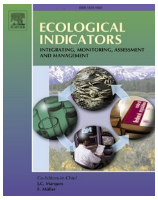
Ecological Indicators 150 (2023) 110243

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Abundance, occurrence and time series: long-term monitoring of social insects in a tropical rainforest

Yves Basset [a,b,c,d,7,*], Philip T. Butterill [b,c,1], David A. Donoso [e,f,2], Greg P. A. Lamarre [a,c,3], Daniel Souto-Vilarós [b,c,4], Filonila Perez [a], Ricardo Bobadilla [a], Yacksecari Lopez [a], José Alejandro Ramírez Silva [a,d,5], Héctor Barrios [d,6]

[a] *ForestGEO, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama*
[b] *Faculty of Science, University of South Bohemia, 370 05 Ceske Budejovice, Czech Republic*
[c] *Biology Centre of the Czech Academy of Sciences, Institute of Entomology, 370 05 Ceske Budejovice, Czech Republic*
[d] *Maestria de Entomologia, Universidad de Panamá, 080814 Panama City, Panama*
[e] *Departamento de Biología, Facultad de Ciencias, Escuela Politécnica Nacional, Quito, Ecuador*
[f] *Centro de Investigación de la Biodiversidad y Cambio Climático, Universidad Tecnológica Indoamérica, Quito, Ecuador*

ARTICLE INFO

Keywords:
Army ant
Formicidae
Orchid bee
Passalidae
Termite
Time series

ABSTRACT

The magnitude of worldwide insect decline is hotly debated, with multiple examples of stable or increasing insect populations. In addition, time series data for tropical insects are scarce, notably in rainforests where insect diversity is poorly known but reaches a peak. Despite social insects (ants, termites, bees and allies) being key organisms in these habitats, long-term monitoring data for these groups are crucially lacking. For many of these insects, the difficulty of locating nests in rainforests could be one reason. In this context, species occurrence in samples is often used as a surrogate for abundance to evaluate species distribution in space/time, but the loss of information is difficult to assess. In a tropical rainforest in Panama, we employed various sampling methods to examine the time series of seven insect assemblages with differing degrees of sociality: termite workers and soldiers, termite alates, bess beetles, litter ant workers, army ant alates, orchid bees, and nocturnal sweat bees. We used five community variables and six models related to occurrence and abundance, to test for significant trends in assemblages over a 13-year period (2009–2021). While assemblages of bess beetles increased, those of termite workers and soldiers, army ant alates, and orchid bees remained relatively stable. Termite alate, litter ant worker, and nocturnal bee assemblages showed signs of decline, demonstrating the need for monitoring distinct assemblages. Significant trends in generalized additive mixed models (GAMM) were observed in three out of five assemblages that could be tested. Our study indicates that trends in assemblages may be more informatively reported with abundance than with occurrence. We recommend (1) monitoring multiple insect assemblages as ecological indicators responsible for diverse ecosystem services; and (2) reporting species richness, changes in faunal composition, occurrence, and, when possible, using time-explicit analyses (such as GAMM models) for evaluating population trends over time.

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* Corresponding author at: ForestGEO, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama.
E-mail address: bassety@si.edu (Y. Basset).

[1] ORCID number: 0000-0002-5554-6591
[2] ORCID number: 0000-0002-3408-1457
[3] ORCID number: 0000-0002-7645-985X
[4] ORCID number: 0000-0002-8803-5173
[5] ORCID number: 0000-0001-6799-5207
[6] ORCID number: 0000-0002-0542-1731
[7] ORCID number: 0000-0002-1942-5717

https://doi.org/10.1016/j.ecolind.2023.110243
Received 21 December 2022; Received in revised form 7 April 2023; Accepted 10 April 2023

1. Introduction

Concerns about worldwide insect decline are growing (Hallmann et al., 2017; Wagner et al., 2021), with possible catastrophic consequences for a variety of ecosystem services (van der Sluijs, 2020). This decline is frequently attributed to a range of factors such as habitat loss and fragmentation, pesticide and light pollution, invasive species and pathogens, as well as climate change and the frequency of extreme climatic anomalies (e.g., Wagner et al. 2021). However, insect decline is not without controversies (Thomas et al., 2019; Schowalter et al., 2021) and some authors have also provided recent and convincing examples of stable or increasing insect populations (e.g., Macgregor et al., 2019: moths in U.K.; Roubik et al., 2021: bees in Panama; Lamarre et al., 2022: tiger moths in Panama). In this context time series for tropical insects are scarce and limited in temporal range (Basset & Lamarre, 2019), particularly in rainforests where most insect diversity is concentrated (Basset et al., 2012). Such time series are urgently needed for a balanced assessment of global insect decline, or lack thereof.

In tropical rainforests, social insects such as ants, termites and bees are responsible for crucial ecosystem services related to the maintenance and regeneration of the forest. Ants represent a large proportion of animal biomass in tropical rainforests and exert formidable predation pressure in this ecosystem (Philpott & Armbrecht, 2006). Likewise, the biomass of termites in tropical rainforests is considerable, as a group of dominant detritivorous invertebrates (Bignell & Eggleton, 2000). The pollination services of bees are also an important component of tropical rainforests (Roubik, 1983). Hence, ants, termites and bees have all been routinely used as ecological indicators of forest fragmentation and/or habitat quality in the Neotropics (e.g., Underwood & Fisher, 2006; Alves et al., 2011; Gonçalves and Faria, 2021), as they are highly abundant, easily sampled, closely connected with ecosystem function, and respond to environmental changes (Lawes et al., 2017). However, these taxa have been infrequently used to indicate long-term temporal disturbance. The long-term monitoring of these social organisms, along with analyses of their potential decline in tropical rainforests should be a scientific priority.

Although the paucity of time series for social insects in tropical rainforests calls for immediate action, it is not clear which variables would be most pertinent and information-rich when reporting time series analyses. Colony census may represent the best estimate of population levels for social insects, especially because the relationship between worker abundance and the number of nests may be valid only for common species (Gotelli et al., 2011). However, accurate censuses of often small and concealed colonies are problematic in tropical rainforests. Accordingly, few long-term data are available for social insects in these forests (Wolda & Roubik, 1986; Roubik, 2001; Dejean et al., 2011; Roubik et al., 2021). Despite a plethora of studies that have recorded the response of ants to management techniques or ecological disturbance (reviewed in Underwood & Fisher, 2006), long-term data on tropical ant populations are scarce (Lamarre et al., 2022). The situation is broadly similar for termites for which population size is often estimated by counting, mapping, or excavating termite mounds (e.g., Josens & Soki, 2010) and, more rarely, by collecting alates at light (e.g., Robello & Martius, 1994). Surveying individual workers and soldiers often appears more feasible than locating and counting nests. Still, since social ants and termites have strongly aggregated distributions, abundance data and estimates of variability may be highly dependent on the distance to the colony and related factors, such as behavior and speed. Hence, species occurrence in samples (i.e., the number of samples in which a species is present) is usually used as a surrogate of species colony abundance (Longino, 2000; Bourguignon et al., 2009; Gotelli et al., 2011).

However, as selected studies indicate, this issue is not universally accepted and may depend on the degree of sociality, the protocol used, the availability of spatial replicates and pseudoreplicates (i.e., temporal replicates), and the caste targeted (Table S1). Depending on these factors, authors may favor either an approach based on occurrence (Longino, 2000; Roisin & Leponce, 2004; Bourguignon et al., 2009; Gotelli et al., 2011) or abundance (e.g., Levings and Franks, 1982; Levings, 1983; Donoso, 2017). Gotelli et al. (2011) stress that in a particular ecological context abundance-related variables may be useful, for example when evaluating the collective ecosystem services that are contributed by a particular species. For the estimation of local diversity, Gotelli et al. (2011) recommend an occurrence-based approach. In another example, Donoso et al. (2022) considered male ant abundance as a surrogate for reproductive investment. Although the choice of abundance- or occurrence-related variables may ultimately depend on the aims of the study (Gotelli et al., 2011), some trends are apparent (Table S1) and can be used to suggest different strategies for analysing abundance or occurrence data (Fig. S1).

First, many studies related to solitary or weakly social insects favour a protocol based on traps with spatial and temporal replicates. In this case, abundance-related variables or models are favoured (Fig. S1), as they may be more sensitive than occurrence-related variables. Abundance data converted to occurrence data may also allow the estimation of species detectability with hierarchical occupancy models (MacKenzie et al., 2003; Dorazio et al., 2006, Kéry, 2011). Second, for true social insects, protocols may target either workers (or soldiers, especially for identification of termite species) or alates. Since the purpose of alates is reproduction and dissemination, they are often easily collected in numbers with different traps (e.g., Malaise, light or flight-interception traps, Table S1). Surveys with traps often include spatial replicates as well as temporal pseudoreplicates, hence may be reported with abundance-related variables. Conversely, protocols used to survey mostly workers may not necessarily include temporal pseudoreplicates (e.g., nest count, transects, plot-based surveys) and may need to report population trends with occurrence-based variables.

In addition, social insects may show two categories of responses over time, which may interact with each other: (1) the number of colonies may fluctuate over time or not; (2) colony size (i.e., the number of workers) may fluctuate over time or not. Because of the difficulty of censusing accurately nests in tropical rainforests over time and the lack of information about colony size, it is difficult to discuss well the interaction between the two categories of responses.

In this contribution, we report significant changes in abundances or occurrences but refrain from discussing whether they are caused by changes in colony number, colony size or both. We also do not consider biomass-related variables, which are estimated with time-consuming protocols (e.g., Dahlsjö et al., 2014). We present relatively long time series (13 years) based on community metrics, abundance, and occurrence of different assemblages of social or subsocial insects, obtained from a tropical rainforest. We are not interested in inferring the drivers of the time series patterns presented here. Rather, our aims are twofold: (1) we use these data to suggest statistical methods adequate for reporting annual censuses of whole assemblages of social insects and of the populations of their common species, especially when censuses of nests are impractical. For assemblages for which these comparisons are possible, we ask whether trends reported by variables/models related to community metrics, occurrence or abundance are similar. (2) We compare the trends observed over time for these assemblages to evaluate whether one or several of them may be useful as ecological indicators. Ultimately, we seek to recommend a set of simple analytical protocols for the analysis of long-term monitoring data for social insects, which represent important ecological indicators in tropical rainforests.

2. Material and methods

2.1. Study site and organisms

Insect data were obtained from Barro Colorado Island in Panama (BCI; 9.15°N, 79.85°W; 120–160 m asl). BCI receives an average annual rainfall of 2,662 mm, with an annual average daily maximum and minimum air temperatures of 31.0 °C and 23.6 °C, respectively (https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado). The 1,542 ha protected island is covered with evergreen wet lowland rainforest and was created around 1910, when the Chagres River was dammed to fill the Panama Canal. Insects were collected within and near the 50 ha ForestGEO plot, which is thoroughly described in Anderson-Teixeira et al. (2015). Social or near-social insects monitored on BCI included (Table 1): alates, workers and soldiers of Isoptera (termites), Passalidae (bess beetles), nocturnal Halictidae (sweat-bees), Euglossini (orchid bees), alates of the Dorylinae genera *Eciton*, *Labidus*, *Neivamymex* and *Nomamyrmex* (army ants), and workers of litter ants (Formicidae). While Isoptera and Formicidae are eusocial or hypersocial insects (Table S1), Passalidae are subsocial (Alencar *et al.*, 2022). Nocturnal sweat-bees of the genus *Megalopta* (Halictidae) collected in Panama have a facultatively social behavior (Arneson & Wcislo, 2003), while euglossine bees censused by baits may be solitary, communal, or quasisocial (Michener, 1974).

2.2. Insect protocols and datasets

Our protocols targeted specific insect assemblages in the understory (Table 1). All protocols were performed at 10 independent locations (spaced by at least 300 m) within and near the ForestGEO permanent plot, with an equal number of spatial and temporal replicates each year (Table 1). Details on locations and analyses of spatial pseudoreplication are provided elsewhere (Basset et al., 2013). Protocols to collect the focal assemblages used standard methods in entomology and are detailed in Appendix S1. All insect protocols spanned 13 years (2009–2021) and their scope in terms of individuals and species collected are indicated in Table 1. All specimens collected were identified and vouchered within the reference collections of the ForestGEO Arthropod Initiative at the Smithsonian Tropical Research Institute in Panama. Additionally, DNA Cytochrome *c* oxidase subunit I (COI, "DNA barcode") sequences were obtained from ForestGEO specimens collected on BCI. Specimens were sequenced at the Biodiversity Institute of Ontario, University of Guelph. Sequences were deposited in the project BCIAR of the database of the Barcode of Life Data System (https://www.barcodinglife.org/index.php). Molecular data were used to confirm identifications based on morphology and to examine the possible occurrence of cryptic species.

Table 1
Summary of datasets used in analyses, ordered by assemblages, sites and protocols, along with the number of individuals and species collected. All datasets cover 13 years (2009–2021). Replicates = number of replicates per year, s = spatial, t = temporal.

Assemblage (cast)	Protocol	No. samples per year	No. individuals	No. species	Replicates
Weakly social					
Passalidae	Light trap	80	1218	12	s = 10,t = 4
Halictidae	Light trap	80	9194	6	s = 10,t = 4
Euglossini	Cineole bait	40	57,199	24	s = 10,t = 4
Eusocial or hypersocial					
Isoptera (alates)	Light trap	80	29,335	28	s = 10,t = 4
Isoptera (workers)	Transect	40	4762*	27	none
Dorylinae (alates)	Light trap	80	7552	13	s = 10,t = 4
Formicidae (workers)	Winkler	50	17,114	142	s = 10

* Indicative only as no effort was made to optimize collection of workers and soldiers in quadrats.

2.3. Statistical methods

In this contribution we do not consider analyses for individual species but rather for whole assemblages, including community metrics, occurrence and abundance. A wide range of techniques have been used to model insect abundance over time such as, for example, least square regressions (e.g., Roubik et al., 2021), loglinear Poisson regression models (e.g., Van Swaay & van Strien, 2005), generalized linear mixed models (GLMM; e.g., Aldercotte *et al.*, 2021; Ohyama and Redak, 2022) or generalized additive mixed models (GAMM; e.g., Bell et al., 2020; Gardiner & Didham, 2020). To evaluate the consistency of trends for one assemblage, we selected 11 variables/models (identified by numbers below) and for each of them tested whether trends existed over the study period towards decline, increase or stability. We consider three categories of variables/models over the study period: community metrics, and variables related to occurrence/occupancy and abundance. The first category includes data collected at the species level, whereas the two other categories only include data relevant to the whole of assemblages. However, the latter are perfectly applicable for analysing the population dynamics of common species. Analyses were performed with the software R (R Development Core Team, 2022) and all packages and functions used are indicated in Appendix S1, along with other details.

2.3.1. Community variables

(a) We first calculated the observed species richness as well as mean species richness per sample over the study period (i.e., mean species richness per location and survey). (b) Second, we estimated species turnover (appearance, disappearance and total turnover) over years, as well as (c) mean rank shifts, which is a measure of the relative change in species rank abundances and indicates shifts in relative abundances over time (Collins et al., 2008). (d) We also calculated the rate of community change over successive time intervals. This is the slope of the differences in species composition within a community over increasing time intervals, and it provides a measure of the rate of directional change in community composition (Collins et al., 2000). (e) Last, we computed a Nonmetric Multidimensional Scaling (NMDS) ordination where the abundance of species was ordered by years (samples) and the similarity between years was calculated with the Bray-Curtis distance.

2.3.2. Variables related to occurrence and occupancy

(f) We first calculated the occurrence of assemblages over the study years. Since the total number of samples is fixed per year (Table 1), the proportion of occurrence may theoretically reach 1.0 in years of abnormally high population levels, thus impeding the resolution of monitoring. Hence, we reported occurrence with alpha = 1 (samples with at least 1 individual) and alpha = 5 (samples with at least 5 individuals). (g) Second, we calculated an asymptotic estimator of "true" occurrence. We used the matrix of occurrence of assemblages in samples and calculated a sample-based estimation of occurrence (estimated occurrence, Chao et al., 2014).

(h) We computed hierarchical Bayesian site-occupancy models. In the field observers or traps may overlook any species, and consequently the probability p of species detection is often < 1. Therefore "true" species occupancy is underestimated and nearly always > naive species occupancy (Kéry, 2011). If pseudoreplicates are available, they can be used with zero-inflated binomial models ("site occupancy models") to estimate true species distribution and its confidence limits, as opposed to apparent species distribution (MacKenzie et al., 2003; Dorazio et al., 2006). We report the detection probability, the probability of finding a species at time t if it is present at site i (Fiske & Chandler, 2011), in contrast to species occurrence which is the proportion of samples occupied. We built 7 dynamic (multi-season) occupancy models (MacKenzie et al., 2003; details in Appendix S1). Goodness-of-fit of the models were estimated by a bootstrapping procedure and Chi-square tests, and the best model was selected according to the lowest Akaike Information Criterion (AIC).

2.3.3. Variables and models related to abundance

(i) We first considered the mean abundance per location (10 sites), survey (4 surveys per year) and year (13 years) as time series for each taxon. Along with mean abundance, we also plotted a locally estimated scatterplot smoothing (loess) to help assessing visually trends over the study period. (j) Next, we used the package rtrim ("Trends and Indices for Monitoring Data", TRIM; Bogaart et al., 2020). TRIM models have been widely used for estimating growth and decline of animal populations based on (possibly sparsely available) count data (Van Strien et al., 2004). TRIM computes four loglinear Poisson regression models to estimate population totals over time, based on a set of counts at n sites and during m years. A Chi-squared test was used as goodness-of-fit measure (details about models in Van Strien et al., 2004; Bogaart et al., 2020; Appendix S1). (k) Last, we built Generalized Additive Mixed Models (GAMMs; Wood, 2017). GAMM models may incorporate nonlinearity and temporal autocorrelation of responses across years and with varying seasonal phenology (Wood, 2017). We considered six competitive models and selected the best one with the lowest AIC (details in Appendix S1). Goodness-of-fit of the models were also estimated by an Analysis of variance (ANOVA).

For each assemblage, we also detailed the identity of the dominant species and the Berger-Parker index of dominance (Berger & Parker, 1970). Variables and models were calculated for all assemblages but, because of lack of spatial or temporal replicates, mean abundance and TRIM could not be estimated for termite workers, and occupancy and GAMM models could not be estimated for both termite and ant workers (Fig. S1). We used a modified non-parametric Mann-Kendall trend test (Mann, 1945; Kendall, 1975) with the sieve-bootstrap enhancement for potentially autocorrelated data to evaluate consistently increasing or decreasing (monotonic) trends over the study years. For variables/models (i) and (k), which included ≥ 30 data points, we further performed a WAVK trend test (Lyubchich et al., 2013) with the sieve-bootstrap enhancement to test for any trend (monotonic or non-monotonic) over the study period. Significant trends were evaluated visually as being increasing or decreasing with lowess regression (locally weighted scatterplot smoothing). Eventually we also report the % change for all assemblages and variables such as species richness, occurrence and abundance, comparing the baseline year (2009) with 2021.

3. Results

Our various datasets included 126,374 individuals representing 252 species (Table 1). Plots of variables and models over time for representative assemblages are detailed in Figs. 1-4 (bess beetles, ant workers, termite workers and alates, respectively). Plots for other assemblages are in supplementary Fig. S2-4 (sweat bees, orchid bees and army ant alates, respectively). Results of trend tests for all variables and models are summarized in Table 2, and results of the best occupancy, TRIM and GAMM models in Tables S2 to S4. Table 3 also indicates the percent change in different variables in 2021 as compared to the base year (2009), for each assemblage.

3.1. Comparisons of models and variables

Regarding community variables, the only clear indication of a significant trend in our 13-year datasets concerned species richness and community change for Passalidae and mean rank shift for workers of Formicidae (Table 2). Variables related to occurrence were the least sensitive to changes, and rarely exhibited a significant trend (occurrence for Passalidae, Table 2). For most assemblages, but Passalidae and Halictidae, estimated occurrence was not useful since it indicated that all samples would be occupied. This pattern was broadly similar for occupancy models. More significant trends were recovered for variable and models related to abundance (mean abundance, TRIM and GAMM models), although this mainly concerned GAMM models (Table 2). TRIM models, with no significant results, were the least prone to show changes in time (Table 2). Contrasting occurrence vs abundance variables/models (Table 2), indicated that abundance data modeled with GAMM were more likely to recover a significant trend than could occurrence variables. The few significant trends recovered overall contrast with the percentage difference between year 2021 and the base year, which were often substantial (Table 3).

3.2. Comparisons of trends in assemblages

Over the study period, Passalidae (Fig. 1) showed significant increasing trends in species richness, community change, occurrence, and GAMM model. This was reflected by often strong differences in various variables between the base year and 2021 (Table 3). Overall, this suggests an increase in passalid population during the study period. Mean rank shifts and mean abundance for ant workers decreased significantly (Fig. 2, Table 2; WAVK test). The drop in ant abundance appeared to be sharper during the period 2017–2021. A GAMM model could not be fitted because of lack of temporal replicates within years. Percentage differences for ants between the base year and year 2021 were mostly negative (Table 3). No significant trends were observed for the variables recorded for termite workers and soldiers, in the absence of variables and models accounting for abundance (Fig. 3, Table 2). We noted a drop in mean species richness, reflected by a negative difference between the base year and 2021 (Table 3). Although the abundance of termite alates modeled by a GAMM model indicated a significant decreasing trend, the model itself had a very low R^2 (0.004) and was not significant (Fig. 4, Table 2). Trends of variables/models were also not significant over the study period for Halictidae (Fig. S2, Table 2), except for the GAMM model, indicating a significant decreasing trend (WAVK test). No significant trends were detected for variables and models with orchid bee data (Fig. S3, Table 2). Eventually no significant trend existed for variables and models for army ant alates, except for the values of the first axis of the NMDS (Fig. S4, Table 2).

4. Discussion

As far as we know, this study represents one of the first datasets to include relatively long-term monitoring data (13 years) for various assemblages of social insects ($n = 7$) at a single rainforest location in the tropics. We analyzed the data at the community level to compare trends of assemblages over time and evaluate whether one or several of them may be useful as ecological indicators. While the variables and models considered here can easily be calculated at the species level, we refrained from doing so due to the large number of species ($n = 252$). To maximize interpretation, further analyses at the level of species should consider each assemblage separately, assign species to functional groups and interpret trends in time series of functional groups (e.g., Basset et al., 2017). However, this goes beyond the scope of this contribution.

4.1. Methodological considerations and statistical models

Nest censuses (counting colonies) yield ideal data with which to evaluate the population dynamics of social insects (e.g., Levings & Franks, 1982; Roubik, 1983; Dejean et al., 2011), but this sampling method is impractical for most termite and ant species in tropical rainforests. In preference, we obtained statistical estimates of occurrence and abundance from specific protocols targeting specific assemblages (light traps, cineole baits, Winkler, quadrats). Other methods are available and may be more efficient depending on whether taxa may be epigeic or hypogeic (Table S1). Pitfall traps may be used effectively to monitor ant workers over time (Donoso, 2017), and pseudoreplicates (temporal replicates) can be included in abundance models such as

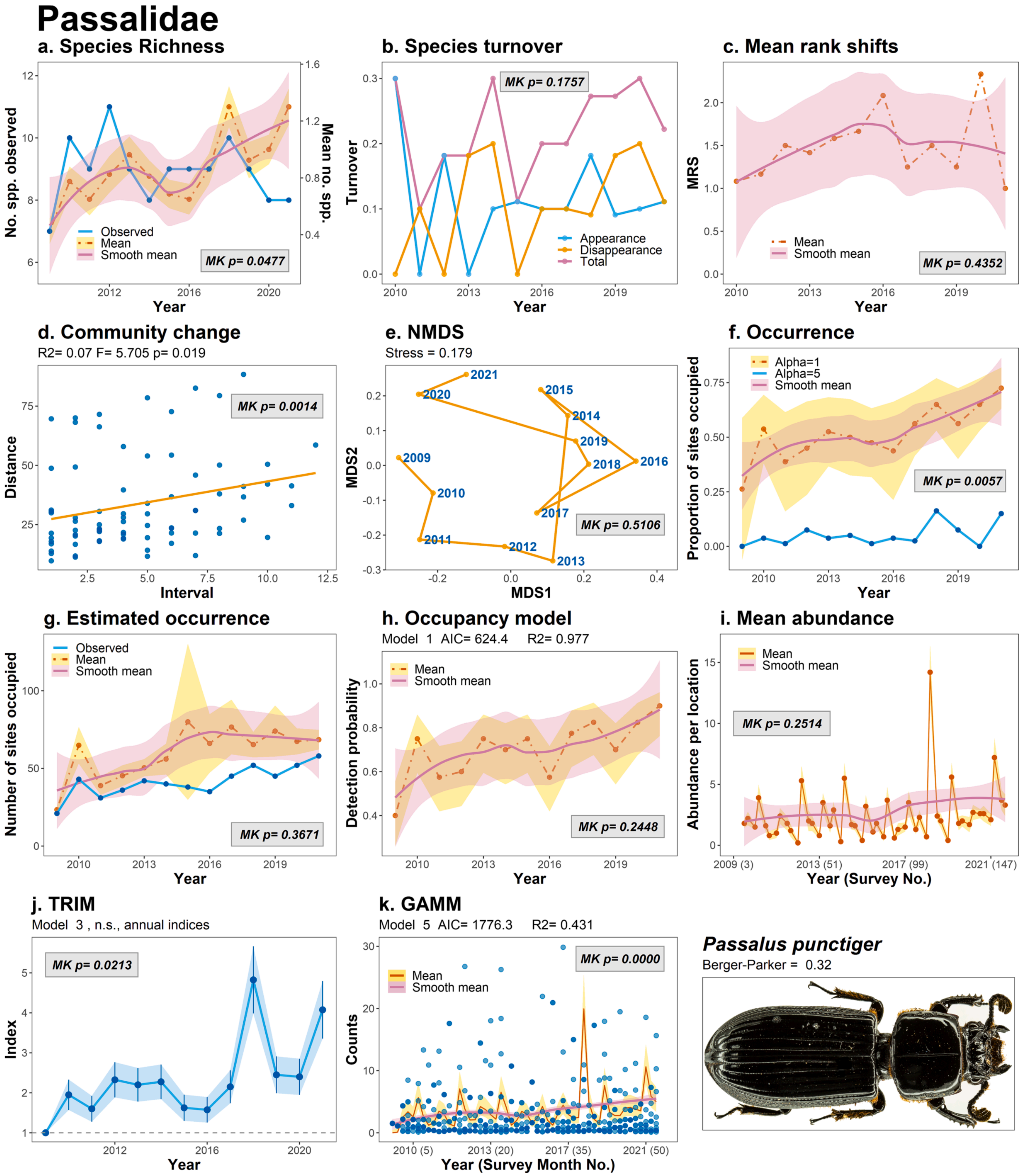

Fig. 1. Time series 2009–2021 for bess beetles, an assemblage collected with light traps, including spatial and temporal replicates. (a)-(e) community variables; (f)-(g) variables related to occurrence; (h)-(k) variables and models related to abundance; (l) dominant species in the assemblage (photo by Francisco Serrano). Pink ribbons denote lowess regressions for visualization of the main variable, plotted in red. For the GAMM, residuals are plotted across all sites. MK = modified Mann-Kendall trend test. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

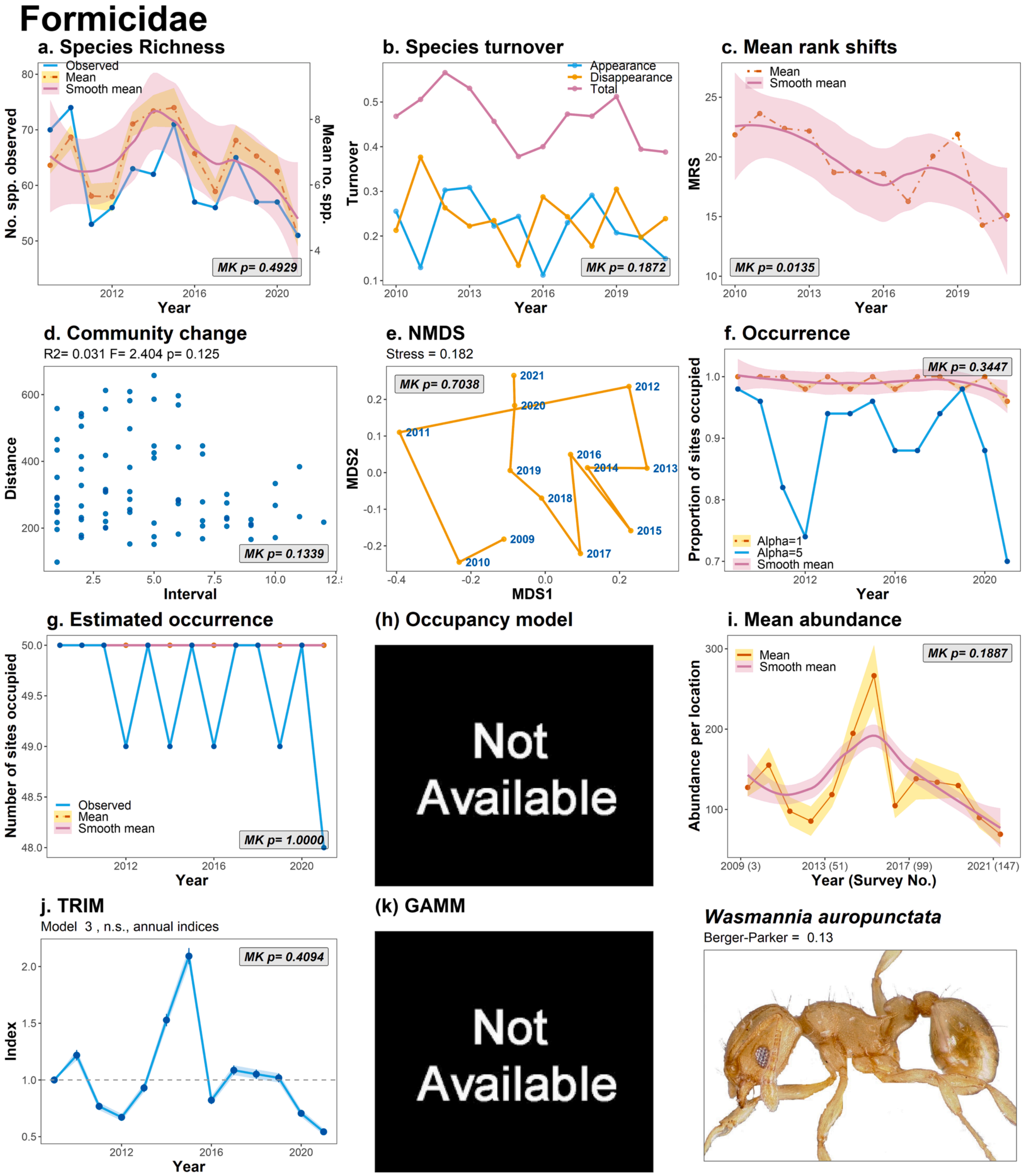

Fig. 2. Time series 2009–2021 for litter ant workers, an assemblage collected with Winkler, including spatial replicates but no temporal replicates. Presentation follows Fig. 1. *Wasmannia auropunctata*: photo by April Nobile, AntWeb, https://www.antweb.org.

GAMM. The only drawback is that pitfall traps collect a smaller proportion of local litter ant assemblages than Winkler does (Bestelmeyer et al., 2000), often the larger and more mobile species (Donoso & Ramón 2009).

Over the study period, community variables for most assemblages were stable, except for species richness, community change for Passalidae, and mean rank shifts for ant workers. When comparing arthropod assemblages along disturbance gradients, community variables such as species richness have often been considered less discriminating than abundance (e.g., Basset et al., 2008). Our data confirm this when

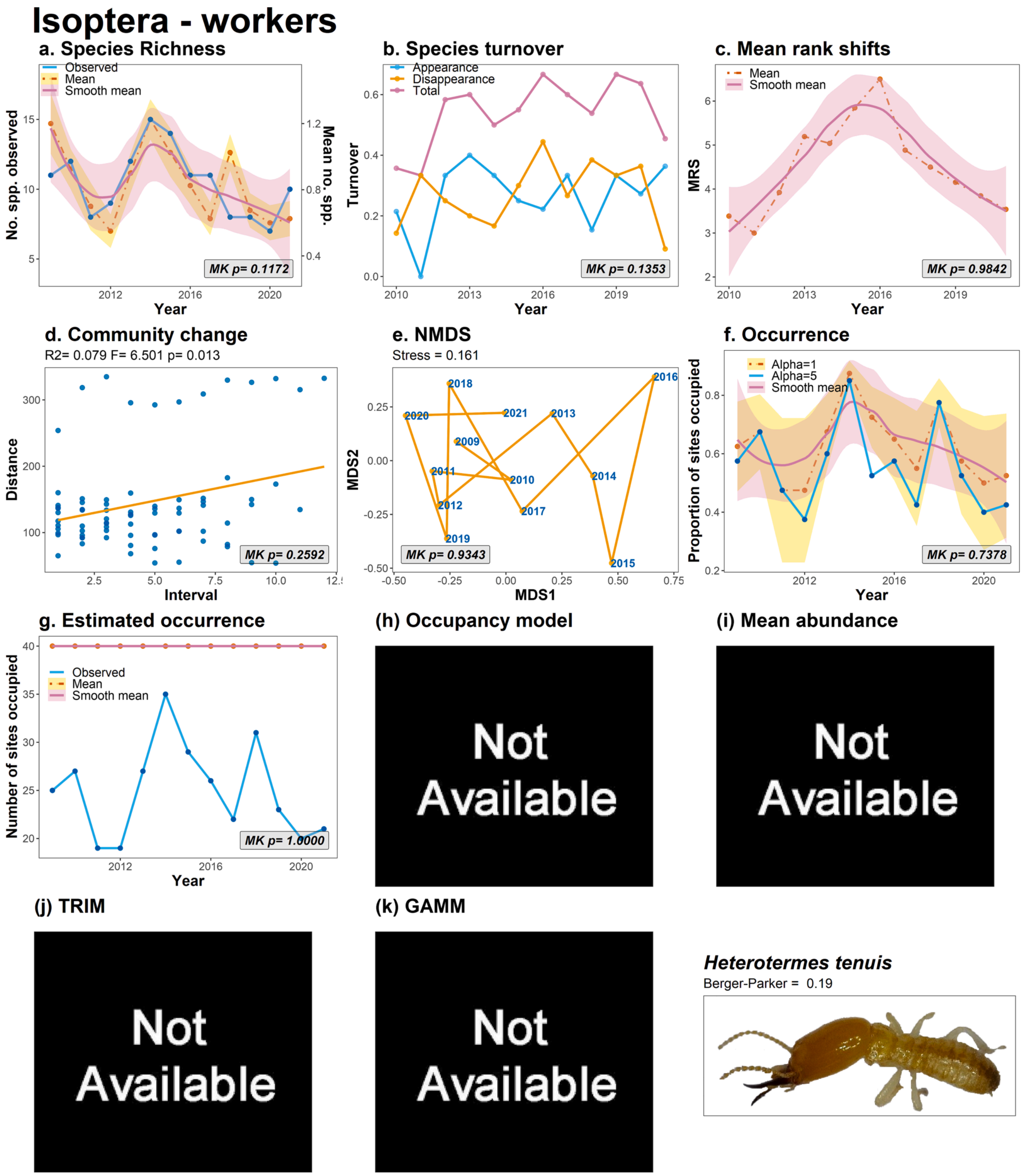

Fig. 3. Time series 2009–2021 for termite workers and soldiers, an assemblage collected with transects without spatial and temporal replicates. Presentation follows Fig. 1. Heterotermes tenuis: photo © ForestGEO Arthropod Initiative.

comparing insect assemblages over time. Species turnover, mean rank shifts, and the rate of community change often varied considerably over the study period (especially for ant and termite workers), but monotonic trends were mostly not significant. Further, there was no obvious indication for any assemblage that the disappearance rate in species turnover increased towards the latter years of the study period. Similarly, Donoso (2017) concluded that, despite considerable variation in the community variables of an assemblage of rainforest litter ants in Ecuador, the temporal dynamics of the assemblage were mostly stable. The NMDS results, representing faunal similarity between years, were

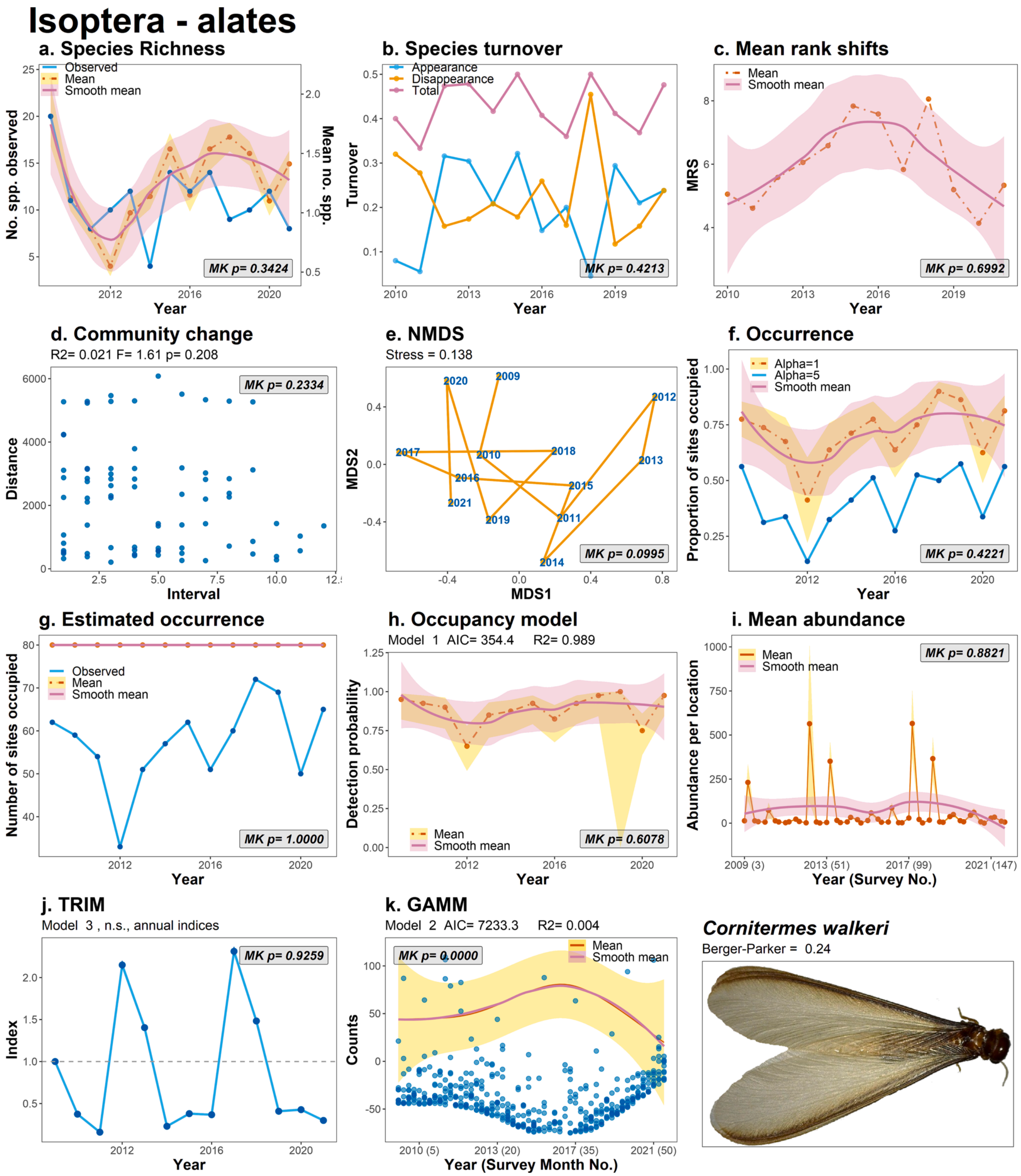

Fig. 4. Time series 2009–2021 for termite alates, an assemblage collected with light traps, including spatial and temporal replicates. Presentation follows Fig. 1. *Cornitermnes walkeri*: photo © ForestGEO Arthropod Initiative.

presented here in the form of visual summaries.

The ecological interest in reporting occurrence within samples clearly depends on whether data are reported at the species level or higher resolution (such as here), the taxa themselves, the affinity of taxa for the sampling method, and the number of samples collected. In the conditions of our study, occurrence proved to be very informative for Passalidae collected at light (average yearly occurrence < 0.50), informative for termite workers collected in quadrats, termite alates, and army ant alates collected at light (occurrence 0.50–0.80), less informative for Halictidae collected at light (occurrence > 0.80), and practically

Table 2
Results of trend tests (p-values) for different variables and models. Unless indicated by "WAVK" (WAVK test), results refer to Man-Kendall tests corrected for potential autocorrelation. For significant trends (in bold), "+" and "-" denotes increasing and decreasing trends, respectively.

Variable/model/test	Passalidae	Halictidae	Euglossini	Isoptera-alates	Isoptera-workers	Dorylinae-alates	Formicidae-workers
i) Community variables							
Mean species richness	**0.0478** +	0.246	0.706	0.342	0.117	0.808	0.493
Total species turnover	0.176	0.439	1.0000	0.421	0.135	0.079	0.187
Mean rank shifts	0.435	0.378	0.257	0.699	0.984	0.155	**0.014 -**
Community change	**0.014** +	0.646	0.384	0.233	0.259	0.757	0.134
NMDS	0.511	1.000	0.157	0.096	0.934	**0.028** +	0.704
ii) Occurrence and occupancy							
Occurrence (alpha = 1)	**0.006** +	0.157	1.000	0.422	0.738	0.951	0.345 (2)
Estimated occurrence	0.367	0.480	1.000	1.000	1.000	1.000	1.000
Occupancy model	0.245	0.190	1.000	0.608	NA	0.521	NA
iii) Abundance							
Mean abundance	0.251	0.468	0.631	0.882	NA	0.756	0.189
Mean abundance -WAVK	0.528	0.117	0.933	0.407	NA	0.629	**<0.0001 -**
TRIM	0.021 (1)	1.000 (1)	0.041 (1)	0.923 (1)	NA	0.734 (1)	0.409 (1)
GAMM	**<0.0001** +	0.099	0.279	**<0.0001 –** (1)	NA	0.405	NA
GAMM - WAVK	**<0.0001** +	**<0.0001 -**	0.663	**<0.0001 –** (1)	NA	0.300	NA

(1) Model not significant.
(2) Calculated with alpha = 5 since alpha = 1 values all close to 1.

Table 3
Percent change in different variables for year 2021 as compared to the base year (2009), detailed by assemblage. SR = species richness, Occ = occurrence, Ab = abundance.

Assemblage	SR	Mean SR	Occ	True Occ	Mean Ab
Passalidae	+14	+206	+176	+192	+104
Halictidae	0	−19	–22	−29	−55
Euglossini	−20	+6	0	0	+79
Isoptera-alates	−60	−22	+5	0	−70
Isoptera-workers	−9	−48	−16	0	NA
Dorylinae-alates	−11	−27	−5	0	+1
Formicidae-workers	−27	–32	−4	0	−46

meaningless for ant workers in Winkler samples and baited orchid bees (occurrence near 1.0). However, occurrence may be far more informative when data are reported at the species level and when many samples are available. Didham et al. (2020) proposed that occurrence data may represent the logical target for citizen science monitoring. We agree, but only when species can be easily identified. At the level of assemblages, occurrence data reported with alpha = 5 individuals largely paralleled data reported with alpha = 1 individual but may nevertheless be useful at the species level. On the other hand, estimated occurrence does not appear very informative unless a very large number of spatial replicates are available.

A variety of variables and methods can be used to model abundance. Here, we considered Bayesian site-occupancy, mean abundance over spatial replicates with loess regression, TRIM, GAM and GAMM models. In addition to spatial replicates, site-occupancy and GAMM models also require temporal replicates within study years. Bayesian site-occupancy models could not be fitted to ant workers in Winkler samples because temporal replicates are impossible to obtain from identical locations, since the litter needs to be harvested for extraction. Moreover, these models were difficult to implement because of our relatively low number of spatial replicates (Welsh et al., 2013). Significant trends over the study period were not recorded with mean abundance, except for ant workers. However, the loess regression allowed us to conveniently visualize the overall data. Although trends over annual indices computed with TRIM models were sometimes significant, none of the models themselves were significant. Linear models such as TRIM may represent a good fit for long time series of bird abundance (Van Strien et al., 2004) but they are clearly not useful for short insect time series, which may vary substantially within years.

Significant trends in GAMM models were observed in three out of five assemblages tested. Since percentage changes in abundance in 2021 relative to the baseline year were not trivial for these assemblages, we conclude that GAMM models, if they can be fitted to the data, provide an efficient way to summarize data and trends over the study years. However, we note that because of the high variation in insect abundance within and among years, changes in abundance between the baseline year and later years may often be apparently spectacular without necessarily being mirrored by a significant increasing or declining trend (Didham et al., 2020; Aldercotte et al., 2022).

4.2. *Trends over time of assemblages*

BCI is a protected area since 1923, embedded into the larger 12,000 ha Parque Soberania in the Panama Canal Watershed (Anderson-Teixeira et al., 2015). As such the island is buffered against some of the main threats to insect populations, such as habitat loss, insecticide and light pollution, but not immune to the effects of climate change. Since 1981 BCI has experienced an increase of 0.36 °C in mean annual temperature and a 17.9 % increase in mean annual precipitation (Anderson-Teixeira et al., 2015). A moderate increase in temperature and rainfall may benefit insect populations, such as tropical ants (Donoso et al., 2022), but only up to a certain point (Deutsch et al., 2008). Thus, for the study period considered, we should not be surprised that none of our insect time series on BCI indicated drastic decline. However, this does not preclude future changes in the population dynamics of the assemblages studied.

As compared to solitary insects, eusocial insects may have a higher buffering capacity for mitigating changes in environmental conditions, since they can wait out dangerous temperatures in their nest (Kaspari et al., 2015). In support of this, the Passalidae, which can be considered the least social of the assemblages studied (Alencar *et al.*, 2022) and hence with the least buffering capacity and high propensity to variation in population dynamics, exhibited a series of significant trends suggesting an increase in population. This may be related to increasing air temperatures and the activity of adults. Recent time series for solitary insects on BCI likewise indicated stable populations (Reduviidae: Lucas et al., 2016) with very few species declining (Arctiinae: Lamarre et al., 2022), or slightly increasing populations for species assigned to particular functional groups (Saturniidae: Basset et al., 2017). This further suggests that, to date, increasing air temperatures on BCI have not yet risen above critical temperatures for tropical ectotherms (Deutsch et al., 2008).

The assemblage of termite workers did not show any significant trend over the study period, but models related to abundance could not be fitted to these data. The GAMM model for termite alates suggested a decrease in abundance in later years. Future monitoring data may indicate whether this translates into a population decrease for termite workers and, similarly, for ant workers. The assemblage of orchid bees appeared to be stable during the study period, largely concurrent with the conclusions of Roubik et al. (2021) in the Canal Zone of Panama. Many of the loess curves for Halictidae appear superficially similar to those of orchid bees. Still, sweat bees exhibited a decreasing trend, perhaps indicating a lower resilience to climate change than orchid bees. Although divergences in the trends of assemblages occurred, it is difficult to interpret them without analyses at the level of species, further assigned to functional groups (e.g., Basset et al., 2017). This issue is beyond the scope of this study.

4.3. Ecological indicators

Insects have often been used as ecological indicators of spatial changes, such as forest fragmentation or land use conversion (e.g., Underwood & Fisher, 2006). Owing to short generation times, they should be also used as indicators of change over time. How do we judge which of the 7 assemblages examined could be considered the best ecological indicator of temporal changes in this relatively undisturbed rainforest? Many authors have reviewed and discussed the criteria that make insects good ecological indicators. These can be summarized as i) a well-known taxonomy and biology, ii) an important role in ecosystem functioning, iii) ease of collection and study, iv) a broad geographical distribution, v) specialized biology, and vi) being of potential economic importance (Gonçalves and Faria, 2021). All these criteria are, to some extent, satisfied by our focal assemblages, with the exception that economic importance is only relevant to orchid and sweat bees via pollination services. As best ecological indicators, we would be inclined to select passalids, termite alates, and worker ants, which showed to some extent trends over the study years. Other assemblages may be at a disadvantage in this regard: orchid bees and *Megalopta* are limited to the Neotropics, protocols are difficult to adapt to termite workers to measure abundance, and army ant alates showed no significant trend over the study period. However, all the assemblages in our study have merit as ecological indicators, since they represent complementary ecological services, such as pollination, decomposition, and predation. Hence, we recommend considering assemblages of ecological indicators that reflect a variety of life histories and are responsible for a diversity of ecosystem services.

4.4. Conclusions

Insect monitoring data are often reported at a low-resolution level or even as biomass (orders or families, e.g., Hallmann et al., 2017; Macgregor et al., 2019). This results from high diversity and complexity of assemblages and the relative lack of interest in insect data at higher resolution (Basset & Lamarre, 2019). Our study indicates that trends in assemblages may be more informatively reported with abundance than with occurrence. Further, species-level data can be reported with community variables which may complement the use of more sophisticated models, such as GAMM. For maximizing information and sake of brevity in monitoring reports, we recommend reporting mean species richness, changes in faunal composition (NMDS), occurrence and GAMM. Further, GAMM models can be improved by including abiotic and biotic factors as covariates and used for forecasting future population dynamics, as did Gardiner and Didham (2020) with fireflies in the U.K. Ultimately this may help to identify winners and losers in the face of anthropogenic changes (e.g., Lamarre et al. 2022).

Author contributions

Y.B. and H.B. conceived and designed the study. F.P., R.B., Y.L. and J.A.R. provided insect data. Y.B. and P.B. analyzed the data. Y.B., D.A.D., P.B., G.P.A.L. and D.S-V. wrote the manuscript. All authors read and approved the manuscript.

Declaration of Competing Interest

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

Data availability

Data relevant to this contribution have been deposited in FigShare DOI: 10.25573/data.21719933. Sequences were deposited in the project BCIAR of the database of the Barcode of Life Data System https://www.barcodinglife.org/index.php.

Acknowledgments

We thank ForestGEO and the Smithsonian Tropical Research Institute for logistical support. This study was supported by ForestGEO and the Czech Science Foundation (GAČR 20-31295S to YB, GAČR19-15645Y to GPAL). Grants from the Smithsonian Institution Barcoding Opportunity FY013, FY014, FY018 and FY020 (to YB) and in-kind help from the Canadian Centre for DNA Barcoding allowed to sequence beetle specimens. YB, HB, JARS and GPAL were supported by the Sistema Nacional de Investigación, SENACYT, Panama. Olivier Missa kindly wrote the R script to estimate confidence limits with species proportions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110243.

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