1   Title

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3   **Breakdown in seasonal dynamics of ant communities with land-cover change**

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5   Authors

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14

15   Abstract

16   Concerns about widespread human-induced declines in insect populations are mounting, yet little
17   is known about how land-use change modifies the dynamics of insect communities, particularly
18   in understudied biomes. Here we examine how the seasonal patterns of ant activity, key drivers
19   of ecosystem functioning, vary with human-induced land cover change on a subtropical island
20   landscape. Using trap captures sampled biweekly from a biodiversity monitoring network
21   covering Okinawa Island, Japan, we processed 1.2 million individuals and reconstructed activity
22   patterns within and across habitat types. We determined that communities inside the forest
23   exhibited more variability than those in more developed areas. Using time-series decomposition
24   to deconstruct this pattern, we found that ant communities at sites with greater human
25   development exhibited diminished seasonality, reduced synchrony, and higher stochasticity
26   compared to those at sites with greater forest cover. We demonstrate that our results cannot be
27   explained by variation in either regional or *in situ* temperature patterns, or by differences in
28   species richness or composition among sites. We conclude that the breakdown of natural
29   seasonal patterns of functionally key insect communities may comprise an important and
30   underappreciated consequence of global environmental change that must be better understood
31   across Earth's biomes.

32

33   Keywords

34   ant, insect, monitoring, Japan, subtropics, synchrony, temporal, variability

35

Introduction

37   Insects comprise 95% of described terrestrial animal species on Earth and are key drivers of a
38   multitude of ecosystem functions and services, including pollination, food provisioning, pest
39   control, water filtration, carbon sequestration, and decomposition (Schowalter, 2013). There is
40   also mounting concern about the possibility of long-term global insect declines due to human-
41   induced environmental change, which can disrupt key functions and services (Goulson, 2019;
42   Wagner, 2020). But while such trends measured over broad timescales are informative for
43   monitoring populations (Dornelas et al., 2013), they overlook changes in natural seasonal
44   patterns that can only be detected at fine temporal resolutions. When these seasonal patterns are
45   broken down by human pressures, it can result in the erosion of biodiversity (Tonkin et al., 2017)
46   and degradation of the ecosystem functions and services on which human societies depend (Ross
47   et al., 2021; Stevenson et al., 2015). For this reason, a better understanding is needed of how
48   fine-scale temporal patterns of insect communities are affected in this era of global change.
49
50   Land-cover modification is a major driver of biodiversity loss (Cardinale et al., 2012), and many
51   studies have examined its consequences for insect diversity (e.g., Castro et al., 2018; Corro et al.,
52   2019; Knop, 2016; Oliver et al., 2016; Senapathi et al., 2015). However, the corresponding
53   effects on temporal dynamics of insect communities are not well-known. For example, human-
54   altered land cover with higher densities of alien species can lead to boom-and-bust dynamics that
55   cause high variability (Lester & Gruber, 2016; Simberloff & Gibbons, 2004). At the same time,
56   urbanization can lead to biotic homogenization and reduced community variability over time
57   (Hung et al., 2017; McKinney, 2006). Although these documented effects of land-cover change
58   on insect temporal dynamics differ, investigations into how insect communities are affected are
59   crucial for tropical and subtropical biomes undergoing rapid land-cover change (Janzen &
60   Hallwachs, 2021), and also for islands that have restricted land area, frequent introductions of
61   alien species, and exposure to increasingly extreme weather events (Russell & Kueffer, 2019).
62
63   Here, we examine the effects of anthropogenic land-cover change on the fine-scale temporal
64   variability of ant community activity. Ants are a dominant insect group in the many
65   environments they inhabit around the world, underpinning a broad spectrum of ecological
66   interactions and playing a major role in regulating ecosystem function (Hölldobler & Wilson,
67   1990), which makes them ideal bioindicators for ecosystem change (Andersen & Majer, 2004).
68   Community seasonality is linked to the maintenance of key ecosystem functions and services
69   (Stevenson et al., 2015). However, even though ants can exhibit significant seasonality in
70   tropical and subtropical regions (Basu, 1997; Samways, 1990), little is known about how land-
71   cover change affects ant community seasonality in these diverse biomes.
72
73   To address this, we used high-resolution (biweekly) monitoring data on ant activity for
74   subtropical Okinawa Island in southern Japan to examine whether, and how, the temporal
75   variability of ant communities varies with land cover change. We then determined which
76   temporal components of variability (i.e., seasonality, trend, or stochasticity) contribute the most
77   to differences across the gradient (Fig. S1). We also tested whether other potential drivers,
78   including differences across sites in climate seasonality, species richness, and community
79   composition, could be responsible for observed differences in temporal community variability,
80   and additionally examined the roles played by invasive species in moderating these effects.

Materials and Methods

Study sites and land-cover data

Our study focuses on the subtropical main island of Okinawa in the southern Ryukyu archipelago of Japan. The island has a historical land-cover gradient, spanning from the minimally developed north to the more urban south (Fig. 1). Okinawa's extensive Yambaru Forest in the north was recently recognized as part of Japan's newest Natural World Heritage Site for its high endemism and biodiversity. Although the island is only 0.3% of Japan's total land area, it provides habitat to more than one-third of the country's ant species (Terayama et al. 2009, Terayama et al. 2014). The few studies of ant communities in Okinawa include biodiversity surveys (e.g., Ito et al., 1998) and comparisons between native and alien ant populations in Yambaru (Katayama & Tsuji, 2010; Suwabe et al., 2009; Yamauchi & Ogata, 1995). This study, the first to sample island-wide ant diversity and temporal patterns in Okinawa, uses data from a biodiversity monitoring system covering the land-cover gradient of the island, administered by the Okinawa Environmental Observation Network (OKEON) Churamori Project (https://okeon.unit.oist.jp/).

We used a land-cover map for Okinawa (year 2015) to calculate representative land-cover values for the 24 OKEON monitoring sites. The sites (pairwise distances: minimum = 389 m, mean = 33 km, maximum = 102 km) are located in or near forested areas across multiple land-cover types varying from broadly contiguous forest to highly agricultural or urban areas (Fig. 1). To characterize each site, we calculated the proportion of seven main land-cover classes (forest, agriculture, urban, grass, sand, freshwater, miscellaneous) around circular buffers with radius 1 km (see Ross et al., 2018 for details). Buffers with this size were chosen to characterize representative land-cover values for areas surrounding sites without including regions that may have resident unsampled colonies. Sites near the coast included ocean area within the buffer, so we used relative proportions for all sites that considered only land area. As correlations were high between the main land-cover classes of interest (that is, forest, agriculture, and urban; Table S1), we used principal component analysis (R function *prcomp*) after applying an arcsine transformation to the proportions to improve normality (e.g., Van Buskirk, 2005) and retained the first and second axes (variance explained: PC1 = 81% and PC2 = 11%) for use as explanatory variables. PC1 represents the forested (high) to developed (low; urban and/or agriculture) gradient, while PC2 represents the rural (high; agriculture and/or grass) to urban (low) gradient (Fig. S2). All analyses were conducted in R (R Core Group, 2021), and spatial analyses were conducted with R packages *sf* (Pebesma, 2018) for vector data and *raster* (Hijmans, 2021) for gridded data.

Ant activity data

We sampled worker ant activity biweekly with Sea, Land, and Air Malaise (SLAM) traps for two years and identified samples to species level, resulting in 1,378,324 classified individuals. Specifically, we sampled one SLAM trap (Large BT1005, MegaView Science Co., Ltd.) at each of three stations per OKEON site (pairwise distances within sites: mean = 90 m, minimum = 19 m, maximum = 195 m) every two weeks from March 2016 to March 2018 (further details in Supporting Information A). The stations are predominantly deployed under forest canopy, though several are in nearby open areas. This sampling method mainly targets terrestrial browsing species, though does occasionally catch arboreal and subterranean individuals. Insect

125   count data sampled with passive traps are usually interpreted as a measure of activity, or the rate
126   at which individuals intersect a point in space, rather than direct estimates of abundance, though
127   changes in abundance are generally reflected in ant activity data (Kaspari et al., 2022a).
128
129   We additionally categorized all species by invasive status as either native, alien, or uncertain
130   based on expert opinion and biogeographical databases (Guénard et al. 2017, Janicki et al. 2016,
131   Terayama et al. 2009, https://www.antwiki.org/, https://www.antweb.org/). Native refers to
132   species with enough data to establish historical occupancy in Okinawa without human-aided
133   dispersal from other regions. Alien refers to species that definitively have native ranges in
134   different regions and have dispersed to Okinawa via human activity. Uncertain species lack
135   sufficient data to make such determinations.
136
137   Some prevalent species had extreme count outliers, such as *Technomyrmex brunneus*
138   (representing counts greater than 5,000), likely caused by large colony sizes and/or increased
139   activity following mating flights, heterospecific competition, or other biological phenomena. We
140   avoided bias in variability estimates by limiting count values to a conservative threshold of 500
141   individuals for a given species at a station within a two-week period. We also examined changes
142   in our results for a range of thresholds. For each species during each sampling period, we
143   summed counts over the three stations per site to determine site-level activity (Fig. 2), and over
144   all sites per land-cover group for grouped species-level activity. We then calculated total site
145   density as the sum of all counts per site.
146
147   Sampled abundance and variability can be correlated due to sampling error alone because of
148   mean-variance scaling (McArdle & Gaston, 1995). For example, even if species dynamics are
149   identical across two sites, if we sample fewer individuals from site A than site B (e.g., due to
150   effects of sampling station placement), site B may have a higher temporal variability simply
151   because its counts are higher. While in some sense this could reflect the actual variability of
152   observed species at specific locations (that is, at the stations), we wanted to disentangle
153   differences in community variability from those attributable to sampling error. Thus, we rarefied
154   the data from all sites so that the total count (sum of all samples across the two years) for each
155   site equals the total count at the site with the least abundance (Fig. S1, Supporting Information B;
156   Gaston & McArdle, 1994). Finally, to determine whether species richness differences could
157   drive any observed differences in temporal variability, we calculated site-specific total species
158   richness, and the richness of each invasive status group from the observed and rarefied data,
159   making extrapolations to account for incomplete sampling using Hill numbers ($q = 0$) with the R
160   package *iNEXT* (Hsieh et al., 2016).
161

Temporal variability and time-series decomposition
163   We calculated two aspects of temporal variability: functional and compositional (Supporting
164   Information C). Functional variability refers to activity changes at the aggregate scale (e.g.,
165   Hillebrand & Kunze, 2020) and is calculated as the coefficient of variability (ratio of the
166   standard deviation to the mean) of total ant counts across all species per site (McArdle & Gaston,
167   1995). Compositional variability estimates the variation in community composition over time
168   and is calculated as temporal beta diversity (Legendre & De Cáceres, 2013) using the R package
169   *adespatial* (Dray et al., 2022), which additionally records species' individual contributions to

170   beta diversity. As we use ant count data, compositional changes would thus represent changes in
171   relative activity rates of different species in the local species pool, which in turn is a function of
172   the abundance and patterns of behavior (Kaspari et al., 2022a).
173
174   Next, we used temporal decomposition models to determine the relationships of temporal
175   variability components with observed patterns. Time series can be decomposed into components
176   describing different underlying temporal patterns in the data: "seasonal" processes that repeat
177   cyclically over some temporal scale (i.e., phenology), "trend" that describes directional change,
178   and "remainder" that represents any residual variation not captured by the other components (i.e.,
179   short-term stochastic fluctuations; Hyndman & Athanasopoulos, 2021). A community with high
180   temporal variability may have strong cyclical patterns, increasing or decreasing trends, high
181   stochasticity, or some combination of these. For temporal datasets spanning many annual cycles,
182   models that can estimate complex seasonal responses (e.g., wavelet analysis; Tonkin et al., 2017)
183   are often employed, but for studies spanning few annual cycles at a fine temporal resolution,
184   simpler models with fewer assumptions and problems with overfitting are preferable. We
185   estimated additive temporal components for the ant activity data by fitting time-series linear
186   models with temporal predictors using the R package *fable* (O'Hara-Wild et al., 2021). As our
187   time-series was short, we used simple predictors consisting of a linear trend and a seasonal signal
188   approximated with an annual Fourier term with the simplest maximum order (K) of 1—this
189   models seasonality as a sine wave (Hyndman & Athanasopoulos, 2021). We fitted this model to
190   the rarefied data at both the site-level and species-level for land-cover groups, then decomposed
191   the count value at each time-step. For each site, we measured the absolute variance of each
192   temporal component, but also the relative component variance, defined here as the individual
193   component variance divided by summed variance of all components (Supporting Information D).
194
195   Finally, as spatial autocorrelation between sites did not affect results (Table S3; Supporting
196   Information E), we used simple linear models to estimate relationships between land cover and
197   our focal metrics of temporal variability. Specifically, we fitted models for total ant counts
198   (before rarefaction), functional and compositional temporal variability, and absolute and relative
199   variances of time-series components. To explore differences between native and alien species,
200   we also fitted models separately by invasive status for site richness and summed species'
201   contributions to beta diversity. We performed model selection on linear combinations of the
202   predictor variables land-cover PC1 and PC2 using the Akaike Information Criterion corrected for
203   small sample sizes (AICc).
204

205   *Assessing effects of differences in temperature and community composition on observed*
206   *seasonality patterns*
207   To determine if other differences among sites may be responsible for any observed variation in
208   ant community activity and relationships with land cover, we additionally examined differences
209   in 1) regional and site-level temperature and 2) tested whether seasonality differences persisted
210   after standardizing community composition between land-cover groups. For (1), we downloaded
211   regional climate data for the collection period from the Japan Meteorological Agency (JMA)
212   database (http://www.jma.go.jp/en/amedas_h/map65.html, accessed 04/01/2020) and calculated
213   temperature means and extremes from the six climate stations that collect temperature data
214   (Miyagijima, Itokazu, Naha, Ashimine, Nago, Oku). We also collected *in situ* site-level data

215 throughout the collection period at one station per site to characterize local air and soil
216 temperature patterns (WatchDog 2900ET Weather Station 1.5 m above ground and SMEC
217 WaterScout 300 Soil Sensor 10 cm below ground, Spectrum Technologies). With the same
218 workflow as for the ant activity data, we calculated absolute variance of seasonality for regional
219 and site-level temperature time-series, then estimated relationships with land-cover PC1 using
220 linear models.
221
222 For (2), we conducted analyses to test whether differences in community composition alone,
223 without variation in seasonality within species, could be driving the observed patterns in
224 seasonality, or alternatively if habitat-dependent dynamics of species occurring in both habitat
225 types were responsible. We used land-cover PC1 to partition the sites into two groups with eight
226 sites each—forested and developed (comprising sites with more agricultural and/or urban land
227 cover)—and retained only those species shared between groups and with total counts greater
228 than 100. We excluded the eight sites with intermediate values of PC1 to better represent the
229 most characteristic sites for each land-cover group. To make balanced comparisons between
230 land-cover groups, we rarefied each species' activity data to the minimum count of that species
231 between groups (Fig. S1, Supporting Information B). To determine whether community
232 composition affected our results, we fitted time-series linear models to each species in the land-
233 cover groups and calculated the relative variance of their seasonality (forested versus developed
234 sites). As differences between the land-cover groups were not normally distributed (Shapiro-
235 Wilk test; $p = 0.011$), we used the nonparametric Wilcoxon signed-rank test to determine
236 whether the same species between groups exhibit significant differences in relative seasonality
237 variance. Additionally, to determine how temporal mismatch changes with invasive status, we
238 calculated the synchrony of seasonality for each invasive status between land-cover groups and
239 standardized them to the same scale. We used the R package *codyn* (Hallett et al., 2016) to
240 calculate synchrony using the method described by Loreau & De Mazancourt (2008). We then
241 compared seasonal curves to the average seasonality curve for each land-cover group to visualize
242 the degree of temporal mismatch by invasive status.
243

244 Results

245 Our sampling for 2016–2018 resulted in the recovery of >1.2 million individuals (before
246 thresholding) and 16,595 unique count records at the site-level across 91 ant species. Total count
247 was less than 5 individuals for 21 species and greater than 10,000 individuals for 15 species, with
248 a minimum of 1 (*Aenictus ceylonicus*, *Crematogaster* c.f. *matsumurai*, *Ectomomyrmex sp.*,
249 *Erromyrma latinodis*, *Hypoponera* sp., *Leptogenys confucii*, *Strumigenys hirashimai*,
250 *Strumigenys mazu*) and a maximum of 259,180 (*Tetramorium bicarinatum*). The pattern of ant
251 activity dropping in the winter and rising in the summer qualitatively diminished as human
252 disturbance increased (Fig. 2). Total ant activity (after thresholding to 500) had a nearly 23-fold
253 difference between the site with the minimum count (Yona Forest, $n = 3616$) and that with
254 maximum count (Sueyoshi Forest, $n = 82,781$). The natural log of total density had a strong
255 negative relationship with land-cover PC1 ($R^2 = 0.71$, $p < 0.001$), indicating that ant activity
256 overall was higher in developed areas than forested areas (Fig. 3). Rarefaction resampled all sites
257 to the minimum site count before analysis.
258

259 The linear models suggested strong relationships with the land-cover PC1 for most metrics of
260 temporal variability (Figs. 3, 4). Based on model selection via AICc, all models included PC1 as
261 the sole predictor except the relative variances of seasonality and stochasticity, which also used
262 PC2 (Table S3). Functional and compositional temporal variability both had strong positive
263 relationships with PC1 (functional: $R^2 = 0.67$, $p < 0.001$; compositional: $R^2 = 0.60$, $p < 0.001$;
264 Fig. 3), and these two variabilities also had a strong relationship to each other ($R^2 = 0.62$, Fig.
265 S3). The species' contributions to beta diversity (Fig. S4) that explained individual species'
266 impacts on compositional variability were also positively correlated with PC1 for native species
267 ($R^2 = 0.40$, $p < 0.001$), but uncertain ($R^2 = 0.28$, $p < 0.01$) species had a weaker, negative
268 relationship (alien species showed no relationship). Absolute seasonality and stochasticity
269 variance had positive relationships with PC1, though that for seasonality ($R^2 = 0.57$, $p < 0.001$)
270 was stronger than that for stochasticity ($R^2 = 0.15$, $p < 0.05$; Fig. 4). On the other hand, relative
271 seasonality variance ($R^2 = 0.23$, $p < 0.05$) was positively related to PC1, while relative
272 stochasticity variance ($R^2 = 0.36$, $p < 0.01$) had a negative relationship (both had $p > 0.05$ for
273 PC2; Fig. 4). All linear regression results are found in Table S3.
274
275 We found no evidence that differences in species richness, temperature at different scales, or
276 species composition are candidates as drivers of observed differences in ant community temporal
277 variability. We found no relationship between PC1 and total species richness (either observed or
278 extrapolated), and a weak correlation with rarefied richness ($R^2 = 0.15$, $p < 0.05$) due to the loss
279 of rare species during the rarefaction process, though we consider this unlikely to bias our results
280 (Fig. S5). We did find strong positive relationships with PC1 for native richness values
281 (observed: $R^2 = 0.47$, $p < 0.001$; extrapolated: $R^2 = 0.35$, $p < 0.005$; rarefied: $R^2 = 0.61$, $p <$
282 0.001) indicating that more native species can be found in the more forested sites, and weaker
283 negative relationships with alien richness values (observed: $R^2 = 0.29$, $p < 0.005$; extrapolated:
284 $R^2 = 0.20$, $p < 0.05$; rarefied: $R^2 = 0.20$, $p < 0.05$) (Table S3, Fig. S5). Moreover, we found no
285 clear patterns in the absolute variance of regional temperature seasonality from JMA climate
286 stations spanning the island from north to south, nor did we find relationships between the
287 absolute seasonality variance of *in situ* air or soil temperature and PC1 (Fig. S6). Only two sites
288 had exposed sensors that were not located below canopy cover (Oyama Park and OIST Open
289 [OYA and OIT, respectively, in Fig. S6]), and these had higher absolute variances than the other
290 sites. Concerning the tests of different threshold sizes, although we observed some differences,
291 our results remained similar (Supporting Information F, Fig. S7).
292
293 Lastly, individual species showed differing seasonality between land-cover groups (more
294 forested and more developed). Comparisons revealed that, in general, the same species have a
295 higher relative seasonality variance at forested sites than at sites with more human development
296 ($p < 0.005$), though the alien species *Tetramorium lanuginosum* was a notable exception (*Tlanu*
297 in Fig. 5). While seasonality was stronger in the forested group for all species, when separated by
298 invasive status we observed higher synchrony in the forested group for native ($n = 11$, forested:
299 0.75, developed: 0.58) and uncertain species ($n = 8$, forested: 0.5, developed: 0.28), but the
300 opposite pattern for alien species ($n = 4$, forested: 0.73, developed: 0.86) (Fig. 5).
301

302 Discussion

303 Our study sheds light on how ant community activity dynamics vary across a gradient of human-
304 induced land-cover change in a subtropical island environment. Our results complement an
305 extensive number of recent studies focusing on the temperate zone that examine change of insect
306 populations over time (Hallmann et al., 2017; Kaspari et al., 2022a; Seibold et al., 2019; Uhler et
307 al., 2021), including those with enough intra-annual sampling to examine changes to seasonality
308 (Kaspari et al., 2022b). The notable difference is that because climatic seasonality is much
309 weaker in the subtropics, differences in seasonality of insect populations across environmental
310 gradients are likely to be more difficult to detect than for populations in the temperate zone that
311 experience stronger seasonal contrasts (Kishimoto-Yamada & Itioka, 2015).
312
313 We found that temporal variability diminishes for the subtropical ant communities of Okinawa
314 Island as land cover transitions from forested to more developed, and that this is related to a
315 breakdown in seasonality. Forested sites were more variable overall, but their resident ant
316 communities were more seasonal and synchronous, while community variability for developed
317 sites (i.e., urban and agricultural) was characterized by stochastic variation. Although native ant
318 richness was higher in forested sites, we determined the observed differences in seasonality
319 across the land-cover gradient were not due to differences in regional or local temperature
320 patterns, nor to species composition among sites. Compositional differences between
321 communities in different land-cover types, such as the prevalence of one or more highly seasonal
322 species, could drive observed relationships between community seasonality and land cover.
323 However, we found that populations of the same species occupying forested sites were more
324 seasonal than those with more human development. Further, when we separated species by
325 invasive status, we found that the strong seasonal patterns we observed in the forest were more
326 synchronous for native than alien species, though both synchrony values are reasonably high and
327 the considerably smaller sample size for alien species should be taken into consideration.
328
329 Our results suggest that increasing agricultural and urban development can dampen seasonal
330 community variability and thus disrupt phenological patterns for insects. In a number of studies,
331 loss of seasonality has been explained by biotic homogenization, whereby communities become
332 more similar and generalist, and this has been linked with urbanization for a variety of taxa,
333 including bees (Hung et al., 2017), bugs and leafhoppers (Knop, 2016), flowering plants and
334 butterflies (Uchida et al., 2018), and birds (La Sorte et al., 2014; Leveau, 2018). However, the
335 majority of studies on the temporal variability of natural communities compare measurements
336 between years and rarely within them (e.g., Cottingham et al., 2001; de Mazancourt et al., 2013;
337 Olivier et al., 2020; Tilman et al., 2006), meaning that loss of seasonality due to environmental
338 or anthropogenic factors may be overlooked. Yearly samples taken for highly seasonal
339 communities at peak productivity over many annual cycles should show higher stability than for
340 a more stochastic community, yet more frequent sampling would reveal considerable variation
341 due to higher synchrony and seasonality. As other studies have demonstrated, temporal scale is a
342 crucial factor that determines how stability should be interpreted (Clark et al., 2021; McArdle et
343 al., 1990), and as community variability and its drivers vary across temporal scales (Hatosy et al.,
344 2013), it is important to measure community responses to the environment and anthropogenic
345 disturbance across scales to improve future predictions.
346

347 We found a positive relationship between functional and compositional temporal variability,
348 meaning that those sites with communities that varied more as a whole tended also to have
349 higher total variation of the individual species in the local pool. The relationship between
350 functional and compositional variability can range from positive to negative depending on the
351 system and exposure to disturbance (Hillebrand et al., 2018; Ross et al., 2022; White et al.,
352 2020). Two characteristics of more forested sites may help explain this positive relationship. The
353 first is that more forested sites had higher variability in general at the biweekly timescale. The
354 second is that, at more forested sites, native species had higher richness and the highest
355 contributions to beta diversity. Sites with high richness that include substantial numbers of alien
356 species can have community dynamics that differ considerably from similar sites in which native
357 species dominate (Krushelnycky & Gillespie, 2008; Sanders et al., 2003), thus including alien
358 species in richness estimates can affect how diversity-stability relationships are interpreted (e.g.,
359 Moore & Olden, 2017).
360
361 Our results raise the question of what mechanisms drive these patterns. We outline several
362 hypotheses for why seasonal variation in activity could vary across the land-cover gradient. First,
363 there is a possibility that ants are simply responding to the temperature they experience on a
364 physiological level, reflecting temperature and microclimatic variation across habitats. Ants are
365 well-known to be sensitive to temperature variation, with foraging limited to certain temperature
366 ranges (Bernstein 1979, Stuble et al., 2013). Regional climatic variation across the island is very
367 modest, and with no consistent differences in seasonality. Further, we found no relationships
368 between the seasonal variance of *in situ* air and soil temperature and the main land-cover
369 gradient PC1. However, differences in canopy openness, vegetation, and urbanization (via heat-
370 island effects, etc.) may create conditions that are relevant for promoting and depressing ant
371 foraging, and the prevalence of such conditions might be higher in more degraded habitats.
372 Comprehensive measurements with small sensors at various habitat strata for representative sites
373 could help elucidate whether this phenomenon could differ across land-cover types. Another
374 possibility is that ants are responding to resource availability patterns. In this scenario, it is
375 possible that resources are more seasonal inside the forest rather than more human-impacted
376 areas. This could occur, for example, because of anthropogenic food sources that are more static
377 throughout the year, or because of differences in phenology of vegetation inside or outside the
378 forest (Penick et al., 2015). A related question is whether these differences in seasonality are
379 limited to ants or are observed across the arthropod community. Were arthropod seasonality
380 responding more generally to land cover, this would provide a resource pattern that could affect
381 ant activity. Related to this, it is unclear why there seems to be little seasonal niche
382 differentiation for ant species in forested areas, which have activity patterns that follow
383 temperature quite closely in synchrony. One possibility is that species become most active at
384 different times during the same warm season to avoid competition—we saw some evidence of
385 this in the standardized seasonal curves (Fig. 5). This could be due to the inability to achieve
386 high activity levels during cooler months due to physiological limitations, which may be absent
387 in more developed environments with anthropogenic temperature refugia. Other potential
388 explanations relating to differences in the ecology or physical environments across the two
389 habitats likely exist, but more targeted research is needed to address this question.
390
391 We measured variability over two years, but there may be other types of variability that only
392 manifest on longer timescales and are also correlated with land cover. For example, introduced

393   ants are known to have boom-bust dynamics when they reach new localities (Lester & Gruber,
394   2016). Over longer timescales, communities in more human-dominated areas may prove to be
395   more dynamic with successive shifts in the community. Indeed, we witnessed such an event in
396   our two-year period at one of our sites (Sefautaki Forest), where *Pheidole megacephala*, a
397   notoriously impactful invasive ant, arrived and quickly reached high abundance, raising
398   variability of this site beyond what was typical of others with similar land-cover characteristics.
399   Recent research in Yambaru Forest has documented resilience of native ant communities to
400   disturbance based on surveys of invasions at developed areas after regrowth (Shimoji et al.,
401   2022), so this site too may eventually recover to its previous structure. Thus, successive regime
402   shifts in these more disturbed communities could occur over longer timescales, but only
403   monitoring over more years would reveal such dynamics.
404

Conclusions

406   This study provides novel insight into the seasonal dynamics of subtropical insect communities
407   across differing levels of human development. Importantly, it is the first study to our knowledge
408   to measure seasonality of ant activity with high-frequency sampling across a human disturbance
409   gradient. The results of our study, which link anthropogenic disturbance in the form of
410   agricultural and urban development to a reduction in intra-annual temporal variability due to
411   weakening seasonality, support the growing evidence that human development reduces natural
412   seasonal patterns (Hung et al., 2017; La Sorte et al., 2014; Leveau, 2018; Uchida et al., 2018).
413   Although this study focuses on correlative relationships and thus cannot fundamentally
414   demonstrate causal mechanisms, it does provide compelling evidence that continuing habitat loss
415   and fragmentation can lead to increasing homogenization of insect communities in parts of the
416   globe with the highest insect diversity, the subtropics and tropics. As loss of seasonal patterns
417   has been linked to a subsequent reduction in key ecosystem functions and services (Ross et al.,
418   2021; Stevenson et al., 2015), increasing development could result in disruptions to nutrient
419   cycling and food security (Bommarco et al., 2013). To better understand the generality of these
420   patterns, future studies using high-frequency sampling should focus on monitoring a greater
421   diversity of insect communities across different habitat strata (i.e., arboreal, subterranean; Gotelli
422   et al., 2011) in a variety of biomes. Greater focus on the impacts of land-cover change on insect
423   community seasonality should aid ongoing management and conservation efforts to help
424   preserve the important ecosystem functions and services insects provide.
425

Data Availability

427   Raw species' count data before processing and R code used for analysis will be found on Data
428   Dryad after article acceptance. Please contact <jamie.m.kass (at) gmail.com> with data requests.

429

Acknowledgments

References

Andersen, A. N., & Majer, J. D. (2004). Ants show the way Down Under: Invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment*, *2*(6), 291–298.

Basu, P. (1997). Seasonal and Spatial Patterns in Ground Foraging Ants in a Rain Forest in the Western Ghats, India. *Biotropica*, *29*(4), 489–500.

Bernstein, R. A. (1979). Schedules of foraging activity in species of ants. *Journal of Animal Ecology*, 921–930.

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67.

Castro, D. M. P. de, Dolédec, S., & Callisto, M. (2018). Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators*, *84*, 573–582.

Clark, A. T., Arnoldi, J., Zelnik, Y. R., Barabas, G., Hodapp, D., Karakoç, C., König, S., Radchuk, V., Donohue, I., Huth, A., Jacquet, C., Mazancourt, C., Mentges, A., Nothaaß, D., Shoemaker, L. G., Taubert, F., Wiegand, T., Wang, S., Chase, J. M., … Harpole, S. (2021). General statistical scaling laws for stability in ecological systems. *Ecology Letters*, *24*(7), 1474–1486.

Corro, E. J., Ahuatzin, D. A., Jaimes, A. A., Favila, M. E., Ribeiro, M. C., López-Acosta, J. C., & Dáttilo, W. (2019). Forest cover and landscape heterogeneity shape ant–plant co-occurrence networks in human-dominated tropical rainforests. *Landscape Ecology*, *34*(1), 93–104.

Cottingham, K. L., Brown, B. L., & Lennon, J. T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, *4*(1), 72–85.

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J. B., Haegeman, B., Wayne Polley, H., Roscher, C., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., & Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*, *16*(5), 617–625.

Dornelas, M., Magurran, A. E., Buckland, S. T., Chao, A., Chazdon, R. L., Colwell, R. K., Curtis, T., Gaston, K. J., Gotelli, N. J., Kosnik, M. A., McGill, B., McCune, J. L., Morlon, H., Mumby, P. J., Øvreås, L., Studeny, A., & Vellend, M. (2013). Quantifying temporal change in biodiversity: Challenges and opportunities. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1750), 20121931.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Thibaut, J., Larocque, G., Legendre, P., Madi, N., & Wagner, H. H. (2022). *adespatial: Multivariate Multiscale Spatial Analysis* (0.3-16). https://CRAN.R-project.org/package=adespatial

Gaston, K. J., & McArdle, B. H. (1994). The temporal variability of animal abundances: Measures, methods and patterns. *Philosophical Transactions of the Royal Society B*, *345*(1314), 335–358.

485 Gotelli, N. J., Ellison, A. M., Dunn, R. R., & Sanders, N. J. (2011). Counting ants (Hymenoptera:
486   Formicidae): Biodiversity sampling and statistical analysis for myrmecologists.
487   *Myrmecological News*, 32.
488 Goulson, D. (2019). The insect apocalypse, and why it matters. *Current Biology*, *29*(19), R967–
489   R971.
490 Guénard, B., Weiser, M. D., Gomez, K., Narula, N., & Economo, E. P. (2017). The Global Ant
491   Biodiversity Informatics (GABI) database: synthesizing data on the geographic
492   distribution of ant species (Hymenoptera: Formicidae). *Myrmecological*
493   *News/Osterreichische Gesellschaft fur Entomofaunistik*, *24*, 83-89.
494 Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F. B., Ripplinger, J.,
495   Slaughter, P., Gries, C., & Collins, S. L. (2016). codyn: An r package of community
496   dynamics metrics. *Methods in Ecology and Evolution*, *7*(10), 1146–1151.
497 Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W.,
498   Müller, A., Sumser, H., Hörren, T., Goulson, D., & Kroon, H. de. (2017). More than 75
499   percent decline over 27 years in total flying insect biomass in protected areas. *PLOS*
500   *ONE*, *12*(10), e0185809.
501 Hatosy, S. M., Martiny, J. B. H., Sachdeva, R., Steele, J., Fuhrman, J. A., & Martiny, A. C.
502   (2013). Beta diversity of marine bacteria depends on temporal scale. *Ecology*, *94*(9),
503   1898–1904.
504 Hijmans, R. J. (2021). *raster: Geographic Data Analysis and Modeling* (3.4-13) [R].
505   https://CRAN.R-project.org/package=raster
506 Hillebrand, H., & Kunze, C. (2020). Meta-analysis on pulse disturbances reveals differences in
507   functional and compositional recovery across ecosystems. *Ecology Letters*, *23*(3), 575–
508   585.
509 Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö., & Striebel, M. (2018).
510   Decomposing multiple dimensions of stability in global change experiments. *Ecology*
511   *Letters*, *21*(1), 21–30.
512 Hölldobler, B., & Wilson, E. (1990). *The Ants*. Harvard University Press.
513 Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and
514   extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*,
515   *7*(12), 1451–1456.
516 Hung, K.-L. J., Ascher, J. S., & Holway, D. A. (2017). Urbanization-induced habitat
517   fragmentation erodes multiple components of temporal diversity in a Southern California
518   native bee assemblage. *PLOS ONE*, *12*(8), e0184136.
519 Hyndman, R. J., & Athanasopoulos, G. (2021). *Forecasting: Principles and practice* (3rd ed.).
520   OTexts: Melbourne, Australia. https://OTexts.com/fpp3
521 Janicki, J., Narula, N., Ziegler, M., Guénard, B., & Economo, E. P. (2016). Visualizing and
522   interacting with large-volume biodiversity data using client–server web-mapping
523   applications: The design and implementation of antmaps. org. *Ecological Informatics*, *32*,
524   185-193.
525 Janzen, D. H., & Hallwachs, W. (2021). To us insectometers, it is clear that insect decline in our
526   Costa Rican tropics is real, so let's be kind to the survivors. *Proceedings of the National*
527   *Academy of Sciences*, *118*(2), e2002546117.
528 Kaspari, M., Weiser, M. D., Marshall, K. E., Miller, M., Siler, C., & de Beurs, K. (2022a).
529   Activity density at a continental scale: What drives invertebrate biomass moving across
530   the soil surface? *Ecology*, *103*(1), e03542.

Kaspari, M., Weiser, M. D., Marshall, K. E., Siler, C. D., & de Beurs, K. (2022b). Temperature–habitat interactions constrain seasonal activity in a continental array of pitfall traps. *Ecology*, e3855.

Katayama, M., & Tsuji, K. (2010). Habitat differences and occurrence of native and exotic ants on Okinawa Island. *Entomological Science*, *13*(4), 425–429.

Kishimoto-Yamada, K., & Itioka, T. (2015). How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? *Entomological Science*, 18(4), 407–419.

Knop, E. (2016). Biotic homogenization of three insect groups due to urbanization. *Global Change Biology*, *22*(1), 228–236.

Krushelnycky, P. D., & Gillespie, R. G. (2008). Compositional and functional stability of arthropod communities in the face of ant invasions. *Ecological Applications*, *18*(6), 1547–1562.

La Sorte, F. A., Tingley, M. W., & Hurlbert, A. H. (2014). The role of urban and agricultural areas during avian migration: An assessment of within-year temporal turnover. *Global Ecology and Biogeography*, *23*(11), 1225–1234.

Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, *16*(8), 951–963.

Lester, P. J., & Gruber, M. A. M. (2016). Booms, busts and population collapses in invasive ants. *Biological Invasions*, *18*(11), 3091–3101.

Leveau, L. M. (2018). Urbanization, environmental stabilization and temporal persistence of bird species: A view from Latin America. *PeerJ*, *2018*(12), e6056.

Loreau, M., & de Mazancourt, C. (2008). Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments. *The American Naturalist*, *172*(2), E48–E66.

McArdle, B. H., & Gaston, K. J. (1995). The Temporal Variability of Densities: Back to Basics. *Oikos*, *74*(1), 165–171.

McArdle, B. H., Gaston, K. J., & Lawton, J. H. (1990). Variation in the Size of Animal Populations: Patterns, Problems and Artefacts. *The Journal of Animal Ecology*, *59*(2), 439.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260.

Moore, J. W., & Olden, J. D. (2017). Response diversity, nonnative species, and disassembly rules buffer freshwater ecosystem processes from anthropogenic change. *Global Change Biology*, *23*(5), 1871–1880.

O'Hara-Wild, M., Hyndman, R., & Wang, E. (2021). *fable: Forecasting Models for Tidy Time Series* (0.3.1). https://CRAN.R-project.org/package=fable

Oliver, I., Dorrough, J., Doherty, H., & Andrew, N. R. (2016). Additive and synergistic effects of land cover, land use and climate on insect biodiversity. *Landscape Ecology*, *31*(10), 2415–2431.

Olivier, T., Thébault, E., Elias, M., Fontaine, B., & Fontaine, C. (2020). Urbanization and agricultural intensification destabilize animal communities differently than diversity loss. *Nature Communications*, *11*(1), 1–9.

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, *10*(1), 439–446.

Penick, C. A., Savage, A. M., & Dunn, R. R. (2015). Stable isotopes reveal links between human food inputs and urban ant diets. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1806), 20142608.

Ross, S. R. P.-J., Arnoldi, J.-F., Loreau, M., White, C. D., Stout, J. C., Jackson, A. L., & Donohue, I. (2021). Universal scaling of robustness of ecosystem services to species loss. *Nature Communications*, *12*(1), 1–7.

Ross, S. R. P.-J., Friedman, N. R., Dudley, K. L., Yoshimura, M., Yoshida, T., & Economo, E. P. (2018). Listening to ecosystems: Data-rich acoustic monitoring through landscape-scale sensor networks. *Ecological Research*, *33*(1), 135–147.

Ross, S. R. P.-J., García Molinos, J., Okuda, A., Johnstone, J., Atsumi, K., Futamura, R., Williams, M. A., Matsuoka, Y., Uchida, J., Kumikawa, S., Sugiyama, H., Kishida, O., & Donohue, I. (2022). Predators mitigate the destabilising effects of heatwaves on multitrophic stream communities. *Global Change Biology*, *28*(2), 403–416.

Russell, J. C., & Kueffer, C. (2019). Island Biodiversity in the Anthropocene. *Annual Review of Environment and Resources*, *44*(1), 31–60.

Samways, M. J. (1990). Species temporal variability: Epigaeic ant assemblages and management for abundance and scarcity. *Oecologia*, *84*(4), 482–490.

Sanders, N. J., Gotelli, N. J., Heller, N. E., & Gordon, D. M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences*, *100*(5), 2474–2477.

Schowalter, T. D. (2013). *Insects and Sustainability of Ecosystem Services*. CRC Press.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674.

Senapathi, D., Carvalheiro, L. G., Biesmeijer, J. C., Dodson, C.-A., Evans, R. L., McKerchar, M., Morton, R. D., Moss, E. D., Roberts, S. P. M., Kunin, W. E., & Potts, S. G. (2015). The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1806), 20150294.

Shimoji, H., Suwabe, M., Kikuchi, T., Ohnishi, H., Tanaka, H., Kawara, K., Hidaka, Y., Enoki, T., & Tsuji, K. (2022). Resilience of native ant community against invasion of exotic ants after anthropogenic disturbances of forest habitats. *Ecology and Evolution*, 12(7), e9073.

Simberloff, D., & Gibbons, L. (2004). Now you see them, now you don't! – Population Crashes of Established Introduced Species. *Biological Invasions*, *6*(2), 161–172.

Stevenson, T. J., Visser, M. E., Arnold, W., Barrett, P., Biello, S., Dawson, A., Denlinger, D. L., Dominoni, D., Ebling, F. J., Elton, S., Evans, N., Ferguson, H. M., Foster, R. G., Hau, M., Haydon, D. T., Hazlerigg, D. G., Heideman, P., Hopcraft, J. G. C., Jonsson, N. N., … Helm, B. (2015). Disrupted seasonal biology impacts health, food security and ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1817), 20151453.

Stuble, K. L., Pelini, S. L., Diamond, S. E., Fowler, D. A., Dunn, R. R., & Sanders, N. J. (2013). Foraging by forest ants under experimental climatic warming: a test at two sites. *Ecology and Evolution*, *3*(3), 482-491.

620 Suwabe, M., Ohnishi, H., Kikuchi, T., Kawara, K., & Tsuji, K. (2009). Difference in seasonal
621   activity pattern between non-native and native ants in subtropical forest of Okinawa
622   Island, Japan. *Ecological Research*, *24*(3), 637–643.

623 Terayama, M., Takamine, H., & Kubota, S. (2009) Ants in Okinawa. 182 pp. Hidetsune
624   Takamine, Naha City.

625 Terayama, M., Kubota, S., & Eguchi, K. (2014) Encyclopedia of Japanese ants. 278 pp. Asakura
626   Shoten, Tokyo.

627 Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a
628   decade-long grassland experiment. *Nature*, *441*(7093), 629–632.

629 Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality
630   and predictability shape temporal species diversity. *Ecology*, *98*(5), 1201–1216.

631 Uchida, K., Fujimoto, H., & Ushimaru, A. (2018). Urbanization promotes the loss of seasonal
632   dynamics in the semi-natural grasslands of an East Asian megacity. *Basic and Applied*
633   *Ecology*, *29*, 1–11.

634 Uhler, J., Redlich, S., Zhang, J., Hothorn, T., Tobisch, C., Ewald, J., Thorn, S., Seibold, S.,
635   Mitesser, O., Morinière, J., Bozicevic, V., Benjamin, C. S., Englmeier, J., Fricke, U.,
636   Ganuza, C., Haensel, M., Riebl, R., Rojas-Botero, S., Rummler, T., … Müller, J. (2021).
637   Relationship of insect biomass and richness with land use along a climate gradient.
638   *Nature Communications*, *12*(1), 1–9.

639 Van Buskirk, J. (2005). Local and Landscape Influence on Amphibian Occurrence and
640   Abundance. *Ecology*, *86*(7), 1936–1947.

641 Wagner, D. L. (2020). Insect Declines in the Anthropocene. *Annual Review of Entomology*,
642   *65*(1), 457–480.

643 White, L., O'Connor, N. E., Yang, Q., Emmerson, M. C., & Donohue, I. (2020). Individual
644   species provide multifaceted contributions to the stability of ecosystems. *Nature Ecology*
645   *& Evolution*, *4*(12), 1594–1601.

646 Yamauchi, K., & Ogata, K. (1995). Social structure and reproductive systems of tramp versus
647   endemic ants (Hymenoptera: Formicidae) of the Ryukyu Islands. *Pacific Science*, *49*, 55–
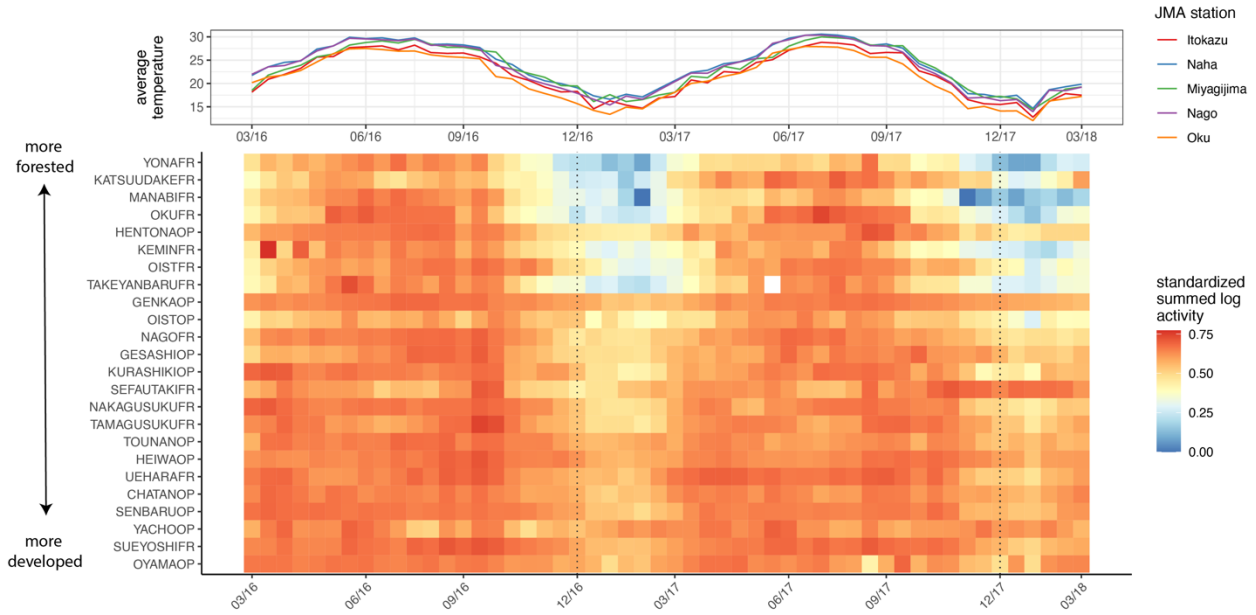648   68.

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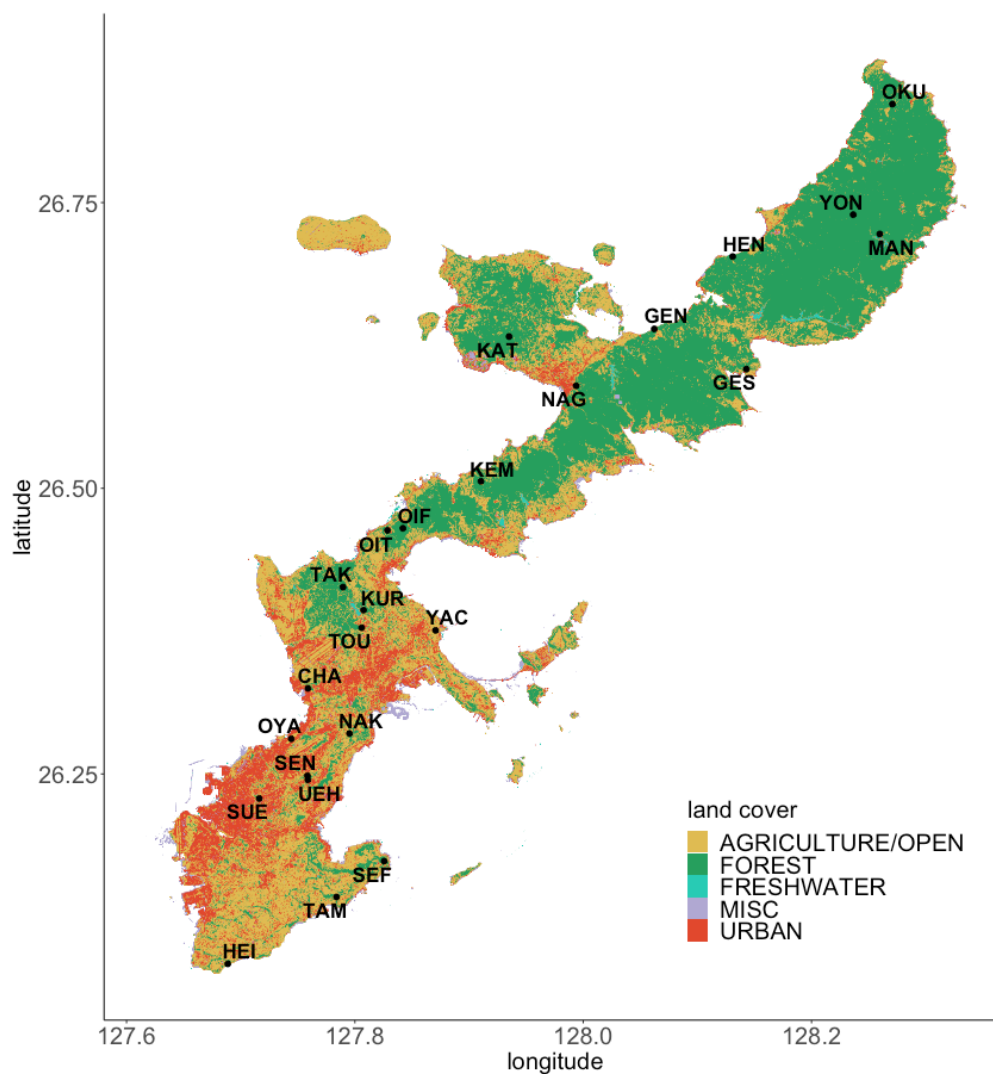
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653 Figure 1. Major land-cover classes of Okinawa Island with locations of the OKEON
654 monitoring stations, which cover the full gradient of human development across the
655 island. Ants were sampled from three stations at each sampling site biweekly from 2016–
656 2018 (total of 52 sampling periods).

657

658

659

Figure 2. Heat map showing the standardized ant activity (i.e., logs of summed site counts divided by the log of the grand total count) over two years in Okinawa. Mean temperature measurements from the Japan Meteorological Agency across the island, ordered from south to north, are included for reference. Heat map sites are ordered by values of land-cover PC1, explaining the anthropogenic stress gradient (top: more forested, bottom: more urban). Dotted lines show the last sampling period before the new year.
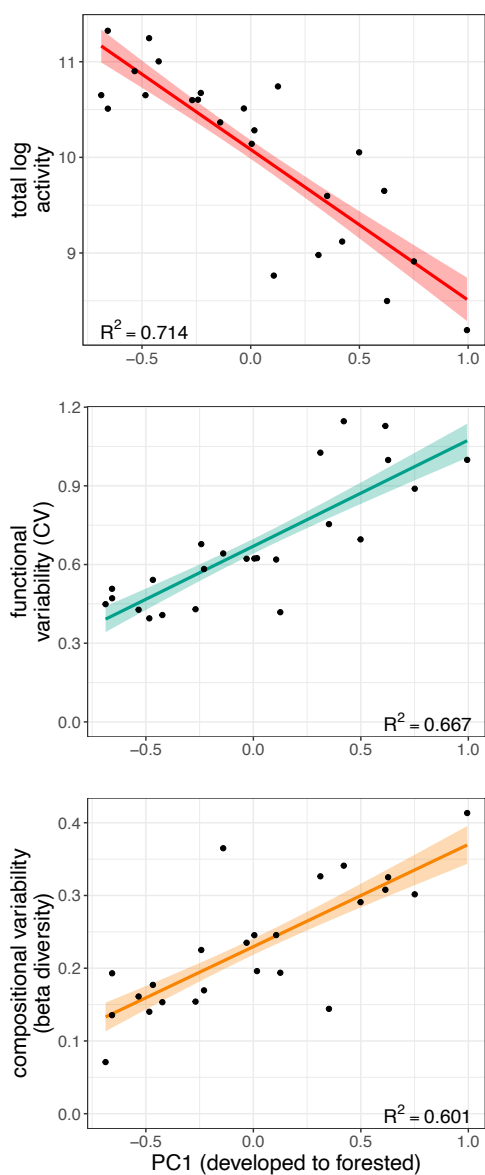
666
667
668 Figure 3. Trends in total log activity, functional variability, and compositional variability for ants
669 across a gradient of anthropogenic impact. Relationships with PC1, explaining the anthropogenic
670 stress gradient (low: more developed, high: more forested). Total log ant activity (before
671 rarefaction) correlates negatively with PC1 while indices of temporal variability (functional:
672 coefficient of variation, compositional: beta diversity) correlate positively.

673

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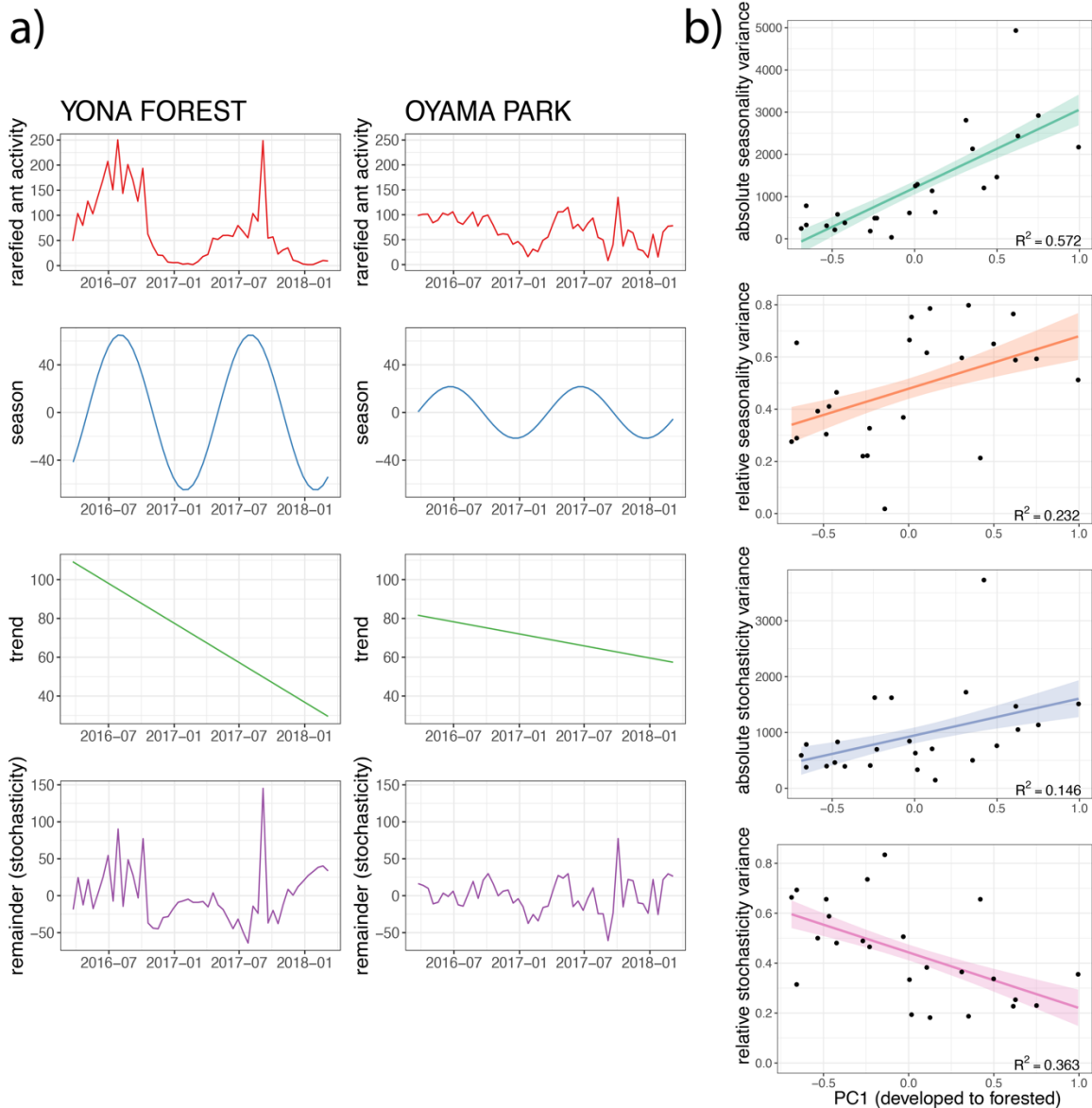
Figure 4. a) Time-series decomposition of rarefied ant activity for the sites with the most forest (Yona Forest) and most human development (Oyama Park) within a 1 km buffer. b) Relationships between absolute and relative variance of seasonality and stochastic temporal components and PC1 across all 24 sites, explaining the anthropogenic stress gradient (low: more developed, high: more forested). Relative variance here is calculated as individual component variance divided by summed variance of all components.

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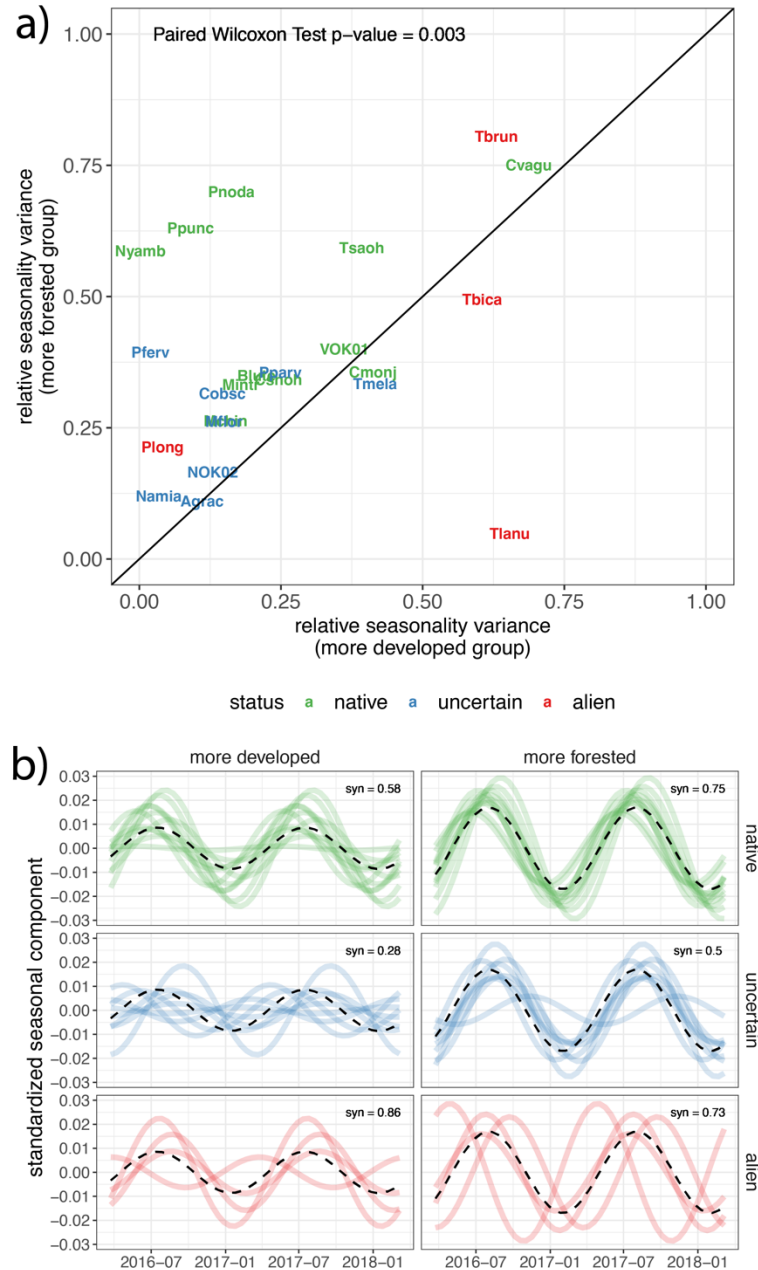
Figure 5. a) Relative seasonality variance calculated per ant species in two representative land-cover groups each containing eight sites: more forested and more developed. Only species shared between groups (abbreviations of those found in Table S2) and with total counts ≥100 were retained, whereupon species counts were rarefied to the minimum between groups. On average, species have a higher relative seasonality variance in the forested group (paired Wilcoxon Test; p = 0.003), and no apparent patterns exist regarding alien status. b) Seasonal component time-series for each species (lines) found in the more forested and more developed groups, standardized by total species activity and separated by invasive species status. The dashed black line shows the mean standardized seasonality across all species per land-cover group, showing much greater temporal mismatch in ant communities at sites with greater human development.

692   Supporting Information

693   A. Ant activity data details

694   As sites across the island were sampled in sequential groups rather than simultaneously for each
695   biweekly period (differences are on the order of 7 days), to allow for appropriate site
696   comparisons, we assigned each sample a time step (52 in total) based on the relative sampling
697   order for that site. To this activity dataset, we filled in absence data when species that were
698   observed at least once at a site were not observed for other time steps for that site in order to
699   calculate temporal variability metrics. Values of NA ($n = 8$) were assigned to samples that
700   experienced trap malfunctions or data loss via extreme weather events and were removed from
701   analyses.
702

703   B. Rarefaction permutations

704   Community samples collected over time are typically biased by sampling error, which results in
705   fluctuations in activity due to site placement or other external factors, but this bias can be
706   reduced via data rarefaction (Gaston & McArdle, 1994). As natural differences in total
707   community count across sites were high (from $n = 3,616$ [Yona Forest] to $n = 82,781$ [Sueyoshi
708   Forest]), we rarefied site- and group-level count while retaining original activity patterns to
709   reduce the effects of sampling error, allowing us to make more even comparisons of temporal
710   variability. For site-level activity, we randomly resampled the individual counts of species i at
711   time t for each site to equal the minimum total site count ($n = 3,616$). For group-level activity,
712   we first limited the species considered to those with total count greater than 100 for the two-year
713   study period, then randomly resampled (with replacement) the individual counts of species i at
714   time t for each group to equal that species' minimum total count between groups. We performed
715   1000 iterations of each rarefaction and conducted all proceeding analyses on these iterations.
716

717   C. Community and compositional variability calculations

718   We measured community temporal variability by calculating the coefficient of variation (CV) of
719   summed ant count by site over the 2-year sampling period. We measured compositional temporal
720   variability by calculating temporal beta diversity for each site community as the total variability
721   of the species composition matrix (here, species × time step) after a Hellinger transformation (to
722   ensure purely relative count data; Legendre & De Cáceres, 2013) using the function *beta.div*
723   from the R package *adespatial* (Dray et al., 2022). As an additional product of this function, we
724   derived species contributions to beta diversity per site, which is calculated as species variance
725   divided by the total community variance (summing to 1). We then summed these contributions
726   for each invasive status category (native, uncertain, alien) to determine the contribution of each
727   category. We calculated both indices of temporal variability on each rarefied site activity dataset,
728   then found the mean values across datasets. These mean rarefied site values were used in
729   subsequent models.
730

731   D. Formulas for temporal decomposition and associated variance

732   We used the TSLM() function in the R package *fable* (O'Hara-Wild et al., 2021) to fit time-
733   series linear models with the following formula:

734

735 $$y_t = \beta_0 + \beta_1 t + \beta_2 x_1$$

736

737 where y_t is the total count of ants at a site, with t equal to the range 1 to T, the number of time

738 intervals; and where x_1 is the 1st order Fourier term $\sin(\frac{2\pi t}{m})$, with m equal to the number of

739 seasonal periods (in this case, $m = 2$ for 2 years).

740

741 We calculated the temporal components in the following ways:

742

743 $$trend = \beta_0 + \beta_1 t$$

744

745 $$season = y_t - trend - resid$$

746

747 $$remainder = resid$$

748

749 where *resid* is the model residuals.

750

751 In addition to calculating absolute variance of temporal components, we calculated relative

752 variance with the following formula:

753

754 $$relative\ var_z = \frac{var(z)}{var(trend) + var(season) + var(remainder)}$$

755

756 where z is one of the temporal components: trend, season, or remainder.

757

758 E. Assessing effects of spatial autocorrelation on models

759 We first built models using ordinary least squares (OLS) regression to estimate the relationships

760 between land cover and the variables of interest. As some OKEON sites are relatively close to

761 others, we assessed the spatial autocorrelation present in the OLS model residuals by calculating

762 Moran's I and testing with random permutations using the function *moran.randtest*() from the R

763 package *adespatial* (999 repetitions; Dray et al., 2022). But as this test was not significant for

764 any of the models ($p > 0.05$), we fitted OLS models instead of more complex generalized least

765 squares (GLS) models with spatial structure. We determined goodness-of-fit with the adjusted

766 coefficient of determination (R-squared) and compared these between different count threshold

767 choices.

768

769 F. Effects of count threshold choice

770 As we avoided bias in temporal variability estimates by limiting all count values to an assigned

771 threshold, we examined how robust our results are over a range of different thresholds. We

772 report results in the main text for the relatively conservative threshold of 500 set at the station-

773 level, but additionally ran the same analyses with no threshold, and with thresholds 100, 200,

774 1000, and 2000, applied at both the station- and site-levels. We observed some differences across

775   the different thresholding schema, but no threshold fundamentally changes our results (which we
776   report for threshold 500 set at the station-level). The adjusted R-squared values for the metrics
777   calculated were sensitive in varying degrees to threshold (Fig. S7), with the exception of
778   compositional temporal variability—this is because our beta diversity calculation includes a
779   Hellinger transformation that mollifies the effects of outliers in the data. Further, thresholding at
780   the station- and site-levels showed the same general trends. The highest threshold considered
781   (2000) for the station-level was most often associated with the lowest R-squared values. The
782   absence of a threshold had the most dramatic differences. This reduced the R-squared value for
783   functional temporal variability to 0.11 from a thresholded minimum of 0.40, and seasonality
784   variance to 0.16 from 0.39. R-squared values for other metrics were similarly reduced, but more
785   closely followed decreasing trends as thresholds became larger. These reductions in correlations
786   with PC1 occurred because, without thresholding, sites with extreme count values for one or
787   several species spike in functional variability (calculated with CV) and lose seasonality, and the
788   existence of such spikes has little to do with land cover.
789

790   Table S1. Pearson correlations between proportions of land-cover classes within 1 km buffers of
791   sampling sites. "MISC" stands for miscellaneous and includes the classes for unclassified pixels
792   and those classified as bare rock or soil. As pairwise correlations were high, we conducted a
793   principal component analysis (PCA) to derive the main orthogonal land-cover gradients.
794
795

	AGRICULTURE	FOREST	WATER	GRASS	SAND	URBAN	MISC
AGRICULTURE	1						
FOREST	-0.89	1					
WATER	-0.05	0.02	1				
GRASS	0.53	-0.44	0.02	1			
SAND	0.54	-0.48	-0.04	0.23	1		
URBAN	0.56	-0.84	-0.08	0.01	0.20	1	
MISC	0.51	-0.73	0.13	0.18	0.53	0.74	1

796

797   Table S2. Invasive status for all observed ant species based on existing literature and expert

798   opinion.

799

species	status
Aenictus ceylonicus	native
Aenictus lifuiae	native
Anoplolepis gracilipes	uncertain
Aphaenogaster concolor	native
Aphaenogaster irrigua	native
Brachyponera chinensis	native
Brachyponera luteipes	native
Camponotus bishamon	native
Camponotus devestivus	native
Camponotus monju	native
Camponotus OK01	native
Camponotus yambaru	native
Cardiocondyla kagutsuchi	uncertain
Cardiocondyla minutior	uncertain
Cardiocondyla obscurior	uncertain
Cardiocondyla wroughtonii	native
Carebara hannya	native
Carebara oni	native
Carebara yamatonis	native
Colobopsis shohki	native
Crematogaster cf. matsumurai	native

Crematogaster nawai	native
Crematogaster vagula	native
Cryptopone tengu	native
Diacamma OK01	native
Discothyrea kamiteta	native
Ectomomyrmex OK01	native
Erromyrma latinodis	native
Euponera pilosior	native
Hypoponera nippona	native
Hypoponera OK01	native
Hypoponera punctatissima	alien
Hypoponera sauteri	native
Leptogenys confucii	native
Lioponera daikoku	native
Monomorium chinense	native
Monomorium floricola	uncertain
Monomorium hiten	native
Monomorium intrudens	native
Monomorium pharaonis	alien
Myrmecina ryukyuensis	native
Nylanderia amia	uncertain
Nylanderia OK02	uncertain
Nylanderia OK03	uncertain
Nylanderia ryukyuensis	native
Nylanderia yambaru	native
Ochetellus glaber	native

Odontomachus kuroiwae	native
Ooceraea biroi	uncertain
Paratrechina longicornis	alien
Pheidole fervens	uncertain
Pheidole megacephala	alien
Pheidole noda	native
Pheidole parva	uncertain
Pheidole pieli	native
Plagiolepis alluaudi	alien
Polyrhachis dives	native
Polyrhachis moesta	native
Ponera takaminei	native
Ponera tamon	native
Pristomyrmex punctatus	native
Proceratium japonicum	native
Protanilla lini	native
Rhopalomastix OK01	native
Solenopsis tipuna	native
Stigmatomma sakaii	native
Stigmatomma silvestrii	native
Strumigenys circothrix	native
Strumigenys emmae	uncertain
Strumigenys exilirhina	native
Strumigenys hexamera	native
Strumigenys hirashimai	native
Strumigenys lewisi	native

|	
Strumigenys mazu	native
Strumigenys membranifera	uncertain
Strumigenys minutula	native
Strumigenys OK01	uncertain
Strumigenys strigatella	native
Tapinoma melanocephalum	uncertain
Tapinoma saohime	native
Technomyrmex brunneus	alien
Temnothorax indra	native
Temnothorax OK01	native
Tetramorium bicarinatum	alien
Tetramorium kraepelini	uncertain
Tetramorium lanuginosum	alien
Tetramorium nipponense	native
Tetramorium simillimum	alien
Tetramorium smithi	alien
Trichomyrmex destructor	uncertain
Vollenhovia OK01	native

800

801 Table S3. Results from linear regression models built with two land-cover PCA axes: PC1,
802 explaining the forested-developed gradient, and PC2, explaining the rural-urban gradient. All
803 model residuals were tested for spatial autocorrelation by calculating Moran's I and testing with
804 random permutations (*moran.randtest*() from the R package *adespatial*; 999 repetitions), yet
805 none had significant results.
806

Response variable	Intercept	PC1			PC2			Adj. R^2	Moran p
		Estimate	Std. Error	p	Estimate	Std. Error	p		
Total activity (natural log)	10.082	-1.575	0.206	0	NA	NA	NA	0.714	0.269
Total richness (rarefied)	22.742	3.453	1.557	0.037	NA	NA	NA	0.145	0.727
Native richness (rarefied)	13.662	8.351	1.367	0	NA	NA	NA	0.612	0.789
Uncertain richness (rarefied)	5.863	-3.585	1.019	0.002	NA	NA	NA	0.331	0.179
Alien richness (rarefied)	3.217	-1.314	0.509	0.017	NA	NA	NA	0.198	0.59
Total richness (observed)	30.708	NA	NA	NA	NA	NA	NA	0	0.887
Native richness (observed)	18.708	7.483	1.686	0	-7.594	4.611	0.114	0.47	0.8
Uncertain richness (observed)	7.875	-5.188	1.516	0.002	NA	NA	NA	0.318	0.312
Alien richness (observed)	4.125	-2.052	0.643	0.004	NA	NA	NA	0.285	0.271
Total richness (estimated)	38.923	NA	NA	NA	NA	NA	NA	0	0.862
Native richness (estimated)	23.781	13.457	3.646	0.001	NA	NA	NA	0.354	0.767
Uncertain richness (estimated)	8.427	-5.717	1.636	0.002	NA	NA	NA	0.328	0.487
Alien richness (estimated)	4.292	-2.092	0.802	0.016	NA	NA	NA	0.202	0.3

|									
Functional temporal variability	0.67	0.405	0.059	0	NA	NA	NA	0.667	0.269
Compositional temporal variability	0.23	0.141	0.024	0	NA	NA	NA	0.601	0.703
Native SCBD	0.53	0.237	0.059	0.001	NA	NA	NA	0.397	0.776
Uncertain SCBD	0.229	-0.16	0.05	0.004	NA	NA	NA	0.283	0.524
Alien SCBD	0.257	-0.087	0.05	0.094	NA	NA	NA	0.082	0.465
Seasonal variability (absolute)	1209.034	1850.927	328.626	0	NA	NA	NA	0.572	0.918
Seasonal variability (relative)	0.478	0.201	0.081	0.022	-0.373	0.222	0.108	0.232	0.39
Trend variability (absolute)	194.354	311.24	90.185	0.002	NA	NA	NA	0.322	0.567
Trend variability (relative)	0.079	NA	NA	NA	NA	NA	NA	0	0.722
Stochastic variability (absolute)	946.566	660.74	297.568	0.037	NA	NA	NA	0.146	0.591
Stochastic variability (relative)	0.443	-0.223	0.066	0.003	0.345	0.18	0.069	0.363	0.403

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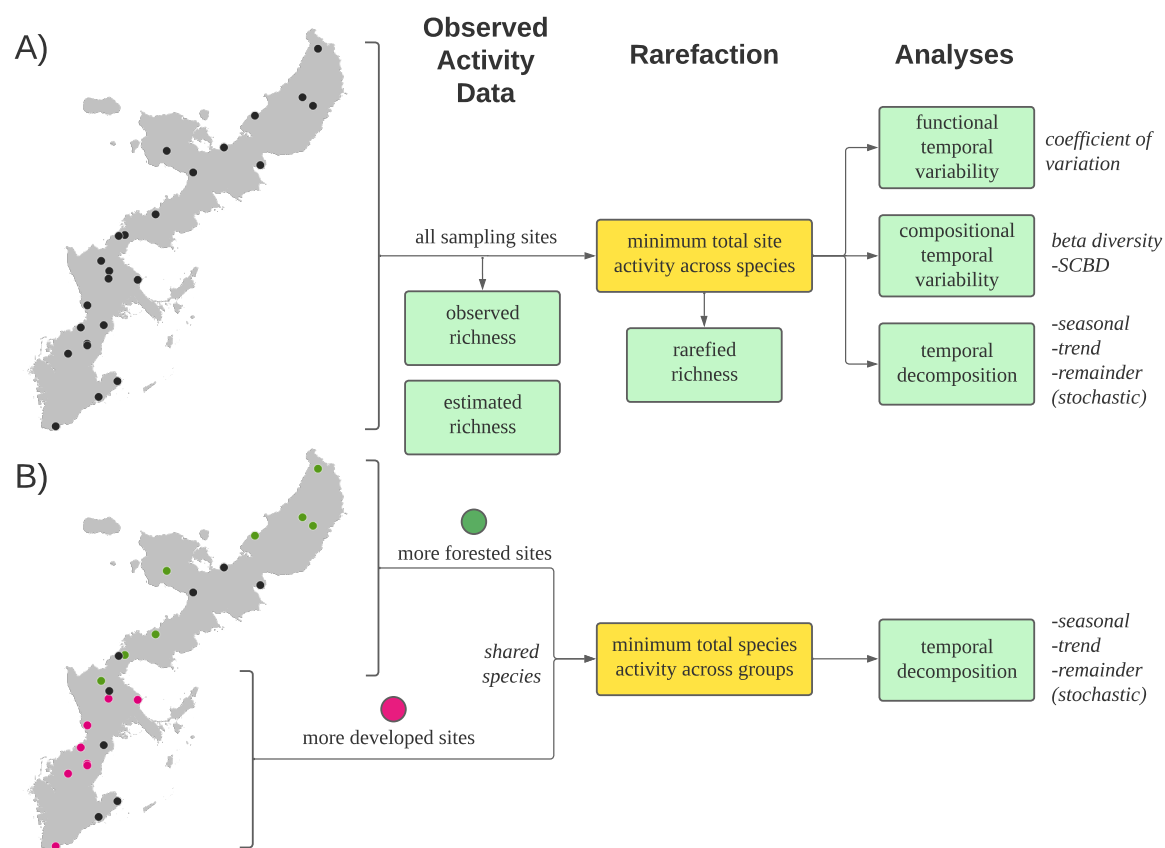
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810

811 Figure S1. Conceptual workflow schematic describing the analysis steps. A) The main analysis
812 uses ant activity data from all sites. Richness is calculated for observed data and estimated via
813 Hill numbers, then the dataset is rarefied by randomly resampling individual workers per site to
814 match the minimum total site activity; rarefied richness is calculated from this rarefied dataset.
815 Next, the following analyses are conducted: functional temporal variability, compositional
816 temporal variability (including species contribution to beta diversity [SCBD]), and temporal
817 decompositions to derive seasonal, trend, and remainder (stochastic) components. B) The group-
818 level analysis first splits sites into two groups (green and pink points) based on land-cover PC1,
819 explaining the forested-developed gradient. Both groups share the same species, and those with
820 mid-level PC1 values are excluded (black points). These grouped data are then rarefied by
821 randomly resampling individual workers per species within each group to match the minimum
822 total species activity between groups. The same temporal decomposition is then conducted on
823 these grouped data.
824
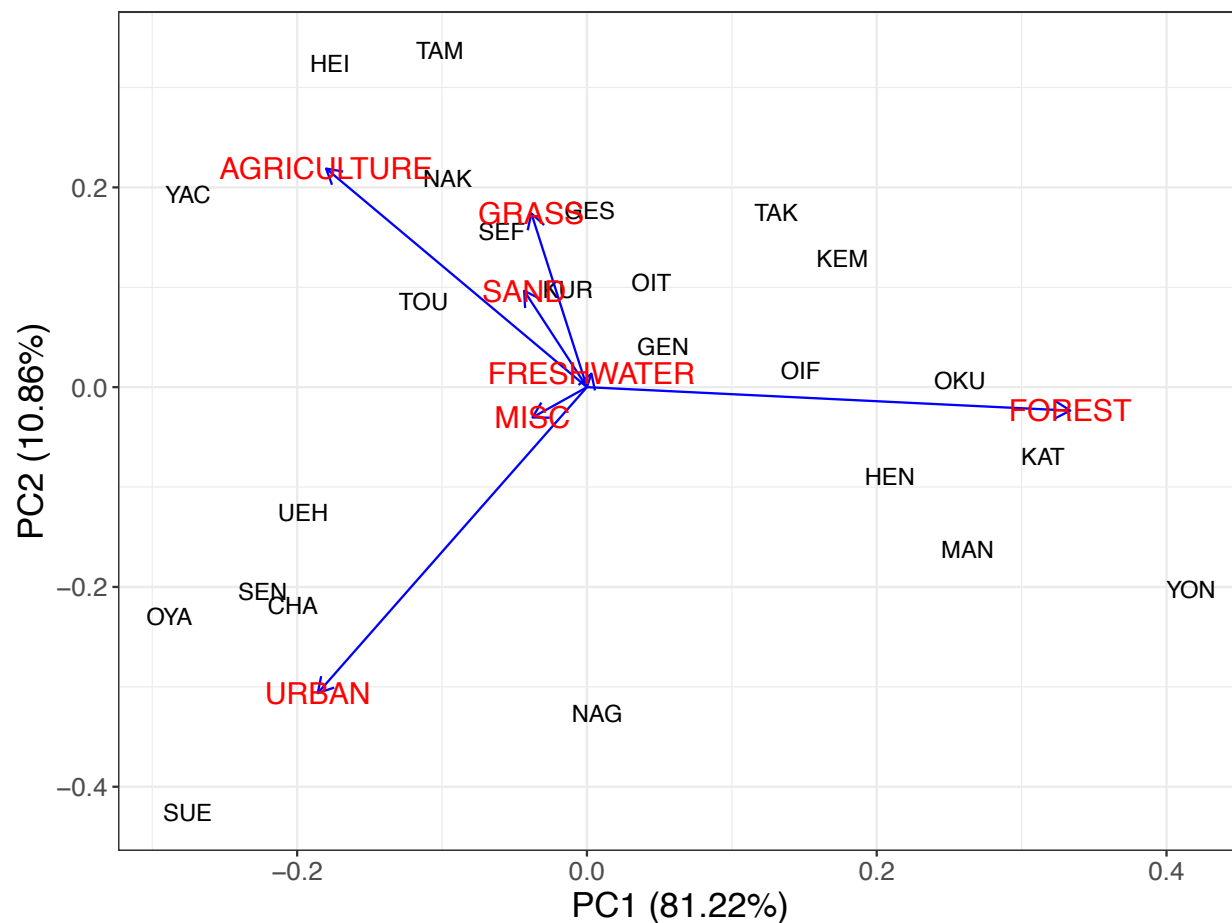
825

826 Figure S2. Biplot of the principal component analysis for the land-cover proportion dataset. PC1
827 explains the main anthropogenic stress gradient (low: more forested, high: more developed),
828 while PC2 explains the rural (high; agriculture and/or grass) to urban (low) gradient.
829
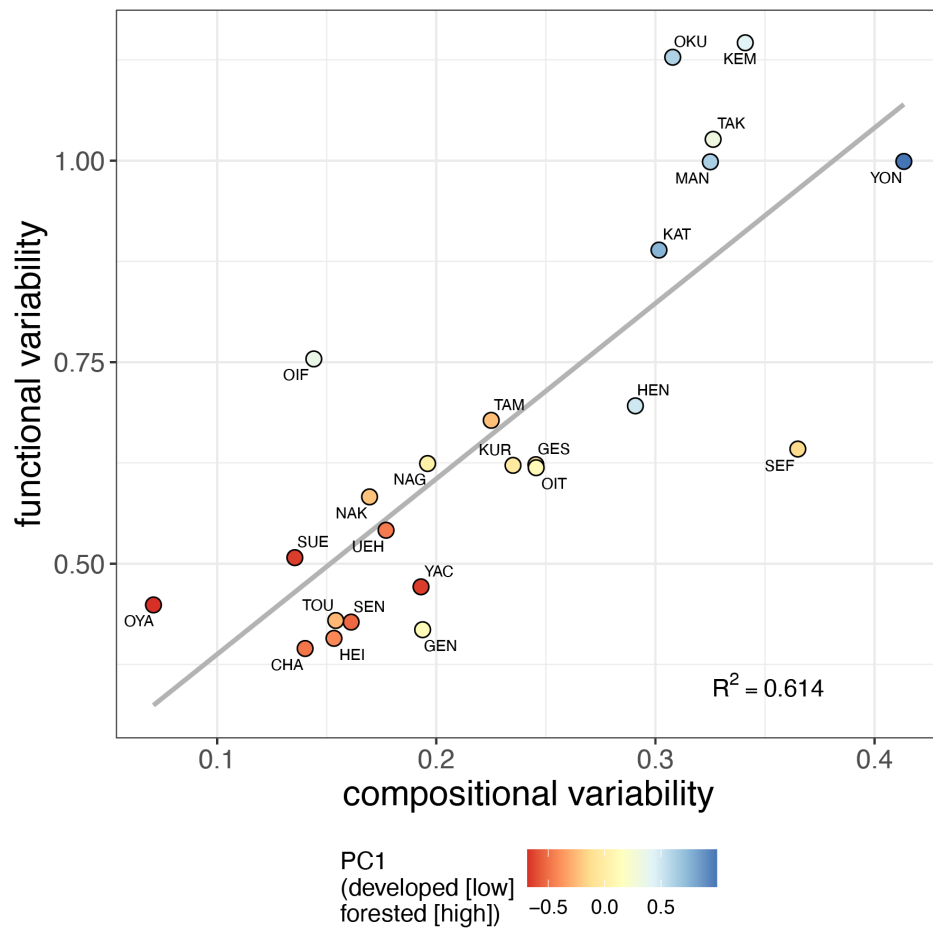
Figure S3. Plot of compositional variability by functional variability, showing the sampling sites with colors corresponding to the forested-developed gradient (PC1), where higher values (blue) are more forested and lower values (red) have more human development. Site abbreviations correspond to those used in Figure 1. The gray line shows the relationship between two variabilities modeled with linear regression.

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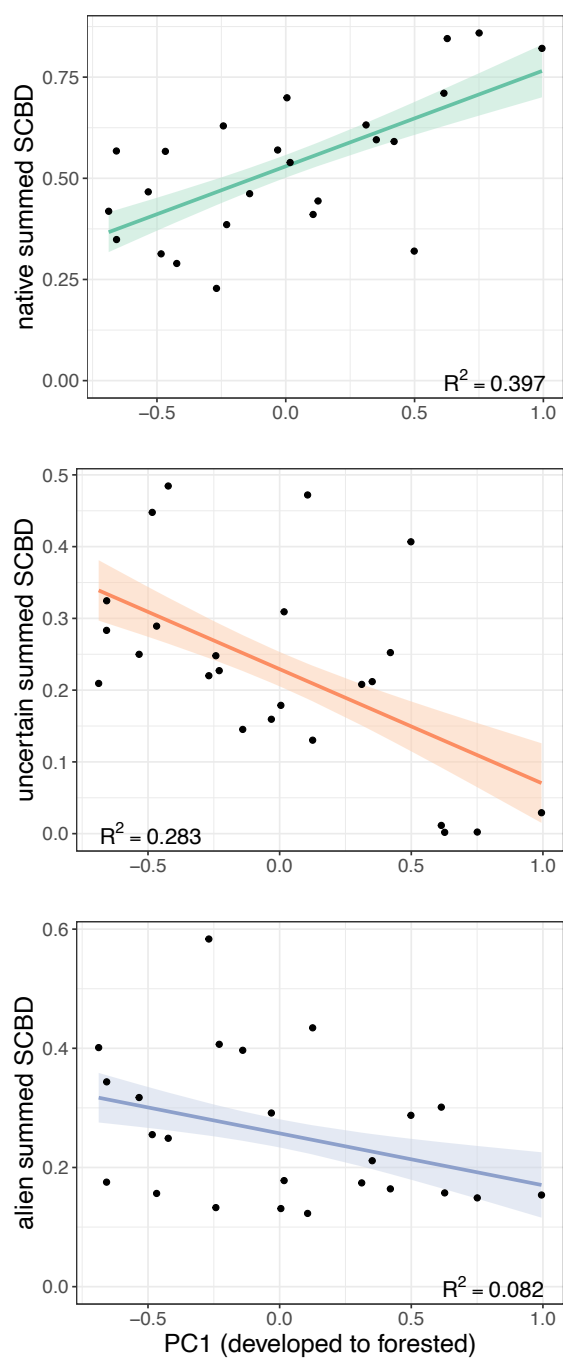
Figure S4. Relationships between PC1 and summed species contributions to beta diversity (SCBD) for native, uncertain, and alien species for the rarefied activity data. PC1 explains the anthropogenic stress gradient (low: more developed, high: more forested).

843
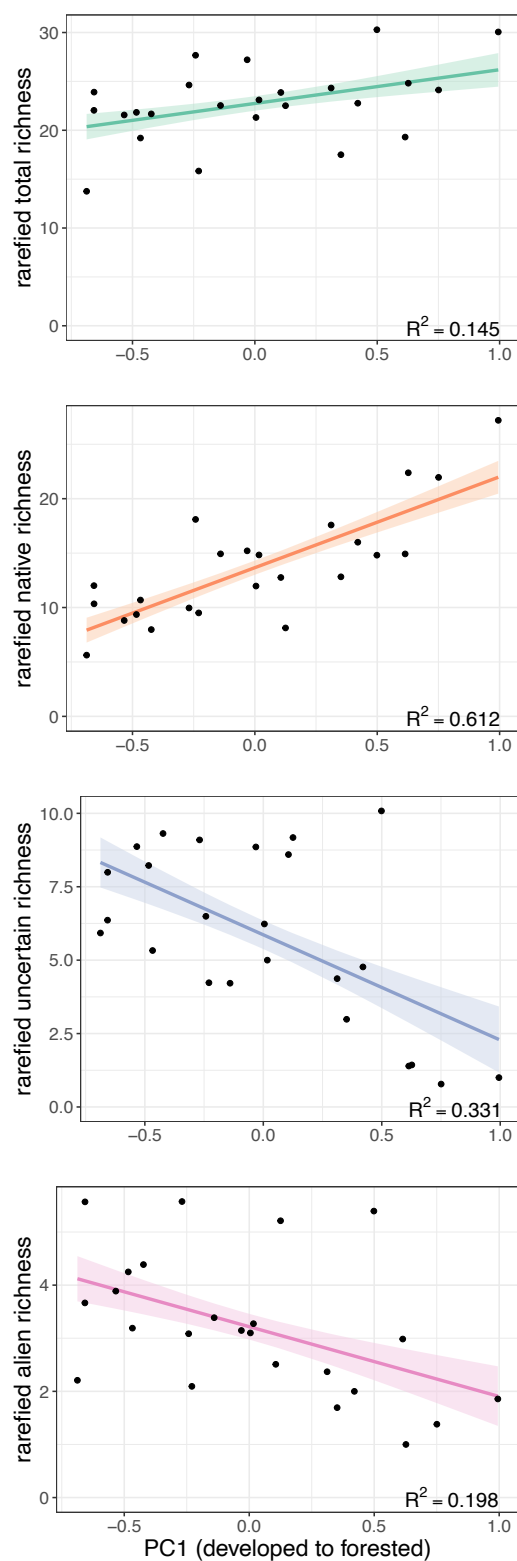
Figure S5. Relationships between PC1 and total richness, as well as richness of native, uncertain, and alien species for the rarefied activity data. PC1 explains the anthropogenic stress gradient (low: more developed, high: more forested).
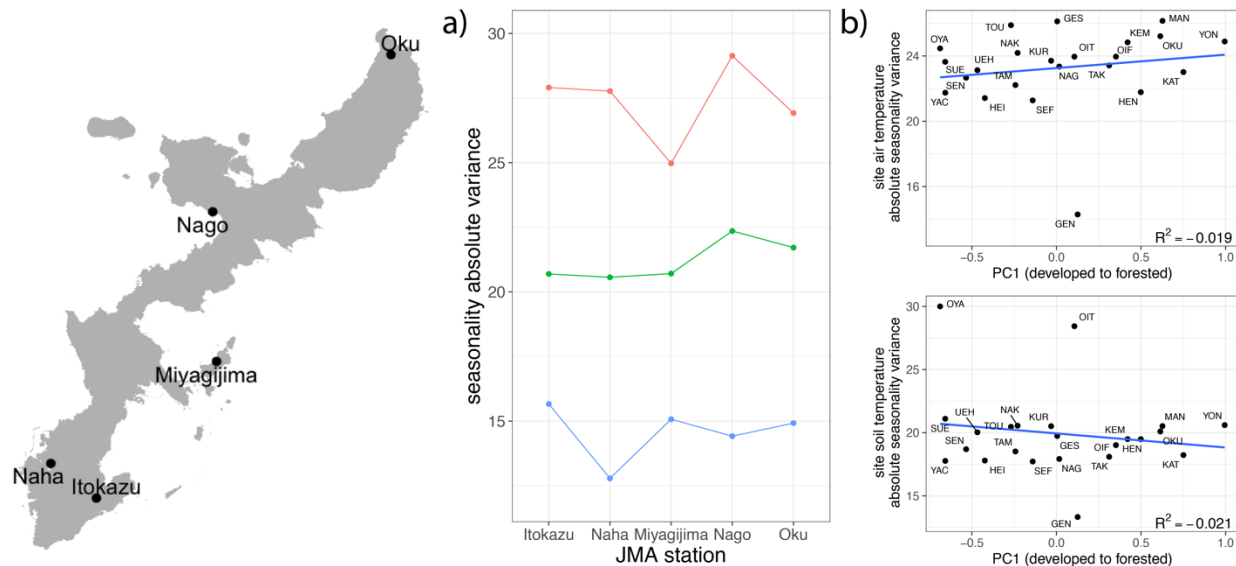
Figure S6. Absolute seasonality variance of temperature at the a) regional and b) site-level scales over the two-year study period (2016 – 2018). Regional temperature measurements were taken from Japanese Meteorological Association weather stations, and station names correspond to those on the map. Site-level temperature measurements were taken for air and soil at one station per sample site. Oyama Park (OYA) and OIST Open (OIT) were the only sites with sensors not located below forest canopy, and thus have higher variance for soil temperature seasonality.

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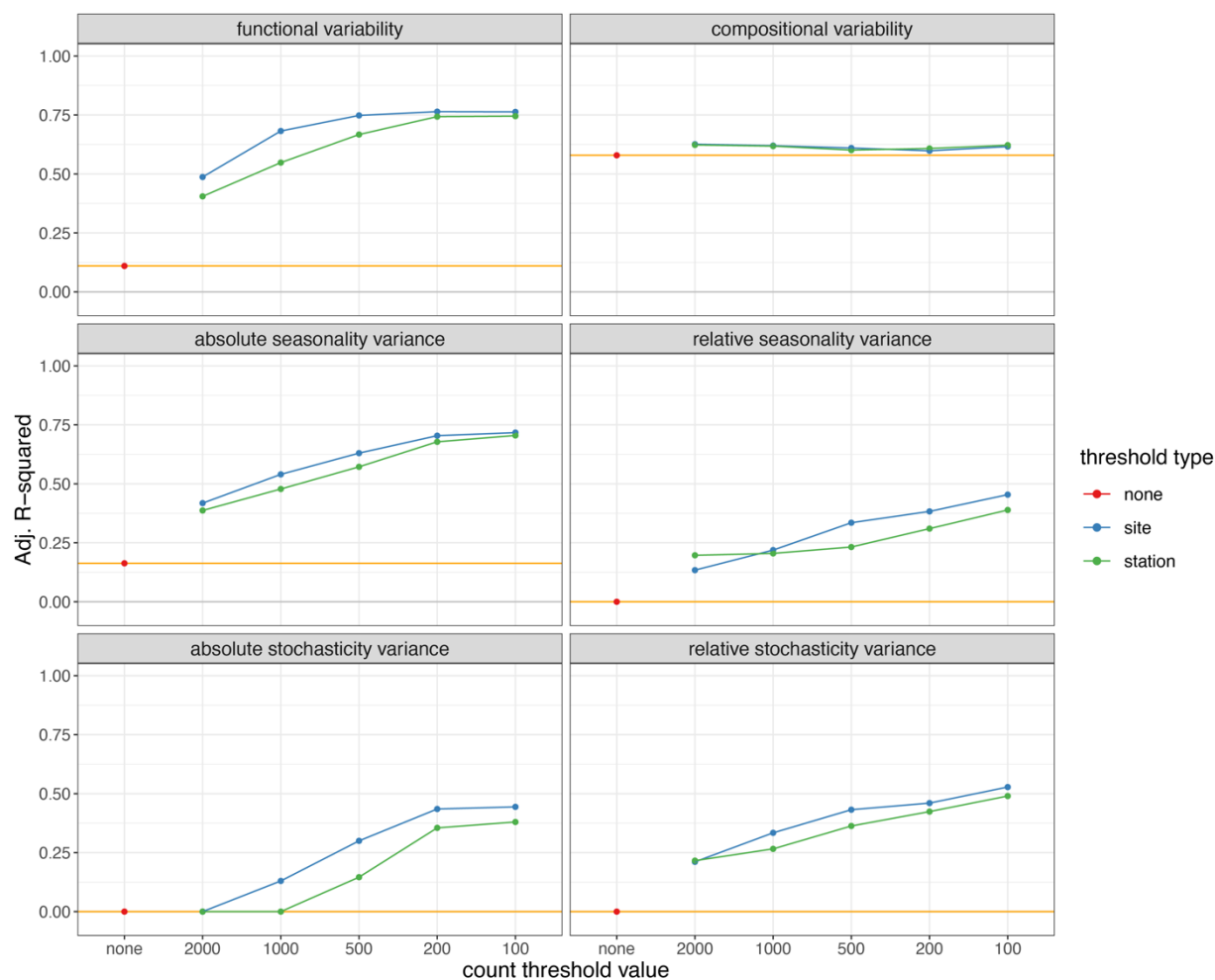
Figure S7. The adjusted R-squared value for the metrics measured in this study at different count thresholds and spatial levels for thresholding (station, site). The threshold value "none" is used as a reference and is symbolized by the red point and orange line. For reference, the analysis described in this paper is a threshold value of 500 at the station level.

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