1 **Title: Global Arthropod beta-diversity is spatially and temporally structured by latitude**

2 **Short running title: Latitudinal arthropod diversity gradient**

3 **Abstract:**

4 Aim: Global gradients in species biodiversity may or may not be associated with greater

5 species replacement closer to the equator. Yet, empirical validation of these patterns has so far

6 focused on less diverse taxa, with comparable assessments of mega-diverse groups

7 historically constrained by the taxonomic impediment.

8 Location: Global

9 Time period: 2010-2017

10 Major taxa studied: Terrestrial arthropods

11 Methods: Here we assess the temporal and spatial dynamics of arthropod communities using a

12 beta-diversity framework, drawing on samples across 129 globally distributed monitoring

13 sites. Overall, we encountered more than 150,000 unique barcode index numbers (BINs) (i.e.

14 species proxies). We assessed between site differences in community diversity using beta-

15 diversity and the partitioned beta-diversity components of species replacement (i.e. turnover)

16 and richness difference (i.e. a measure of nestedness).

17 Results: We show that global differences in community compositional change are linked to

18 latitudinal, spatial, and temporal gradients. General global beta-diversity trends remained

19 consistent across biogeographic regions, with beta-diversity (dissimilarity) increasing with

20 decreasing latitude, greater spatial distance and greater temporal distance. By contrast, species

21 replacement and richness difference patterns varied across biogeographic regions, suggesting

22 different underlying processes are shaping regional biodiversity patterns. Latitudinal effects

23 on species replacement or richness difference were significant for 3 out of 5 regions.

24 Comparably we found significant spatial distance relationships with species replacement or

25 richness difference for 3 out of 5 regions. Temporal distance was significantly associated with

26 species replacement or richness difference for all 5 regions.

27 Main conclusion: The general expectations of the latitudinal diversity gradient (LDG) are

28 supported using a large, extensive global sampling effort. Our findings generally support the

29 global LDG expectations, however, partitioned assessment of beta-diversity indicates the

30 underlying processes driving the general global pattern, here species replacement and richness

31 difference, may be regionally linked to differences in seasonality effects or variation in spatial

32 distribution of environmental factors.

33 **Key words: barcoding, COI, biogeography, biodiversity, metacommunity,**

34 **spatiotemporal**

Introduction

Biodiversity is influenced by many factors, including environmental, evolutionary, biotic interactions, and stochastic, resulting in a global distribution of over 2 million species (IUCN, 2022). The amazing level of global biodiversity is essential for life, including ours, in the form of various environmental services, including nutrient cycling, food security, and waste management, etc. (Felipe-Lucia et al., 2020). As such, understanding what factors shape biodiversity across time and space, particularly at the global scale, is of interest to a wide range of researchers in ecology, evolutionary biology, conservation and invasive species management, agriculture, medical science and many others. In the first instance it is generally accepted that biodiversity is expected to scale with latitude, increasing toward the tropics, a phenomenon referred to as the latitudinal diversity gradient (LDG) (Hillebrand, 2004). The underlying mechanism(s) for the LDG expectation are not definitive, however, with over 30 current hypotheses built on varying degrees of ecological, evolution and environmental complexity (Willig, Kaufman, & Stevens, 2003). More recent efforts have also discovered exceptions to the LDG, which are primarily regional (Dowle, Morgan-Richards, & Trewick, 2013; Mannion, Upchurch, Benson, & Goswami, 2014; Qian & Ricklefs, 2007; Rahbek et al., 2019). The many hypotheses advanced to explain global biodiversity patterns are often difficult to test, particularly across taxonomic groups or at large spatial and temporal scales (Kinlock et al., 2018; Pontarp et al., 2019). However, we can gain insights into biodiversity patterns using pairwise site assessment of total beta-diversity and its associated decomposition components.

The beta-diversity (i.e. β-diversity) framework provides a robust means to assess differences in biodiversity between communities, which can, in turn be used to determine spatio-temporal or environmental response (Borcard, Gillet, & Legendre, 2018). Beta-diversity is the compositional difference (i.e. dissimilarity) between two communities (Borcard et al., 2018). This compositional dissimilarity between communities is expected to arise from two key processes: (i) species replacement (i.e. turnover), quantifies the change in community composition due to non-overlapping species and (ii) richness difference, the species gain or loss between two communities. Communities with high species replacement can result from strong environmental forcing, competition or historical disturbances (Victorero, Robert, Robinson, Taylor, & Huvenne, 2018). Richness difference (i.e. nestedness) can be caused by local species disappearing from a location (i.e. localized extinction), differing niche diversity or other processes resulting in the gain or loss of species (Lazarina et al., 2023; Schmera,

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68   Podani, & Legendre, 2020). Following the beta-diversity framework from Podani *et al.* (2013)

69   total beta-diversity itself can be separated into the components of (i) species replacement and

70   (ii) richness difference, which together sum to the total beta-diversity measure. Subsequently

71   the beta-diversity partitioning framework provides a means to investigate the potential links

72   between global biodiversity patterns and the underlying processes associated with their

73   formation across different species groups and ecological dimensions.

74   While several studies have investigated global biodiversity patterns, predominately using the

75   LDG, they were constrained by three major limitations. First, they were mainly based on

76   meta-analyses, as they combined data collected using different methodologies at different

77   spatial and temporal resolutions (e.g. seasonality) (Hillebrand, 2004; Kinlock et al., 2018).

78   While such data have high heuristic value, they are often affected by biases emerging from

79   the varied sampling techniques underlying the individual data points (Koricheva & Gurevitch,

80   2014). Second, the few studies which have sampled communities using standardized methods

81   to estimate differences in biological communities across broad latitudinal ranges have

82   generally ignored the effects of temporal variability (i.e. seasonality) within or between

83   sampled communities (Rivadeneira et al., 2015; Valdés et al., 2015; Zhang et al., 2020). If

84   differences in biological communities are only assessed across space, estimates of site-

85   specific diversity ignore the well-established importance of local temporal variation in

86   biodiversity (Bista et al., 2018; Fisher, Frank, & Leggett, 2010; Seymour et al., 2021). If site-

87   specific diversity comparisons are made across different time points, the potential estimates of

88   patterns of beta-diversity (i.e. diversity difference between sites) in space will alter patterns of

89   beta-diversity in time, i.e. the scope for spatiotemporal interactions (Gaston, Blackburn, &

90   Spicer, 1998). Third, prior studies have either examined less diverse taxa (Field et al., 2009;

91   Gaston et al., 1998; Hillebrand, 2004) or have generalized patterns emergent from local

92   studies to the global scale (Novotny et al., 2007; Qian & Ricklefs, 2007). Thus far, efforts to

93   assess global patterns with standardized sampling methods have not been undertaken for

94   taxonomic groups that comprise the bulk of global biodiversity.

95   With regards to the LDG, as the most prominent ecological assumption of global biodiversity

96   distribution, species replacement is expected to increase at lower latitudes, reflecting greater

97   habitat specialization and smaller ranges in more seasonally stable environments (Borcard et

98   al., 2018; Qian, 2009; Soininen, Heino, & Wang, 2018). By contrast, richness difference is

99   expected to increase with latitude, reflecting recent recolonization from a shared species pool

100   following deglaciation (Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012). Alternatively,

101   species replacement may increase with latitude, which could reflect historical selection for

102   species adapted for colder periods or to stronger changes in seasonality (Mateo et al., 2016).

103   Different latitudinal patterns in richness difference, be it decreasing with latitude or unimodal,

104   could indicate spatio-temporal disturbance patterns linked to regular or historical extinction

105   events (Socolar, Gilroy, Kunin, & Edwards, 2016). A lack of general patterns across multiple

106   regions or continents may also indicate inconsistent patterns of global biodiversity which may

107   suggest that stochastic processes predominate over expected environmental gradient filtering

108   of community assembly. Hence, comparisons between species replacement and richness

109   difference can provide insights into the processes influencing global biodiversity patterns.

110   In this study, we adopt DNA-based methods to characterize beta-diversity for a highly diverse

111   lineage of animals: terrestrial arthropods (Mora, Tittensor, Adl, Simpson, & Worm, 2011).

112   We comprehensively sample 129 sites across the globe for an average of 22 sequential weeks

113   each, encountering more than 150,000 different Barcode Index Numbers (BINs), a species

114   proxy (Ratnasingham & Hebert, 2013). We calculated and partitioned beta-diversity into its

115   species replacement and richness difference components in both space and time (e.g.

116   seasonality) to determine how global biodiversity patterns relate to latitude, distance, and

117   time.

Methods

119   The Global Malaise Trap Program (GMTP) was initiated in 2007 with the goal of observing

120   global-scale spatiotemporal arthropod biodiversity dynamics (Figures 1 & 2). Between 2010

121   and 2016, one or more Malaise traps were deployed at 129 sampling sites in 28 countries,

122   with repeated weekly sampling ranging from 2-104 weeks (Figure 2). In total, institutions in

123   28 counties contributed to the Global Malaise Trap Program (Figure 1; Table S1), which

124   jointly produced the first set of global biodiversity data for terrestrial arthropods based on a

125   uniform barcode sampling method. Details on GMTP standardized sampling protocols (e.g.

126   trap type, sampling method, data curation) used for this study are outlined in detail in

127   deWaard *et al.* (2019), but we provide a short summary here. A standard Townes-style

128   Malaise trap was deployed at each sampling location (hereafter site) and captured arthropods

129   from each trap were harvested weekly (hereafter trapping event). Arthropod specimens

130   captured from each trapping event were sorted, photographed, and processed individually.

131   Analysis began with each specimen identified morphologically to a taxonomic order and

132   registered on the Barcode of Life Data Systems (BOLD). DNA from each specimen was then

133   extracted and used to amplify and Sanger sequence the standard COI barcode region (Hebert,

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134   Cywinska, Ball, & deWaard, 2003). The resulting COI sequence data was uploaded to the

135   BOLD database, linking each specimen's morphological identification to its COI barcode

136   sequence. For each trapping event, all specimens were sequenced, except when a particular

137   morphospecies was represented by more than 50 individuals, in which case a subset of the

138   individuals were sequenced to confirm that the specimens did indeed represent a single unique

139   BIN (deWaard et al., 2019). The final GMTP dataset includes 1.2 million barcode records and

140   155,185 unique barcode index numbers (BINs) (Ratnasingham & Hebert, 2013). Prior studies

141   have established a strong correspondence between BINs and species identification in insect

142   groups with well-established taxonomy, thereby justifying the recognition of BINs as species

143   proxies (Ratnasingham & Hebert, 2013).

144   Temporal differences (i.e. distance in time) between each pair of sampling events was

145   calculated using circular statistics by first determining the Julian day of the two sampling

146   events and taking two measures (1) the absolute difference between the two Julian days

147   divided by 0.986 (0.986 degrees = 1 day) and (2) 360 minus the absolute difference between

148   the two Julian days divided by 0.986. The minimum value between measure (1) and (2) was

149   then used as the distance in time between the two sampling events. Here we refer to difference

150   in time and seasonality since the study spans multiple seasons (Figure 2) and since seasonality

151   differs drastically between different global locations. Distance between each pair of sampling

152   locations (i.e. distance in space) was calculated as the geographic distance between site pairs

153   using the function distHaversine in the R package geosphere (Hijmans, Williams, Vennes, &

154   Hijmans, 2017). Mean absolute latitude was calculated between each pair of sites along the

155   LDG. To understand how this metric behaves, consider a site pair in which both members are

156   at the Equator. In this case, their mean absolute latitude is 0° - which also applies to two

157   samples from the same trap at the Equator. For a trap pair at the North Pole, the mean

158   absolute latitude is 90°N; for a trap pair with its members on the North vs South Pole, it will

159   be 90°, and for a trap pair of which one member sits on the North Pole and the other at the

160   Equator, mean absolute latitude will be 45°N.

161   Statistical analyses

162   Community data were converted to presence absence data for calculations and analyses of

163   diversity. Beta-diversity and its components were calculated as Jaccard dissimilarity using the

164   Podani family of indices, which is a "true" beta-diversity estimate that is unaffected by the

165   species pool (i.e., gamma-diversity) (Schmera et al., 2020). Total beta-diversity (here Jaccard

166   dissimilarity) and the associated components of species replacement and richness difference

167   were calculated for each site pair using the function beta.div.comp in the R-package

168   *adespatial* (Borcard et al., 2018). We do note that there are alternative beta-diversity

169   partitioning methods (Baselga, 2010b; Borcard et al., 2018; Schmera et al., 2020). The Podani

170   family was utilized here as it is does not overestimate diversity differences and provides a

171   "true" diversity estimate that is unaffected by the total species pool (Borcard et al., 2018;

172   Schmera et al., 2020), but see also alternative true-diversity based partition approaches (Engel

173   et al., 2021; McGlinn et al., 2019). Utilizing a "true-diversity" allows for independent

174   measures of alpha, beta, and gamma diversity. Whereas alpha-diversity reflects within site

175   variation, beta-diversity may either reflect between site variation independently or

176   dependently (i.e. scaling with alpha-diversity) depending on the measure used (Koleff,

177   Gaston, & Lennon, 2003). Using an independent (i.e. "true") measure of beta-diversity

178   becomes more important when comparing beta-diversity measures, dependence of alpha and

179   beta diversities, to avoid compromising interpretation that may actually reflect within-site

180   instead of between site observations (Baselga, 2010a).

181   Pairwise values of total beta-diversity, species replacement, and richness difference were

182   calculated for all trapping event pairs by taking the lower triangle values from the associated

183   distance matrix. As there were 2,412 trapping events in total, N = 2,907,666 pairs of trapping

184   events were included in our analyses.

185   Using linear regression, we modelled each pairwise beta-diversity component as a separate,

186   univariate function of distance in space, distance in time, mean latitude, and the interactions

187   mean latitude × distance in space and mean latitude × distance in time. Here, the two

188   interaction terms are of key interest in explicitly testing whether the rate of beta-diversity,

189   species replacement or richness difference in space or time, respectively, varies detectably

190   with latitude.

191   Our data are not fully balanced as the number of data points per site, and hence pairs of sites,

192   varies. In the analyses, we wished to give each site, and pair of sites, an equal weight in the

193   analyses. If $n_{s_1 s_2}$ is the number of pairs of trapping events for which one trapping event

194   belongs to site s_1 and the other trapping event belongs to site s_2, in an unweighted regression

195   this pair of sites would achieve the total weight of $n_{s_1 s_2}$, and thus sites with more data would

196   contribute disproportionally to our analyses. To account for the unbalanced sampling effort in

197   our models, we applied a weighted linear regression, where the weight for each data point was

198   set to $1/n_{s_1 s_2}$, so that the total weight was equal among all pairs of sites.

199   We note that data points are not independent of each other, because each data point in the

200   linear model involves a pair of samples that are correlated in time and space. For this reason,

201   we did not perform significance tests based on output from the linear model but instead

202   employed the following permutation approach to determine significance for each of the

203   explanatory variables in our models.

204   Given the unequal temporal sampling and spatial sampling design across the multiple GMTP

205   project datasets we used a series of permutation test to assess the significance of each

206   explanatory variable (Chihara & Hesterberg, 2018). For each permutation test we assessed the

207   significance of each explanatory variable individually, including distance in space, distance in

208   time, mean latitude, and the interactions mean latitude × distance in space and mean latitude ×

209   distance in time, by doing the following. We first calculated the log-likelihood ratio between

210   the model where the focal explanatory variable was included (the full model), and the model

211   where the focal explanatory variable was excluded (the reduced model). We compared the

212   observed log-likelihood ratio to its null distribution which we computed by permuting the data

213   N=1,000 times, with the permutation scheme detailed below for each specific test. In general,

214   if the log-likelihood ratio for the full vs. reduced model fitted to the actual data was greater

215   than the log-likelihood ratio for the full vs. reduced model fitted to the permuted data for at

216   least 95% of the permutation outcomes, the explanatory variable was deemed significant

217   (Chihara & Hesterberg, 2018).

218   When testing for the interaction between mean absolute latitude and distance in space, we

219   permuted the sampling sites, keeping all trapping events that belonged to the same original

220   site in the same group. When testing for the interaction between mean absolute latitude and

221   distance in time, we first permuted the sampling sites as described above and permuted the

222   sampling dates within each group of trapping events. When testing for the main (non-

223   interactive) effects of the explanatory variables, we reduced the full model to exclude the

224   respective interaction associated with the explanatory variable being tested. When testing for

225   the main effect of distance in space or for the main effect of mean absolute latitude, we

226   permuted the sampling sites. When testing for the main effect of distance in time, we

227   permuted the dates within sampling locations.

228

Results

230   Overall the project collected 155,185 unique BINs across five geographic regions,

representing regional variation in latitudinal, temporal, and spatial profiles (Figures 2 & S1). BIN diversity (Figure 2) captured a large diversity of terrestrial diversity across 50 orders dominated by Diptera (51% of total BINs; 77,046 unique BINs), Hymenoptera (22% of total BINs; 33,265 unique BINs), Coleoptera (7% of total BINs; 12,550 unique BINs), Lepidoptera (7% of total BINs; 11,899 unique BINs), and Hemiptera (5% of total BINs; 7,783 unique BINs) (Figure 2).

Global beta-diversity (similarity) increased significantly with absolute latitude, which supports the general expectations of the LDG (Table 1; Figure S3 & S4). More generally, site comparisons between communities at higher latitudes were more similar to each other than site comparisons between communities closer to the Equator, with this observation also extending over longer temporal and spatial scales. Total beta-diversity spatio-temporal patterns were generally consistent across biogeographic regions (Table 1; Figure S4). There were some deviations in patterns across the regions, particularly when assessing the partitioned components of species replacement and richness difference (Figure S2). Oceania did not have significant total beta-diversity or species replacement association with latitude, spatial distance or temporal distance, but richness difference was found to increase significantly with increase temporal distance ($p < 0.01$) (Table 1). Eurasia did not have significant latitudinal relationships with total beta-diversity or its partitioned components but did show significant positive association between total beta-diversity dissimilarity and spatial distance ($p < 0.01$) along with significant positive associations between species replacement and spatial distance ($p = 0.4$), temporal distance ($p < 0.01$), and temporal distance x latitude ($p = 0.05$), as well as significant positive associations between richness difference and temporal distance ($p < 0.01$) (Table 1, Figure 3, 4). More generally, latitude, latitude x distance, or latitude x time were significantly associated with species replacement for two of five regions (North America and Eurasia) and for one of five regions for richness difference (South America). Spatial distance or space x latitude was significantly associated with species replacement for Africa and Eurasia, with richness replacement associated with North America and Africa. Temporal distance or time x latitude was significantly associated with species replacement for four of five regions (except Oceania), with richness difference being significant for North America, Oceania, and Eurasia (Table 1; Figures 3 & 4).

Discussion

The dataset generated by the Global Malaise Trap Program offers a unique opportunity to assess the underpinnings of global latitudinal biodiversity patterns using a highly diverse and

dominant group of terrestrial organisms. Our main finding is that total pairwise beta-diversity dissimilarity increases with decreasing latitude, increasing spatial distance, and increasing distance in time. We did not find strong indications of generalized partitioned beta-diversity patterns (i.e. species replacement or richness difference) at a global scale. However, we did find partitioned beta-diversity patterns at the regional scale which differed in the influence of latitude, spatial distance, and time indicating regional factors play a key role in overall beta diversity patterns (Figures 3, 4 & S4).

To evaluate community dissimilarity in space and time, we partitioned overall beta-diversity into its components: richness difference and species replacement. This partitioning framework provides insights into what factors are driving differences in biological diversity between sites, and subsequently overall diversity gradients (Borcard et al., 2018; Lennon, Koleff, GreenwooD, & Gaston, 2001). We expected richness difference to increase with increasing latitude, reflecting the recent recolonization of high latitude environments following deglaciation (Dobrovolski et al., 2012). If species expanded their distributions from a joint source pool in a glacial refugium, communities established along the expansion front should form nested subsets of the source species pool. Consistent with this scenario, we generally found increased richness difference with increasing latitude (Table 1, Figure 3 & 4). We also expected species replacement to decrease with increasing latitude as a direct effect of limiting factors or eco-evolutionary processes, leading to smaller ranges and increased specialization in areas with less seasonal variability (Qian, 2009; Soininen et al., 2018). However, while we found clear support for latitudinal changes in overall beta-diversity, the underlying trends in species replacement and richness difference were inconsistent across regions, suggesting different, regional, ecological or evolutionary process are influencing biodiversity patterns (Table 1, Figures 3 & 4).

Regional trends

The appearance of generally consistent total beta-diversity patterns across geographic regions suggests alternatives to earlier observations pointing to regional rather than global factors influencing changes in community composition. However, the Oceania region seems to be an exception, as we found no association between changes in biodiversity community composition and spatial distance or latitude. This supports findings from Novotny *et al.* (2007), who proposed that regional differences in arthropod communities may actually be lower in Papua New Guinea than in temperate sites, indicating that beta-diversity is unlikely to explain the high diversity of tropical arthropod communities. However, their patterns and

297   ours may suffer from lower site coverage than is needed to confirm the lack of latitudinal

298   gradient, but it is interesting none the less. Past studies have largely focused on temperate

299   sites, drawing some concern that tropical sites may be underestimated in assessing LDG

300   dynamics. The GMTP data includes 30 tropical sampling sites (23% of the sampled sites)

301   with 986 trapping events (40.1% of the total trapping effort), providing a wider assessment.

302   We did find partitioned components of beta-diversity differed across regions, however, which

303   would suggest that although the general global spatial trends in beta-diversity are consistently

304   observed the underlying environmental or biotic drivers of species replacement and richness

305   difference may be regional rather than global (Pontarp et al., 2019). The more frequent

306   association with spatial distance versus latitude, particularly outside North America might

307   also support recent indications that the strength of the LDG may be greater in the western

308   hemisphere (Kinlock et al., 2018).

Temporal beta-diversity trends

310   In stark contrast to previous studies, especially in assessing global scale patterns, our analyses

311   also considered temporal effects on latitudinal beta-diversity dynamics. Temporal species

312   replacement or richness difference were significant for all five regions, including the global

313   scale (Table 1). Temporal ecological dynamics are important for understanding seasonal shifts

314   in habitat and home ranges which can influence spatial biodiversity patterns (Massol et al.,

315   2011; Seymour et al., 2021). While pronounced temporal changes in environmental

316   conditions (i.e. seasonality) in the temperate zone have been well documented, the same may

317   be true for the tropics. Temporal species replacement was noted for several regions, indicating

318   seasonal shifts in community composition likely due to competition and seasonal effects of

319   environmental forcing (Seymour, Brown, et al., 2020; Tonkin, Bogan, Bonada, Rios-Touma,

320   & Lytle, 2017). Here we note variation in rainfall, radiation, leaf flush etc. has been proposed

321   to generate strong seasonality in the activity of arthropods (Basset et al., 2015; Grøtan, Lande,

322   Chacon, & DeVries, 2014). Temporal richness replacement, which predominantly was co-

323   associated with a significant effect of latitude likely attributed to species loss during key

324   seasonal shifts, which may be more prominent at higher latitudes where seasonal shifts in

325   environmental conditions are greater (Tonkin et al., 2017). The observed temporal patterns

326   here attest to finer partitioning of community composition that should be accounted for in

327   determining the mechanistic associations with larger spatial/latitudinal biodiversity patterns.

Spatial beta-diversity trends

329 The prevalence of high beta-diversity values between sites, particularly the high number

330 (88%) of pairwise global sites that were completely dissimilar (i.e. shared no species)

331 highlights the extraordinary diversity of terrestrial arthropods. Communities become more

332 similar at the regional level with 63% dissimilar sites for North America, 69% for Oceania,

333 50% for Eurasia, 51% for Africa and 34% for South America. While most arthropods can

334 disperse by flight, both individual home ranges and species distributions are commonly

335 restricted (Wagner, Grames, Forister, Berenbaum, & Stopak, 2021). Range sizes have been

336 proposed to shrink towards the tropics, following the so-called Rapoport's rule. Nonetheless,

337 the evidence for this assertion is very limited as it has traditionally been derived from studies

338 predominately conducted in the northern hemisphere (Gaston et al., 1998), but some recent

339 support for southern hemisphere trends are available (Dyer, Redding, Cassey, Collen, &

340 Blackburn, 2020; Pintor, Schwarzkopf, & Krockenberger, 2015). Our observation of greater

341 species replacement may reflect greater niche partitioning and specialization allowed by

342 higher productivity or stemming from greater levels of speciation (Hillebrand, 2004).

343 While previous assessments of beta-diversity have largely involved regional assessments

344 (Seymour, Edwards, et al., 2020; Tonkin et al., 2017), which were then used to fuel meta-

345 analyses (Graco-Roza et al., 2022; Hillebrand, 2004; Kinlock et al., 2018), this study

346 represents a true global assessment of temporal-spatial dynamics of the most diverse lineage

347 of terrestrial animals. The consistency in general global patterns which were decomposed at

348 the regional scale enables a mechanistic assessment of the planetary biodiversity patterns.

349 This synthesis was only made possible by our coupling of a standardized sampling method

350 with DNA-based taxonomic assignments (Hebert et al., 2003). Importantly, convincing

351 analyses of beta diversity require an efficient means for rigorously establishing the incidence

352 of species shared across sites in massive sampling programs. Such methods are finally

353 available for our use at a planetary scale.

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Table 1. Statistical significance of patterns detected. To assess the importance of each candidate variable (listed on the left as Covariates), we used a series of permutation tests. We first calculated the log-likelihood ratio between the model where the explanatory variable being tested was included (the full model), and the model with the explanatory variable being tested was excluded (the reduced model). We then compared the observed log-likelihood ratio to its null distribution, which we computed by permuting the data N=1,000 times (see Methods for the exact permutation schemes implemented). This table shows the proportion of permutation outcomes for which the log-likelihood ratio of the model fitted to the actual data was lower than the log-likelihood ratio for the models fitted to the permuted data. Values at or below 0.05 are deemed significant and are indicated in bold face.

| Covariate	Region	Beta	Richness Difference	Species Replacement
Latitude	Global	**<0.01**	0.19	0.18
Distance in space (ΔS)	Global	**<0.01**	0.95	0.91
Distance in time (ΔT)	Global	**<0.01**	1.00	1.00
ΔT × Latitude	Global	**<0.01**	**0.04**	**0.05**
ΔS × Latitude	Global	**<0.01**	**0.03**	**0.03**
Latitude	North America	**<0.01**	**0.02**	**0.01**
Distance in space (ΔS)	North America	**<0.01**	**0.01**	0.45
Distance in time (ΔT)	North America	1.00	**<0.01**	**<0.01**
ΔT × Latitude	North America	**<0.01**	0.07	**<0.01**
ΔS × Latitude	North America	**<0.01**	**0.01**	0.63
Latitude	South America	**<0.01**	**<0.01**	0.17
Distance in space (ΔS)	South America	0.17	0.51	0.66
Distance in time (ΔT)	South America	**<0.01**	1.00	**<0.01**
ΔT × Latitude	South America	0.33	0.49	0.33
ΔS × Latitude	South America	0.85	0.15	0.19
Latitude	Oceania	0.71	0.90	0.81
Distance in space (ΔS)	Oceania	0.57	0.98	0.11
Distance in time (ΔT)	Oceania	1.00	**<0.01**	1.00
ΔT × Latitude	Oceania	0.33	0.37	0.45
ΔS × Latitude	Oceania	0.43	0.08	0.07
Latitude	Eurasia	0.13	0.29	0.37
Distance in space (ΔS)	Eurasia	**<0.01**	0.93	**0.04**
Distance in time (ΔT)	Eurasia	1.00	**<0.01**	**<0.01**
ΔT × Latitude	Eurasia	0.29	0.06	**0.05**
ΔS × Latitude	Eurasia	0.43	0.71	0.85
Latitude	Africa	**0.03**	0.83	0.40
Distance in space (ΔS)	Africa	**<0.01**	**0.01**	**0.01**
Distance in time (ΔT)	Africa	1.00	1.00	**<0.01**
ΔT × Latitude	Africa	0.52	0.60	0.88
ΔS × Latitude	Africa	0.91	0.54	0.22

544 Figures

545 **Figure 1. Sampling sites and five biogeographical regions considered.** Regions are
546 differentiated by color. White points indicate sampling locations.

547

Sampling sites = 129
Trapping events = 2412

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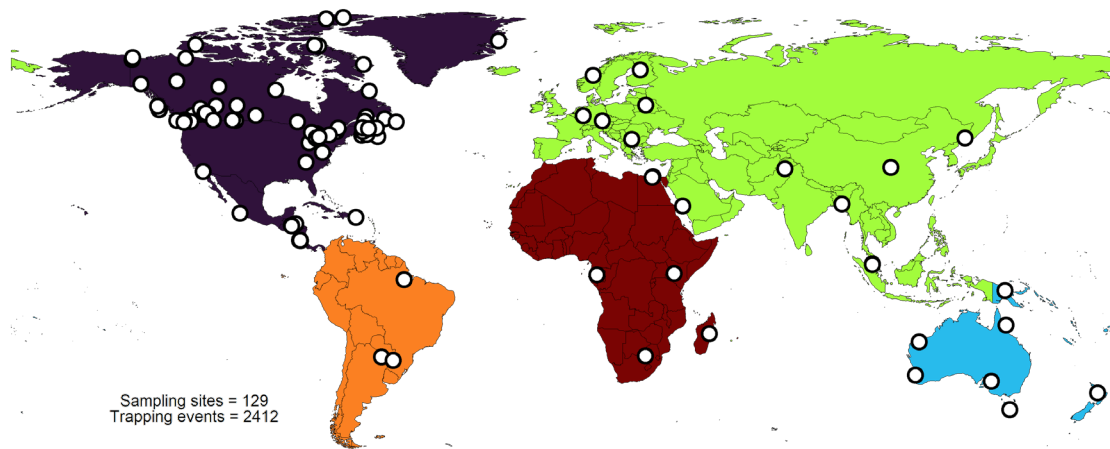
Figure 2. Diversity of BINs (i.e. species proxies) across the sampling sites. top and middle panels: (each vertical bar). Colors shown are unique terrestrial arthropod orders with each height corresponding to the relative abundance (top) or log abundance (middle) of unique BINs across the given site. The absolute latitude is provided on the x-axis with sites arranged from low to high. Bottom panel, each circle represents a sampling unique event, with colors corresponding to the region. Each horizontal line shows a unique sampling location with latitude (absolute) indicated on the y-axis. Colors correspond to regional groups following the same color scheme as Figure 1.
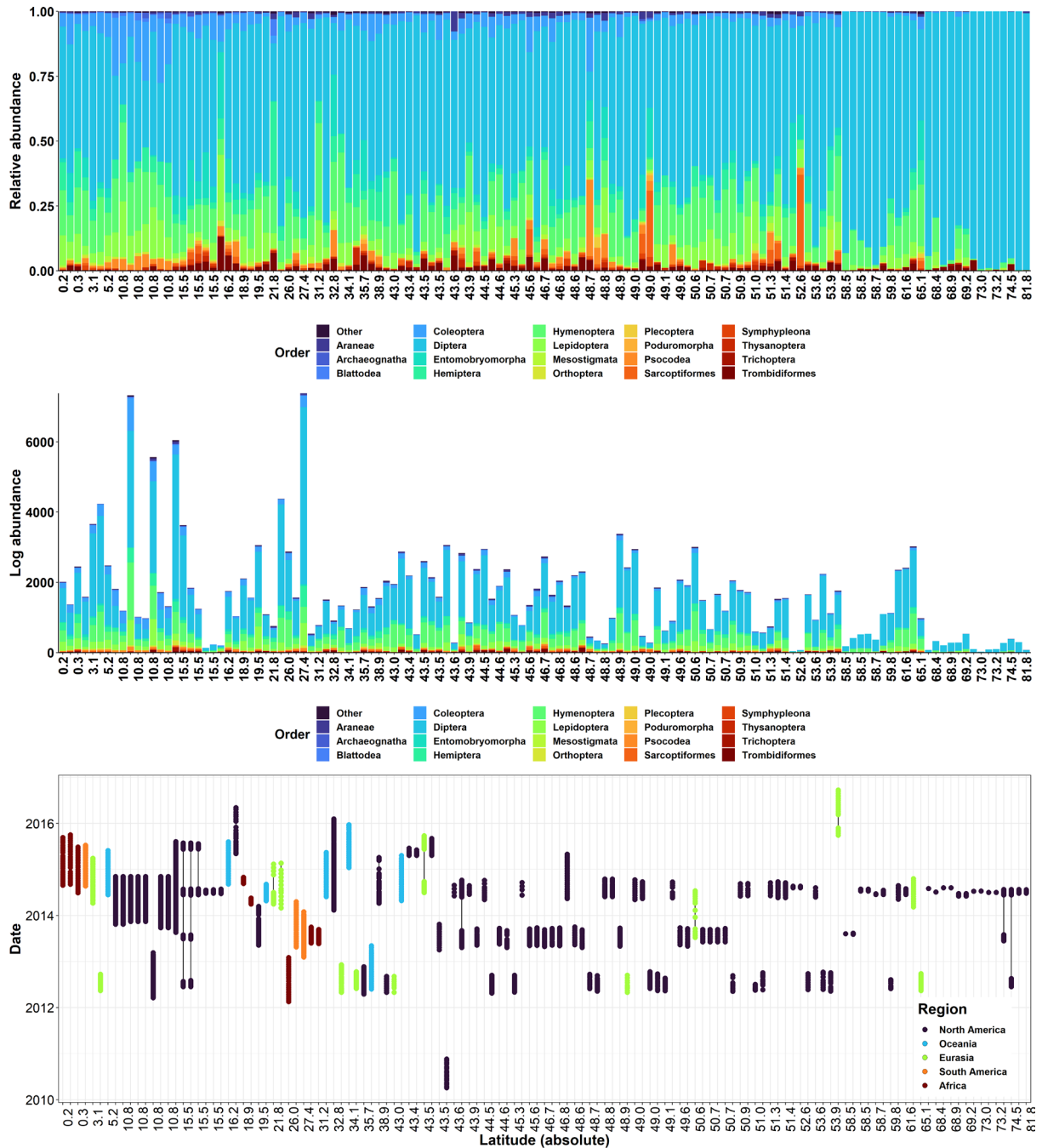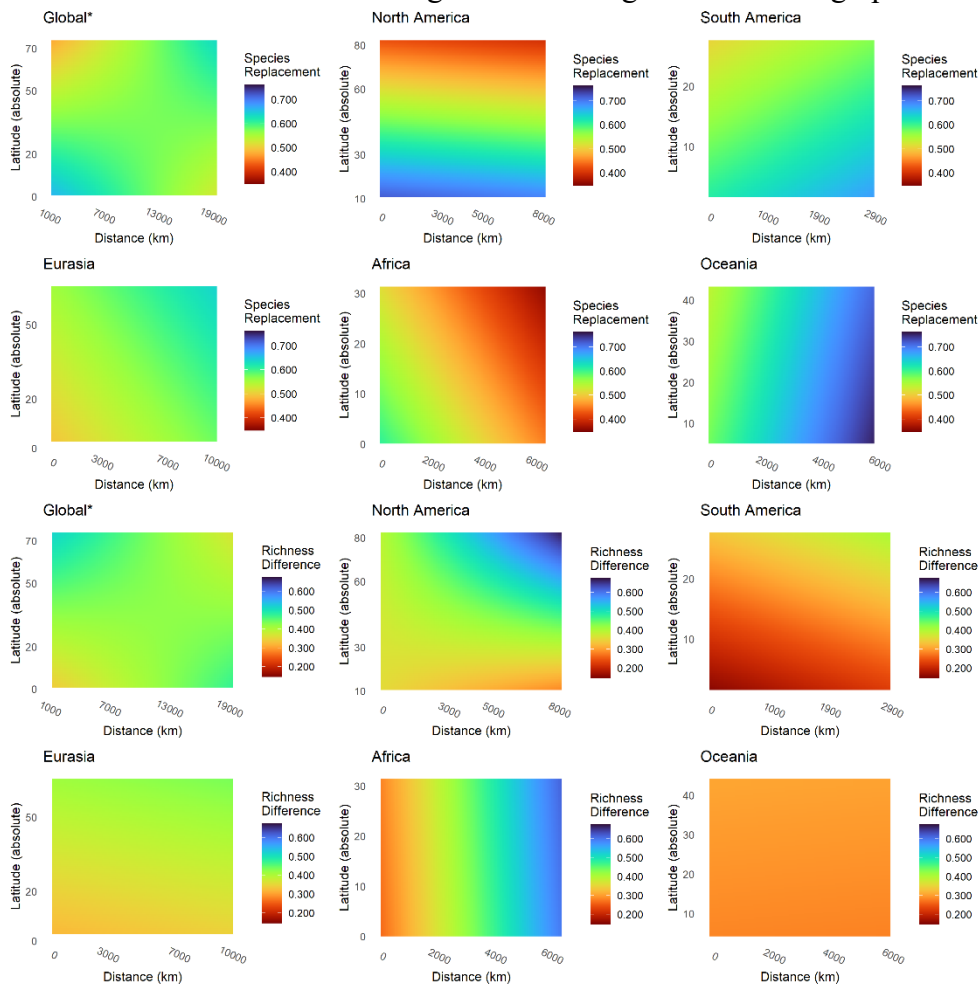
Figure 3. Impacts of pairwise distance in space and latitude on community dissimilarity.
This figure shows the species replacement and richness difference components of beta-
diversity, plotted from the fitted values of a linear model of the metric in question as a
function of distance in space, distance in time (here set to zero), mean absolute latitude, and
the interactions mean latitude × distance in space and mean latitude × distance in time (see
Table 1 for statistical significances). In this figure, we explicitly test whether spatial patterns
of community beta-diversity *in space* (in terms of overall beta-diversity, species replacement
or richness difference) varies detectably with latitude. Regions with a significant interaction
between pairwise difference in latitude and pairwise distance are indicated by an asterisk.
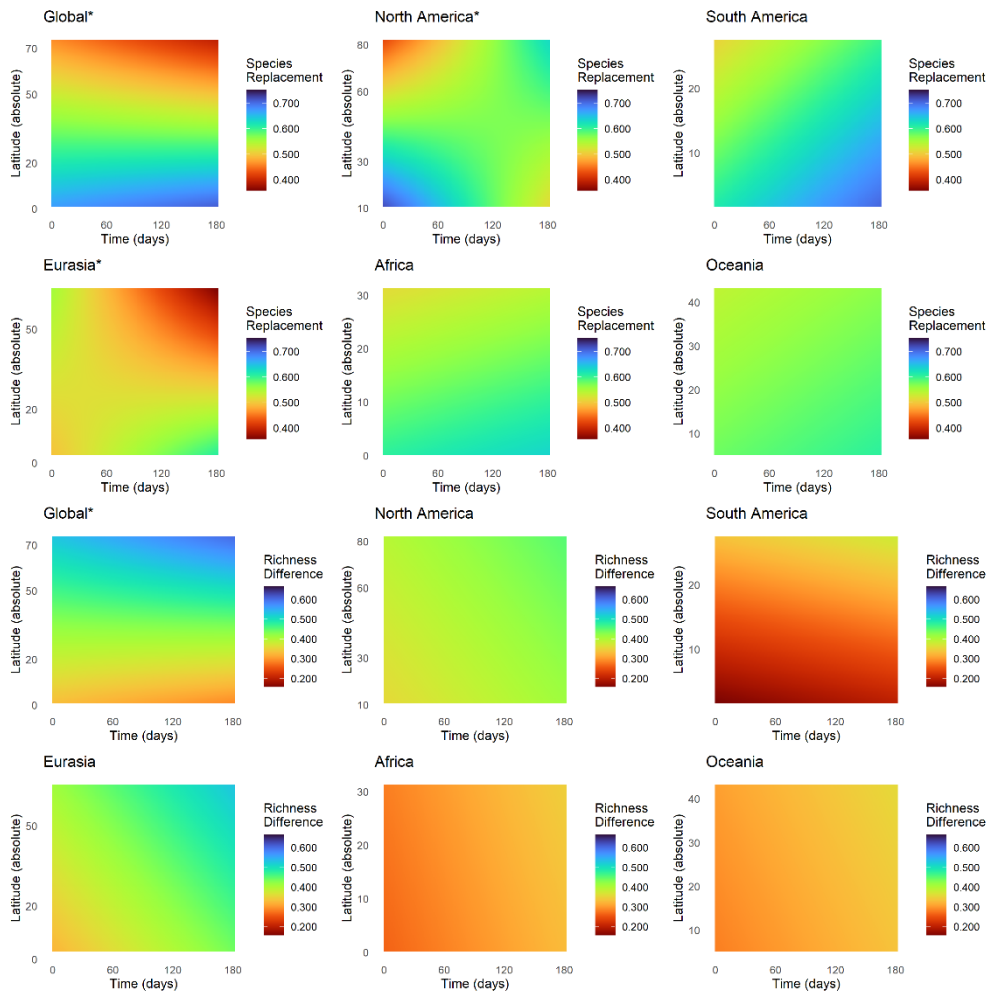Note the differences in the scaling of axes among the individual graphs.

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Figure 4. Impacts of pairwise distance in time and latitude on community dissimilarity. This figure shows the species replacement and richness difference components of beta-diversity, plotted from the fitted values of a linear model of the metric in question as a function of distance in space (here set to zero), distance in time, mean latitude, and interactions between mean latitude × distance in space and mean latitude × distance in time (see Table 1 for statistical significances). In this figure, we explicitly test whether temporal patterns of community beta-diversity *in time* (in terms of overall beta-diversity, species replacement and richness difference) varies detectably with latitude.