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1	Differential effects of vegetation and climate on termite diversity and damage
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11 Abstract

12	1.	Species diversity shapes ecosystem services, yet few studies have investigated the
13		relationship between species diversity and infrastructure damage, for guiding pest
14		management more effectively. It is not clear that which proportion of species
15		diversity (total/functional-dominant/common/rare) contributes most to infrastructure
16		damage and how biodiversity effect interacts with environmental factors.
17	2.	We correlated termite species richness with termite infestation throughout 83 cities in
18		Zhejiang Province, eastern China. Species was classified as wood-feeder or not, and
19		as common or rare based on distributional range. We analyzed the relative
20		contributions and the direct/indirect effect of climate, vegetation and anthropogenic
21		activities on four metrics (total/wood-feeder/common/rare) of termite species richness
22		and damage level of eight infrastructure types that distributed in populated and
23		remote areas.
24	3.	Common species, with preferences for deciduous vegetation, caused more damage to
25		the infrastructure of densely populated area. Rare species, with preferences for
26		evergreen vegetation, caused more damage in sparsely populated area. While
27		increasing population density favored common against rare species richness,
28		reforestation activities promoted rare but decreased common species richness.
29	4.	Whilst vegetation was the main driver of termite damage via affecting common
30		species richness in densely populated area, climate was the main and direct driver of
31		rare species richness and damage in sparsely populated area. Notably, rare species
32		richness and infrastructure damage at remote areas were higher in cities of higher
33		drought risk and maximum elevation.

5. *Synthesis and applications*. Our study reveals that managing vegetation, such as

- 35 increasing evergreen proportions, can sustainably suppress common termites and
- ³⁶ infrastructure damage in populated area. Meanwhile, future climate change would not
- 37 only threaten rare species richness but increase infrastructure damage in remote area,
- thus more frequent inspections will be necessary.
- Keywords: termites, pest damage, biodiversity conservation, biodiversity and ecosystem
 functioning, climate, vegetation, anthropogenic activities
- 41

42 Introduction

Species diversity is directly responsible for many ecosystem processes and services 43 (Tilman et al., 2014). Very few studies have considered the relationship between species 44 diversity and damage, even though this ecosystem process causes considerable socio-45 economic losses globally like damaging infrastructures (Diagne et al., 2021). A major 46 47 problem is that, although pest diversity correlates with damage levels at the local scale (Dangles et al., 2009), this relationship cannot be extrapolated reliably to the regional 48 scales at which governments typically plan control measures (Lustig et al., 2019). 49 Moreover, control measures applied at regional scales, such as widespread pesticide 50 spraying, are highly problematic. For example, agricultural pesticides have caused $\sim 42\%$ 51 loss of stream invertebrate diversity in Europe and Australia (Beketov et al., 2013). We 52 must understand the scaling relationships between species diversity and damage at 53 regional scales before we can develop a more targeted and sustainable approach to global 54 55 pest control.

Firstly, we must establish the relationship between species diversity and damage. A major 56 question is whether total or a specific group contribute more to ecosystem functioning. 57 The positive 'biodiversity-ecosystem functioning' (BEF) relationship is generally due to 58 the complementarity or selection effect of biodiversity (Tilman et al., 2014). Therefore, 59 when complementarity effect dominates, one could expect that the increase of total 60 species richness could enhance ecosystem functions. When selection effect dominates, 61 the increase of species richness of functionally dominant species could be more important 62 for driving ecosystem functions. In addition, it is also suggested that common and rare 63 species diversity could be both important for driving ecosystem functions (Mateo-Tomás 64

65	et al., 2017). The mass-ratio hypothesis suggests that common species, with their superior
66	abundance, biomass or range sizes, exert greater impacts on functioning (Grime, 1998).
67	However, communities of rare species, which include multiple unique and possibly
68	keystone species, may also contribute disproportionately to ecosystem functions (Lyons
69	et al., 2005). Moreover, rare species, at greater risk of extinction (Seibold et al., 2019),
70	are more likely to impact ecosystem functioning. It therefore makes sense to compare the
71	relative contributions of common and rare species to the amount of damage, in addition
72	to that of total species richness and functionally important species richness.
73	Secondly, if there is a link between species diversity and damage, we must establish the
74	relationship between species diversity and the environment. While it might be hard to
75	predict how the whole communities or functionally important species respond to
76	environmental changes, common and rare species seems to diverge in response.
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 76 77 78 79 80 81 82 83 84 85 86 	environmental changes, common and rare species seems to diverge in response. Population declines are often caused by climate change (Enquist et al., 2019), vegetation degradation (Sekercioglu & Sodhi, 2007) and anthropogenic activities (Harrison et al., 2019). Interestingly, climate change seems not to have consistent effects on the distribution and population sizes of common and widely-distributed pests; instead it leads to complex outcomes depending on species identity and physiological characteristics (Lehmann et al., 2020). Nevertheless, climate warming could lead to phenological changes that favor the persistence and population growth of common pests by expanding overwintering ranges (Ma et al., 2021). Vegetation degradation (Guo et al., 2019) and anthropogenic activities such as land-use intensification (Seibold et al., 2019) tend to

88 eventually become pest species. It therefore remains unclear whether vegetation,

anthropogenic activities or climate will have the greatest impacts on pest diversity, and

90 whether vegetation and anthropogenic activities will have different impacts on different

91 proportions of pest diversity, such as common and rare.

92 Thanks to their diversity, global distribution and economic importance, termites (Insecta: Isoptera) are an ideal model. Termites are eusocial insects, ubiquitous throughout tropical 93 94 and subtropical regions (Cerezer et al., 2020). Of the world's ~3,000 extant species, 371 have been reported as destructive, 104 species are considered serious pests (Krishna et 95 al., 2013), and there are 28 globally invasive species (Evans et al., 2013). A diet of wood 96 97 combined with their tunneling behavior means that termite species cause global losses of 15-40 billion dollars per year (Govorushko, 2019). Termites contribute to the widespread 98 99 damage of different properties, including social and economic infrastructures such as buildings, dams, roads and power supplies. Therefore, it is important to know which 100 proportion of termite diversity (total/wood-feeder/common/rare) contributes the most to 101 102 infrastructure damage and to know its environmental drivers.

We asked three questions: 1) how does different metrics of termite species richness respond to climate, vegetation and anthropogenic activities? 2) is termite species richness a better predictor of infrastructure damage than environmental factors? And which richness metric is the best predictor of infrastructure damage? 3) do climate, vegetation and anthropogenic activities affect termite damage directly, or indirectly by influencing termite species richness? To answer these questions, we compiled the first dataset linking termite species richness (63 species in total) with termite infestation for eight different

110 types of infrastructure in populated and remote areas, spanning 83 cities in Zhejiang

111 Province, eastern China (Figure 1). We realized that there was a change of land-use

intensity from remote (or natural) to densely populated areas within each city, where

- 113 community composition, assembly rule and ecosystem function/services would be
- significantly different (Filgueiras et al., 2021). Therefore, we selected four infrastructure
- 115 types in both populated and remote areas to test if termite species richness and
- 116 environmental drivers would have different effects (i.e. relative contributions and
- 117 direction of effects) on infrastructure damage in populated vs. remotes areas.

118 Materials and Methods

119 Study region

120 Zhejiang Province, located in eastern China, covers an area of 105,500 km² (Fig. 1a). The

population size reaches 50,690,000 in 2020. In total there are 83 'city' units in Zhejiang,

some of which consist of multiple districts per administrative city and others of which are

123 counties with comparative and even larger administrative area (Fig. 1b). City area ranges

124 from 86 to 4452 km². The climate is typical for subtropical monsoon regions. Mean

- annual temperature is 16-19°C and mean annual precipitation is 1200-1800mm. With an
- l26 elevational range between 0 and 1921 m a.s.l., Zhejiang province is mostly mountainous
- 127 (rugged terrain covers 70.4% of the land area; see Fig. 1c) and forested (covering 61.17%
- 128 of the land area).

129 Termite diversity and damage level

130 Since 1998, the urgent need for termite control led to a province-wide systematic

investigation of termite taxonomy and distribution in Zhejiang. Transect methods,

132	subterranean and arboreal nest sampling were combined to fully determine termite
133	species composition. The sampling among cities did not follow a standardized approach,
134	e.g. fixed number and area of searching effort at the same time period (season; weather).
135	Instead, termite control station per city tried to sample the fullest number of termite
136	species by visiting both natural and disturbed habitats as many as possible from 1998 to
137	2014. Therefore, species richness might not be comparable from the perspective of fixed
138	sampling effort. However, it is reasonable for us to believe that the majority of species
139	occurring in each city has been documented. In 2015, termite species composition for
140	each city was reported (Song, 2015). See Table S1 for detailed information (e.g. pest
141	status and feeding type) of each species. As city area varies substantially, we used
142	adjusted species richness (or species density) to control for the influence of city area
143	using the equation $D = S/ln(A)$, where S is the total species richness for a given city,
144	and A is city area (Qian et al., 2021). The one-quarter rule, i.e. the first quarter of range
145	size or abundance ranking among species, is often used as the threshold for classifying
146	common (> threshold) and rare (< threshold) species (Gaston, 1994). However, since
147	$63/4 \approx 16$ species would be defined as rare species but there were 24 species only occurred
148	in one city (Table S1), it was impossible to differentiate common and rare termites by the
149	one-quarter rule. We calculated the proportion of cities in which termites occurred, and
150	from this we defined five thresholds of occupancy (i.e. 0.5, 0.25, 0.1, 0.05, 0.025), which
151	we then used to classify each species as common (> threshold) or rare (< threshold)
152	species. The sum of these common and rare species gave the total species richness per
153	group for each city. Seven species were reported to be major pest species (Krishna et al.,
154	2013: H. Li et al., 2010), with five species (<i>Reticulitermes flavicens, Contotermes</i>

formosanus, *Odontotermes formosanus*, *Macrotermes barneyi*, *R. chinensis*) as the most
 common ones in Zhejiang Province (Table S1).

Meanwhile, eight types of infrastructures were inspected by termite control stations 157 during 1998-2014 for termite infestation, including urban and rural buildings, green space 158 (i.e. roadside trees and city parks) and sea walls in densely populated area, and also 159 including ancient buildings, large-old trees (including scattered trees in rural area and 160 161 clustered trees in forests), reservoir dams, and agroforests (i.e. orchards and commercial forests) in sparsely populated (or remote) area. An inspection unit was defined as an 162 individual (e.g. building, large-old tree and reservoir dam), a section (sea wall; 1km) or a 163 164 patch (green space and agroforest; 100m²). At least 20 units for each type of infrastructure per city were selected in different locations so as to assess termite damage 165 at city-level each year (Hu et al., 2017). Each unit was investigated via observation, 166 baiting and detector to find the following signs of termite activities: 1) occurrence of 167 termite workers/soldiers; 2) termite nest; 3) destruction (feeding marks) caused by 168 termites; 4) occurrence of symbiotic fungi (Termitomyces); 5) soil sheeting and tube built 169 by termites. If one of these signs was found, the inspection unit would be defined as 170 'infested'; otherwise as 'safe'. The city-level damage level of a specific infrastructure 171 was defined as the ratio between the number of infested units and the number of total 172

- 173 units under inspection. The average damage level for each specific type of infrastructure
- 174 during 1998-2014 was used for analysis.
- 175 We realized that the 'damage' metric in our study is indeed occupancy. Therefore, we
- 176 tested the linear relationship between each of eight termite occupancy metrics with true

177	damage metric	for houses (i.e. the actual	l area of infested	houses/ar	partments	versus the
	0						

total area under inspection). We found that three occupancy metrics in populated areas,

179 including urban buildings, rural buildings and green space, was significantly and

- 180 positively correlated with the true damage metric for houses, but other infrastructures
- 181 showed no correlations (Fig. S1). Therefore, we believed that the occupancy metrics were
- 182 robust enough to reflect termite damage under different scenarios, e.g. in populated vs.

183 remote areas.

184 Environmental variables

185 A total of 33 environmental variables, averaged across 2001-2014, were included for

186 analyses (see Table S2 for detailed descriptions). Sixteen climate variables were extracted

187 from ClimateAP, an application for dynamic local downscaling (1km×1km for our study)

188 of historical climate data in the Asia Pacific region (T. Wang et al., 2017).

189 Ten vegetation variables were compiled from three databases. The first database provided

the tree canopy cover for 2000, forest cover gain during 2000-2012 and forest cover loss

during 2000-2020 based on global Landsat data at a 30m×30m resolution (Hansen et al.,

192 2013). The second database was extracted from the Moderate Resolution Imaging

193 Spectroradiometer (MODIS) at monthly intervals and 1km×1km resolution (Didan,

194 2015). Both the Normalized Difference Vegetation Index (NDVI) and Enhanced

195 Vegetation Index (EVI) per month were extracted. Since the two indices were lowest in

196 January and February but highest in August and September, we calculated the difference

197 between lowest and highest vegetation index as deciduousness (NDVI.deci and

198 EVI.deci). This approach has been proven to be a robust estimate of deciduousness

- 199 (Buitenwerf & Higgins, 2016). Evergreenness was calculcated as the highest vegetation
- 200 index since the zonal mature vegetation in Zhejiang Province is mainly subtropical
- 201 evergreen broad-leaved forest (Wu et al., 2017). The third database was extracted from
- the MODIS Land Cover Type per year at 0.5km×0.5km resolution (Friedl & Sulla-
- 203 Menashe, 2019). The percent cover of forest was calculated using Arcgis 10.2.2 (ESRI,
- 204 2014). The average value of forest patch size and gyration radius per city was calculated
- using FRAGSTATS v4 (McGarigal et al., 2012).
- 206 Seven anthropogenic variables were compiled. The percent cover of urban area and crop
- area was extracted from the MODIS Land Cover Type database. The calibrated version
- of annual nighttime light intensity at 1km×1km resolution were used (X. Li & Zhou,
- 209 2017). The Gross Domestic Product per capita (GDPper; total GDP divided by
- 210 population) and population density (total human population divided by city area) was
- 211 compiled from the statistical yearbook of each city. The cumulative sum of reforestation
- area was extracted from the China Forestry Statistical Yearbook (National Forestry
- Administration, 2015). The city history (i.e. age since establishment) was compiled from
- 214 historical documents.
- Topography was extracted from the ASTER Global Digital Elevation Model at 30m×30m
- 216 resolution (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science
- Team, 2019). The average, maximum and range of elevation as well as the ratio of
- surface to horizontal area was calculated using Arcgis 10.2.2.
- 219 Principal Component Analysis (PCA) showed that the first three principal components
- explained 95.6% variation of climatic variables (n = 16), 89.8% of vegetation variables (n

221	= 10) and 89.7% of anthropogenic variables (n = 7). We excluded topography from the
222	analysis because topography was highly correlated ($r > 0.7$) with many environmental
223	variables (Fig. S2; see Fig. S3 for correlation matrix among PCAs), especially vegetation
224	and anthropogenic activities. However, the bivariate relationship of topographic variable
225	with termite species richness and infrastructure damage was reported.

226 Statistical analysis

- All statistical analyses were carried out using R 4.1.1 software (R Core Team, 2021). The
- 228 percentage of termite damage and some predictors (see Table S2) were Ln-transformed to
- 229 achieve normality. Principal Component Analysis (PCA) was used to extract the first
- three main components for climate, vegetation and anthropogenic activities with the R
- package 'vegan' (Oksanen et al., 2018). See Table S3-S6 for the correlation between
- 232 PCA and specific predictors. Since PCA could only be compared for the relative
- 233 importance but give little biological and ecological information, we preselected nine
- variables from 33 predictors based on 4 criteria: 1) three variables for each group
- 235 (climate/vegetation/anthropogenic); 2) containing the variable(s) which is(are) the most
- correlated with response (species richness and damage); 3) low multicollinearity (r < r
- 0.07) and variation inflation (VIF < 4) for multiple linear regression analyses; 4)
- 238 biologically and ecologically related to termites. For climate, climatic moisture deficit
- 239 (CMD), Hargreaves reference evapotranspiration (Eref) and number of frost-free days
- 240 (NFFD) were selected; for vegetation, evergreenness (NDVI), deciduousness
- 241 (NDVI.deci) and forest patch size were selected; for anthropogenic activities, we selected
- the cover of crop field, the cumulative sum of reforestation area during 1998-2014, and
- 243 city history. These nine variables would be used to conduct the following analyses for

capturing the directions (positive vs. negative) of effects, rather than comparing their
relative importance.

246	Spatial simultaneous autoregressive error models (SARs) were used to remove the spatial
247	autocorrelation of adjusted species richness and Ln-transformed damage level (Kissling
248	& Carl, 2008). SARs were fitted using the R package 'spdep' (Bivand & Wong, 2018).
249	We first fitted the SARs models without any predictors but an intercept. Then, we
250	extracted the residuals of fitted values of response, through which the spatial
251	autocorrelation component was removed. Finally, we used the residuals as the new
252	response variable for multiple linear model analyses (Belmaker & Jetz, 2011). The spatial
253	weight matrices of the SARs were calculated with the nearest polygon neighbor and a
254	row-standardized coding style. We didn't use SARs models to compare the effects of
255	predictors because no available packages could decompose the R^2 of SARs models. We
256	thus used a 'LMG' approach to yield 'natural' decompositions of the model R^2 in
257	multiple linear regression models to evaluate the relative importance of each predictor
258	with the R package 'relaimpo' (Grömping, 2007). These analyses were conducted for the
259	first and second hypotheses. For the second hypothesis, we selected the termite diversity
260	predictor that contributed to the highest model R^2 for each infrastructure type. Given that
261	Vegetation.PCA1 and Anthropogenic.PCA1 were highly correlated ($r = 0.795$, $p < 0.795$)
262	0.001), we divided our analyses into two models by excluding either one variable, while
263	predictors other than Vegetation.PCA1 and Anthropogenic.PCA1 were repeated in both
264	models. The mean and standard error of the relative importance and R^2 of two models
265	were used for reporting results.



- ²⁶⁷ unadjusted (or the raw) species richness and termite damage without transformation as
- ²⁶⁸ response. We used the generalized linear mixed effect model with penalized quasi-
- ²⁶⁹ likelihood approach (glmmPQL) from the R package '*MASS*' (Venables & Ripley, 2002)
- 270 to fit the relationship tested. Quasi-poisson (allowing overdispersion) and binomial error
- 271 was used for richness and damage data, respectively. The upper administrative level (i.e.
- some cities of the same administrative region) was treated as random effect. Moreover,
- the spatial autocorrelation structure could be included by assuming a spatial correlation
- 274 structure (e.g. spherical) with spatial coordinate of city centroid as input. Given that city
- area was highly correlated with some predictors, e.g. Climate.PCA3, Vegetation.PCA1

and Anthropogenic.PCA1, we used a similar approach to multiple linear regression

- 277 model analyses by averaging models with only each of correlated predictors. The r2beta
- ²⁷⁸ function of R package '*r2glmm*' (Jaeger et al., 2017) was used to separate the relative

279 contribution.

For the third hypothesis, we constructed piecewise structural equation models to

decompose the direct and indirect (via altering termite diversity) effects of environmental

- 282 predictors on infrastructure damage with the R package 'piecewiseSEM' (Lefcheck,
- 283 2016). The termite diversity variable used was the same as for hypothesis 2. Shipley's d-

284 separation test was used to evaluate model fit through the Fisher's C statistic and χ^2 -based

- *p*-value (Shipley, 2013). We refined the initial model by dropping non-significant links,
- starting with the least significant and continuing stepwise until the decrease in AICc (i.e.
- $\Delta AICc$) associated with dropping one step was less than 2 units. We did not use the
- spatially explicit SEM because the only available package 'sesem' (Lamb et al., 2014) is

289	designed for point- rather than polygon-neighbors. We analyzed the original variables
290	without removing spatial components. The piecewise SEM results should therefore be
291	interpreted qualitatively by focusing only on whether there were direct or indirect effects
292	of environmental predictors.

293 Results

- Sixteen-three species were found in Zhejiang Province, with 8.37 ± 4.80 (mean \pm SE) 294
- 295 species found per city. The damage level for the eight types of infrastructures across
- cities was: $13.2 \pm 12.4\%$ (urban building); $16.2 \pm 16.9\%$ (rural building); $26.4 \pm 22.6\%$ 296
- (green space); $21.5 \pm 19.7\%$ (sea wall); $40.0 \pm 26.3\%$ (ancient building); $33.3 \pm 25.9\%$ 297
- (large-old tree); $18.6 \pm 15.9\%$ (agroforest); $47.2 \pm 27.4\%$ (reservoir). 298

299 **Drivers of termite species richness**

Both total species richness and wood-feeder species richness was predominantly driven 300

301 by climate, with Eref and forest patch size showing positive effects (Fig. 2a, 2g).

Vegetation, followed by anthropogenic activities, explained most of the variation in 302

303 common species richness for the first three thresholds (0.5, 0.25, 0.1; see Fig. 2b-2d). At

304 lower threshold values, where relatively more species were classified as common, climate

- 305 was most closely correlated with common species richness for the latter two thresholds
- 306 (0.05, 0.025; see Fig. 2e, 2f). In the case of rare termites, climate was most closely
- 307 correlated with species richness across all five thresholds (Fig. 2h-2l), with Eref showing
- 308 significantly positive correlation with rare species richness (Table S7). Similar patterns
- were found for the results of generalized linear mixed models of unadjusted species 309
- 310 richness (Fig. S4). Notably, common and rare species richness responded differently to

311	several vegetation and anthropogenic factors. For instance, common species richness
312	responded negatively to evergreenness (NDVI), whereas rare species richness responded
313	negatively to deciduousness (NDVI.deci; Fig. 2 and Table S7). Furthermore, reforestation
314	reduced the diversity of common termites, but it increased rare species richness.
315	Increasing human population density increased the species richness of common termites
316	but reduced the diversity of rare termites. Finally, forest patch size had positive effects
317	for both common and rare species richness. Topography was not the best predictor of
318	termite species richness, except that rare species richness of the '0.05' and '0.025'
319	threshold was best and positively predicted by the maximum elevation (Table S7).
320	Drivers of termite damage
520	
321	Based on Pearson correlation analysis between species richness metric and damage level
322	(Table 1), we found that common species richness was the best predictor of the damage
322 323	(Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species
322 323 324	(Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and
322323324325	(Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and reservoirs. No significant correlation is detected between any species richness metric and
 322 323 324 325 326 	 (Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and reservoirs. No significant correlation is detected between any species richness metric and sea wall damage. Generalized linear mixed models with unadjusted species richness as
 322 323 324 325 326 327 	 (Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and reservoirs. No significant correlation is detected between any species richness metric and sea wall damage. Generalized linear mixed models with unadjusted species richness as predictors showed that common species richness was the best predictor of green space
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 322 323 324 325 326 327 328 329 	 (Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and reservoirs. No significant correlation is detected between any species richness metric and sea wall damage. Generalized linear mixed models with unadjusted species richness as predictors showed that common species richness was the best predictor of green space damage while rare species richness for reservoir damage (Table S8). Based on the hierarchical partitioning of <i>R</i>² of multiple linear regression models of damage, common
 322 323 324 325 326 327 328 329 330 	 (Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and reservoirs. No significant correlation is detected between any species richness metric and sea wall damage, Generalized linear mixed models with unadjusted species richness as predictors showed that common species richness was the best predictor of green space damage while rare species richness for reservoir damage (Table S8). Based on the hierarchical partitioning of <i>R</i>² of multiple linear regression models of damage, common species richness was the best predictor for urban buildings (Fig. 3a), rural buildings (Fig.
 322 323 324 325 326 327 328 329 330 331 	 (Table 1), we found that common species richness was the best predictor of the damage level of urban buildings, rural buildings and green space. Meanwhile, rare species richness was the best predictor for ancient buildings, large-old trees, agroforests and reservoirs. No significant correlation is detected between any species richness metric and sea wall damage. Generalized linear mixed models with unadjusted species richness as predictors showed that common species richness was the best predictor of green space damage while rare species richness for reservoir damage (Table S8). Based on the hierarchical partitioning of <i>R</i>² of multiple linear regression models of damage, common species richness was the best predictor for urban buildings (Fig. 3a), rural buildings (Fig. 3b) and green space (Fig. 3c), which located in densely populated area. Sea wall damage
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buildings (Fig. 3e) and large-old trees (Fig. 3f) correlated most closely with climate, i.e.
positively correlated with Eref. Agroforest damage was mainly driven by rare species
richness (Fig. 3g). Reservoir damage is predominantly driven by anthropogenic activities,
i.e. positively correlated with city history (Fig. 3h). None of topographic variables was
the best predictor of infrastructure damage (Table S9). Similar patterns were found for
the results of generalized linear mixed models of damage (Fig. S4). The only difference is
that climate became the best predictor of sea wall damage (Fig. S4o).

341 Termite species richness mediates environmental effects on termite damage

In densely populated area, vegetation was primarily (Fig. 4a, 4c) or partially (Fig. 4b) 342 343 correlated with damage via indirect effects on common species richness. Specifically, forest patch size and NDVI increased and decreased infrastructure damage indirectly 344 through increasing and decreasing common species richness, respectively. Vegetation 345 and climate exerted direct effects on sea wall damage, with NDVI.deci showing the 346 strongest and negative effect (Fig. 4d). In contrast, climate exerted direct effects on the 347 damage levels of remote infrastructures (Fig. 4e, 4f, 4h). Agroforests were the only 348 exception, in that their damage levels were affected indirectly by climate altering rare 349 species richness (Fig. 4g). Specifically, Eref increased infrastructure damage at remote 350 351 areas directly (Fig. 4e, 4f, 4h) or indirectly through positive correlations with rare species richness (Fig. 4g). 352

353 **Discussion**

354 Zhejiang Province is listed as one of the six most extremely infested provinces in China

355 (Ahmad et al., 2021). Since 1958, provincial government has organized a series of local

- 356 control measures in each city, including chemical pesticides, nest excavation, anti-termite
- 357 materials for new constructions and systematic baiting grids (Song, 2015). Among them,
- 358 chemical control was most widely used and undoubtedly the most effective measure.
- 359 During 1988-2008, Zhejiang Province consumed the largest amount of Chlordane (~980
- 360 t; termiticide), which was 35.7% of total usage in China (Q. Wang et al., 2013). Given
- that Chlordane is one of the persistent organic pollutants with high toxicity, bio-
- 362 accumulation and long-range transport potential, China has banned Chlordane production
- ³⁶³ for all purposes since 2009. During recent years, the integrated termite management has
- 364 been proposed to control termite damage with not only chemical approaches but also
- 365 non-chemical measures which are economically, socially and environmentally safe
- 366 (Ahmad et al., 2021). Nevertheless, there is still a lack of knowledge about how regional
- 367 factors like termite diversity and environmental setting influences termite damage,
- 368 especially the occupancy of termite infestation in different kinds of infrastructures. By
- 369 tackling this problem, managers could determine the most ideal combinations of local
- 370 control measures under a specific regional setting, and even modify key drivers at
- 371 regional scale for long-term termite control.

372 Contrasting responses of common vs. rare termites to environmental factors

- 373 Our study reveals the differential effects of climate, vegetation and anthropogenic
- activities on termite diversity, and the correlation between termite diversity and termite
- damage. While forest patch size increased all four metric of termite species richness, it is
- interesting to learn that common and termite species richness showed contrasting
- 377 responses to vegetation composition, i.e. evergreen and deciduous vegetation.
- 378 Meanwhile, most common termites feed on deadwood and wooden constructions,

whereas some of the rare species feed on humus (Table S1). These results make 379 biological sense because the deciduous and evergreen trees of subtropical China (J. Li et 380 381 al., 2021) and elsewhere (van Ommen Kloeke et al., 2012) divide into two functional groups based on their life history strategies and multiple traits. Deciduous trees, which 382 are resource-acquisitive, have higher nutritional value and are therefore more attractive to 383 384 wood-feeding termites (C. Guo et al., 2021). Evergreen trees, which are resourceconservative, have stronger defenses, are slower to decompose and easier to accumulate 385 as humus (Joly et al., 2017), and are therefore more attractive to the relatively less 386 common humus-feeding termites. Correspondingly, we found that common species 387 richness correlated negatively with evergreen vegetation, whereas rare species richness 388 correlated negatively with deciduous vegetation. Reforestation projects of Zhejiang 389 Province favor subtropical evergreen broad-leaved trees (e.g. Schima superba, Phoebe 390 391 chekiangensis and Cyclobalanopsis gilva). Consequently, we found that reforestation correlated positively with evergreen vegetation (Pearson's r = 0.682, p < 0.001) and 392 negatively with deciduous vegetation (r = -0.401, p < 0.001), which might explain why 393 reforestation reduced common species richness but increased rare species richness. 394 395 Moreover, reforestation projects tended to focus on less populated cities, which explains the negative correlations between reforestation and human population density (r = -0.685, 396 397 p < 0.001), and which may also explain the coincidental gradients between vegetation 398 and human population density in which more populated cities exhibit less evergreen vegetation (r = -0.522, p < 0.001) and more deciduous vegetation (r = 0.609, p < 0.001). 399 400 In summary, anthropogenic changes linked with human population density such as 401 shifting vegetation could increase the diversity of wood-feeding termites and reduce the

diversity of the relatively rare species of termites feeding on humus in human-disturbed 402 areas (Jones et al., 2003). 403

Vegetation affects damage in densely populated area via common termite diversity 404 Climate is often cited as the dominant driver of common termite distribution and damage 405 406 (Cerezer et al., 2020; Reddy & Sammaiah, 1991). However, our results suggest that vegetation could play a more important role than climate, which explains why common 407 408 termites, especially species which grow fungi on dead and decaying plant material, could mitigate climate change effect in both tropical forests (Ashton et al., 2019) and savannas 409 (Veldhuis et al., 2017). Accordingly, we found that vegetation composition (evergreen vs. 410 411 deciduous) and forest loss (indicated by the average size of forest patches) reduced common species richness more than climate variables (Table S7). One possible 412 explanation is that forests not only serve as sources of food and nests, but also exert 413 greater control of understory microclimate than regional climate (De Frenne et al., 2019). 414 415 It is therefore unsurprising that vegetation rather than climate affected the infestation of populated infrastructures in Zhejiang Province by altering common species richness. This 416 finding will help inform termite control measures in populated areas, offering an effective 417 control measure other than environmentally hazardous pesticides (Ahmad et al., 2021). In 418 419 particular, our results suggest that planting and maintaining small to moderate sized patches of evergreen trees, which are less palatable to common termites, may reduce 420 421 colony establishment and population growth of these species in populated area.

422

Climate directly affects damage in remote area and threatens rare termite diversity

423	Unlike common termites, climate does affect the distribution of rare termites in Zhejiang
424	Province. Specifically, we found more species of rare termites in cities with greater
425	drought risk (estimated by the Hargreaves reference evapotranspiration, i.e. vegetation
426	water demand; see the variable 'Eref' in Fig. 2), particularly at higher elevations ($r =$
427	0.769, $p < 0.001$; Fig. S1). All termites are vulnerable to desiccation (Woon et al., 2019),
428	meaning that populations of rare termites might decline if drought events become more
429	frequent in China (Su et al., 2018). Meanwhile, the notion that the ectotherms at higher
430	elevations would have wider thermal niches and thus be less vulnerable to climate
431	warming(Walters et al., 2012), has been dispelled by molecular evidence revealing that
432	these 'species' are in fact complexes of cryptic species occupying discrete elevational
433	zones and adapting to local temperature (García-Robledo et al., 2016). It is therefore
434	likely that climate warming will eradicate cryptic species of rare termites. Unfortunately,
435	with the exception of agroforests, rare termites caused less damage to remote
436	infrastructures, suggesting that these species should not even be recognized as pests.
437	Instead, they contribute to functions like litter decomposition and soil bioturbation, and
438	thus should be targets of conservation. Climate (e.g. Eref) is more strongly linked with
439	termite damage of remote infrastructures, probably because physical challenges, e.g.
440	swelling and shrinking caused by heat-cold or dry-wet cycles (Naumann et al., 2021),
441	cause deformation and crevices, thus rendering the deteriorating infrastructures more
442	susceptible to termite infestation. Compared with infrastructures in populated area (e.g.
443	urban buildings), mechanical failures are more difficult to detect in remote area (e.g.
444	reservoir dams). Climate change will therefore cause termite damage to become more
445	frequent and unpredictable, especially in remote area.

446 Conclusions

We show that common and rare termite diversity was more strongly correlated with 447 448 infrastructure damage in populated area and remote area, respectively. Meanwhile, common species richness was more strongly correlated with vegetation factors while rare 449 species richness with climatic variables. Notably, whilst common species richness 450 451 outweighed environmental factors in explaining infrastructure damage in populated area, climate posed the major and direct effect on termite damage in remoted area. 452 Consequently, we conclude that common, widely-distributed termites should be targeted 453 for pest control to mitigate infrastructure damage in populated area, through increasing 454 the proportions of evergreen trees in city forests and green spaces as the sustainable 455 alternative of pesticides. In contrast, rare termites and infrastructures in remote area 456 should be targets for conservation with frequent inspections, since they are more 457 susceptible to climate change. Therefore, we recommend the initiation of a cross-region 458 459 and long-term investigation of termite distributions and infestation at higher resolutions along different environmental gradients. Such a large network would simultaneously 460 461 support pest control and advance species conservation by pinpointing each termite 462 species as common or rare.

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- 468 conceived the study and developed the methodology. DW collected and analyzed the

469	metadata. DW and MDFE wrote the first draft. All authors reviewed and edited,
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471	financial interests. Data Availability: Data will be deposited in Dryad if the manuscript is
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686 Figures and Tables



Fig. 1. Data overview. Total termite species richness (a), infrastructure damage level (i.e.
percent ratio of infrastructure units infested by termites, using urban buildings as
examples) (b), five threshold values (blue vertical dashed lines) for classifying common
and rare termite species (c) and the topography and location of Zhejiang Province (d).
Note that each polygon in (a) and (b) refers to a city unit. Two grey polygons in (b)
denote two cities with missing values. Threshold value in (c) refers to the proportion of

694	occupancy (cities with occurrence record) for a species. For each threshold value, species
695	with occurrence records above threshold (i.e. right of blue dashed line) is classified as
696	common species while species with occurrence records below threshold (i.e. left of blue
697	dashed line) as rare. Two termite species with the lowest (Incisitermes minor; N=1;
698	worker) and highest (Reticulitermes flaviceps; N=83; dealate) occupancy are shown. The
699	semi-transparent white polygon with red outline in (d) denotes the administrative area of
700	Zhejiang Province, while its location within China is shown as the red-filled polygon in
701	the bottom-right subpanel.



30%

20%

10%

0%





 $R^2 = 0.2206$

0%- I

30% -

20%

10%

30% -

20%

10%

0%





(d) Common termite_0.1







30%

20% -

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0%

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R² = 0.1782









(i) Rare termite_0.25



(j) Rare termite_0.1



(k) Rare termite_0.05 R² = 0.1264 209 10%





Clife

40% -R² = 0.1846 30% 20% 10% 0%











703

10%

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704	Fig. 2. The effects and relative importance of environmental predictors in explaining
705	the species richness of common (left two panels) and rare termites (right two

panels). Five different threshold values (i.e. proportion of cities with occurrence record;

ranging from 0.025 to 0.5 designated in each sub-title) were used to classify each species

708as common (> threshold) or rare (< threshold). Number of total, wood-feeder, common or</th>

rare species per city divided by (Ln-transformed) city area is treated as the response. Nine

environmental factors (left sub-graph) or the first three principal components for climate,

vegetation and anthropogenic activities (right sub-graph) are treated as environmental

712 predictors. Marginal R^2 is reported. Based on the hierarchical partitioning of model R^2 ,

the relative importance of each predictor, i.e. the percentage of model R^2 explained by

714 individual predictor, is shown and scales with bar height. The "+" and "-" above each bar

indicates the effect sign of each predictor, i.e. positive and negative respectively. The

spatial autoregressive component of response variables has been removed. Error bars

denote the ± 1.96 SE, i.e. the 95% confidence interval of mean value.

718



Fig. 3. The effects and relative importance of environmental predictors and termite diversity in explaining the damage level of eight infrastructure types at populated (left two panels) and remote areas (right two panels). The percentage of infrastructure units infested by termites after Ln-transformation is treated as the response. Nine environmental factors (left sub-graph) or the first three principal components for climate, vegetation and anthropogenic activities (right sub-graph) are treated as environmental

726	predictors. The damage level of four infrastructure types in the left panel explained more
727	variation (i.e. contributed to a higher model R^2) predicted by common species richness,
728	while the right panel by rare species richness. Marginal R^2 is reported. Based on the
729	hierarchical partitioning of the model R^2 , the relative importance of each predictor, i.e.
730	the percentage of the model R^2 explained by individual predictors is shown and scales
731	with bar height. The "+" and "-" above each bar indicates the effect sign of each
732	predictor, i.e. positive and negative, respectively. The spatial autoregressive component
733	of the response variables has been removed. Error bars denote the ± 1.96 SE, i.e. the 95%
734	confidence interval of mean value.



Fig. 4. The piecewise structural equation models for decomposing the direct and indirect effects of termite diversity and environmental factors on infrastructure damage. Each subfigure corresponds to the one in Fig. 3. "Clim", "Vege" and "Anth" are the abbreviations of climate, vegetation and anthropogenic activities, respectively. Significant (p < 0.05) and insignificant (p > 0.05) path relationships are designated with solid and dashed lines. Black and red paths indicate positive and negative relationships. Standardized path coefficients scaled by deviations are reported, proportional to the size of the path. Model fit, including Marginal R^2 , Fisher's C statistic, *p*-value and AICc are also reported. See Table S10 (with nine preselected environmental predictors) and S11 (with

742 nine environmental PCA predictors) for model summaries.

Table 1. Pearson correlation between termite species richness and termite damage. Significant (p < 0.05) relationships are printed in bold.

	Predictor	Urban building	Rural building	Green space	Sea wall	Ancient building	Large-old tree	Agroforest	Reservoir
		(N=81)	(N=70)	(N=77)	(N=33)	(N=76)	(N=75)	(N=62)	(N=59)
	Total	0.17	0.36	0.35	0.10	0.25	0.31	0.25	0.21
	Wood-feeder	0.17	0.38	0.34	0.14	0.25	0.31	0.28	0.14
	Common_0.5	0.13	0.29	0.05	-0.27	-0.27	-0.14	-0.08	-0.20
	Common_0.25	0.23	0.34	0.34	-0.12	0.09	0.16	0.03	-0.07
	Common_0.1	0.25	0.40	0.39	0.02	0.17	0.23	0.20	0.06
	Common_0.05	0.27	0.41	0.40	0.04	0.19	0.24	0.25	0.11
	Common_0.025	0.22	0.39	0.38	0.05	0.21	0.27	0.24	0.15
	Rare_0.5	0.14	0.31	0.35	0.16	0.32	0.35	0.28	0.25
	Rare_0.25	0.08	0.28	0.27	0.21	0.30	0.33	0.34	0.34
	Rare_0.1	-0.02	0.16	0.17	0.13	0.28	0.31	0.23	0.33
	Rare_0.05	-0.18	-0.03	0.04	0.10	0.24	0.26	0.10	0.29
	Rare_0.025	-0.13	-0.01	0.05	0.13	0.20	0.24	0.14	0.28

The predictor with the highest correlation coefficient with response is printed in red. Number (N) of replicates is reported.