**Yes, a non‐random distribution, but why do dragonflies and damselflies not follow latitudinal gradient rules?**

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**Summary**

1. Latitudinal diversity gradient (LDG) is the increase in species richness towards the equator and is one of the most consistent patterns in biogeography, where current and historical processes contribute to shape the pattern.

2. Despite that LDG patterns have been described for some insects, the underlying mechanisms associated with community assembly and diversification along modern latitudinal diversity gradient pattern remain unknowledge for many groups.

3. Odonata is an old order of insects that originated during the Carboniferous and has diversified through different eras. Here, we defined co-occurrence based on the presence in ecoregions and 1°×1° grid cells of Odonata species in North America NA, to address their species richness, phylogenetic structure, and species diversification rate along the latitudinal gradient.

4. For the whole order, we found the highest species richness at mid-latitudes, while phylogenetic diversity showed a linear positive pattern along the gradient. Our results showed dragonfly assemblages were clustered along all the gradient, suggesting that environmental filtering sorted the assemblages. Whereas damselfly species assemblages were clustered at mid-latitude and overdispersed into both extremes of gradient, probably community assembly is driving by thermal gradients at mid-latitude, by competitive exclusion at south extreme, and by different origins of the biota at the boreal zone. Our results show that apparently most ancestral lineages of Odonata inhabit tropical zones, where diversified and dispersed to the temperate region, although likely also have been diversified into regions of NA, which might be linked with the highest species richness at mid-latitude for both suborders.

Keywords: Latitudinal richness, Odonata, Zygoptera, Anisoptera, North America

**Introduction**

One of the most consistent patterns in biogeography is the increase in species richness towards the equator, named the latitudinal diversity gradient (LDG) - a trend that is actually stronger at regional than at local scales (Mannion, Upchurch, Benson, & Goswami, 2014). The pattern of LDG describes how biodiversity changes geographically (Stevens & Tello, 2018) from which the following generalizations emerge: 1) the processes that drive LDG operate at different spatial and temporal scales; 2) LDG permeates most taxa regardless of their ecological and/or bionomic (i.e. aquatic, terrestrials, macro, and micro-organisms) properties; and 3) the factors that explain LDG patterns are diverse.

Several explanations have been advanced to explain the LDG (Etienne et al., 2019; Owens et al., 2017), which can be framed in three groups of hypotheses: 1) ecological limits (present-day conditions, as net primary productivity [NPP] or environmental stability). This refers to Mittelbach et al. (2007) and focuses on mechanisms of species coexistence and maintenance of species diversity due to abiotic settings and biotic interactions. According to this, in some cases taxa would be originated in the tropics and expand toward the poles without losing their tropical presence, which is the case for trees (Chu et al., 2019); 2) diversification rates. The hypotheses grouped here (*sensu* Morlon 2014– the balance between speciation and extinction) point out that diversity may be greater in regions where diversification has taken place over a longer period. This means that environmental stability affects the rate of diversification (Pontarp et al., 2019). This would allow the tropics to act as cradle, that is, a center of origin for species, due to a high origination/speciation rates (as found in swallowtail butterflies and oribatid mites; Condamine et al., 2012; Pachl et al., 2017); and finally, 3) time of species’ accumulation (*sensu* Pontarp et al. 2019). This group of hypotheses assumes that, barring major disturbances or climatic shifts, species richness will continue to increase unbounded over time (Massante et al., 2019). Under this conceptual framework, tropics are viewed as a museum, meaning that such areas are regions with a high number of old species with larger geographic range (as found in gastropods; Rivadeneira et al., 2015). Notice, however, that within a region, more than one evolutionary hypothesis could act (Moreau & Bell, 2013), and some well-known examples for this have been found in ants (Moreau & Bell, 2013), leaf beetles (McKenna & Farrell, 2006), and birds (Diniz-Filho, Rangel, Bini, & Hawkins, 2007).

Measuring and comparing phylogenetic diversity offers the possibility to integrate present-day ecological processes (hypothesis group 1), and the role of evolutionary drivers including origin, speciation and extinction of species (hypothesis groups 2 and 3) via the addition of evolutionary relationships and species’ history to the analysis (Mannion et al., 2014; Massante et al., 2019). This addition is key as two regions may share species richness but differ considerably in the phylogenetic structure and history of their constituent species (Economo, Narula, Friedman, Weiser, & Guénard, 2018; Massante et al., 2019). For instance, localized speciation results from long-term accumulation of closely-related lineages, leading to low phylogenetic diversity (i.e., clustered model). In contrast, low extinction rates result in communities with high phylogenetic diversity due to coexisting distantly-related lineages (i.e., overdispersed model) (Massante et al., 2019). Thus, the integration of ecological and evolutionary data provides new findings that allow a better understanding and the possibility of distinguishing the mechanisms that shape LDGs (Condamine et al., 2012; Economo et al., 2018).

Odonata (dragonflies [suborder Anisoptera] and damselflies [suborder Zygoptera]) is an old insect order likely originated during the Carboniferous, more specifically the Pennsylvanian (323–298 Mya) or the Permian (298–251 Mya). The highest diversification rates of both odonate suborders coincided with periods of warmer global climate (Song et al., 2020) associated with two mass extinction events in the Permian-Triassic ~251 Mya and Cretaceous-Paleogene ~66 Mya (Suvorov et al., 2020). We have used odonate insects to test for the shape of species richness, structure and diversification rates of communities along the latitudinal gradient. We chose these animals given their relatively high taxonomic knowledge and available large datasets of species distribution (Abbott & Broglie 2005). We also chose them as their two main odonate suborders differ in morphology, ecology, and ecophysiology (Bybee et al., 2016), which has led them to evolve distinct distribution areas, thermal tolerance, and vulnerability to threats (Rocha-Ortega, Rodríguez, Bried, Abbott, & Córdoba-aguilar, 2020). These differences imply that the patterns of latitudinal gradients may vary between suborders so that distinguishing among mechanisms that structure the community of each suborder is still an open question. Odonate communities are taxonomically segregated along the latitudinal gradient, going from high to low latitudes at regional scale, a patterns that is not followed at a local scale (Cerini, Stellati, & Vignoli, 2020). Nonetheless, to date, the evaluation of the role of evolutionary drivers including origin, speciation, and extinction in structuring the odonates community, is missing. Consequently, we badly need hypotheses that explain latitudinal gradient shape for Odonata diversity, particularly for each suborder. Filling in this knowledge gap will improve the identification and discrimination of the underpinning evolutionary and ecological mechanisms beyond the patterns (e.g. segregated assemblages) (Pavoine et al., 2014; Winter, Devictor, & Schweiger, 2013).

In particular, we were interested in responding the following questions: 1) What kind of latitudinal gradient do odonate communities follow? At the community diversity level, we expect to corroborate the latitudinal patterns that are somehow classical in the literature, that is, a monotonic increase in the number of species from northern to southern latitudes (Mittelbach et al., 2007). According to this, the resulting pattern would be more evident with a regional control, because historical factors, geology, and climate determine the size and composition of the regional species pool (Scott, Barton, Evans, & Keating, 2011; Shah, Tonkin, Haase, & Jähnig, 2015). Besides, the pattern shown by both suborders may vary due to their difference in morphology, ecology, and ecophysiology. For this, we do not have suborder-specific predictions but that, simply, differences will emerge; 2) What can the phylogenetic structure and history of their constituent species tell us about the latitudinal patterns? At the phylogenetic level, we expect a reverse pattern, that is, an increasing diversity from southern to northern latitude given the next reasoning: if the order has a tropical origin and this region maintains more stable climate conditions, thus their species are phylogenetically clustered.

**Materials and Methods**

*Data sampling*

We gathered records from all Odonata species inhabiting North America (NA) - from Canada to the south of Mexico. The records were obtained from OdonataCentral, a storage and distribution hub for adult odonate records throughout NA (Abbot & Broglie, 2005) and from CONABIO (CONABIO, 2009) a storage site for, mainly, Mexican diversity. We removed duplicated and incorrectly georeferenced records, rendering a total of 300,896 records (97,398 Canada; 65,647 Mexico; 137,851 United States) for 603 species (400 for dragonflies and 203 for damselflies as listed in Appendix I). Synonyms were checked using the Integrated Taxonomic Information System (ITIS, 2020).

*Units of analysis*

We contrasted the latitudinal gradient of all Odonata species, and for both suborders separately measured in two units: latitudinal bands and ecoregions. We used eco-regions as a regional control. The eco-regions are units that consider biogeographic relationship of assemblages, reflecting the spacing and strength of environmental barriers to survival or dispersal (Chen & Srivastava, 2014). The region generates the pool of potentially colonizing species. We overlaid odonate records on Level II ecoregions of NA (<http://www.cec.org/north-american-environmental-atlas/terrestrial-ecoregions-level-ii/>) and selected for analysis those ecoregions with a completeness higher than 50%. We used this scale because Level II ecological regions are useful for national and subcontinental overviews of ecological patterns. Completeness was calculated using the ICE and Chao2 nonparametric estimators as implemented in EstimateS v8.2 (Colwell, 2013). These estimators are recommended for incidence data (Colwell & Coddington, 1994). The number of ecoregions with completeness higher than 50% was 48, which represents 96 % of NA ecoregions. The average area of all ecoregions was 4.02653E+11 km with a large variation (SD ± 4.07373E+11 km) (Appendix II. List of ecoregions included in the study and the number of records of each eco-region). We calculated the number of species in the geographic midpoint of each of the 48 ecoregions considered in this study.

We calculated the number of species inhabiting each 1° × 1° cell by counting the species in the geographic midpoint of each cell. This unit of spatial co-occurrence is because cells of this size are likely to have accumulated the large majority of their species by range expansions, rather than in situ speciation (Kennedy, Price, Fjelds, Rahbek, & Kennedy, 2016). Whereas we used latitudinal bands as units that do not consider biogeographic relationships of assemblages or regional control, longitudinal bands were used as a measure of area.

*Phylogenetic data*

A phylogeny for all species in our database was obtained by using the informatics tool Phylomatic (Webb & Donoghue, 2005). Phylomatic uses the Odonata mega-tree (Waller & Svensson, 2017) as a backbone onto which species are added based on their taxonomy. The phylogeny produced had little resolution within genera. For families missing in Waller & Svensson (2017), we took into account the fossil dating dates proposed by Davis et al. (2011), while nodes with no estimated dates were estimated by *bladj* algorithm in Phylocom (Webb et al., 2008).

*Phylogenetic structure and ancestry*

To evaluate the phylogenetic structure for bands and ecoregions, we calculated a widespread used metric—the Net Relatedness Index (NRI) not weighted by species abundance (Webb et al., 2008). The NRI index calculates the mean phylogenetic distances (MPDs) among all co-occurring individuals of records and, therefore, it indicates the ‘basal’ dispersion of the lineages within the community. To standardize the observed MPD to that expected given the species richness observed, we compared each metric with a null distribution of 1000 random communities constructed using the phylogeny-pool null model in the software R. The regional pool used in these randomizations included all species occurring in the study. We multiplied the NRI results by −1 such that if the transformed values were >0, then communities were phylogenetically clustered (closely related individuals co-occurring), yet if the values were negative, then communities were phylogenetically overdispersed (distantly related individuals co-occurring) (González-Caro, Umaña, Álvarez, Stevenson, & Swenson, 2014).

A detailed Odonata phylogeny with corrected branch lengths does not exist yet, so we used a simple metric of net diversification rates. For this, we used the root-to-tip of each species which represents the number of nodes on the path between the nodes. The mean root-to-tip of all odonates (MRD) found in a latitudinal band or ecoregion was used as a measure of the level of the evolutionary development of the local fauna (Borges et al., 2018; Hawkins & Devries, 2009). Taxa with low MRD represent lineages with low rates of net evolutionary diversification (i.e., old relict lineages), while taxa with high RD belong to lineages with high rates of net evolutionary diversification (i.e., more derived linages).

*Statistical analysis*

We estimated species richness using a first-order non-parametric Jackknife estimator (Jackknife 1) per latitudinal band and ecoregion. This procedure reduces the intrinsic bias present on occurrence records that were collected without a specific sampling design. Jackknife is a re-sampling technique that provides an estimate for the species richness (Silva, De Marco, & Resende, 2010) and was estimated using the PAST software (available at http://folk.uio.no/ohammer/ past/).

We used generalized linear models (GLMs) and generalized additive models (GAMs) to test the linear and non-linear relationship respectively, between estimated species richness, to which NRI, and MDR were entered as response variables, and 1° band of latitude plus the number of 1° band of longitudinal within the bands of latitude (excluding interactions between them) to discard that pattern are regulated by area (longitudinal extend). According to our prediction (i.e., the existence of a latitudinal gradient of species richness), we expected a significant negative linear model in the band analyses. Using independent models, we tested the relationship between estimated species richness, NRI and MRD, and mean latitudinal point of ecoregion plus ecoregion area, as explanatory variables, excluding interactions between them, to dismiss that patterns are regulated by the area. The best-fit model was selected based on the highest R2 value and the smallest AIC value. Finally, we tested the relationship between NRI as a function of estimated species richness. We performed all analyses for the entire Odonata order as well as for both suborders, dragonfly and damselfly separately.

**Results**

*Geographical patterns*

Overall, non-linear models (GAMs) had more explanatory power than linear models (GLMs). Given this, species richness, NRI, and MDR were better explained by latitude than ecoregion for all groups (Table 1; Fig. 1, 2). Moreover, the highest species richness took place in the middle of the continent, from 32 ° N to 35 ° N, for all groups (Table 1; Fig. 2 a,b,c).

NRI showed a linear positive pattern for Odonata but a non-linear pattern for both suborders (Table 2; Fig. 1, 2). Dragonfly species were more clustered (i.e., most closely related) along all the gradient, and less clustered at intermediate latitudes (Fig. 2 e). This was opposite to damselfly species which were more clustered at intermediate latitudes and dispersed at the extremes (Fig. 2 f).

We did not find a significant relationship between NRI with estimated species richness for Odonata (F = 1.92e-05, p = 0.99). Moreover, while the relationship for dragonflies was linear and negative (F = 5.2, b = -0.01, p < 0.01), for damselflies it was linear and positive (F = 31.05, b = 0.02, p < 0.001).

MRD for Odonata showed a positive linear pattern (Table 3: Fig. 2 g). Nevertheless, this pattern was not linear for both suborders (Table 3; Fig. 2 h, i). Models of latitudinal bands explained the pattern better than ecoregion. MRD had a strong spatial structure for Odonata: while northern areas were dominated by species of more derived taxa, MRD steadily decreased towards the south (Fig. 2 g). For dragonflies, the pattern also showed derived taxa among the latitudinal bands, until 50° where there was a non-linear increase (Fig. 2h). For damselflies, MDR showed more derived taxa at intermediate latitudes (Fig. 2 i).

**Discussion**

Our results indicate that Odonata species richness did not follow the latitudinal gradient usually found for most species (i.e., unimodal tropic model), and contrary to expected, latitudinal bands were more explanatory than ecoregions. Patterns of odonate species richness were non-linear, with a peak at intermediated latitudes (at 32-35 °N), rather than tropical, without relevance of the area (longitudinal extent or area of ecoregion). The peak of biodiversity for the whole order and both suborders corresponded to the zone of transition between the Neotropical and Nearctic biota, especially for dragonflies. In this regard, the highest dragonfly richness in Eastern USA seems to be the result of the continuous connection of this region with the wet tropics from the south. Interestingly, numerous tropical species have moved into southeastern USA, including species from the uplands of the Mexican Plateau, which is a pattern also shown by other arthropod groups (Morrone & Márquez, 2008; Morrone, 2010; Rueda et al., 2013). Actually, the complexity of the mountain ranges from Mexico to South America, provides varying climates and thus habitats that have served as speciation hotspots for dragonflies and damselflies (Kalkman et al., 2008).

The species richness patterns we have documented might also be explained by the mid-domain effect hypothesis, which assumes that species distribution is truncated by physical or climatic barriers (Šizling, Storch, & Keil, 2009). Thus, for instance, life history strategies of Odonata species that inhabit high latitudes (where extreme environmental conditions prevail), consequently have a lower number of generations per year than species found at low latitudes. This latitudinal difference ultimately implies species abundance and stability (Dalzochio, Périco, Dametto, & Sahlén, 2020; Zeuss, Brunzel, & Brandl, 2017). In this sense, environmental characteristics that are latitudinally-shaped have likely contributed to colonization of few linages in higher latitudes.

Phylogenetic diversity for the entire order showed a linear positive pattern along the gradient. From a mechanistic point of view, community assembly vary with latitude (Boyero et al., 2015) and the shape of any latitudinal pattern might be explained by encompassing evolutionary and ecological time scales, and also several non-mutually excluding processes (Pontarp et al., 2019). Unlike, Cerini et al., (2020) who pointed out segregated or overdispersed odonate assemblages along the gradient, we found that dragonfly assemblages were clustered all over the continent, but less similar at intermediate latitudes which was the opposite for damselfly assemblages. Our findings could be explained by differences in the time and region of diversification in dragonflies and damselflies. In this sense, possibly for dragonflies, clustering along all the gradient may be explained by environmental filtering based on similar niche requirements (see De Araújo Martins et al., 2015). However, at mid-latitude the mixture of dragonfly species from both Nearctic and Neotropical origin reduces such clustering (Kalkman et al., 2008). Conversely, damselfly assemblages being clustered at mid-latitude might be explained by thermal gradients (Rocha-Ortega et al., 2020), where co-occurrent species are more closely related that in the rest of the gradient and share temperature-based adaptations (Pinkert, Brandl, & Zeuss, 2017). At the south extreme of the latitudinal gradient, phylogenetic overdispersion is explain by competitive exclusion of closely related species, joined to dispersal limitation, and/or niche parameters that are highly divergent in sympatry (Ackerly et al., 2006; Morlon et al., 2011).While, at the boreal zone, species assembly could be structured by the biota with different origins, thereby phylogenetically less related (Corser, White, & Schlesinger, 2014).

Although the origin of the order Odonata has been widely discussed, it is commonly accepted to be tropical (Corser et al., 2014). Indeed, our results show that apparently most ancestral (i.e., less derived) lineages of Odonata inhabit tropical zones. Although our results indicate that the lesser derived linages for dragonflies and the most derived for damselflies, occurs at mid-latitude, the major trend suggests that most ancestral lineages of both suborders live in southern latitudes. In NA, dragonflies have been established much longer than damselflies, with the former containing crown group endemic taxa and other very old lineages since the Mesozoic era before the breakup of Pangaea (Corser et al., 2014). The recent era has had low gene flow with other regions (e.g., Europe; Kohli et al., 2021). This means that dragonflies have remained more isolated inside NA than damselflies. This could explain why even when older linages inhabit the south, assemblages are phylogenetically closely-related across the gradient. It also explains why dragonflies have diversified across NA, with low extinction rate at mid-latitude (e.g., Appalachian Mountains, Corser et al., 2014), and all lineages remaining more isolated than damselflies. These regions may also be linked to the highest species richness at mid-latitude for both suborders. Damselflies from NA are mainly of neotropical origin (~60 Mya), but with a burst of recent endemic speciation for certain groups, coinciding with extreme climate deterioration during repeated Plio–Pleistocene glaciations since ~ 5 Mya (Corser et al., 2014). Moreover, it is likely that Central America played an important role in the early diversification of some damselfly families (Sánchez-Herrera, Beatty, Nunes, Salazar, & Ware, 2020). Therefore, at the extremes of latitudinal gradient assemblages are phylogenetically distantly-related, while assemblages at mid-latitude have faced fewer changes over evolutionary time.

In summary, the most salient result of our study is the support of the species accumulation time hypothesis, which assumes that ancestral species originated in the tropics where they diversified and dispersed to the temperate region. This implies a higher per-species flow into the tropics than off the tropics, a pattern that can be categorized as a dispersal hypothesis (Etienne et al., 2019). Nonetheless, community assembly processes are scale depend (Münkemüller et al., 2014), so that our results can change if, for example, South America odonate fauna is added. Furthermore, our results of community phylogenetic structure can also change with the improvement in branch length measurement in the Odonata phylogeny and the use of more complete techniques to record diversification. Despite this, our protocol is the first to integrate both taxonomic and phylogenetic diversity and the structure of odonate communities to explain the assembly mechanisms through the latitudinal gradient.

**Acknowledgements**

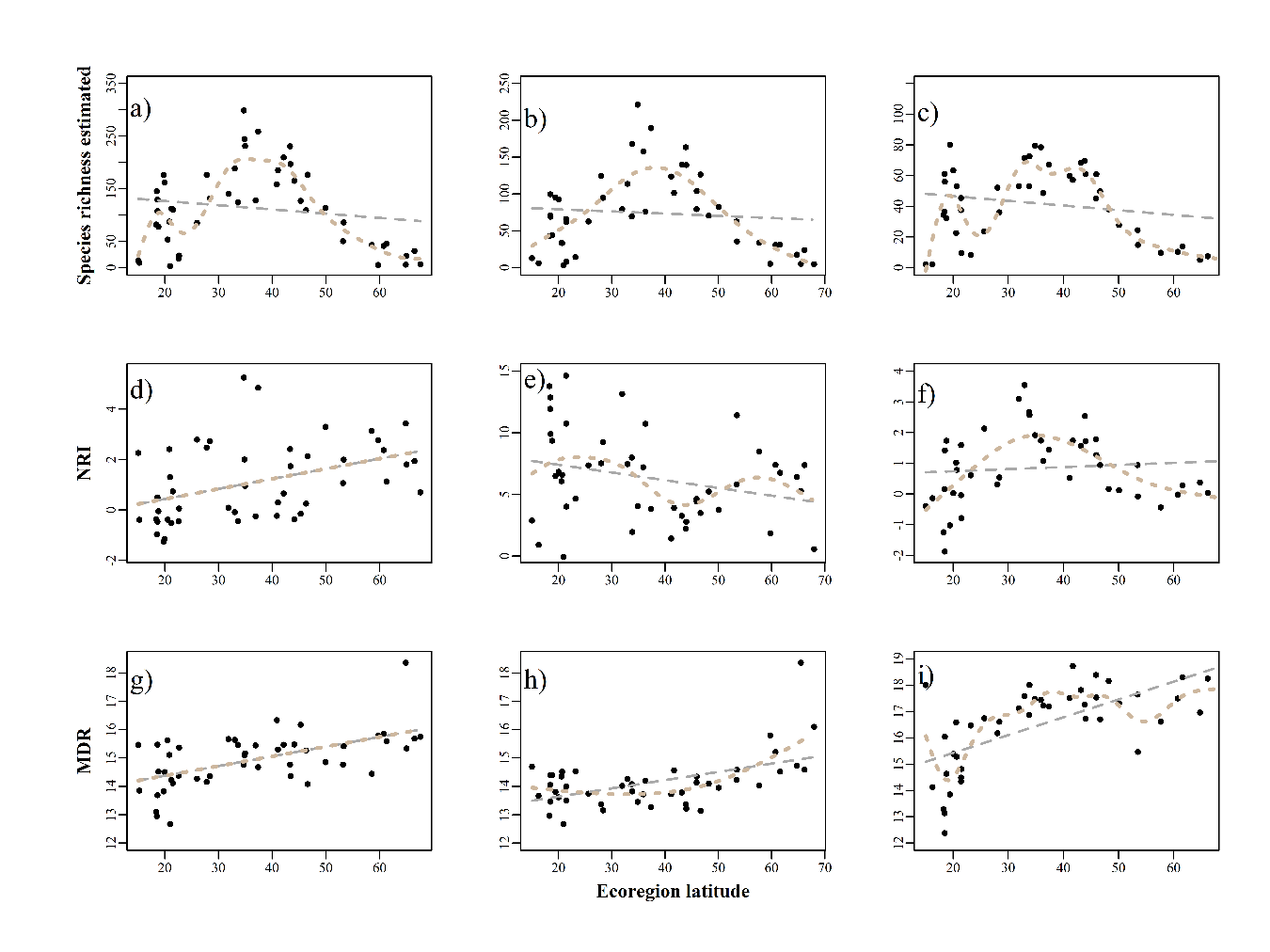
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Data accessibility statement: data can be accessed from <https://doi.org/10.6084/m9.figshare.16958473>

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| **Table 1.** Results of GLMs and GAM of estimated species richness as mean latitudinal points of ecoregion plus ecoregion area, and 1° bands of latitude plus 1° bands of longitudinal. Bold letters indicate significant results. | | | | | | | | |
| **Ecoregion** | | | | | | | | |
| Estimated species richness (Odonata) | | | | | | | | |
|  | **GLM** | | | | **GAM** | |  |  |
| Variable | F | *p* | R2 | AIC | F | *P* | R2 | AIC |
| Mean latitudinal point of ecoregion | 1.58 | 0.21 | 0.22 | 537.38 | **13.52** | **< 0.001** | **0.64** | **502.82** |
| Ecoregion area | 11.09 | < 0.001 |  |  | 2.45 | 0.12 |  |  |
| Dragonfly estimated species richness | | | | | | | | |
| Mean latitudinal point of ecoregion | 0.44 | 0.51 | 0.20 | 504.58 | **12.34** | **< 0.001** | **0.62** | **471.67** |
| Ecoregion area | 10.88 | < 0.001 |  |  | 2.18 | 0.14 |  |  |
| Damselfly estimated species richness | | | | | | | | |
| Mean latitudinal point of ecoregion | 1.73 | 0.19 | 0.15 | 394.47 | **9.0** | **< 0.001** | **0.57** | **368.66** |
| Ecoregion area | 5.82 | < 0.01 |  |  | 1.22 | 0.27 |  |  |
| **1° band of latitude** | | | | | | | | |
| Odonate estimated species richness | | | | | | | | |
|  | **GLM** | | | | **GAM** | |  |  |
| Variable | F | *p* | R2 | AIC | F | *P* | R2 | AIC |
| 1° bands of latitude | 12.11 | < 0.001 | 0.34 | 662.91 | **45.46** | **< 0.001** | **0.88** | **573.15** |
| 1° bands of longitudinal | 16.07 | < 0.001 |  |  | 0.05 | 0.82 |  |  |
| Dragonfly estimated species richness | | | | | | | | |
| 1° bands of latitude | 8.90 | < 0.001 | 0.34 | 620.14 | **57.35** | **< 0.001** | **0.90** | **517.31** |
| 1° bands of longitudinal | 18.69 | < 0.001 |  |  | 0.06 | 0.80 |  |  |
| Damselfly estimated species richness | | | | | | | | |
| 1° bands of latitude | 21.18 | < 0.001 | 0.37 | 516.36 | **20.72** | **< 0.001** | **0.76** | **469.57** |
| 1° bands of longitudinal | 9.29 | < 0.001 |  |  | 0.21 | 0.64 |  |  |

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| **Table 2.** Results of GLMs and GAM of estimated NRI as mean latitudinal points of ecoregion plus ecoregion area, and 1° band of latitude plus 1° band of longitudinal. Bold letters indicate significant results. | | | | | | | | |
| **Ecoregion** | | | | | | | | |
| Odonate NRI | | | | | | | | |
|  | **GLM** | | | | **GAM** | |  |  |
| Variable | F | *P* | R2 | AIC | F | *p* | R2 | AIC |
| Mean latitudinal point of ecoregion | 9.15 | <0.01 | 0.18 | 172.63 | 4.18 | 0.04 | 0.14 | 172.62 |
| Ecoregion area | 0.87 | 0.35 |  |  | 0.87 | 0.35 |  |  |
| Dragonfly NRI | | | | | | | | |
| Mean latitudinal point of ecoregion | 3.70 | 0.06 | 0.09 | 258.03 | 1.09 | 0.30 | 0.05 | 258.03 |
| Ecoregion area | 1.09 | 0.30 |  |  | 1.09 | 0.32 |  |  |
| Damselfly NRI | | | | | | | | |
| Mean latitudinal point of ecoregion | 0.31 | 0.57 | 0.04 | 141.37 | **5.74** | **<0.001** | **0.55** | **135.27** |
| Ecoregion area | 1.67 | 0.20 |  |  | 0.74 | 0.39 |  |  |
| **1° band of latitude** | | | | | | | | |
| Odonate NRI | | | | | | | | |
|  | **GLM** | | | | **GAM** | |  |  |
| Variable | F | *p* | R2 | AIC | F | *p* | R2 | AIC |
| 1° bands of latitude | **12.93** | **<0.001** | **0.31** | **165.83** | 1.37 | 0.24 | 0.33 | 164.87 |
| 1° bands of longitudinal | 11.58 | <0.01 |  |  | 1.36 | 0.24 |  |  |
| Dragonfly NRI | | | | | | | | |
| 1° bands of latitude | 0.52 | 0.47 | 0.01 | 285.07 | **8.29** | **<0.001** | **0.56** | **243.33** |
| 1° bands of longitudinal | 0.07 | 0.78 |  |  | 2.45 | 0.12 |  |  |
| Damselfly NRI | | | | | | | | |
| 1° bands of latitude | 25.72 | <0.001 | 0.48 | 162.5 | **17.18** | **<0.001** | **0.70** | **122.95** |
| 1° bands of longitudinal | 21.45 | <0.001 |  |  | 0.01 | 0.90 |  |  |

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| **Table 3.** Results of GLMs and GAM of mean divergence rates (MDR) as mean latitudinal points of ecoregion plus ecoregion area, and 1° bands of latitude plus 1° bands of longitudinal. Bold letters indicate significant results | | | | | | | | |
| **Ecoregion** | | | | | | | | |
| Odonate MDR | | | | | | | | |
|  | **GLM** | | | | **GAM** | |  |  |
| Variable | F | *p* | R2 | AIC | F | *P* | R2 | AIC |
| Mean latitudinal point of ecoregion | **20.60** | **< 0.001** | **0.31** | **119.99** | 13.73 | < 0.001 | 0.28 | 119.98 |
| Ecoregion area | 0.04 | 0.82 |  |  | 0.04 | 0.82 |  |  |
| Dragonfly MDR | | | | | | | | |
| Mean latitudinal point of ecoregion | 17.03 | < 0.001 | 0.31 | 114.2 | **10.92** | **< 0.001** | **0.44** | **105.36** |
| Ecoregion area | 3.52 | 0.06 |  |  | 0.01 | 0.91 |  |  |
| Damselfly MDR | | | | | | | | |
| Mean latitudinal point of ecoregion | 29.49 | < 0.001 | 0.45 | 142.61 | **5.74** | **< 0.001** | **0.55** | **135.27** |
| Ecoregion area | 2.93 | 0.09 |  |  | 0.74 | 0.39 |  |  |
| **1° bands of latitude** | | | | | | | | |
| Odonate MDR | | | | | | | | |
|  | **GLM** | | | | **GAM** | |  |  |
| Variable | F | *p* | R2 | AIC | F | *P* | R2 | AIC |
| 1° bands of latitude | **64.55** | **< 0.001** | **0.54** | **77.09** | 46.16 | < 0.001 | 0.53 | 77.19 |
| 1° bands of longitudinal | 0.04 | 0.83 |  |  | 0.04 | 0.83 |  |  |
| Dragonfly MDR | | | | | | | | |
| 1° bands of latitude | 55.84 | < 0.001 | 0.64 | 73.07 | **32.94** | **< 0.001** | **0.72** | **60.33** |
| 1° bands of longitudinal | 40.40 | < 0.001 |  |  | 3.98 | 0.051 |  |  |
| Damselfly MDR | | | | | | | | |
| 1° bands of latitude | 25.72 | < 0.001 | 0.48 | 162.5 | **3.91** | **< 0.01** | **0.60** | **150.92** |
| 1° bands of longitudinal | 21.45 | < 0.001 |  |  | 0.47 | 0.49 |  |  |

Figure 1. Patterns at ecoregional level for Odonata: a) species richness: d) NRI, and g) MDR. For dragonflies: b) species richness, e) NRI, and h) MDR. For damselflies: c) species richness, f) NRI, and i) MDR.

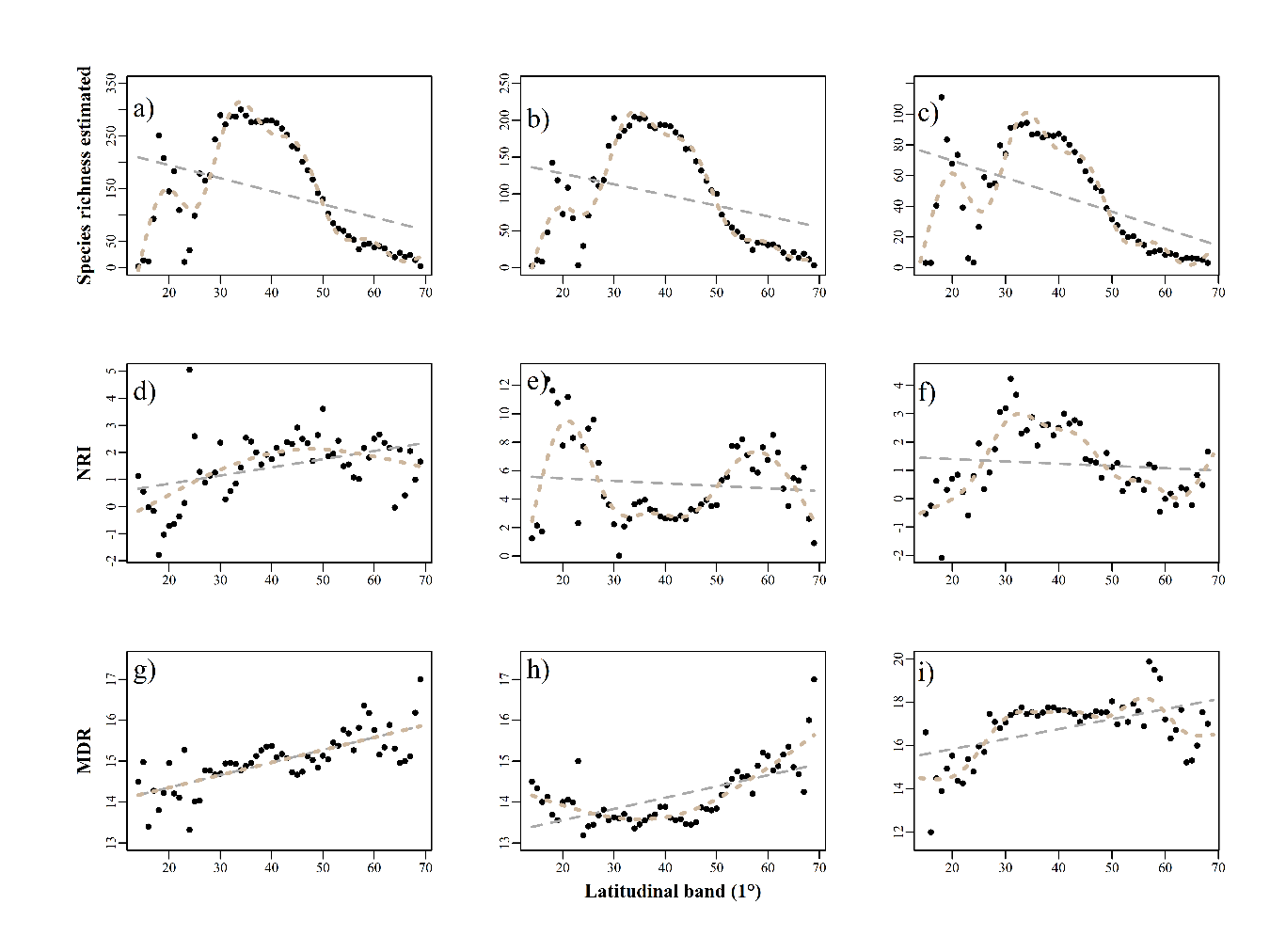
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Figure 2. Patterns at latitudinal band level for Odonata: a) species richness: d) NRI, and g) MDR. For dragonflies: b) species richness, e) NRI, and h) MDR. For damselflies: c) species richness, f) NRI, and i) MDR.

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