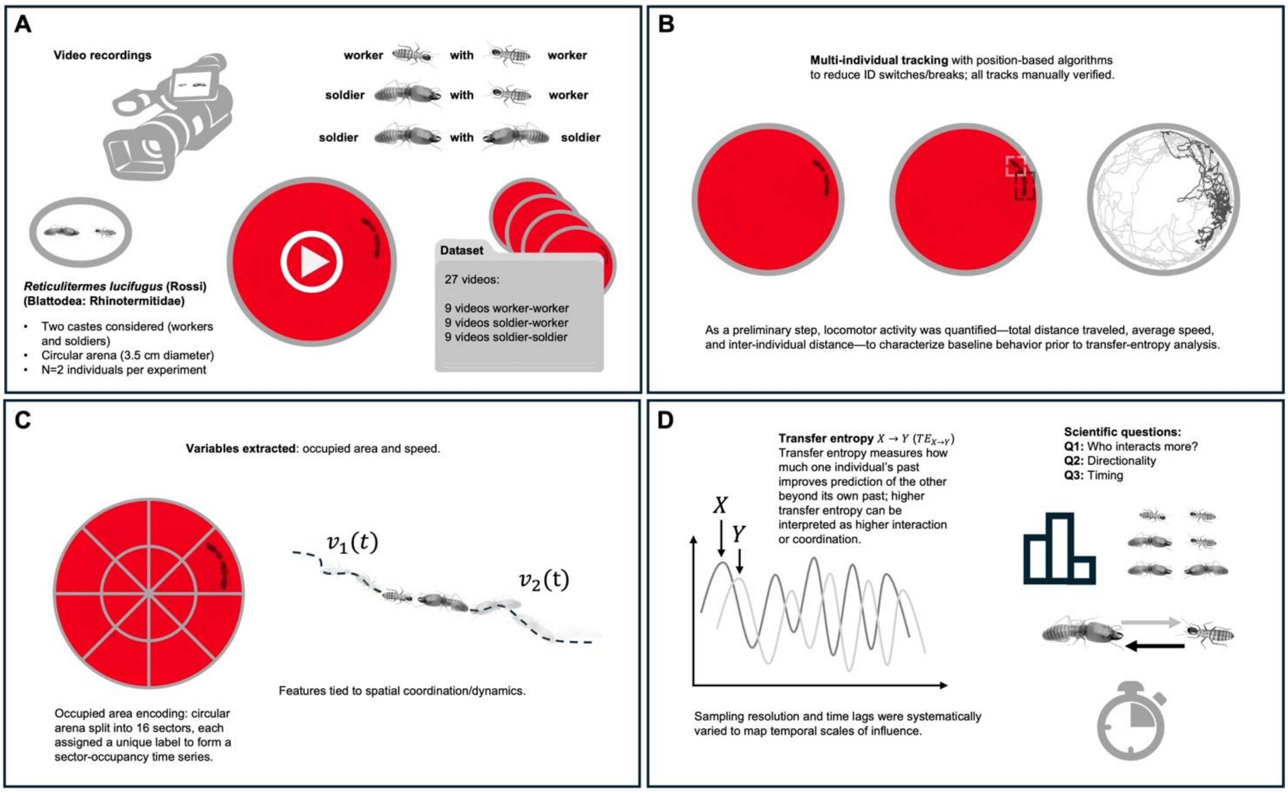

Fig. 2 Workflow of the proposed approach: Experimental set-up and video recordings (**A**); multi-individual tracking (**B**); features extraction (**C**); transfer entropy analysis (**D**).

Methods

Termite collection and rearing

Samples of *Reticulitermes lucifugus* were collected in May 2023 from infested pine wood in Pontedera, Pisa (Italy) (43°40'56.8"N 10°36'41.3"E). The pine stumps in which the colonies were living were placed in acrylic boxes (30x40x30 cm), and reared in laboratory conditions at a temperature of 25±2°C. *Reticulitermes lucifugus* subjects were identified according to Clément et al (2001). Only individuals from the same colony were used in experimental pairings to avoid inter-colony aggression, which is a known behavioral response in the genus *Reticulitermes* (Simkovic et al., 2018) and would confound interaction analyses.

Experimental set-up and procedure

The experimental set-up consisted of a video acquisition platform incorporating a Petri dish with a diameter of 3.5 cm. A red-light emitting diode (LED) was used because insects do not possess receptors for that wavelength (Briscoe & Chittka, 2001). An RGB camera (12MP camera, telephoto: f/2.8 aperture) was positioned above the arena to record the termites' motor activities. Each experiment involved two individuals, and three different pairings were considered: worker-worker, soldier-soldier, and worker-soldier. Prior to testing, individuals were randomly selected (according to the target caste) and kept isolated in Petri dishes (Ø 5.5 cm) for 5 minutes to allow for acclimation and to reduce potential stress from handling. Following acclimation, pairs were gently introduced into a clean observation arena for behavioral recording. Each experiment was recorded for 20 minutes. The recording duration was selected based on preliminary observations, during which we noted that different behavioral dynamics consistently occurred within this time frame. This interval provided a balance between behavioral richness and minimizing potential fatigue or stress effects on the individuals. Videos were recorded at a resolution of 1080 × 1920 pixels. All experiments were conducted during May and June 2023, during the active season for *R. lucifugus*, under laboratory conditions, and over multiple days to account for any daily variability. The experiment was repeated nine times for each pairing, in line with sample sizes found in the literature involving the application of transfer entropy analysis (Porfiri, 2018; Shaffer & Abaid, 2020). Videos were collected throughout the day (9:00 a.m. - 7:00 p.m.) at a temperature of 25±1°C. The arena was cleaned with alcohol and water after the experiments to remove any residual stimuli.

Data acquisition and extraction

The videos were processed using the USE Tracker free software for tracking individuals within the arena (Campo, 2015-2016). USE Tracker utilizes several open-source software libraries such as FFMPEG, OpenCV, and WxWidgets. This software provides a variety of image processing algorithms that can be parameterized and subsequently combined in a pipeline (Bologna et al., 2017). The image processing pipeline used is presented in Fig. 2. A region of interest was selected, and a difference with the background was considered (sensitivity to this difference=20). An erosion process was applied to shrink borders by 2 pixels, followed by a dilation process to grow borders by 2 pixels. Blobs were then extracted with a minimum blob size of 350 pixels. The software employed is a valid choice for tracking multiple individuals simultaneously (Bles et al., 2017; Quque et al., 2021).

The software utilized specialized algorithms based on position estimation to minimize track ID switches and breaks. However, the data obtained were manually verified for each video to ensure the accuracy and reliability of the tracking data. The data obtained through the tracking software were then processed and analyzed using the numerical computation software MATLAB. Data originally acquired at 30 fps were downsampled to a sampling interval of 120 ms. Although each video lasted 20 minutes, the first 30 seconds were excluded to allow the stabilization of the software used during acquisition, while the final 30 seconds were removed to standardize the effective duration of the analyzed segments across all recordings.

Subsequently, two key variables of interest were derived: the occupied area and the speed. To quantify the occupied area, the circular arena was divided into 16 distinct sectors. This was achieved by first partitioning the circular area into eight equal angular segments. Each segment was then further subdivided by introducing a concentric circle with a radius equal to half that of the original arena, creating an inner and outer region for each segment. Each sector was assigned a unique value, which was used to represent the area occupied by the individuals over time. This spatial representation was designed to capture dynamic patterns of movement and interaction within the standardized experimental context. These variables, occupied area and speed, were selected as they are inherently linked to spatial interactions and dynamic behaviors (Valentini et al., 2020). This approach ensured consistency across all videos and aimed to provide a robust framework for analyzing the mechanisms underlying interaction in the observed scenarios.

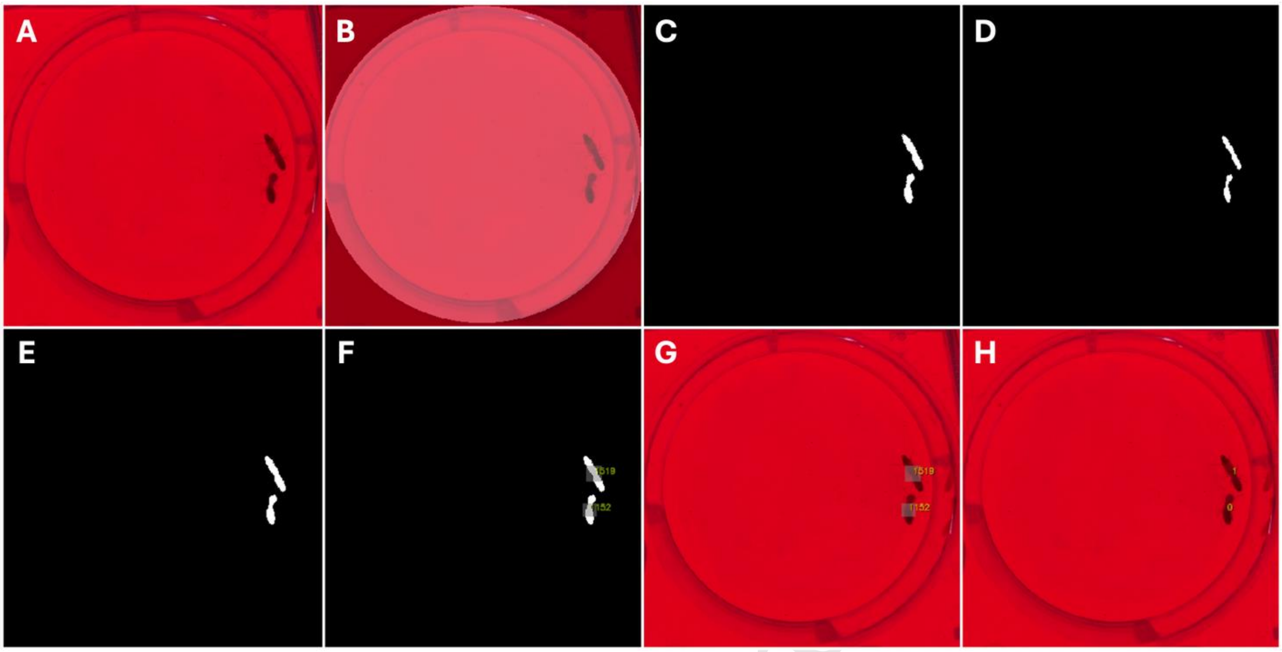

Fig. 2 Image processing pipeline for tracking individuals: sample frame (**A**); zone of interest (**B**); background difference (**C**); erosion (**D**); dilation (**E**); blobs extraction (**F**); blobs representation on the frame (**G**); individuals' identification on the frame (**H**).

Data analysis

Information theory provides a robust framework for quantifying uncertainty and the information flow in complex systems (Cover & Thomas, 2012). To investigate directed dependencies between individuals, transfer entropy was employed. Transfer entropy quantifies how much the state of one variable (e.g., the position or speed of an individual) contributes to predicting the future state of another. Crucially, this approach captures directionality in the interaction, allowing the identification of who influences whom, and to what extent. Unlike correlation-based methods, which assess symmetric associations, transfer entropy can reveal asymmetric and potentially causal interactions over time (Porfiri, 2018). Higher transfer entropy values reflect a higher amount of information that one termite's behavior provides about the future behavior of another, which can be interpreted as higher interaction or coordination between the two. Transfer entropy has been analyzed from the collected data. Given two time series (sampled at T_s), $X = \{x_1, x_2, \dots, x_N\}$ and $Y = \{y_1, y_2, \dots, y_N\}$, the conditional entropy $H(x_i|y_i)$ can be defined as:

$$H(x_i|y_i) = \sum_{x_i,y_i} p(x_i, y_i) log \frac{p(y_i)}{p(x_i,y_i)} \quad (1)$$

The transfer entropy according to the direction of flow $X \rightarrow Y$ $(TE_{X\rightarrow Y})$ can be defined as:

$$TE_{X\rightarrow Y} = H\left(y_i\middle|y_{i-\tau_y}^{l}\right) - H\left(y_i\middle|y_{i-\tau_y}^{l}, x_{i-\tau_x}^{k}\right) = \quad (2)$$

$$= \sum_{y_i, y_{i-\tau_y}^l} p\left(y_i, y_{i-\tau_y}^l\right) log \frac{p(y_{i-\tau_y}^l)}{p(y_i, y_{i-\tau_y}^l)} - \sum_{y_i, y_{i-\tau_y}^l, x_{i-\tau_x}^k} p\left(y_i, y_{i-\tau_y}^l, x_{i-\tau_x}^k\right) log \frac{p\left(y_{i-\tau_y}^l, x_{i-\tau_x}^k\right)}{p\left(y_i, y_{i-\tau_y}^l, x_{i-\tau_x}^k\right)}$$

where i denotes time, τ_x and τ_y represent the time lags, while k and l are the block lengths in variables X and Y, respectively. Since:

$$p\left(y_i, y_{i-\tau_y}^l\right) = \sum_{x_{i-\tau_x}^k} p\left(y_i, y_{i-\tau_y}^l, x_{i-\tau_x}^k\right) \quad (3)$$

thus, the transfer entropy results in:

$$TE_{X \to Y} = \sum_{y_i, y_{i-\tau_y}^l, x_{i-\tau_x}^k} p\left(y_i, y_{i-\tau_y}^l, x_{i-\tau_x}^k\right) log \frac{p\left(y_i \middle| y_{i-\tau_y}^l, x_{i-\tau_x}^k\right)}{p\left(y_i \middle| y_{i-\tau_y}^l\right)} \quad (4)$$

The estimation was based on the adaptive partitioning method introduced by Darbellay and Vajda (D-V), as implemented by Lee et al. (2012). This approach extends the D-V algorithm to three-dimensional space defined by y_i, $y_{i-\tau_y}$, and $x_{i-\tau_x}$ for computing the transfer entropy. This method dynamically adjusts the partitioning of the data space to compute probability distributions more efficiently and accurately than traditional fixed-bin approaches—an advantage in cases where parameter tuning can be challenging or time-consuming. Two main temporal parameters were considered:

- Downsampling factor: This determines how frequently data points are sampled from the original time series. Lower downsampling values retain fine temporal resolution and are suited to capturing frequent, rapid interactions. Higher values reduce the temporal resolution, enabling the analysis of slower dynamics.
- Time lags (τ_x and τ_y): These indicate the temporal delay between a potential cause (in one individual) and its effect (in another). By testing different lag values, it becomes possible to characterize how quickly information is transferred within a pair. Short time lags suggest fast responses, while longer lags reflect delayed interactions.

The analysis was carried out in two phases: first, by varying the downsampling factor while keeping the time lags constant; and second, by exploring different values of τ_x and τ_y to assess the impact of delay on information transfer, as suggested also by Faes et al. (2014). Transfer entropy estimation and the subsequent analysis were conducted in MATLAB, using the available online code developed in Lee et al. (2012). For the statistical analysis comparing results between groups, due to the sample size, a nonparametric analysis was employed. The Kruskal-Wallis test followed by a Dunn's test with Bonferroni correction for post-hoc analysis was used for comparisons involving multiple groups, whereas the Wilcoxon test was utilized for comparisons between two groups. A significance level of p=0.05 was used as the threshold for determining statistical significance. Statistical analyses were conducted in R.

Results

Locomotion analysis

To characterize the behavioral patterns emerging from different caste pairings, a set of quantitative features was extracted from the recorded trajectories of the individuals during the experiments. This analysis aimed to capture aspects of mobility and interaction, including spatial paths, movement speed, and the distance maintained between individuals over time. These parameters were selected to provide a comprehensive overview of the locomotion activity and social dynamics within each pairing. The extracted features were then compared across experimental groups to identify statistically significant differences. The outcomes of these analyses are summarized in Fig. 3. Figure 3**A** shows the path on the x-y axis from a sample involving a worker-soldier pair. Figure 3**B** displays the speed of the two specimens in the video sample, and Fig. 3**C** shows the distance maintained between individuals over time. For the comparison among all video samples, the total distance traveled (Fig. 3**D**), the average speed (Fig. 3**E**), and the average distance maintained between individuals during the experiment (Fig. 3**F**) were considered as features. When analyzing the distance traveled and the average speed, it is evident that workers paired with individuals of the same caste cover longer distances and exhibit higher average speeds compared to both soldiers paired with soldiers (p=0.0018) and soldiers paired with workers (p=0.0021). However, regarding the average distance between individuals during the experiment, a significant difference emerged between same-caste pairings of workers and soldiers (p=0.0247). Specifically, soldiers maintained a smaller average distance than workers.

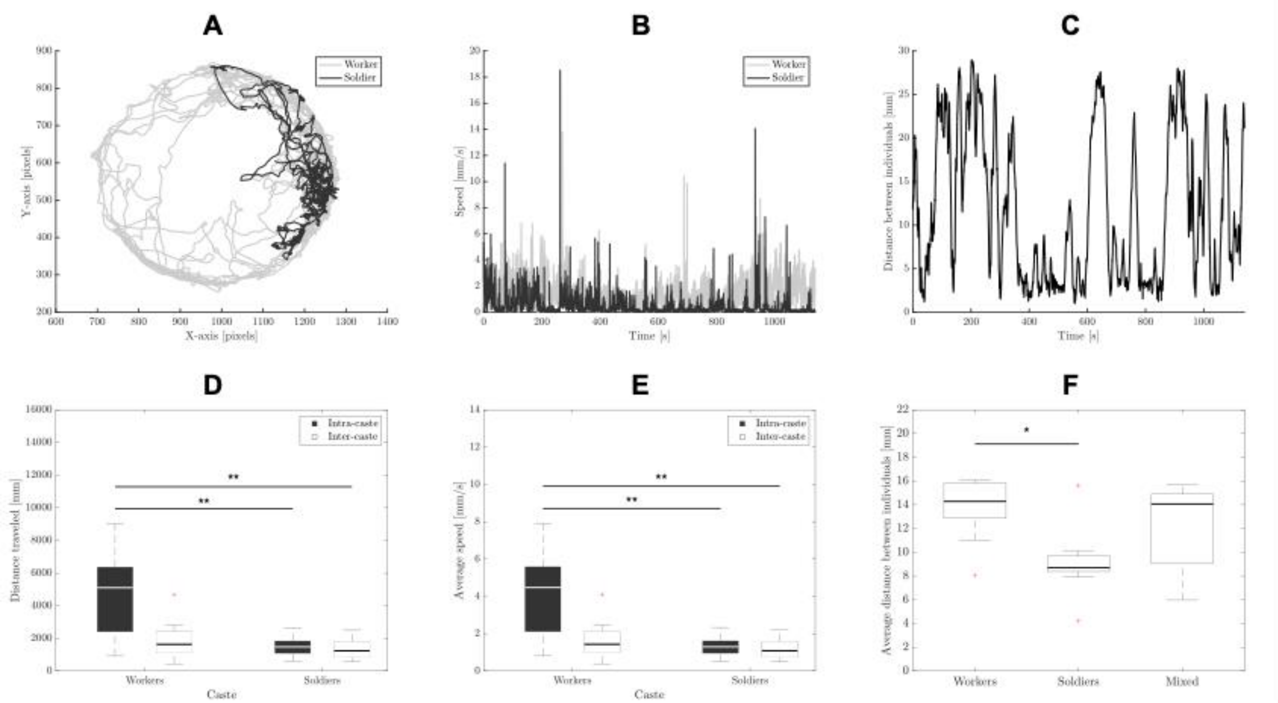

Fig. 3. Feature comparison: Video sample of a mixed pairing showing the path traced in the x-y plane during the experiment (**A**); speed over time for the mixed pairing (**B**); distance maintained between individuals over time for the mixed pairing (**C**); comparison of the total distance traveled during the experiment across different castes and pairings (**D**); comparison of the average speed across different castes and pairings (**E**); comparison of the average distance maintained between individuals across different castes and pairings (**F**). A single asterisk (*) indicates $p < 0.05$, two asterisks (**) indicate $p < 0.01$.

Transfer entropy across different downsampling factors

Transfer entropy analysis was performed considering two variables: the areas occupied by individuals during the experiment and their speed. To better understand both the quantity of the information transfer and the timing of interactions, different downsampling factors (N) were assessed while keeping the time lags fixed at $\tau_x = 1,$ and $\tau_y = 1$. Figure 4 presents the results of the transfer entropy analysis across various downsampling factors, where a downsampling factor of 1 corresponds to a sampling interval of 120 ms. Focusing on the occupied areas, the total transfer entropy illustrated in Fig. 4**A** reveals distinct trends across different caste pairings. Identifying peak values— representing the highest levels of information exchange— allows the association of each caste combination with specific temporal interaction dynamics. Paired workers display a peak of 0.59 bits at N=7, corresponding to 0.84 seconds, with values declining for higher N. Up to N=13, their total transfer entropy remains higher than that of both the soldier-soldier and mixed (worker-soldier) pairings. Soldier-soldier pairs reach their maximum transfer entropy (0.55 bits) at N=17, while the mixed pairing (worker-soldier) peaks at 0.53 bits at N=41, corresponding to 2.04 and 4.92 seconds, respectively. When comparing the peak total transfer entropy values across the three pairings (Fig. 4**B**), no statistically significant differences are observed. The same holds true for the net transfer entropy (Fig. 4**C**). Additionally, when examining the directionality of information transfer within the mixed pairing (Fig. 4**D**), no significant asymmetry is found between the two directions (worker-to-soldier vs. soldier-to-worker). When considering speed (Fig. 4**E**), a general decrease in total transfer entropy is observed across all pairings. For each group, the peak transfer entropy occurs at N=1, indicating that the most immediate interaction window—corresponding to 120 ms or less—carries the highest level of information exchange. A comparison of the maximum total transfer entropy values (Fig. 4**F**) reveals a significant difference between same-caste pairings of workers and soldiers (p=0.0081), with values of 0.25 and 0.20 bits, respectively. A significant difference is also found between worker-worker and mixed pairings (p=0.0119), with the latter exhibiting a lower transfer entropy (0.20 bits). No significant differences are detected when comparing the net transfer entropy among the three groups (Fig. 4**G**). Focusing on directionality within the mixed pairing (Fig. 4**H**), the information flow from soldiers to workers is significantly higher than in the opposite direction (p=0.0315).

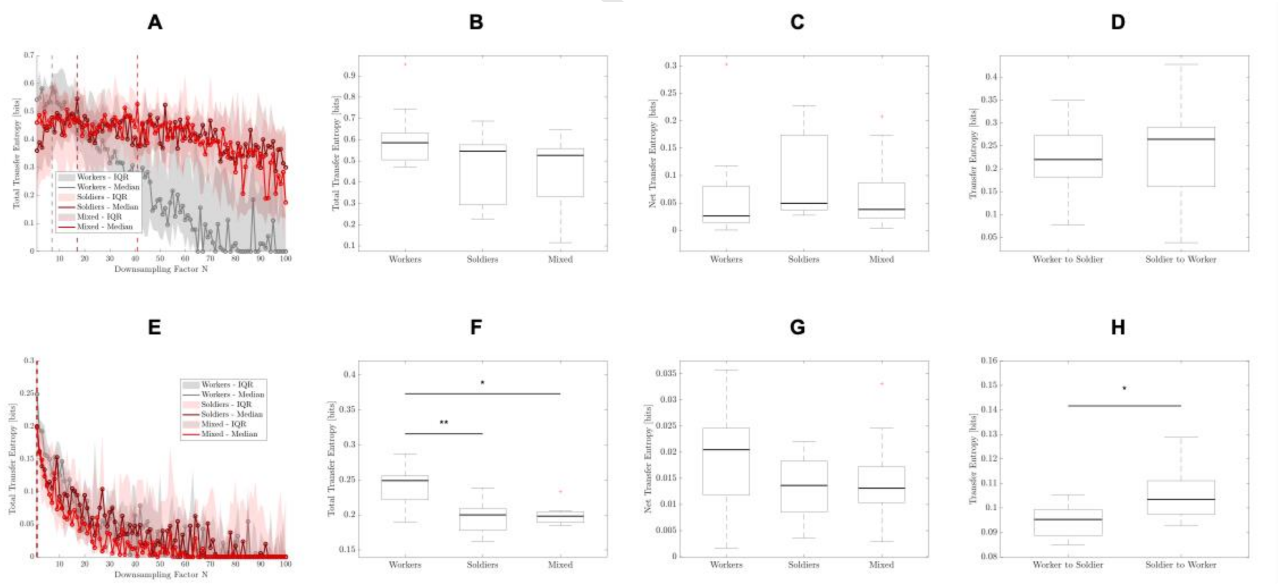

Fig. 4. Transfer entropy analysis across varying downsampling factor: Total transfer entropy as a function of the downsampling factor, using occupied area as the variable (**A**); comparison of maximum total transfer entropy among pairings (**B**); comparison of net transfer entropy at maximum total transfer entropy values (**C**); directional transfer entropy (worker to soldier and soldier to worker) for mixed pairs at the maximum total transfer entropy (**D**); total transfer entropy as a function of the downsampling factor, using speed as the variable (**E**); comparison of maximum total transfer entropy among pairings based on speed (**F**); comparison of net

transfer entropy at maximum total transfer entropy values based on speed (**G**); directional transfer entropy for mixed pairs at the maximum total transfer entropy based on speed (**H**). A single asterisk (*) indicates $p < 0.05$, two asterisks (**) indicate $p < 0.01$.

Transfer entropy across varying time lags

Next, the analysis focused on the minimum downsampling factor (N=1), while systematically varying the time lags τ_x and τ_y. Figure 5 shows the median values of total transfer entropy obtained under these conditions, helping to identify the time lag combinations that lead to the highest information exchange and reveal the timing characteristics of the interaction. Considering the occupied area, paired workers exhibit a maximum total transfer entropy of 1.04 bits at $\tau_x = 44$ and $\tau_y = 30$ (Fig. 5**A**). Soldier-soldier pairs show a lower maximum of 0.67 bits at $\tau_x = 48$ and $\tau_y = 35$ (Fig. 5**B**), while mixed-caste pairings reach their maximum of 0.68 bits at $\tau_x = 28$ and $\tau_y = 35$ (Fig. 5**C**). When analyzing individuals' speeds, the maximum total transfer entropy values are associated with shorter time lags, indicating quicker information transfer between individuals. Specifically, worker-worker pairs reach their maximum of 0.25 bits at $\tau_x = 2$ and $\tau_y = 1$ (Fig. 5**D**), while soldier-soldier pairs achieve a slightly lower maximum of 0.20 bits at $\tau_x = 6$ and $\tau_y = 1$ (Fig. 5**E**). Mixed-caste pairs similarly display a maximum of 0.20 bits, occurring at $\tau_x = 3$ and $\tau_y = 1$ (Fig. 5**F**).

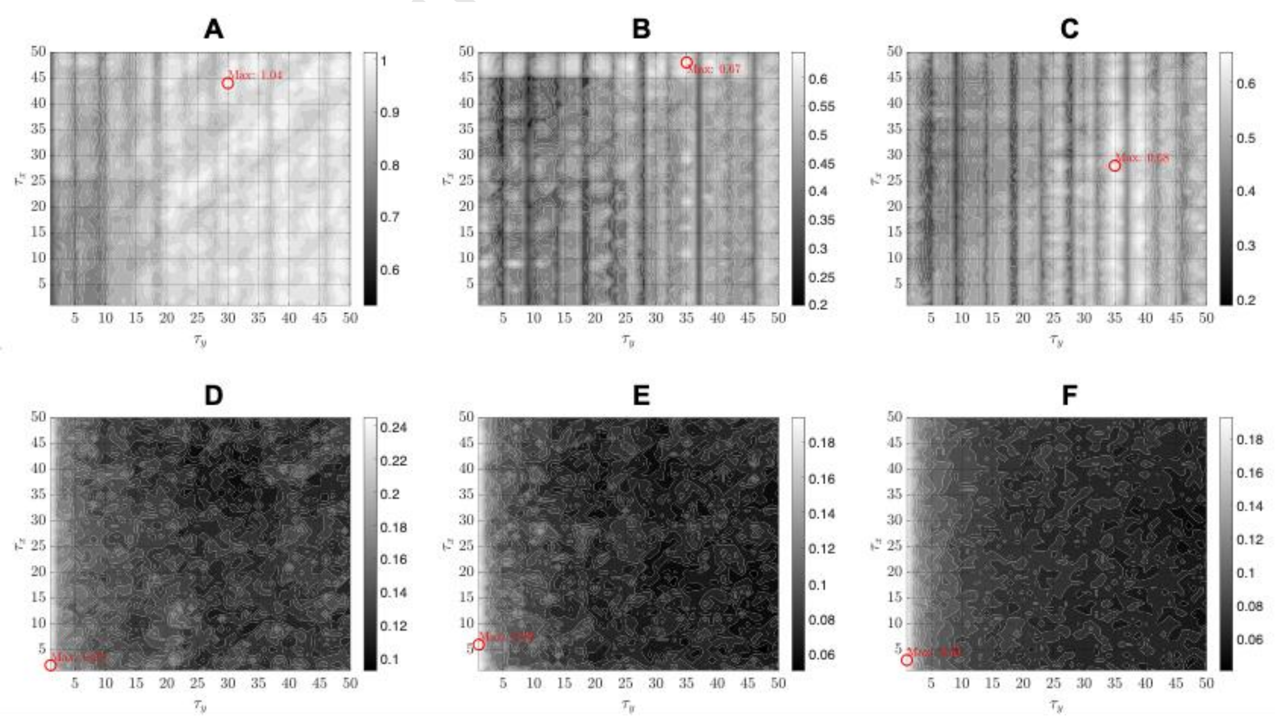

Fig. 5 Transfer entropy analysis across varying time lags (τ_x and τ_y): Median transfer entropy values for worker-worker (**A**), soldier-soldier (**B**), and mixed pairs (**C**), using occupied area as the analyzed variable; median transfer entropy values for worker-worker (**D**), soldier-soldier (**E**), and mixed pairs (**F**), using speed as the analyzed variable.

Finally, the maximum total transfer entropy values obtained for each pairing were compared and are summarized in Fig. 6. When considering occupied area (Fig. 6**A**), a significant difference emerges between worker-worker and soldier-soldier pairings (*p*=0.0108). Additionally, a significant difference is observed between worker-worker and mixed pairings (*p*=0.0207). No significant differences were detected in terms of net transfer entropy (Fig. 6**B**) or in the directional information flow within mixed pairings (Fig. 6**C**). Regarding speed as the analyzed variable, a significant difference is again observed between worker-worker and soldier-soldier pairings (*p*=0.0108, Fig. 6**D**). Additionally, a significant difference is observed between worker-worker and mixed pairings (*p*=0.0119). No significant differences were detected in terms of net transfer entropy (Fig. 6**E**) or in the directional information flow within mixed pairings (Fig. 6**F**).

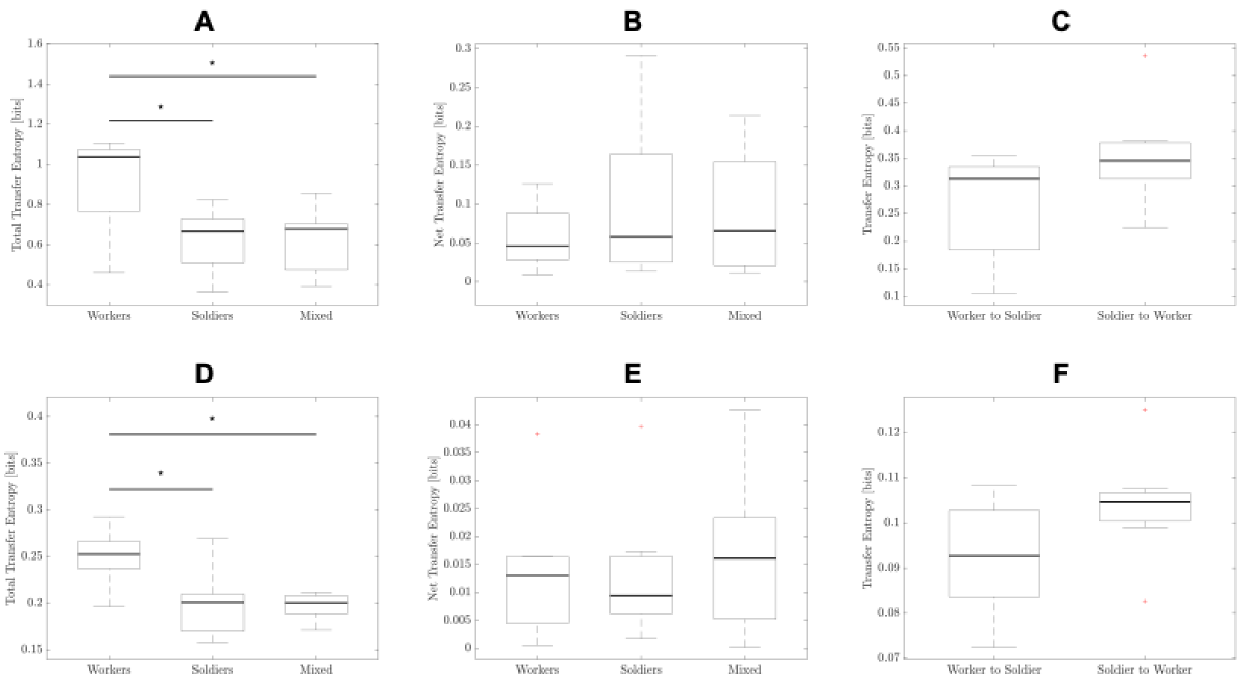

Fig. 6 Transfer entropy comparison at optimal time lags: Comparison of total transfer entropy among pairings (**A**), net transfer entropy (**B**), and directional transfer entropy (worker-to-soldier and soldier-to-worker) for mixed pairs (**C**), considering occupied area as the variable; comparison of total transfer entropy among pairings (**D**), net transfer entropy (**E**), and directional transfer entropy for mixed pairs (**F**), considering speed as the variable. A single asterisk (*) indicates $p < 0.05$, two asterisks (**) indicate $p < 0.01$.

Discussion

In this study, the primary aim was to explore the interaction dynamics within termites from different castes—specifically workers and soldiers—by applying a computational and information-theoretic framework. The underlying hypothesis was that the quantity and direction of information transfer differ depending on the caste composition of the interacting individuals. We expected that individuals from the same caste (e.g., worker-worker or soldier-soldier) would exhibit more intense and symmetric information exchange due to shared behavioral traits and roles. In contrast, mixed pairs (worker-soldier) were hypothesized to display asymmetric information transfer, with one caste exerting higher influence in the interaction. By quantifying the intensity, directionality, and temporal characteristics of information transfer, this study aimed to uncover caste-specific interaction patterns and provide new insights into termite social organization. To ensure consistency across experimental trials, the video context and analytical conditions were standardized. Two features were selected as proxies for interaction: the spatial area occupied and the movement (speed) of individuals. These variables were chosen because they are tightly linked to spatial coordination and social behavior (Valentini et al., 2020), allowing the capture of subtle dynamics in individual-to-individual interactions. The results confirm that transfer entropy, a central concept in information theory, is an effective tool for analyzing interaction patterns in biological systems. Unlike correlation-based methods, transfer entropy captures both the directionality and magnitude of information exchange, providing deeper insights into social responsiveness and coordination (Porfiri, 2018). Within this framework, the present study adopts a comparative interpretation of transfer entropy across caste pairings. Inference is drawn from between-pairing differences and supported by statistical tests.

In the broader context of computational approaches to insect behavior, artificial intelligence and information theory offer complementary strengths. While artificial neural networks excel at species identification and multi-level classification (Manduca et al., 2023a; Manduca et al., 2025a; Santaera et al., 2025) and at uncovering complex patterns in data (Fazzari et al., 2025; Galotti et al., 2025; Manduca et al. 2023b; Manduca et al. 2025b), information-theoretic tools allow for causal inference and mechanistic interpretation of interaction dynamics. Seo et al. (2024), for example, used an agent-based model to simulate tunneling behavior in incipient termite colonies, and a convolutional neural network (CNN) was trained to predict the number of individuals in the simulation based on the resulting tunnel structures. Lee & Lee (2020) proposed another modeling-based approach to optimize termite control strategies through bait deployment, showing that placing bait stations at intermediate distances from the nest maximizes diffusion efficiency. Information-theoretic methods have been employed in ecological modeling to relate ecological modeling to relate species behavior and spatial predictors, supporting decision-making in habitat management (Yost et al., 2008). Transfer entropy has also proven useful in biological systems without nervous systems. Ray et al. (2019) used it to investigate information flow within the contractile membrane of *Physarum polycephalum* during decision-making tasks, showing how leading regions emerge depending on environmental asymmetries. This demonstrates the versatility of transfer entropy in capturing decentralized coordination across biological domains. In social insects, Mizumoto et al. (2021) investigated coordination dynamics during heterospecific tandem runs between *Coptotermes formosanus* and *C. gestroi*. Their study demonstrated that male responsiveness to female pheromone release influences pair stability, and that post-separation movement speed reflects mate evaluation strategies. While their analysis integrates behavioral observations with transfer entropy measures, it centers on reproductive interactions and mate selection. In contrast, the present study examines interaction dynamics between workers and soldiers, using a quantitative, information-theoretic approach based on motion trajectories. By applying transfer entropy, the magnitude, direction, and temporal characteristics of interaction are inferred without relying on explicit interaction signals. This perspective complements previous findings by extending the use of information-theoretic tools to caste-specific social organization beyond the reproductive context. Other approaches have focused on termite detection using environmental signals. Nanda et al. (2021) developed a system that uses acoustic and temperature data, combined with feature selection algorithms, to accurately detect termite presence and estimate population size. While that method emphasizes external monitoring, our study targets internal interaction dynamics—two complementary approaches to understanding termite colonies.

Initial analyses showed that worker termites, when paired with individuals of the same caste, traveled longer distances and exhibited higher average speeds compared to soldiers paired with either other soldiers or workers. Regarding spatial proximity, a notable difference emerged in same-caste pairings: soldiers tended to maintain a smaller average distance from each other than workers did. Transfer entropy analysis offered a deeper perspective on these patterns. To better understand the interaction dynamics between termite castes, this study assessed the amount of information exchanged, the direction in which it flows, and the temporal characteristics of this exchange. This was achieved by systematically varying two key parameters: the sampling resolution (via downsampling) and the temporal delay between individuals (via time lags). Adjusting the downsampling factor allowed the investigation of interactions across different temporal scales—from rapid, frequent exchanges to slower, more gradual ones. Modifying the time lags helped determine how quickly the behavior of one individual influenced that of the other, providing insight into the immediacy or delay in their responses. In the first analysis, the downsampling factor was varied while keeping time lags fixed. When considering the spatial area occupied by individuals, worker-worker pairs exhibited the highest levels of information exchange, characterized by faster interaction dynamics compared to other pairings. Mixed pairings exhibited the less frequent interaction dynamics. While the differences in total transfer entropy based on spatial occupancy were not statistically significant, the analysis of speed as a behavioral variable revealed more distinct patterns. All groups demonstrated similar temporal dynamics, but significant differences emerged in total transfer entropy values. Worker-worker pairings showed the highest levels of information exchange, significantly exceeding those of soldier-soldier and mixed pairs. Moreover, within mixed pairs, the flow of information was significantly higher from soldiers to workers than in the reverse direction. In the second analysis, the downsampling factor was held constant and time lags were systematically varied. Results remained consistent: higher optimal time lags were associated with delayed responses and slower interactions, while lower lags indicated more immediate, tightly coupled exchanges. Again, worker-worker pairs demonstrated faster interaction dynamics and higher transfer entropy values. Experiments involved two individuals, focusing on inter-individual interaction. Transfer entropy allowed comparison and evaluation of interaction dynamics across caste pairings by measuring directionality and timing. Information theory can also be applied to group-level aggregates. Extensions to multi-agent settings are a promising direction for future works.

The investigation of communication networks within termite colonies offers promising opportunities to improve current pest management strategies (Su & Scheffrahn, 1998; Tonini et al., 2014). A deeper understanding of the complex social behaviors and interaction patterns of termites can inform the development of more refined, efficient, and sustainable control methods designed to disrupt their organizational structure, ultimately enhancing treatment effectiveness (Angon et al, 2023; Boulogne et al., 2017; Bouri et al., 2023). Although traditional approaches often emphasize the rapid dissemination of active compounds throughout the colony, targeting coordination mechanisms does not necessarily conflict with this objective. On the contrary, impairing local communication may weaken the colony's coordination and responsiveness to environmental stimuli, thereby increasing vulnerability. In some cases, a temporary slowdown in the spread of active compounds may be offset by reduced organizational resilience. Alternatively, leveraging social interactions to promote the internal distribution of compounds—such as influencing how termites share information about food sources or threats—may further enhance treatment efficacy. These strategies represent promising avenues for future research, and could support more targeted pest control solutions.

Beyond pest management, the broader implications of this research extend into fields such as robotics and engineered systems. For instance, recent work on heat sink design has adopted morphological principles derived from termite nests to generate self-organized structures that outperform traditional pin-fin configurations (Hu et al., 2023). Termites, like many other social insects, exhibit swarm intelligence to navigate complex environments and carry out collective tasks (Majumder, 2023). Understanding their coordination mechanisms can inspire the design of robotic systems that rely on similar decentralized principles (Blum & Groß, 2015). This knowledge has potential applications in autonomous navigation, drone fleet coordination, and distributed sensor networks, where multi-agent cooperation is essential (Ajith et al., 2006; Zungeru et al., 2012). As such, insights gained from termite social dynamics may contribute not only to biological research and pest control but also to the advancement of bio-inspired engineering and intelligent systems.

Conclusions

This study contributes to a deeper understanding of information transfer dynamics within termite colonies, with a particular focus on the interactions between castes. By applying transfer entropy, the directional flow of information was quantified, enabling a precise assessment of how individuals within and across castes influence one another. This methodological approach provided not only a measure of information exchange but also insight into the temporal and directional characteristics of inter-individual interaction. Through the systematic variation of downsampling factors and time lags, both total and net transfer entropy values were evaluated. First, varying the downsampling factor for speed revealed highest information transfer in worker–

worker pairs and directional asymmetry in worker-soldier pairs, with influence from soldiers to workers exceeding the reverse. Worker–worker pairs consistently exhibited the highest information transfer also varying time lags: for occupied area, total transfer entropy reached 1.04 bits versus 0.67 (soldier–soldier) and 0.68 (mixed); for speed, total transfer entropy was 0.25 bits versus 0.20 (soldier–soldier and mixed. Results also indicate faster responsiveness in workers. Beyond the biological insights, the findings offer potential applications in pest management. A more granular understanding of termite social organization could inform the development of targeted, efficient, and sustainable control strategies. Furthermore, the principles uncovered through this study may inspire innovations in bio-inspired robotics and distributed artificial systems, particularly those leveraging swarm intelligence for coordinated behaviors.

Ethical statement

This study follows the established ethical guidelines for the treatment of animals in behavioral research and education, as outlined by ASAB/ABS (2014), as well as the relevant Italian regulations (D.M. 116, 192) and European Union directives (European Commission, 2007). All experiments involved behavioral observations. No special permits were required from the Italian government for tests involving *Reticulitermes lucifugus*.

Declaration of competing interest

The authors declare that they have no competing interests.

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Data availability

Data and code used in this study are publicly available at: **https://github.com/GianlucaManduca/Transfer-entropy-analysis-reveals-interaction-dynamics-between-termite-castes-.git**

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Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Highlights:

- Termite societies rely on caste-based roles and intricate communication strategies
- Transfer entropy revealed termites' caste-specific communication dynamics
- Worker termites showed the highest levels of information exchange
- Information flow was stronger from soldiers to workers in mixed pairs
- Findings support improved pest control strategies and swarm robotics design