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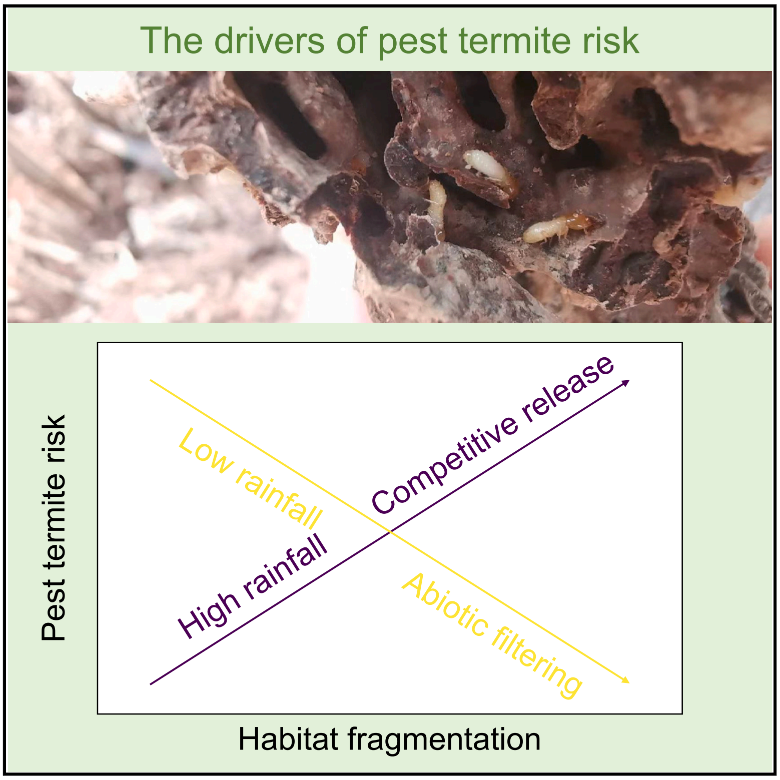
Habitat fragmentation drives pest termite risk in humid, but not arid, biomes

Graphical abstract



Highlights

- Habitat fragmentation and climate change may interactively alter pest termite risk
- The hypothesis is tested across 625 island assemblages and 813 local communities
- Habitat fragmentation drives pest termite risk at high but not low precipitation
- Humid intact forests control pest termite risk via competitively superior species

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In brief

Habitat fragmentation and climate change affect both pest and engineering species of termites that are widely distributed from the tropics to temperate regions. Our study mechanistically uncovered how these two stressors interactively changed the pest species risk in termite communities and highlighted that competitively superior species preferring humid intact forests are critical for controlling pest termite risk. As large-scale deforestation can drive regional desiccation, it is urgent to preserve and restore intact forests to prevent the outbreak of pest termites.

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Article

Habitat fragmentation drives pest termite risk in humid, but not arid, biomes

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SCIENCE FOR SOCIETY Termites play key roles in natural ecosystems, but some pest species cause global annual economic losses up to 40 billion US dollars. Climate change shapes pest termite distribution, and the loss and fragmentation of natural habitats replace beneficial species with pest termites. However, it is unknown how the two stressors interactively alter the pest proportion of termite communities and whether biotic interactions (e.g., competition) mediate such effects. Competitively superior species (i.e., winners in resource acquisition and agonistic conflicts) may prefer more intact habitats and a warmer, wetter climate due to higher resource quality and availability. In turn, superior species may limit pest outbreaks. We found that habitat fragmentation facilitated pest termites solely in humid biomes by threatening competitively superior species. As deforestation in humid tropics is driving regional desiccation, it is urgent to adopt reforestation as the eco-friendly means for pest termite control.

SUMMARY

Predicting global change effects poses significant challenges due to the intricate interplay between climate change and anthropogenic stressors in shaping ecological communities and their function, such as pest outbreak risk. Termites are ecosystem engineers, yet some pest species are causing worldwide economic losses. While habitat fragmentation seems to drive pest-dominated termite communities, its interaction with climate change effect remains unknown. We test whether climate and habitat fragmentation interactively alter interspecific competition that may limit pest termite risk. Leveraging global termite co-occurrence including 280 pest species, we found that competitively superior termite species (e.g., large bodied) increased in large and continuous habitats solely at high precipitation. While competitive species suppressed pest species globally, habitat fragmentation drove pest termite risk only in humid biomes. Unfortunately, humid tropics have experienced vast forest fragmentation and rainfall reduction over the past decades. These stressors, if not stopped, may drive pest termite risk, potentially via competitive release.

INTRODUCTION

Termites are one of the dominant invertebrate taxa. They are distributed from the tropics to temperate regions,[1] with a global biomass higher than other soil arthropod taxa[2] and similar to humans (0.05 vs. 0.06 Gt C).[3] Termites play key roles as ecosystem engineers, contributing to necromass decomposition[4] and soil bioturbation.[5,6] Some species can even mitigate extreme drought impacts on forest ecosystems.[7] Of the nearly 3,000 living termite species, however, more than 300 species are reported as damaging pests of forestry, agriculture, and urban structures, causing global economic losses up to ∼15–40 billion US dollars per year.[8,9] At least 28 species are highly invasive and spread across continents,[10,11] with 27 registered as pests (Table S1). To predict pest termite risk, it is critical to understand how multiple stressors interact on termite communities under global change.[12] Previous research has shown that habitat fragmentation and land use intensification increased pest termite

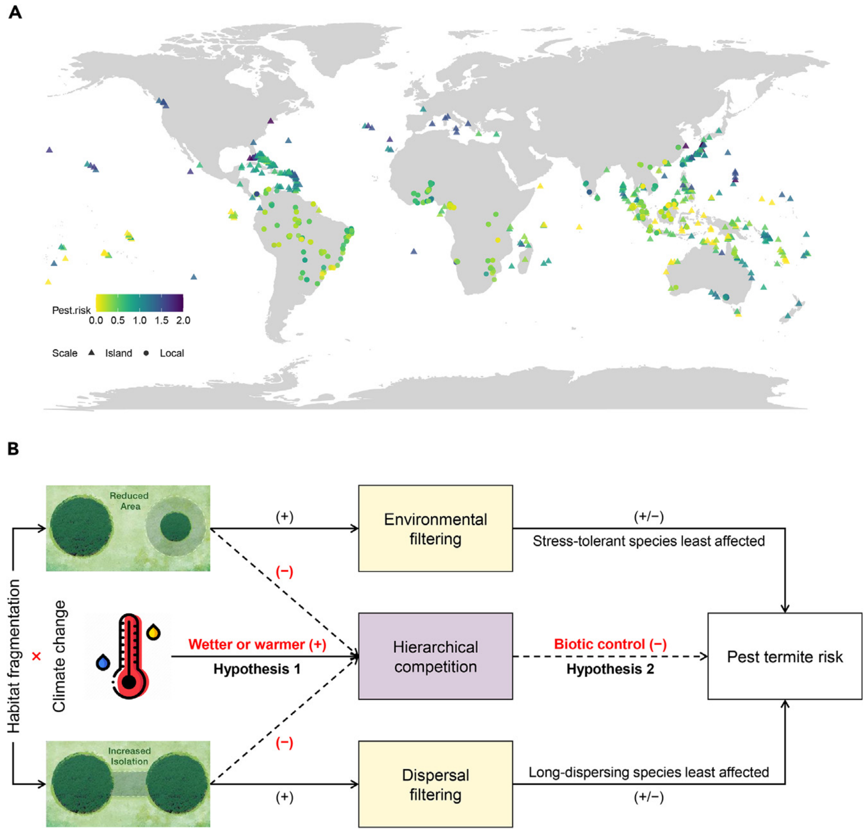

Figure 1. Global patterns of pest termite risk and the hypotheses regarding the interacting effects of climate and habitat fragmentation

The community-weighted mean of pest risk level within island species assemblages and local communities are both shown in (A), with symbols denoting spatial scale and color gradient denoting pest risk. A conceptual diagram of driving mechanisms is shown in (B), indicating that climate and habitat fragmentation interactively alter the importance of hierarchical competition, thus changing pest termite risk.

invasion and activities in some regions.[11,13–15] Although global warming is predicted to facilitate termite decomposing activities and expand the future distribution range of invasive species,[4,15,16] it remains unknown if and how climate change, interacting with habitat fragmentation, alters the pest species proportion of termite communities at a global scale (Figure 1A).

Understanding the dominant community assembly processes (i.e., abiotic filtering and competition; Figure 1B) is key to predicting the hotspots of pest risk.[12] Classic ecological theory posits that functional dissimilarity or phylogenetic distance among co-occurring species could be used for discerning assembly processes, with abiotic filtering causing more similar species assemblages and competition resulting in dissimilar assemblages.[17] However, recent studies have suggested that different assembly processes could cause the same patterns of species dissimilarity,[18,19] and one plausible solution is to match the assembly processes with the trends of species dissimilarity along the gradients of abiotic stressors.[20] Habitat fragmentation causes a reduction in habitat area (i.e., habitat loss) and an increase in habitat isolation (i.e., habitat fragmentation per se), thus filtering out species that are more sensitive to environmental stress (i.e., environmental filtering) or limited by dispersal capacity (i.e., dispersal filtering), based on the theory of island biogeography and empirical evidence, and leading to more similar species assemblages in small and isolated habitats than expected (i.e., random sampling from the species pool; Figure 2A).[20–22] Indeed, the majority of global pest termites are wood feeders (281 of 368 registered pests; see Table S1 for more details), which are less sensitive to habitat fragmentation[23,24] or probably better at dispersing across oceans (via rafting wood) than other feeding groups.[25] Nevertheless, the ability to endure abiotic filtering does not necessarily indicate that all pest termites prefer fragmented habitats than continuous habitats under any conditions, and thus abiotic filtering may decrease pest termite risk (Figure 2B). Alternatively, some termite species (e.g., Macrotermitinae) are competitively superior than others, and thus their decrease or even local extinction following habitat fragmentation may free extra niches for competitively inferior species (e.g., *Coptotermes*), which turn into pest termites via competitive release.[11] For instance, studies have suggested that large-bodied *Macrotermes* species are competitively superior than others[26] and that their presence leads to the exclusion of phylogenetically dissimilar species in pristine savannas.[27] A recent study in island systems further confirmed that competitive superiority was strengthened on larger and less isolated islands, which led to lower termite diversity and more similar species assemblages than expected.[28] Different from niche-driven competitive exclusion (or the limiting similarity hypothesis[29]), where species with similar niches cannot coexist due to limited niche space, resulting in more dissimilar species assemblages (Figure 2A), fitness-driven competitive exclusion (or hierarchical competition) generally leads to the dominance of a few species that have superior competitive ability and reduce other species in number, thus resulting in more similar species assemblages.[30] It is thus critical to discern two different types of competition, since they could pose different effects on pest species, with fitness-driven competition being more likely to limit pest species.

Climate change and habitat fragmentation, by altering environmental conditions and resource supply, can trigger changes in interspecific competition and, thus, species coexistence.[31,32] Coexistence occurs when the niche difference between two species is strong enough to overcome the competitive ability difference (or competitive superiority); i.e., the difference in the ability to win in agonistic conflicts and acquiring local resources.[33] Increasing environmental breadth (e.g., a key resource) can drive the eco-evolutionary divergence of competitive ability between species,[34] which, in turn, would select competitively inferior species with a sufficient niche difference to coexist with superior

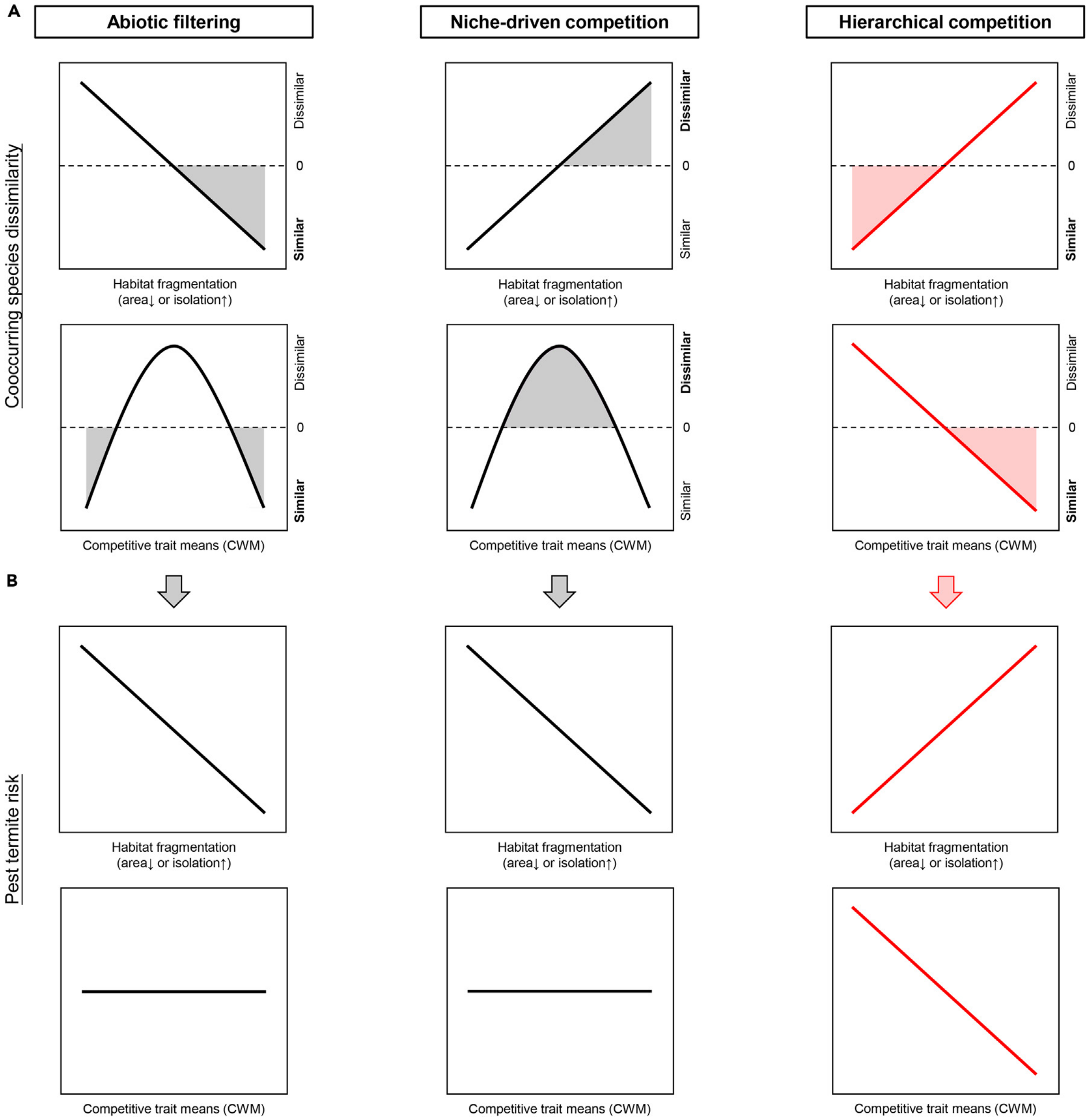

Figure 2. Identifying the dominant assembly process and the respective pattern for pest termite risk

(A and B) By regressing co-occurring species dissimilarity (observed vs. random) or pest termite risk against the gradients of habitat fragmentation (i.e., area reduction or isolation increase) and community-weighted mean (CWM) of competitive traits at different levels of climate conditions, we can infer the respective process of community assembly that drives the change of pest termite risk. We hypothesize that the dominant assembly process depends on the climate conditions, with hierarchical competition (red) being more important in wetter or warmer climates. Note that the shaded areas in (A) indicate the effects of the assembly process on termite communities. For instance, abiotic filtering following habitat fragmentation causes more similar species assemblages than expected.

species.[34,35] Inferior species may reduce the competitive difference (or disadvantage) if they disperse to the new habitats (e.g., with a warmer climate) much earlier than superior species so that inferior species can build up the numerical advantage and increase in fitness traits with sufficient time.[36] Alternatively, limited resource availability may reduce the survival rate and, thus, population size of all co-occurring species, but competitively superior species would be disproportionately suppressed due to the loss of control over multiple key resources.[37] For instance, a shortage in key elements like nitrogen reduces both the colony size and the individual body size of termites,[38] while anthropogenic disturbances and habitat fragmentation have been shown to disproportionately threaten competitively superior species (e.g., *Macrotermes*), probably via resource limitation.[26,28] Therefore, we posited that large continuous habitats in a wetter/warmer climate may have higher environmental suitability and resource availability that favor the evolution and ecological dominance of competitively superior species in termite communities (hypothesis 1; Figure 2A), which imposes stronger biotic control on pest species (hypothesis 2; Figure 2B).

Specifically, we assumed that habitat fragmentation under a wetter or warmer climate triggers more extensive loss of competitively superior species and, thus, a faster shift to pest-dominated communities. In contrast, abiotic filtering following habitat fragmentation is more important in structuring termite communities under drier or colder climate, yet pest termite risk becomes less sensitive to habitat fragmentation. To further distinguish hierarchical competition from other assembly processes (i.e., niche-driven competition and abiotic filtering), we regressed co-occurring species dissimilarity and pest termite risk along two gradients (i.e., habitat fragmentation and community-weighted mean of competitive traits) across different climate conditions and hypothesized that only hierarchical competition will simultaneously lead to more similar species assemblages in large and continuous habitats (Figure 2A, top right), negative relationships between co-occurring species dissimilarity and competitive trait means (Figure 2A, bottom right), and negative relationships between pest termite risk and competitive trait means (Figure 2B, bottom right). For competitive traits, we expected that competitive ability may scale with body size at individual levels where large-bodied species outcompete small-bodied species in agonistic interactions[26,39–41] or scale with nesting strategy complexity at the colony level[42] (Figure S1; related to larger colony size, better nutritional status, and a higher degree of diet differentiation among intrageneric species). Notably, termite body size evolution is independent of nesting strategy complexity and colony size,[43] which contradicts the traditional hypothesis that advanced sociality or colony size is at the cost of individual body size.[44]

Here we tested how habitat fragmentation and climate gradients interactively determine termite species dissimilarity, competitive trait means, and pest termite risk (i.e., community-weighted mean of pest risk level) by compiling termite co-occurrence data (1,596 species, including 280 pest species) at the island scale (i.e., species checklist of 625 oceanic islands) and at the local scale on both mainland and oceanic islands (i.e., 813 communities surveyed by standardized transects or quadrats; Figure 1A). We found that hierarchical competition was strengthened in humid biomes, where competitively superior species preferred larger and less isolated habitats. As the increase of competitively superior species suppressed pest termite risk, we found that habitat fragmentation caused more pest species in humid but not arid biomes. Our findings suggest that habitat fragmentation might drive pest termite outbreaks via competitive release, especially in humid biomes. Considering that humid tropics are experiencing vast forest loss and fragmentation,[45] which, in turn, causes regional desiccation,[46] we are concerned that pest termites could gain dominance and cause more severe damage in these regions.

RESULTS

Climate metrics included mean annual temperature, mean annual precipitation, and climate change velocity. Although our hypotheses did not involve climate change velocity, there have been studies stressing or at least considering the effects of climate change velocity on the current patterns of biodiversity.[47,48] Therefore, we included climate change velocity to account for the historic effects of climate change in shaping current termite communities and pest termite risk. Two metrics for habitat fragmentation, habitat area and isolation, were represented by island area (km^2) and distance to the nearest mainland (km, island isolation) for island species assemblages and by percentage tree cover (within 30 × 30 m range) and land use proportion (within 5 × 5 km range) for local communities, with local metrics more related to human disturbance.[45] Considering that percent tree cover of natural habitats is different across biomes, we also calculated the Z score of percent tree cover within the 5 × 5 km range per site, representing the relative level of percentage tree cover against adjacent grids (30 × 30 m) of the same climate condition.

For co-occurring species dissimilarity, we calculated mean functional and phylogenetic differences among all species pairs per termite community and transformed the difference value into a Z score so that zero value was the mean level of species dissimilarity by random sampling from the species pool. Positive and negative values, respectively, indicated more dissimilar or similar species assemblages than expected. Nine functional traits were complied, including body size (i.e., maximum head width of the soldier caste, mm), nesting strategy complexity (0 = one-piece nester, 1 = multiple-piece nester, 2 = central-piece nester), and pest risk level (0 = non-pest, 1 = pest, 2 = major pest). There was only weak correlation between pest risk level and nesting strategy complexity at the species level (Kendall's $\tau = -0.148$, $p < 0.001$) and between pest risk level and body size (Kendall's $\tau = 0.108$, $p < 0.001$; Figure S2). To improve trait data normality, we extracted the first four principal components (81.52% of trait variations; Table S2). We calculated the community-weighted mean of principal component 1 (PC1), PC3, and PC4 to reveal the shift in nesting strategy complexity (Pearson's $r = -0.96$), body size ($r = -0.78$), and pest risk ($r = 0.93$) per termite community. Details regarding the datasets and statistical analyses can be found in the experimental procedures.

Competition is the dominant assembly process in humid but not arid biomes

Notably, island- and local-scale models showed similar patterns where termite species assemblages were more similar in functional traits and phylogeny than expected in large and continuous habitats at high precipitation but more dissimilar at low precipitation (Figures 3 and S3; see Tables S3 and S4 for effects of other climate variables). The opposite patterns were detected in small and isolated habitats. If environmental or dispersal filtering is the dominant assembly process, we would observe more similar species assemblages in small or isolated habitats. As expected, this is the case for termite communities at low precipitation. In contrast, more similar species assemblages occur in large and continuous habitats at high precipitation, suggesting that competition becomes the dominant assembly process (supporting hypothesis 1; Figure 2A). Importantly, species dissimilarity calculated based on the full (Figure 3) and dispersion-field species pool (Figure S3) showed the same patterns, suggesting the robustness of our conclusions. We also analyzed the effects of another metric of island isolation, landmass proportion at island perimeter, which was negatively correlated with the distance to the nearest mainland ($r = -0.804$, $p < 0.001$; Figure S4). We found that both functional and phylogenetic dissimilarity increased with landmass at island perimeter at high precipitation but decreased with landmass at island perimeter at low precipitation (Figure S5; Table S3). One exception is that phylogenetic dissimilarity of local communities based on the full species pool tended to consistently

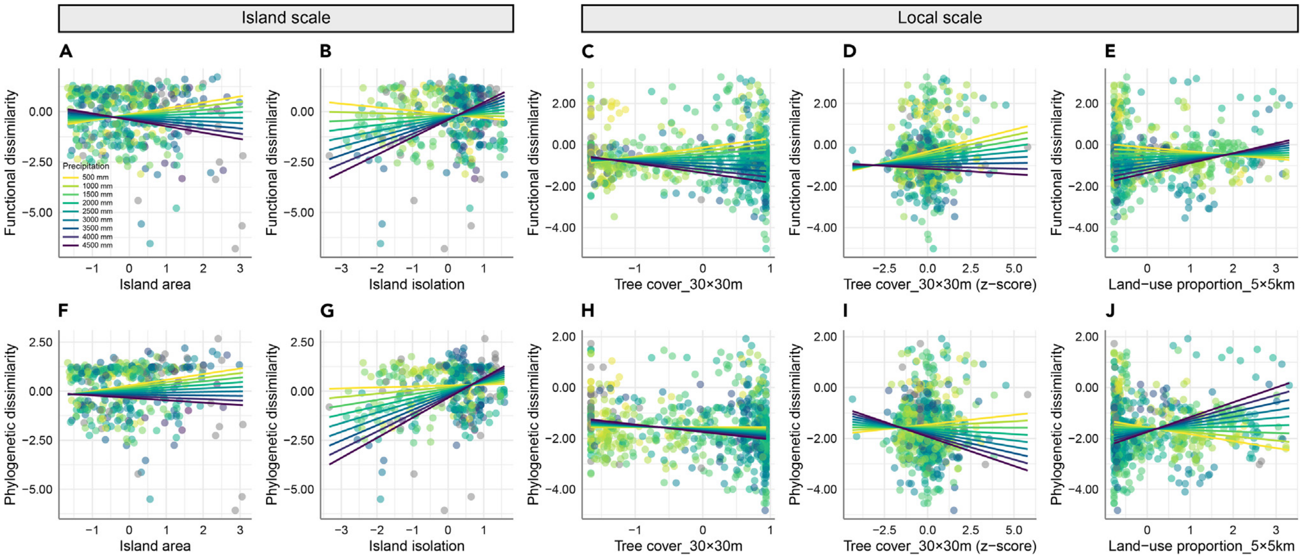

Figure 3. Co-occurring species dissimilarity along the gradients of habitat fragmentation

Precipitation gradient is denoted by the color bars in (A). Shown at the top and bottom are the patterns of functional and phylogenetic dissimilarity calculated based on the full species pool. The same patterns are detected for species dissimilarity calculated based on the dispersion field species pool (Figure S3; see experimental procedures for more details). All predictors are scaled to zero mean and unit variance. Island area (km^2) in (A) and (F) was measured as the polygon area of landmass surrounded by ocean. Island isolation (km) in (B) and (G) refers to the distance to the nearest mainland. See Figure S4 for the patterns of co-occurring species dissimilarity along the gradients of landmass proportion at the island perimeter, which is used as another metric for island isolation. Note that percentage tree cover (30 × 30 m, C and H) and land use proportion (5 × 5 km, E and J) are calculated at different spatial scales. As a different definition of habitat area for local communities, the Z score of percentage tree cover in (D) and (I) is calculated as the difference of tree cover between the target grid (30 × 30 m) and the mean of all grids within a 5 × 5 km range, which is then divided by the standard deviation of all grids. The respective assembly process could be inferred from the patterns of co-occurring dissimilarity (Figure 2A). See Tables S3 and S4 for model summaries.

decrease with increasing percentage tree cover across precipitation gradients (Figure 3H). Nevertheless, we still kept the interaction term of percentage tree cover because the difference in Akaike Information Criterion (AIC) values between models with (2211.334) and without the interaction (2211.289) was not large enough for variable exclusion (ΔAIC = 0.045 < 2). Furthermore, we detected marginally significant (p = 0.071) interaction effects between precipitation and the Z score of percentage tree cover on phylogenetic dissimilarity (Figure 3I), suggesting that habitat area effect still depended on precipitation level.

Hierarchical competition is enhanced as precipitation increases and weakened as habitat fragmentation increases

To further distinguish hierarchical competition from niche-driven competition, we regressed co-occurring species dissimilarity along the gradients of competitive trait means (Figure 2A). If hierarchical competition is the dominant process, then we would observe the monotonically negative relationship between species dissimilarity and competitive trait means, with the high values of competitive trait means leading to less diverse and more similar species assemblages than expected. If niche-driven competition is more important, then we should observe a hump-shaped pattern instead, with the intermediate values of competitive trait means leading to more diverse and dissimilar species assemblages than expected. We found that termite communities in humid biomes tended to show monotonically negative relationships, while communities in arid biomes tended to show hump-shaped relationship (supporting hypothesis 1; Figure 2A), and that nesting strategy complexity and body size were the key competitive traits at island and local scale, respectively (Figures 4A–4D and S6; see Tables S5 and S6 for model summaries). Meanwhile, it is more obvious that high but not low values of competitive trait mean in humid biomes were accompanied with more similar species assemblages (i.e., larger negative values of species dissimilarity). These findings indicate that hierarchical competition is more important in structuring termite communities in humid biomes. In accordance, we found that the community-weighted mean of nesting strategy complexity at island scale increased with precipitation and decreased with island isolation (Figure 4E; see Table S7 for model summaries), while mean body size at local scale increased with percentage tree cover at high precipitation but decreased with percentage tree cover at low precipitation (Figure 4F; see Table S8 for model summaries). These findings demonstrate that increasing precipitation may favor more competitively superior species, especially in large habitats.

Habitat fragmentation effect on pest termite risk depends on precipitation

As expected, we found that pest termite risk at island and local scale both decreased with habitat area at high precipitation (>2,000 mm/year), but increased with habitat area at low precipitation (Figures 5A and 5B; Tables S9 and S10; see also Figure S7A and Table S11 for the patterns of proportion-weighted pest risk at local scale). These findings indicate that the ecological resistance of large habitats to pest termites is greatest in

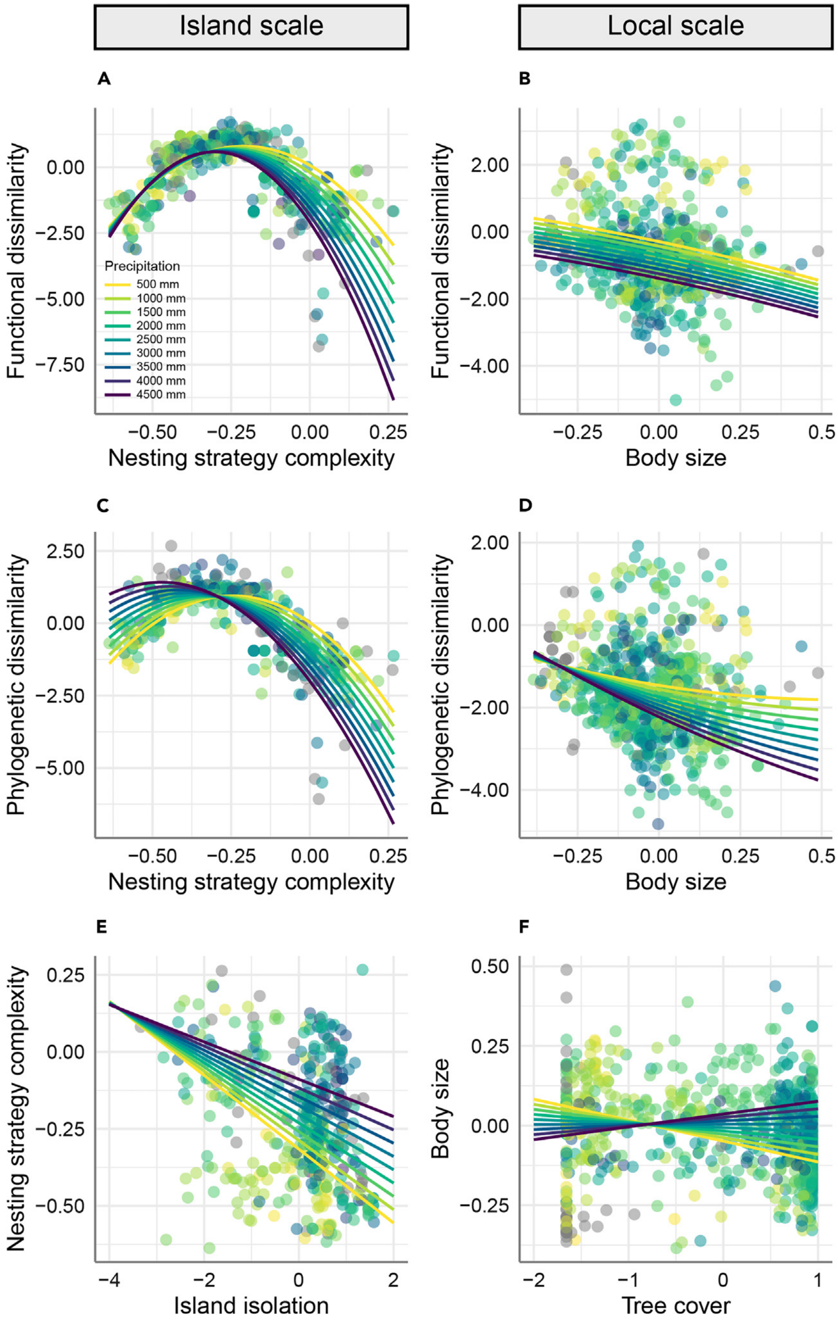

Figure 4. Co-occurring species dissimilarity along the gradients of competitive trait means

Precipitation gradient is denoted by the color bars in (A). (A)–(D) show the patterns of functional and phylogenetic dissimilarity calculated based on the full species pool, respectively. Similar patterns are detected for species dissimilarity calculated based on the dispersion field species pool (Figure S6; see experimental procedures for more details). (E) and (F) show the patterns of competitive trait means along the gradient of habitat fragmentation. The metrics of climate and habitat fragmentation are all scaled to zero mean and unit variance. See Tables S5–S8 for model summaries.

humid but not arid biomes (supporting hypothesis 2; Figure 2B). Notably, we found that the community-weighted mean of nesting strategy complexity and body size, respectively, showed negative relationships with pest termite risk at island and local scale (supporting hypothesis 2 in Figures 2B, 5C, and 5D; Tables S9 and S10; see also Figure S7B and Table S11 for the patterns of proportion-weighted pest risk at local scale). Meanwhile, mean body size had stronger negative effects on pest termite risk at higher precipitation, suggesting that competitively superior species build up stronger biotic resistance of large habitats to pest termites in humid than arid biomes. These findings reveal that habitat fragmentation in humid biomes may threaten the ecological dominance of competitively superior species and thus facilitate pest termites via competitive release.

DISCUSSION

Increasing rainfall drives hierarchical competition, especially in large habitats

Our study highlights that precipitation is a key climate factor that changes the major process (hierarchical competition vs. abiotic filtering) for the assembly of termite communities and has cascading effects on ecosystem function, such as pest outbreak risk. As termite fitness is limited by food resources[38,49] and desiccation[50] to some extent, increasing rainfall may benefit termites by increasing net primary productivity[51] and ameliorating soil moisture limitation.[52] In humid biomes, where environmental conditions are more habitable during longer time spans, investing in competitive ability may benefit termites more than in arid regions. In other words, some traits are more likely to reflect the hierarchy in competitive ability in humid than arid biomes. First, we found that overall nesting strategy became more complex with increasing rainfall at island scale, with central-piece nesters becoming dominant. These species build a central nest composed of soil or carton materials and gather food resources from tens to hundreds of meters away (Figure S1A), thus occupying a much larger territory and having larger colony size (Figure S1B) than one-piece nesters (which nest and feed in the same piece of wood) and similar to multiple-piece nesters (i.e., nesting in different pieces of deadwood inter-connected by foraging galleries). Due to their superior competitive ability, central-piece nesters may be more capable of acquiring resources and, thus, have better nutritional status than the other two nesters, e.g., lower tissue carbon-to-nitrogen (C/N) ratio (Figure S1C). Nevertheless, the trait-trait coevolution among these functional traits requires more in-depth studies incorporating the geographic distribution overlap and phylogenetic

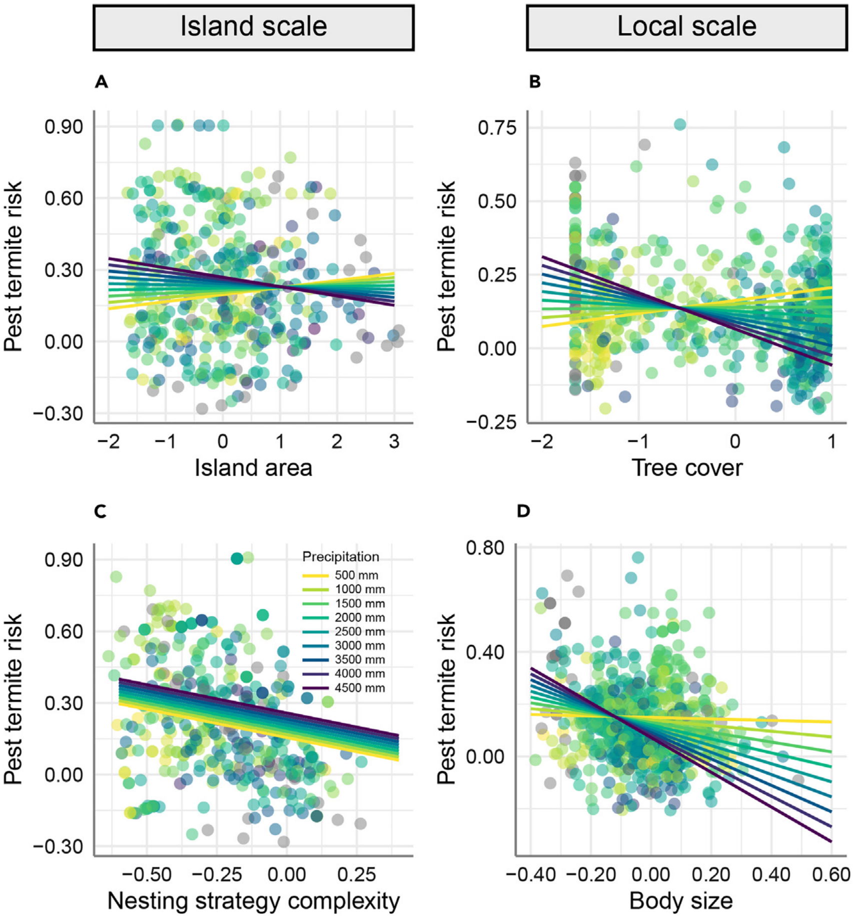

Figure 5. Pest termite risk along the gradients of habitat fragmentation and competitive trait means

Precipitation gradient is denoted by the color bars in (C). (A) and (B) and (C) and (D) show the patterns of community-weighted mean of pest termite risk along the gradients of habitat fragmentation and competitive trait means, respectively. The metrics of climate and habitat fragmentation are all scaled to zero mean and unit variance. See Tables S9 and S10 for model summaries.

non-independence among termite species (see Table S12 for the phylogenetic signals of nine functional traits covered in this study). Notably, some studies have reported that increasing rainfall in southern Africa increases the diversity of fungus-growing and soil-feeding termites, which are all central-piece nesters, but decrease the diversity of wood-feeding species, which belong to one-piece or multiple-piece nesters.[53] Likewise, increasing rainfall promotes the occurrence of central-piece nesters (e.g., arboreal and mound-building species) but not one-piece nesters (e.g., inside trees) in Australia.[54] Therefore, higher precipitation seems to favor central-piece nesters more than other nesters. Second, competitive ability may scale with termite body size under some circumstances, with the largest species winning overwhelmingly in paired aggression contests with equal numbers of individuals of smaller species.[26,39] We observe a positive interaction effect between rainfall and percentage tree cover on termite body size, suggesting that large-bodied species are more likely to occupy large habitats in humid biomes. Our study thus suggests that hierarchical competition among termite species may be strengthened, particularly in large habitats with increasing precipitation. Meanwhile, we do not imply that nesting strategy complexity and body size will always cause a difference in competitive ability and shape community structure under any condition. Instead, our study indicates that these two traits could reflect the hierarchy of competitive ability mostly in humid biomes.

Habitat fragmentation drives pest termite risk by competitive release in humid biomes

Pest responses to climate change are multifaceted and ecologically complex.[55] Moreover, climate change interacts with multiple anthropogenic stressors, including land use intensification and habitat fragmentation, to affect insect populations.[56] However, a unified theory or analytical framework is still lacking to understand and predict how climate change and habitat fragmentation interactively alter insect pest dynamics. From the perspective of community assembly, our study suggests that increasing rainfall may enhance hierarchical competition and, thus, strengthen the ecological resistance of continuous habitats (e.g., primary forests) to pest termites. Since tropical forests experienced a net cover loss[57] and severe forest fragmentation[45] over the past decades, we call for more attention to the functional degradation and pest risk increase within termite communities,[11] especially in humid tropics. Furthermore, there is increasing concern that at least six invasive termite species (also major pests; Table S1) have spread from urban into peri-urban forested habitats and that native termites and predators in invaded areas may not limit these invasive species.[11] This is probably because of the lack of shared evolutionary history among native and invasive species, leading to the collapse of ecological resilience.[58] This phenomenon further stresses that the competition-driven ecological resistance to pest termites, if not all pests, is formed through eco-evolutionary dynamics and is particularly important in natural forests of humid biomes, based on our findings.

We predict that future changes of rainfall regimens might have long-lasting impacts on the assembly process and, thus, pest risk of termite communities. Unfortunately, the massive loss of natural habitats can trigger the desiccation of regional climate. For example, large-scale forest loss has caused rainfall reduction and agricultural losses up to 1 billion US dollars annually in the southern Brazilian Amazon.[59] Besides, it is suggested that rainfall reduction below 2,000 mm/year would drastically decrease gross primary productivity, aboveground biomass, and tree cover in the Amazon rainforest.[60] Such a feedback loop between forest loss and rainfall reduction may gradually switch the community assembly from hierarchical competition to abiotic filtering and, thus, reduce the ecological resistance of forests to pest termites. It is reported that forest fragmentation restructures termite communities from soil-feeding species to wood/litter-feeding species and causes the loss of termite diversity.[23,24,61] Given that most pest termite species reported are wood/litter feeders (76.4%; Table S1), habitat fragmentation is likely to increase pest risk by favoring wood/litter-feeding termites against soil feeders. Furthermore, desiccation of the regional climate may be detrimental to forest-dwelling termites, as they are soft bodied,[50] and, thus, may reduce competition intensity among termite species. This is in accord with our findings that increasing rainfall increases the overall proportion of central-piece nesting species at island scale (Figure 4E) and increase the proportion of large-bodied species at local scale, especially in large forests (Figure 4F). While competitively superior species can have suppressing effects on pest termite risk (Figures 5C and 5D), we are deeply concerned that competitive species may be more sensitive to rainfall reduction and habitat fragmentation than pest species. Unfortunately, rainfall reduction by large-scale deforestation is common in global monsoon regions,[46,62] and it is thus urgent to conserve and restore continuous forests for maintaining humid climates and reversing functional degradation of termite communities.

Conserving large and continuous areas for natural or less disturbed habitats might not only reduce pest damage but also contribute to more sustainable management and economics. Larsen et al. reported that the spatial clustering of surrounding organic fields can significantly reduce the overall pesticide use in the focal organic field, while conventional fields surrounded by organic fields would increase pesticide use.[63] This is because organic fields may harbor more beneficial organisms, such as natural enemies that force pests to invade other areas with fewer enemies,[64] or because the reduced reliance on chemical pest control in organic agriculture could result in organic fields having higher levels of pests that spill over to other fields.[65] Therefore, increasing the spatial clustering of organic fields at the landscape scale could not only reduce pest damage but also reduce broad-spectrum pesticide use, which may further reduce environmental pollution and biodiversity loss.[66] Similarly, it is a common practice to spray insecticides for pest termite control.[67] Although there have been rapid developments in the research and registration of effective and environmentally friendly products, most consumers purchase products that are not only ineffective but also harmful to human and environment health because these ineffective products proliferate with greater market share.[68] Based on our findings, conserving natural habitats could be a more sustainable approach for pest termite control without sacrificing human and environment health.

Taken together, our findings suggest that precipitation is important in determining how habitat fragmentation drives pest termite risk. This climate change effect is mediated by the strengthened role of hierarchical competition in community assembly. The biotic control service provided by natural enemies and competitors against pest species is ecologically and economically important yet greatly threatened by anthropogenic stressors.[69,70] Our study suggests that conserving large and continuous forests, especially in humid biomes, can restore the hierarchical competition against pest termites and, thus, improve termites' engineering role as a whole. This could be important and urgent, as a recent study shows that termites are becoming more active under global warming.[4] Nevertheless, our study is based on observations across static climate gradients and inferring competition processes from species dissimilarity patterns but not direct measurements (e.g., interaction coefficients). Therefore, we call for more observational studies to cross-validate the patterns we found and more experimental studies involving climate change (e.g., warming and drought events) to monitor anthropogenic impacts on biotic interactions and functional change of termite communities. Besides, land management practice generally depends on the benefit-cost ratio, yet our study did not estimate the net cost or benefit by restoring the natural habitats to limit the damaging effects of pest termites. Future studies should develop cost-benefit analyses to determine whether and to what extent we should restore natural habitats to limit the damaging effects of pest termites without compromising the economic benefits of local industries or land uses. Finally, our analyses did not include the natural enemies of termites, such as ants,[71] which should be emphasized in future studies.

EXPERIMENTAL PROCEDURES

Global datasets

Island dataset

We compiled the co-occurrence data of 1,026 termite species on 625 (continental and oceanic) islands from four major sources: (1) Treatise on the Isoptera of the world,[9] (2) University of Florida Termite Collection (https://www.termitediversity.org/), (3) Global Biodiversity Information Facility (https://doi.org/10.15468/dL.yd4edv), and (4) individual studies and records searched from the Web of Science with the keyword combinations "Termite OR Isoptera" AND "Island" (see the island dataset for reference list). Morphospecies and records at coarser taxonomic levels were excluded. Most records for island termites are species specific and without spatial coordinates, making it impossible to define and distinguish local communities based on the spatial distance. We thus treated the species checklist per island to be the island species assemblages as a whole. Meanwhile, we included exotic species that successfully establish on islands because human-aided transport should be considered for the island biogeography of the Anthropocene.[72] Moreover, we acknowledged that many termite species on large islands may not co-occur in the same local habitats. Given that the relative contribution of assembly processes varies with spatial scale,[73,74] we anticipated that competition could be more important at local scale, while abiotic filtering or adaptive evolution (i.e., more similar species assemblages in large and isolated habitats)[20] could be more important at island scale.

Local dataset

Different from the island dataset, we only compiled the standardized survey data (e.g., transects and quadrats) of termite communities so that co-occurring species experience similar abiotic and biotic conditions and could be defined as local communities by study sites. This dataset was compiled from two major sources: (1) a previous dataset compiled for understanding latitudinal patterns of termite diversity by Cerezer et al.,[75] (2) recent studies and records searched from the Web of Science with the keyword combinations "Termite OR Isoptera" AND "transect OR survey OR community" (see the local dataset for the reference list). In total, we compiled standardized survey data for 813 study sites covering 738 species and 133 morphospecies. We included morphospecies at the genus level because (1) the proportion of morphospecies was considerable for some study sites, and (2) some genera were unique and should not be left out.

Functional traits and phylogeny

Functional traits

We compiled nine functional traits from existing datasets and individual studies to reveal different aspects of termites. For morphology, the maximum head width (mm) of the soldier caste (or worker caste for soldierless termites) was selected to represent termite body size.[43] For species displaying polymorphism within the soldier or worker caste, we used the measurements from the largest subcaste (i.e., major soldiers or major workers) to keep consistency across species and to reveal the advantage gained from enlarging body size. We did not use the maximum head width of alate imagoes to indicate competitiveness because alates never fight. Instead, we chose the soldier caste (or workers for soldierless termites) in particular, as they are responsible for colony defense. For undefined species at genus level, maximum head width was estimated as the average of species within the respective genus. For defense strategy, the number of size morphs for the soldier caste was used to reveal the defensive polyethism within the colony,[76] ranging from 0 (soldierless[77]) to 1 (one size morph) and 2 (at least two size morphs). We acknowledged that the number of size morphs was not enough to describe the difference in colony defense among species, as there are various types of mechanical[78] and chemical defenses.[79] However, given the considerable diversity (≥ 9) of defense types, it is difficult to use only one trait (either continuous or ordinal variable) to represent, and thus we chose not to include mechanical or chemical defense strategies in our analysis. For pest risk, each termite species was classified as one of three types according to a previous report[9]: non-pest (n = 0), pest (n = 1), and major pest (n = 2). The pest risk of undefined species at genus level was calculated as the average value of pest risk among all defined species of the same genus. Pest risk assignment was based on previous literature that reported termite damage to agroforestry (e.g., tea/coffee, rubber, cocoa, oil palm, groundnut, sugarcane, fruit trees, forest trees, and field crops), pastures, grains, buildings, and timber (Table S1). Species with higher pest risk generally caused greater economic loss across larger geographic ranges. Notably, we did not suggest that pest species (n = 1 or 2) would always cause damage in any given context. Instead, we aimed to suggest that there will be a higher risk of pest damage where these species accumulate more, and, thus, these areas should be given priority for pest pre-control.

For nesting strategy complexity (see Figure S1A for graphical illustrations), we grouped each species into one-piece nesters (n = 1), multiple-piece nesters (n = 2), and central-piece nesters (n = 3) based on a genus-level checklist.[42] For foraging activity, we further distinguished species: whether they are foragers that search for food outside the nest (0 or 1) and whether they have access to soil (0 or 1).[42] For feeding substrates of termites, we extracted three traits at genus level: (1) the dominant feeding group along the humification gradient,[80] including wood/grass-feeding lower termites (n = 1, evolutionary primitive families other than Termitidae); higher termites feeding on fresh or partially decayed organic material, including deadwood, grass, litters, dung, epiphytes, and fungi (n = 2); humus soil-feeding termites (n = 3); and mineral soil-feeding termites (n = 4); (2) intrageneric diet differentiation (ranging from 1 to 5) by summing the number of diet types per genus reported by individual studies of termite surveys; and (3) with or without soil-feeding habit (n = 1 or 0), with soil-feeding species including humus-soil feeders, mineral-soil feeder, and wood/soil-interface (or intermediate) feeders. As the feeding substrate trait is unavailable for some termite species, we used these three genus-level traits to reveal the difference in diet evolution history among termites at coarser taxonomic levels. For instance, feeding diet differentiation can avoid fierce competition and, thus, enable stable coexistence.[81,82] High diet differentiation at genus level may indicate that sympatric species of the same genus confronted intense competition during the evolutionary history and, thus, diverge into different diets. Alternatively, different environmental conditions and major food sources would also drive allopatric diet divergence among closely related species.[83] In addition, we realized that several traits were highly correlated (Figure S2). For instance, genera with soil-feeding habits included some of feeding group 2 (e.g., *Amitermes*)[23,80,84,85] and all species from groups 3 and 4. Given that the soil-feeding habit was not entirely the subset of the dominant feeding group gradient, we included both traits for quantifying functional dissimilarity among species. In addition, not all one-piece nesting species are foragers, while all multiple-piece and central-piece nesters are foragers. Nevertheless, we still kept the forager trait, as it had a different definition and focus compared with nesting strategy complexity, and we used principal-component analysis to account for the collinearity among nine functional traits.

Phylogeny

Phylogenetic information was obtained from the most complete species-level phylogeny of termites.[86] Nevertheless, there are many species without public records of genetic data. Meanwhile, the local dataset contained undefined species at genus level. To address these issues, we employed a method called Taxonomic Addition for Complete Trees (TACT),[87] which can incorporate species without genetic data as well as undefined species at genus level. First, we extracted the phylogeny that contained exclusively all extant termite species with genetic data and calibrated the phylogeny by using four alternative schemes (with the fourth scheme finally used because the resulting estimates were largely congruent between calibration schemes).[86] Second, we used the TACT method to randomly place the species without genetic data within their corresponding genera, subfamilies, or families by taking into account branch lengths determined by local diversification rates.[87] Third, we pruned the species present in the trees but missing from our datasets. Finally, 1,000 pseudo-posterior trees are generated. We acknowledged that each of the pseudo-posterior trees might not reflect the actual phylogeny of termite species in our study. Therefore, we used 1,000 pseudo-posterior trees for calculating the mean values of phylogenetic dissimilarity across a considerable range of possible topologies.

Co-occurring species dissimilarity

For each island species assemblage or local community, we used tree-based approaches to calculate functional and phylogenetic dissimilarity. We first computed functional distances between all species pairs using Gower's distance[88] and constructed a functional dendrogram (comparable with a phylogenetic tree) using hierarchical clustering and the unweighted pair group method with arithmetic means algorithm. We calculated the correlation between the mean pairwise functional distance based on the dendrograms and functional diversity metrics based on the trait convex hull.[89] For island datasets, functional distance was positively correlated with functional richness (r = 0.383, p < 0.001), functional dispersion (r = 0.648, p < 0.001), and Rao's Q (r = 0.582, p < 0.001). For local datasets, functional dissimilarity was positively correlated with functional richness (r = 0.401, p < 0.001), functional dispersion (r = 0.677, p < 0.001), and Rao's Q (r = 0.620, p < 0.001). While functional diversity metrics did not strongly (r > 0.7) covary with functional distance, we deemed that functional distance basically revealed the same trends of functional diversity metrics.

Species dissimilarity was defined as the departure of functional or phylogenetic distances of co-occurring species within an assemblage relative to a random sampling of species from the species pool.[17] The island species pool was defined as all species occurring on all islands, while the local species pool was defined as all species present in all local-scale habitats, so that different species had the same chance to colonize any given island or local-scale habitat without ecological or evolutionary constraints (i.e., null hypothesis that no deterministic process matters). In addition to the "full" species pool, we also constructed the dispersion field that represents the pool of species with geographic extents overlapping the focal assemblage.[90] Given that the geographic ranges of many termite species were quite limited, we used the genus-level dispersion field as the species pool, which included all species within the genera that occur at least once within the dispersion field.[20] By comparing the results based on the full species pool and the dispersion field pool, it would be more robust to make the inference on how species dissimilarity varied along the gradients of climate and habitat fragmentation.

The standardized effect size (SES) for species dissimilarity was calculated as [observed − mean(null)]/SD(null), which was analogous to normalized Z values. Null values were calculated from 1,000 random communities using the tip-shuffling null model that randomizes species identity (i.e., the names of taxa on the functional or phylogenetic topologies) while maintaining the community data matrix that captures the distribution of species richness per island or local site.[20] Randomization was carried out for one functional dendrogram but each of 1,000 phylogenetic pseudo-posterior trees. As there were no abundance data for island communities, and different definitions of abundance were used for local communities (e.g., occurrence frequency across sampling units vs. total individual number), we chose not to incorporate non-random abundance distributions for sampling null communities.[91] SES values of phylogenetic dissimilarity were further averaged across all pseudo-posterior trees. Some island species assemblages (n = 201) and local communities (n = 15) only had one termite species (or morphospecies), and, thus, species dissimilarity was not calculated. These islands and local communities only included six unique species in total that did not occur in the rest of islands and local habitats. Besides, these one-species islands and local sites were distributed around the other sites and could also contribute to the species pool. Therefore, we did not exclude the six species from the species pool.

Given that tip-level community structure, i.e., pairwise distance between nearest species, reveals subtle differences in functional traits and evolutionary history among species, we expected that tip-level species dissimilarity in our study might not capture the true pattern because several traits were gathered at genus level, while many species in the phylogenetic trees were randomly placed based on the taxonomic constraints. Therefore, we calculated root-level functional and phylogenetic dissimilarity instead, which reveals a root-level community structure that is more sensitive to splits deeper in tree topologies. Specifically, we calculated the SES of mean pairwise distances (i.e., all species pairs per community) based on functional dendrogram or phylogenetic trees.

Climate and habitat fragmentation

Island dataset

We obtained island variables from a standardized dataset of the world's islands,[92] including area, isolation, and climatic factors (temperature, precipitation, and climate change velocity). Island area (km^2) was measured as the polygon area of landmass surrounded by ocean using a cylindrical equal-area projection. Isolation (km) was calculated as the distance from an island's mass centroid to the nearest mainland coast (excluding Antarctica, which is permanently covered by ice). In addition, landmass at island perimeter was calculated as the $\log_{10}$-transformed sum of the proportions of landmass within buffer distances of 100, 1,000 and 10,000 km around the island perimeter. Higher values of landmass at island perimeter indicate lower levels of island isolation. The maximum values per island polygon of mean annual temperature (°C) and mean annual precipitation (mm) were included to adjust for potential confounding effects of climate on community structure. Climate change velocity (CCVT; 30-s resolution, from Sandel et al.[93]) was calculated as the ratio between the temporal change in temperature per year (°C/year) and the contemporary spatial change in temperature (°C/m) and expressed in distance units per time (m/year). The temporal change was the difference of mean annual temperature between current and the last glacial maximum divided by 21,000 years. CCVT per island was averaged across the island polygon. We log-transformed island area, isolation, and CCVT to improve normality. Although our study did not make hypotheses about how CCVT affected termite diversity, we deemed it necessary to include this confounding factor, given that climate stability can increase biodiversity and phylogenetic turnover, while rapid climate changes favors generalist species and phylogenetic homogenization.[47]

Local dataset

Compared with islands, it is harder to find analogous characteristics of habitat area and isolation for local sites. This is because most indexes for quantifying habitat fragmentation are based on the strict definition of habitat patches and the delineation of their boundaries.[94,95] For instance, we can use the size of continuous forest patches as the indicator of habitat area for termite communities in forest biomes, but the same metric may not be applied to savanna biomes, where trees are scattered within grass matrix. While a habitat patch could not be defined universally, the degree of habitat isolation (e.g., distance between patches) remains questionable. Therefore, we proposed two standardized metrics as the rough estimate of habitat area and isolation for local sites. First, we used the percentage of tree cover in 2010 at 30-m resolution[96] (https://glad.umd.edu/dataset/global-2010-tree-cover-30-m) to quantify total habitat amount within 900 m^2. This frame size was comparable to the standardized transects (200 m^2) of local sites and is within the foraging territory size of termites.[97] Even though trees are scattered, termites are still able to reach all tree habitats, as trees provide both food resources and shelters against microclimate stressors.[98] Second, to quantify the landscape-scale isolation level,[99,100] we calculated land use proportion (%) within a 5,000 × 5,000 m area that was covered by human infrastructure, cropland, and water, based on the 2019 global land cover map at 30-m resolution.[101] These land uses could be more hostile to many termite species than forests, plantations, and savannas due to human activities (e.g., resource scarcity and pesticides) or impassable matrix (e.g., dam construction). We selected this frame size (5,000 m) as a previous study suggests that the maximum record of termite dispersal flight distance is 1,300 m by *Coptotermes formosanus*.[102] By calculating the land use proportion within this frame size, we could quantify the degree of dispersal limitation for prospective colonists outside this frame to reach the focal habitat at the frame center. As the supplement to habitat area, we also calculated the Z score of percentage tree cover by comparing the observed tree cover to the mean values of all grids (30 × 30 m) within the 5 × 5 km. Specifically, the difference between observed and mean values was divided by the standard deviation of percent tree cover among all grids. This metric was independent of the cross-regional difference in natural tree cover and, thus, could be used to assessed the relative level of habitat area across regions. Finally, we extracted three climate metrics for local sites. Mean annual temperature and precipitation were extracted from WorldClim 2 at 30-s resolution.[103] Climate change velocity was extracted from the raster products of Sandel et al.[93] We extracted these metrics according to the spatial coordinates per study site.

Statistical analyses

All statistical analyses were conducted in R v.4.2.3.[104] No collinearity (Pearson's $|r| > 0.7$[105]) was found among climate and habitat variables for islands (see Figure S4A for the correlation matrix) and local sites (Figure S4B), except for island isolation (i.e., distance to nearest mainland) and landmass at island perimeter ($r = -0.804$, $p < 0.001$). By compiling trait data from existing literature,[25,42] we computed the nonparametric relative contrast effects (R package "nparcomp"[106]) of termite nesting strategy complexity on three functional traits, showing that species with a more complex nesting strategy have a larger colony size, lower tissue C/N ratio, and higher degree of intrageneric diet differentiation (Figure S1). The phylogenetic signal of continuous traits (i.e., body size and diet differentiation) and other categorical traits were quantified using Pagel's λ[107] and δ statistics,[108] respectively. After excluding morphospecies, all traits showed phylogenetic signals (Table S12), which were especially strong for body size ($\lambda = 0.902$), diet differentiation ($\lambda = 0.985$), nesting strategy complexity ($\delta = 7{,}047$), foraging ($\delta = 4{,}756$), and soil access ($\delta = 1{,}320$). However, only continuous traits showed significant signals ($p < 0.05$) by comparing them with trait randomization in phylogeny, suggesting that the level of phylogenetic relatedness could be different from functional similarity. Therefore, it is necessary to study how functional and phylogenetic aspects of termite communities responded separately to climate and habitat fragmentation. If the function- and phylogeny-based models yielded similar results, then we could make a more robust conclusion. The following analyses were carried out to test the main hypotheses (Figures 2A and 2B).

First, we conducted principal-component analysis to extract four PC axes of nine functional traits for all island and local species ($R^2 = 81.52\%$; PC1∼PC4: 41.37%/17.72%/12.33%/10.09%). We then calculated the community-weighted mean of PC1, PC3, and PC4 per community to quantify competitive and pest risk, since these axes are well correlated with nesting strategy complexity ($r = -0.96$), body size ($r = -0.78$), and pest risk, respectively ($r = 0.93$; see Table S2 for more details).

Second, we ran multiple linear regression models to test the significance of two-way interactions between climate and habitat fragmentation on species dissimilarity, community-weighted mean of functional traits, and pest risk. To test whether species dissimilarity would show different trends (nonlinear vs. linear) along the gradient of competitive trait means, we included the two-way interaction between climate variables and the linear and quadratic term of community-weighted mean nesting strategy complexity or body size as the predictors. Backward selection was carried out until the final model reached the lowest AIC value. Given that local-scale communities reported the relative proportion (calculated based on species-specific occurrence frequency or the total individual number) per species co-occurring in the same local habitats, we also calculated proportion-weighted pest risk for local communities. We tested whether proportion-weighted mean and community-weighted mean pest risk showed similar responses to habitat fragmentation and climate. Finally, we tested whether the community-weighted mean of competitive traits had negative effects on pest termite risk and whether this effect changed with climate gradients. To do so, we carried out multiple linear regression analyses by including competitive traits, climate, and their two-way interactions as predictors. Backward selection was carried out to obtain the best models. We acknowledged that backward selection may inflate the type I errors due to the multiple hypothesis testing, but it should be noted that none of the models excluded the main effects of any predictors

(Tables S3–S12), with only some two-way interaction terms being excluded during the selection. Nevertheless, we still adopted the model selection approach because it is critical to test whether there were meaningful interaction effects among predictors. If not, then the visualization procedure based on the full model will plot the two-way interactions between climate and other predictors, making it difficult for readers to understand the results.

Third, we extracted the residuals from each multiple regression model and tested for spatial autocorrelation by calculating the global Moran's I index, with the "moranI" function of the "Rfast2" package.[109] The residuals of all models showed weak but significantly negative spatial autocorrelation (approximately -0.119 to -0.003; Table S13), indicating the dispersion pattern of species dissimilarity and the community weighted mean of competitive traits and pest risk level.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Chengjin Chu (chuchjin@mail.sysu.edu.cn and dhwoo@foxmail.com).

Materials availability

This study did not generate new unique materials.

Data and code availability

Raw data and code are archived in Dryad: https://doi.org/10.5061/dryad.k98sf7mdt.

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AUTHOR CONTRIBUTIONS

D.W., Y.L., M.Y., C.L., and C.C. conceived the idea and methodology of this manuscript. F.S.C. and M.R.P. constructed the phylogeny. D.W. compiled the datasets of termite co-occurrence and functional traits. D.W. and C.L. analyzed the data. D.W. wrote the first manuscript draft with considerable input from P.E. and C.C. and finalized the manuscript. All authors commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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