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45 **Abstract:** The outstanding biodiversity found in the American tropics (the Neotropics) has attracted the
46 attention of naturalists for centuries. Despite major advances in the generation of biodiversity data, many
47 questions remain to be answered. In this review, we first summarize some of the knowns and unknowns
48 about Neotropical biodiversity, and discuss how human impact may have drastically affected some of the
49 patterns observed today. We then link biodiversity to landscape, and outline major advances in
50 biogeographical research. In particular, we argue that it is crucial to test the effect of landscape and
51 climatic evolution to biotic diversification and distribution in order to achieve a comprehensive
52 understanding of current patterns. In this context, it is also important to consider extant and extinct taxa,
53 as well as to use probabilistic and parametric methods that explicitly include landscape evolution models.
54 We subsequently explore different scales in Neotropical biogeography, focusing on the intersection
55 between biogeography and community ecology, both of which often address similar questions from
56 different angles. The concepts of community assembly, island biogeography, neutral processes, and
57 ecological interactions are then discussed as important components of the complex processes that
58 determine the patterns observed today. Single-taxon and cross-taxonomic studies are complementary and
59 greatly needed, but achieving synthesis remains challenging. Finally, we argue that phylogenetic
60 approaches hold great potential to connect across taxonomic, spatial and temporal scales, despite current
61 difficulties to generate and cross-analyze large volumes of molecular data. We conclude by outlining
62 major prospects and hindrances for further advancing our knowledge on the rich Neotropical biodiversity.

63

64 **Keywords:** biogeography, biotic diversification, community ecology, human impact, landscape
65 evolution, phylogeny, scale, spatio-temporal evolution.

66 I. WHAT DO WE KNOW ABOUT PATTERNS OF NEOTROPICAL BIODIVERSITY?

67

68 Biodiversity refers to the diversity of life across all levels of biological organization (Gaston & Spicer,
69 2004). The diversity of life is unevenly distributed on Earth and varies among and within geographic
70 regions, between terrestrial and aquatic ecosystems, and among different groups of organisms.

71 Biodiversity increases from the poles to the equator, reaching the highest values in tropical regions, a
72 pattern termed the latitudinal diversity gradient (Willig, Kaufman & Stevens, 2003). This pattern is
73 complex though, with numerous non-diverse tropical or diverse non-tropical areas and taxa. More
74 importantly, there are still numerous uncertainties in the underlying data and in our ability to generalize
75 overall patterns and identify their main determinants.

76

77 For many groups of organisms, the Neotropics are home to outstandingly high levels of biodiversity,
78 when compared to other major biotic realms (Lundberg *et al.*, 2000a; Antonelli & Sanmartín, 2011). This
79 region, extending from central Mexico to central Argentina and including the Caribbean islands
80 (Morrone, 2013), contains a vast range of biomes and habitat types, each with a particular biota and
81 evolutionary history (Hughes, Pennington & Antonelli, 2013) (Fig. 1). As such, understanding
82 Neotropical biodiversity patterns and the processes associated with its origin and maintenance is complex
83 (Magurran, 2013). As result, researchers tend to focus on different aspects of biodiversity such as
84 taxonomic, phylogenetic, and functional diversity (Swenson, 2011). Each of these aspects of biodiversity
85 may vary differently among regions and taxa, and each must therefore be assessed by independent criteria
86 (Strecker *et al.*, 2011).

87

88 **Taxonomic diversity**

89 Taxonomic diversity refers to how many taxa can be found within a given area or higher clade, and how
90 individuals are distributed among these taxa. Taxonomic diversity can be quantified at different
91 taxonomic ranks (e.g., species, genera, families), with the species rank being the most popular by far.

92 Species richness – the number of distinct evolutionary lineages – is widely viewed as a fundamental
93 measure of overall biodiversity (Gotelli & Colwell, 2001). This is due to the fact that the species
94 boundary defines the limits of genetic variation, natural selection, and adaptation (Sexton *et al.*, 2009).
95 While individual organisms live and die, the stable phenotypes recognized as species may persist for
96 millions of years, serving as predictable components of the ecosystems in which all species function and
97 evolve (Eldredge, 2014). As result, species are thought to constitute the basic structural and functional
98 units in ecology and evolution (Tilman & Downing, 1996; Worm *et al.*, 2006).

99

100 Generic and family-level taxonomic ranks are occasionally used in comparative studies, especially when
101 species identification or delimitation is difficult (Bertrand, Pleijel & Rouse, 2006). However, higher-level
102 taxa are only arbitrary constructs, reflecting little biological organization and incorporating further biases
103 and artifacts when compared. Species are thus seen as the “fundamental category of biological
104 organization” despite the multitude of species definitions available (de Queiroz, 2005). Taxonomic
105 diversity is generally measured by taxon richness, i.e., the number of taxa in a given area. However,
106 diversity indices (e.g., Brillouin, Shannon-Wiener, and Simpson Index) that take the relative abundances
107 of taxa into account can also be used. These indices allow us to distinguish habitats with the same species
108 richness but different degrees of dominance. Because quantitative abundance data are so rare, few studies
109 to date have documented patterns of diversity in the Neotropics (but see Tuomisto, 2010; Valdujo,
110 Carnaval & Graham, 2013; Steege *et al.*, 2013; Jenkins *et al.*, 2015; Moura *et al.*, 2016; Azevedo, Valdujo
111 & C Nogueira, 2016).

112

113 For well-studied clades, relatively good estimates of taxonomic diversity are available for the Neotropics
114 as a whole, and for each of the major biomes included therein. These estimates have been used to identify
115 the best predictors of diversity at large scales (Jenkins *et al.*, 2015; Moura *et al.*, 2016). However, the
116 observed taxonomic diversity is sensitive to sampling effort. For the Neotropics, taxonomic diversity is

117 generally underestimated, even though the level of sampling across taxa is comparable or even greater
118 than in other tropical regions (Fig. 2).

119

120 For example, in a few years of increased collection efforts, the *Guide of the Ducke Reserve* (Brazil) (da S
121 Ribeiro, 1999), which covers one of the most thoroughly studied areas of Amazonian forest, increased the
122 number of known vascular plants from 825 (Prance, 1990) to 2079 (Hopkins, 2005). Unless sampling is
123 thorough at a given site, species richness of any community will always be underestimated. The accuracy
124 of estimates of taxonomic diversity depends on the number of individuals sampled, the size of the local
125 species pool, the size of the area, and the status of taxonomic knowledge of the groups surveyed (e.g.,
126 Tuomisto, Ruokolainen & Ruokolainen, 2012).

127

128 Even among Neotropical vertebrates, several examples of species-rich yet incompletely- documented
129 fauna are available, including large clades of freshwater fishes, amphibians, and some groups of reptiles.

130 Although about 5,600 species of freshwater fishes are currently known in the Amazon, the Orinoco, and
131 adjacent river basins of tropical South and Central America, more than 100 new species are described
132 every year. In other words, approximately two new species are described per week, although a higher
133 number of new species would be expected if a greater amount of trained taxonomists were available. This
134 rapid pace of species description is not slowing, and recent estimates for the total number of Neotropical
135 freshwater fishes exceed 8,000 species (Reis *et al.*, 2016). This estimate is remarkable, implying that
136 more than 2,400 fish species remain to be described in the Neotropics alone, a number that exceeds the
137 combined number of rodent species currently known on Earth. This large number of expected, but still
138 hidden, lineages represents an example of the unknown unknowns of Neotropical biodiversity.

139

140 Current knowledge of taxonomic limits of Neotropical amphibians and reptiles is gradually growing.

141 Several molecular studies have shown that known diversity is underestimated in many taxonomic orders
142 by the occurrence of high levels of cryptic diversity, i.e., the existence of two or more lineages within a

143 known species (Bickford *et al.*, 2007; Fouquet *et al.*, 2012) to 350% in some groups (Funk, Caminer &
144 Ron, 2011). Even in the much more densely sampled and well-studied Atlantic Rainforest of Brazil,
145 charismatic species of frogs are still being discovered. For instance, seven new species of *Brachycephalus*
146 were recently described for the Atlantic Rainforest (Ribeiro *et al.*, 2015). Likewise, intraspecific analyses
147 of Neotropical lizards show that the occurrence of cryptic diversity is often manifested across biomes
148 (Geurgas & Rodrigues, 2010; Domingos *et al.*, 2014; Guarnizo *et al.*, 2016; Domingos *et al.*, 2017). This
149 subdivision of broadly distributed taxa into multiple cryptic species with restricted geographic
150 distributions increases the perception of biological diversity of a given region, as well as has numerous
151 implications for biogeography (Werneck *et al.*, 2012a), and conservation (Simões *et al.*, 2014).

152

153 Estimates of local taxonomic diversity can be more accurately compared among areas when based on
154 quantitative and standardized sampling such as metrics of beta diversity, i.e., changes in species
155 composition among sites (Tuomisto, 2010; Leprieur *et al.*, 2011). However, this data is only available for
156 organisms whose taxonomy is relatively well understood, such as vascular plants (e.g., trees, ferns), and
157 some vertebrates (e.g., birds, primates). For these same organisms, we also have a general understanding
158 about species richness gradients (e.g., Rosauer & Jetz, 2014). For most other organisms, however, little
159 data are available, preventing accurate circumscriptions of taxa and reasonable estimates of species
160 richness gradients (e.g., Andújar *et al.*, 2015). Indeed, the smaller and less conspicuous the organism, the
161 poorer the state of knowledge. For instance, very little is known about microbial and fungal diversity, and
162 insect diversity is similarly under studied (Basset *et al.*, 2012).

163

164 Another difficulty in assessing taxonomic diversity is associated with the fact that taxa may not represent
165 comparable units. In organisms for which we have a good understanding of distribution patterns,
166 morphological variation, and phylogenetic relationships, more narrowly defined taxa may be recognized.
167 On the other hand, in poorly-studied organisms, species complexes are generally circumscribed as
168 broadly defined taxa, biasing diversity estimates. Similarly, in well-sampled areas, species are likely to be

169 more narrowly defined than those from poorly-known areas. As result, our understanding of taxonomic
170 diversity and species gradients is biased by our taxonomic knowledge (Brito, 2010). Taxonomic units
171 may also vary according to the taxonomist revising a particular group (e.g., whether a ‘splitter’ or a
172 ‘lumper’), and by the data and methodologies underlying taxonomic revisions and species
173 circumscriptions. This issue becomes obvious when taxonomic treatments of the same group are produced
174 by different researchers independently. For example, the Neotropical palm genus *Attalea* included 29
175 species in one monograph (Henderson & Chávez, 1995), and 65 species in another taxonomic treatment
176 published just four years later (Glassman, 1999). Similarly, the Caribbean palm genus *Coccothrinax*
177 included 14 species in one taxonomic treatment (Henderson, Galeano & Bernal, 1995) and 53 species in
178 another (Dransfield *et al.*, 2008).

179

180 *The commonness of rarity.* Species with low abundances and narrow geographic ranges, as well as those
181 confined to special habits, habitats or areas, represent a sizable portion of tropical diversity. Indeed, a
182 recent study extrapolating population size for Amazonian trees suggests that most species in the region
183 are represented by relatively few individuals (Steege *et al.*, 2013). Another study suggests that a
184 considerable fraction of the rare species in the region may actually have relatively large distribution
185 ranges (Zizka *et al.*, 2017), although many apparently widespread species known from very few scattered
186 records may easily turn out to contain multiple biological species. However, the characteristics of these
187 species and their contributions to diversity patterns are difficult to quantify and remain largely obscure
188 (Coddington *et al.*, 2009), partly because most truly rare species will be completely unknown, and partly
189 because rareness in the ecological sense is hard to define, depending on a variety of aspects, including the
190 species concept adopted and the taxonomic preferences.

191

192 As in others biotas, most Neotropical species are rare, narrowly distributed, and endemic to particular
193 regions or biomes (Steege *et al.*, 2016). Plant endemism seems to be largely related to edaphic conditions,
194 although few studies have attempted to empirically quantify factors that cause range restrictions to

195 particular regions (Ficetola, Mazel & Thuiller, 2017). The geographic distributions of many riverine and
196 floodplain taxa are limited by river basin watersheds, and opportunities for dispersal via river capture
197 events (Albert *et al.*, 2017). Climate change velocity is also thought to be associated with restricted
198 distribution patterns. In other words, how fast a species can expand into similar climatic conditions, can
199 affect the species' range. For instance, most vertebrates with small ranges are restricted to areas of higher
200 climatic stability and/or mountainous areas (Sandel *et al.*, 2011). Patterns of endemism may, however, be
201 one of the most difficult things to document given our limited sampling of biodiversity. It is not enough to
202 know where particular species occur, we also need to know where these species do not occur (Soria-Auza
203 & Kessler, 2008). It is, therefore, difficult to reliably say if the biodiversity patterns known to date really
204 reflect true patterns or simple biases in collection effort.

205

206 *Additional biases and gaps.* For most of the Neotropics, detailed geographical distribution information is
207 restricted to certain well-studied taxa (e.g., primates) and well-studied areas (e.g., Barro Colorado Island
208 in Panama, the Ducke Reserve in Brazil). Interestingly, there is also a bias towards rare species, as most
209 scientific collectors tend to over-collect rare or uncommon taxa (Steege *et al.*, 2011). For the vast
210 majority of groups and areas, knowledge is still scarce. For instance, many places in tropical South
211 America have no occurrence records available (Feeley, 2015). Furthermore, particular large areas of
212 Amazonia remain completely unexplored (Hopkins, 2005; Guedes *et al.*, In press). In general, knowledge
213 of species distributions and diversity patterns are strongly biased towards areas that are more easily
214 accessible by roads, rivers, and research stations (Hopkins, 2005; Albert & Carvalho, 2011; Meyer *et al.*,
215 2015). Although bioinformatic solutions may now assist in cleaning, predicting and validating species
216 occurrence data, taxonomic expertise is still essential but limited (Maldonado *et al.*, 2015; Töpel *et al.*,
217 2016). As a result of our limited knowledge on species distributions patterns, and large gaps in knowledge
218 about climatic and edaphic conditions for large portions of the Neotropics, the ecological requirements for
219 species remain only roughly or even completely unknown for most taxa.

220

221 Phylogenetic diversity

222 Phylogenetic diversity assesses cumulative evolutionary distinctiveness within and among areas and taxa.
223 The use of species as universally comparable units may not always be appropriate due to differences in
224 species concepts, operational criteria of delimitation, and circumscriptions among areas, taxa, and
225 taxonomists. In addition, species differ widely in their evolutionary ages, geographic distributions, habitat
226 tolerances, and degree of genetic structure. Species also differ in the biological attributes of their
227 constituent organisms, and therefore, in the effects that these traits may have on ecological and
228 evolutionary processes. Furthermore, species are really just the tips of larger phylogenetic trees evolving
229 through time. Some Neotropical clades are known from just one or a few species that may represent
230 relictual survivors of ancient and extinct groups. Examples include the leaf cacti (*Pereskia* spp;
231 Cactaceae), the South American lungfish (*Lepidosiren paradoxa*; Lepidosirenidae), the hoatzin
232 (*Opisthocomus hoazin*; Opisthocomidae), and the coral pipe snake (*Anilius scytale*; Aniliidae). Other
233 species are members of species-rich Neotropical clades still in the full bloom of their diversification, like
234 the Bignoniaceae with more than 860 species (Fischer, Theisen & Lohmann, 2004), palms with over 730
235 species (Dransfield *et al.*, 2008), armoured catfishes (Loricariidae) with 680 species (Nelson & Platnick,
236 1980a), Cactaceae with 1400 species (Hernández-Ledesma *et al.*, 2015), and tanagers (Thraupidae) with
237 371 species (Burns *et al.*, 2014). To cope with the differences in diversity among different taxa, many
238 researchers have turned their attention to Phylogenetic Diversity (PD) indices (Faith, 1992).

239

240 The basic idea of PD is to measure the total amount of lineage evolution through time found in a
241 particular area (Faith, 1992). Overall, PD has been shown to provide a better estimate of “feature
242 diversity” than species richness alone (Forest *et al.*, 2007). However, there are many ways of deriving and
243 applying such metrics from phylogenies. As such, researchers should try to choose the most appropriate
244 index for each situation, as well as should acknowledge these differences in cross-taxonomic comparisons
245 (Tucker *et al.*, 2016).

246

247 The evolutionary relationships among major groups of macroscopic organisms (i.e., up to family level)
248 are relatively well understood (e.g., Meredith *et al.*, 2011). Recent efforts to understand the global tree of
249 life have improved substantially our understanding of relationships among genera and species (Hinchliff
250 *et al.*, 2015). For instance, recent phylogenies of birds (Jetz *et al.*, 2012), mammals (Faurby & Svenning,
251 2015a) and squamate reptiles (i.e., lizards and snakes) (Tonini *et al.*, 2016) purport to include all living
252 species. However, a substantial fraction of the species included in these studies was placed within the
253 phylogeny solely based on morphological features due to the lack of genetic data. This is especially
254 common for tropical species, for which genetic data is even more limited (Reddy, 2014). In contrast, other
255 phylogenies have been built exclusively from genetic data, such as the seed plant phylogeny for ca.
256 32,000 species (Zanne *et al.*, 2014) and the Neotropical tree phylogeny (Dexter & Chave, 2016). While
257 this approach eliminates incorrect phylogenetic placements based on morphology, it creates biases given
258 the limited genetic data available for tropical species (Antonelli *et al.*, 2015). More detailed knowledge on
259 evolutionary relationships is available for selected groups of vascular plants, e.g., ferns (Lehtonen, 2011),
260 Bignoniaceae (Lohmann, 2006; Grose & Olmstead, 2007; Olmstead *et al.*, 2009), Orchidaceae (Chase,
261 2003), legumes (Azani *et al.*, 2017) and Cactaceae (Hernández-Ledesma *et al.*, 2015).

262

263 The first trials to map phylogenetic diversity over continental and global scales were conducted for
264 selected vertebrate groups for which phylogenies were available and for which distribution patterns are
265 relatively well known, such as amphibians, birds, and mammals (e.g., Safi *et al.*, 2011). Other than these,
266 large-scale phylogenetic and functional diversity studies in the Neotropics are scarce. Some progress has
267 been made in mapping phylogenetic diversity patterns in the Neotropics for specific clades (Rossatto,
268 2014; Fenker *et al.*, 2014; Bacon *et al.*, In press) or at the intraspecific level in the search for areas of high
269 phylogeographic diversity and endemism (Carnaval *et al.*, 2014; Smith *et al.*, 2017). Several ongoing
270 studies by independent research groups are now working to broaden our knowledge on the spatial
271 distribution of Neotropical phylogenetic diversity.

272

273 Complementary to phylogenetic diversity based on the relationships among taxa, patterns of genetic
274 variation within species also represent a vital but often under-appreciated component of biodiversity.
275 Knowledge of intraspecific genetic variation may also improve the prediction of a species ability to adapt
276 to changing climates, as well as can improve the understanding of the determinants of speciation. This
277 type of information is particularly important in the light of global warming. However, our current
278 knowledge of species genetic diversity is restricted to a few selected species, and overall patterns of
279 intraspecific genetic diversity remain poorly understood. Even among well-studied groups (e.g.,
280 mammals), spatial patterns of genetic diversity are effectively unknown within the tropics. In one study
281 addressing this question at a broad spatial scale (Miraldo *et al.*, 2016), found higher genetic diversity at
282 lower latitudes, and lower genetic diversity in Europe. However, no clear pattern was recovered within
283 the tropics.

284

285 A massive increase in the availability of genetic information is being driven by high throughput
286 sequencing technologies. This data accumulation is likely to significantly improve our understanding of
287 genetic diversity and evolutionary relationships amongst species (e.g., Chakrabarty *et al.*, In press).
288 Furthermore, this data will also greatly improve our understanding of largely under-studied groups, such
289 as soil microbes (Mahé *et al.*, 2017). However, a central challenge to understanding current patterns of
290 evolutionary diversity is the absolute dating of phylogenies, which relies heavily on fossils. Fossils are
291 rare and poorly explored and studied in tropical areas, complicating a detailed understanding of the ages
292 of tropical taxa, especially those from rainforests (Wing *et al.*, 2009; Lovejoy, Willis & Albert, 2011). It
293 is therefore crucial that more efforts are put into the exploration, digitization, and analyses of the
294 Neotropical fossil record, in addition to further exploration and sampling of living species.

295

296 **Functional diversity**

297 Functional diversity measures differences in the physiological, behavioral, and ecological characteristics
298 of organisms, and how biological trait values affect ecological and evolutionary processes. Knowledge

299 about species traits and ecological functions (including the variation within and between species) is a
300 crucial component of biodiversity. However, this is one of the major shortcomings in current biodiversity
301 knowledge, especially in tropical areas. Few studies to date have mapped large-scale patterns of
302 functional diversity, although efforts in this direction are underway (see for fishes e.g., Arbour & Lopez-
303 Fernandez, 2014; Toussaint *et al.*, 2016).

304

305 Apart from the lack of data, the theory behind functional diversity is not yet consolidated. We still do not
306 know which traits are important for different groups, how to compare traits for different sets of
307 organisms, and how functional diversity affects forest productivity, stability, and resilience, especially in
308 the tropics. An additional shortcoming is associated with biotic interactions. Apart from basic information
309 on pollination and dispersal syndromes, we know surprisingly little about biotic interactions. Very few
310 species interaction networks are available to date (see Toju *et al.*, 2017).

311

312 For the terrestrial vertebrate groups studied to date, patterns of phylogenetic diversity and species richness
313 seem to be correlated at a global scale, generally supporting the assumption of the surrogacy of various
314 measures (but see Pardo *et al.*, 2016). At least for birds and mammals, global patterns of phylogenetic and
315 functional diversity seem to be comparable (Safi *et al.*, 2011).

316

317 **The human impact on biodiversity**

318 Even though knowledge of contemporary patterns of biodiversity has improved substantially during the
319 past years, it is still unclear whether the documented patterns are derived from natural processes or driven
320 by human influences. Humans have occupied the Neotropics at least since the end of the Late Pleistocene
321 and likely caused major extinctions in the diverse fauna of large mammals (Sandom *et al.*, 2014). The
322 drastic decrease in the density and diversity of large mammals likely led to major changes in overall
323 vegetation structure (Bond, 2005). For example, in South America, the limits between the Dry Diagonal
324 and the adjacent forests may have shifted significantly compared to where they would have been without

325 any human involvement and its cascading effects (Doughty, Faurby & Svenning, 2015). In addition to
326 anthropogenic extinctions, humans likely also caused drastic range contractions of many other species
327 while reduced the abundance of others to the point of ecological irrelevance (Faurby & Svenning, 2015b).
328 The human-linked reduction in Neotropical megafauna likely also affected the plants that they dispersed.
329 This pattern was recently discussed in the context of the impact of over-hunting of primates and tapirs on
330 the total woody biomass of Amazonia (Peres *et al.*, 2016), and large frugivorous in the Atlantic Forest
331 (Bello *et al.*, 2015). Overall, it seems that the patterns observed reflect past hunting. Humans have
332 restricted the ranges of some species, but actively or passively increased the ranges of others, such as
333 invasives or domesticated species (Levis *et al.*, 2017). The knowledge to date is based on the best-studied
334 groups and still it is not clear whether substantial effects of humans will be frequent among other
335 organisms. Clearly, we are observing just the tip of the iceberg.

336

337 Apart from the effects of past human activity for the assembly of Neotropical biodiversity, current habitat
338 loss, climate change and neglected conservation strategies also pose serious threats to natural landscapes.
339 Indeed, these are presumably the primary drivers of the current global biodiversity crisis. Studies that
340 quantify genetic diversity, vulnerability, and extinction risk derived from the impact of habitat loss and
341 climate change are essential to grasp how current human activities are expected to impact the future of
342 Neotropical diversity at multiple levels. Although we now have a fair understanding of several
343 components of Neotropical biodiversity, for many taxonomic groups, well-defined processes remain
344 elusive and biases loom large; refining these issues will constitute an area of active scientific exploration
345 for the next decade and beyond (Table 1).

346

347 **II. BIOGEOGRAPHIC ADVANCES LINKING BIODIVERSITY AND LANDSCAPES**

348

349 **Early ideas about Neotropical biogeography**

350 The Prussian naturalist Alexander von Humboldt was among the first to realize that biotic and abiotic
351 processes work together to constrain species distributions, and to place these influences into a geological
352 framework. He came to this notion in the Neotropics, most famously during his study of the Chimborazo
353 volcano in Ecuador, where he carefully documented the location of different species along elevational
354 zones (Humboldt & Bonpland, 2010). It was in this study that he first observed that physical parameters
355 such as topography and climate were key for floral distributions (Humboldt & Bonpland, 2010).

356

357 A century later, Wegener (1912) advanced the incipient field of historical biogeography with the theory of
358 continental drift, based in part on past geographic distributions of biotas linked by previously connected
359 continental plates. The striking fit between the coastlines of South America and Africa was one of the
360 pieces of evidence inspiring Wegener's theory of dynamic, non-static landmasses. In the 1960s, a
361 geophysical mechanism for plate tectonics was proposed (Vine & Matthews, 1963; Raven & Axelrod,
362 1974; Rosen, 1975), placing studies of plant and freshwater fish biogeography into a plate tectonic
363 framework. This provided historical biogeography a solid basis for further advancement.

364

365 **Inferring landscape evolution in the Neotropics**

366 Now, early in the 21st century, the field of historical biogeography increasingly relies on geological
367 models that specify the landscape configurations on which species originate, disperse, and go extinct.

368 This is especially true in the Neotropics, where understanding phylogeny and biogeography in the context
369 of landscape evolution requires assessment of geological data, including sedimentary environments,
370 sedimentation rates, paleontological records, and fission track ages, among others (e.g., Hoorn *et al.*,
371 1995; Lundberg *et al.*, 2000b; Figueiredo *et al.*, 2009; Hoorn *et al.*, 2010; Sanín *et al.*, 2016; Jaramillo *et*
372 *al.*, 2017; Hoorn *et al.*, 2017).

373

374 Some recent reconstructions of the Neogene landscape in Amazonia are based on numerical modelling,
375 which create reconstructions based on physical parameters such as erosion and mountain uplift. These

376 reconstructions are useful but often depend on arbitrary and artificial values. An example is the
377 reconstruction of the Amazon River where Sacek, 2014 coupled different physical effects derived from
378 the Andes uplift in a mathematical model to explain the drainage reversal in the Miocene (Sacek, 2014).
379 However, this study ignores the synergic effects of plate movement and surface dynamics which are
380 known to have an impact in wetland formation. Other landscape models rely on dynamic topography, in
381 which mantle movements through time are quantified. The effects of these movements are estimated on
382 surface subsidence and are then related to environmental and landscape changes, such as the model
383 applied to explain the genesis of the Pebas wetland in western Amazonia (Hoorn, Wesselingh &
384 Hovikoski, 2010) which reveals the origin of wetlands trough Amazonia. Landscape models are also
385 extremely useful but also lack specificity. Biological data can also help improve landscape models. In
386 recent years, integrated approaches have built landscape evolution models based on both geological and
387 biodiversity data (Craw *et al.*, 2016; Badgley *et al.*, 2017). Some studies make use of geographic
388 information systems (GIS) and combine these with well-dated palynological databases, such as Neotoma
389 (<https://www.neotomadb.org/>). These models are mainly applied to reconstruct landscapes across the
390 Quaternary timescale. For example, reconstruction of changes in connectivity across the northern Andes
391 enabled the inference of cyclic phases of biotic dispersal and speciation versus extinction (Flantua &
392 Hooghiemstra, 2014). Molecular phylogenetic data can also be used to statistically evaluate the likelihood
393 of competing geological models, such as the closure of the Central American Seaway dividing South and
394 Central America (Bacon, 2013), and the roles of the Caribbean plate margins as dispersal corridors
395 between South and Central America (Tagliacollo *et al.*, 2015a). Similar approaches may prove useful in
396 several cases where geological data are insufficient or ambiguous (Baker & Couvreur, 2013).

397

398 **Effects of landscape and climatic evolution on Neotropical diversification**

399 Given the sheer size of the Neotropical region, Neotropical biogeography and biodiversity can only
400 properly be understood when considering the Andean uplift and the effects of this orogeny on the
401 landscape (Fig. 3), and regional climate (Gentry, 1982; Hoorn *et al.*, 2010). The 7,000 km long Andes is

402 strategically positioned perpendicular to the principal global atmospheric currents and traps the humid air
403 of the Intertropical Convergence Zone (ITCZ). This configuration enhances precipitation along the
404 Andean slopes and in western Amazonia, making them wetter than they would be in a low Andes setting.
405 Moreover, the high Andes also redirects the atmospheric flow inducing the southward deflected South
406 American Low-Level Jet (Garreaud *et al.*, 2005; Insel, Poulsen & Ehlers, 2010; Rohrmann *et al.*, 2016).

407

408 The situation is reversed in southern and in northwestern South America. In these regions the Andes trap
409 the humid air of the Southern Hemisphere westerlies (Garreaud *et al.*, 2005). In contrast to the
410 Amazonian scenario, the eastern margin of the Andes at its northern and southern extremes forms a rain
411 shadow where semi-desert conditions prevail, although this situation is partially reverse during El Niño
412 events. Instead, on the western flank there is increased precipitation with more humid conditions
413 (Blisniuk *et al.*, 2005; Palazzesi, Barreda & Cuitiño, 2014). The monumental Andean barrier has thus a
414 huge impact both on the climate and landscapes of South American lowlands, resulting in the
415 modification of river systems and drastic changes in regional climate and habitats.

416

417 The influence of South American climate on biodiversity is well illustrated in the contrasting
418 development of biodiversity between Amazonia and Patagonia. Over the course of the Miocene, Andean
419 uplift led to a humidification of Amazonia and aridification of Patagonia (Blisniuk *et al.*, 2005; Palazzesi,
420 Barreda & Cuitiño, 2014; Rohrmann *et al.*, 2016). This contrast is particularly well-illustrated by the
421 history of New World monkeys (Platyrrhini), which were widely distributed in Patagonia from early to
422 middle Miocene, including the southernmost non-human primates that ever lived (Tejedor *et al.*, 2006;
423 Tejedor & Novo, 2017). However, those primates were later extirpated during regional aridification and
424 global cooling after the Middle Miocene. The platyrrhine record of the high Chilean Andes indicates that
425 the connection between Patagonia and the northern Neotropics possibly persisted on the western part of
426 South America, as the southern Andean cordillera was not an important barrier in the Middle Miocene
427 (Flynn *et al.*, 1995). This scenario provided primates and other animals with a migration route to the

428 north, facilitating faunal turnover (Tejedor & Muñoz-Saba, 2013). This connection may also have
429 contributed to the subsequent Amazonian diversification of crown platyrrhines, including some
430 Patagonian lineages (Rosenberger *et al.*, 2009). Three extant platyrrhine subfamilies were already present
431 in Patagonia by the early Miocene, later represented in the middle Miocene of Colombia (Tejedor &
432 Novo, 2017), which are diverse and widely distributed today.

433

434 The rise of the northern Andes had a major impact on Neotropical biodiversity, as documented for many
435 taxa (e.g., Hughes & Eastwood, 2006; Santos *et al.*, 2009; Antonelli *et al.*, 2009; Tagliacollo *et al.*,
436 2015b; Sanín *et al.*, 2016; Chazot *et al.*, 2016; Diazgranados & Barber, 2017). Recent studies that
437 explicitly integrate surface uplift and climatic changes as a function of speciation and extinction include
438 work on the Andean bellflowers (Lagomarsino *et al.*, 2016), Neotropical orchids (Perez-Escobar *et al.*, In
439 press) and Neotropical hummingbirds (Condamine *et al.*, 2017). A similar approach could be applied to
440 many other taxa and systems, such as the recent cross-taxonomic study on the flora of the Hengduan
441 Mountains by Xing & Ree (2017).

442

443 At an intercontinental scale, the uplift of the Andes can be compared to the Eastern Arc orogeny in
444 Central Africa, which started during the Eocene but reached its maximum in the Pliocene (Pokorný *et al.*,
445 2015). Both of these events resulted from the slow collision of two plates and contributed to the
446 ‘humidification’ of Amazonia and Central Africa, respectively. However, the northeastward movement of
447 Africa brought the continent close to the Equator, closing the Tethys Seaway and precipitating an
448 aridification that remains today (Pokorný *et al.*, 2015). Advances on climatic reconstructions via historical
449 records and climatic modeling (Cheng *et al.*, 2013; Wang *et al.*, 2017) or biome paleo-distribution
450 modeling (Carnaval & Moritz, 2008; Werneck *et al.*, 2011; 2012b; Ledo & Colli, In press) allow for
451 direct hypothesis testing based on independent biodiversity data.

452

453 **Methodological approaches for estimating biogeographic histories**

454 Inferring spatial and temporal dimensions of evolution are fraught with difficulties, especially due to the
455 lack of abundant and evenly sampled biological and geological data. This is particularly critical for the
456 Neotropics due to the region's size, limited access, extraordinary biodiversity levels, landscape
457 heterogeneity, and complex evolutionary and geo-climatic histories. To tackle these problems, we
458 summarize some of the main issues associated with the analyses of biogeography and diversification,
459 focusing on how those issues affect Neotropical biodiversity research.

460

461 *Definition and use of operational units.* Defining units of study in biogeography, sometimes called “areas
462 of endemism,” is not an easy task, especially when diverse systems are involved such as the Neotropics.
463 Sympatry or the geographic congruence among the distribution areas of taxa, is often used as a criterion
464 to define sound units for these studies. The identification of such areas has long been based on expert
465 opinion, with data-driven approaches that use actual species distribution data only becoming available
466 more recently (Holt *et al.*, 2013; Vilhena & Antonelli, 2015; Edler *et al.*, 2016; Antonelli, 2017). These
467 approaches to bioregionalization are of great importance as they allow for more objective, reproducible
468 and informative analyses. Areas have also been defined using geologically explicit criteria, including
469 information on the geological history of landmasses or geographic barriers, both of which are not
470 exclusive to the group under study (Antonelli *et al.*, 2009; Albert & Carvalho, 2011; Töpel *et al.*,
471 2016 ;Bacon *et al.*, In press). Areas defined based on species distribution patterns and geological history
472 are of particular interest (Perret *et al.*, 2007; Givnish *et al.*, 2014).

473

474 The use of areas as discrete entities is useful in parametric biogeographic models where areas are
475 considered as biogeographic traits that evolve along the phylogeny, and whose ancestral areas are inferred
476 at speciation nodes. In these models, the spatial units of analysis are defined by the biogeographic
477 hypothesis under examination. For example, it is possible to determine whether diversification rates have
478 been historically higher in Andean or non-Andean taxa (Chazot *et al.*, 2016). However, defining areas as
479 discrete entities is difficult when there are overlapping boundaries and an excess of widespread taxa.

480 Models have been proposed to objectively define areas of endemism by overlapping taxa with “fuzzy”
481 boundaries (Szumik *et al.*, 2002; Szumik & Goloboff, 2004). Similarly, biotic element analyses have also
482 been proposed to test for non-random distributions of species ranges (Hausdorf & Hennig, 2003). Some
483 of these methods have been applied to Neotropical taxa (Casagrande M, Roig-Juñet & Szumik, 2009;
484 Noguera-Urbano & Escalante, 2015; Azevedo, Valdujo & C Nogueira, 2016).

485

486 Another possibility is to use vicariance -- geographic barriers -- rather than areas as units of analysis
487 (Hovenkamp, 1997; Arias, Szumik & Goloboff, 2011; Arias, In press). This approach explicitly
488 introduces the spatial (landscape) aspect missing from the predefined areas-as-discrete entities used in
489 parametric biogeography. Since this approach is based on taxon-defined ranges, biogeographic
490 reconstructions are not dependent on different area definitions (Arias, in press). A parametric version of
491 this approach allows geographic (dispersal) barriers to evolve over time within the landscape (Albert *et*
492 *al.*, 2017).

493

494 An alternative to using discrete areas in biogeographical analyses is the spatial diffusion approach, which
495 conducts spatial-temporal reconstructions under random walk models within likelihood (Lemmon &
496 Lemmon, 2008) or Bayesian (Lemey *et al.*, 2010) frameworks. This approach has been used to study taxa
497 from open and dry Neotropical biomes (Werneck *et al.*, 2011; 2012b; Nascimento *et al.*, 2013; Camargo
498 *et al.*, 2013), and taxa with broad continental distributions (Gehara *et al.*, 2014). A further development of
499 this approach has been applied to the Neotropical bird genera *Psophia* and *Cinclodes* (Quintero *et al.*,
500 2015). The method uses georeferenced point-localities to infer ancestral areas and thus does not make
501 assumptions about species ranges and operational units that fit many taxa. On the other hand, this method
502 suffers from the common issue of ancestral lineages occupying average values of the descendant lineages.
503 For instance, analyses with this method have reconstructed the ancestral of *Cinclodes* ovenbirds to a
504 region in-between the western and eastern margins of South America, where no such species occur today
505 (Quintero *et al.*, 2015).

506

507 Considering the complex and dynamic nature of the Neotropical region across multiple temporal and
508 spatial scales, spatial diffusion biogeographic analyses would greatly benefit from the incorporation of
509 landscape-explicit models that allow the reconstruction of actual paths along branches (McRae *et al.*,
510 2008). These developments would allow the incorporation of spatial heterogeneity via dispersal
511 constraints, derived from estimated ecological niche models or landscape evolution models, among
512 others.

513

514 *Single lineage approaches.* These provide detailed reconstructions of the temporal and spatial evolution
515 for individual clades, species, or lineages. The focus is not on generalities but on contingencies or events
516 that are idiosyncratic to the group under study. Methodological advances in single lineage approaches
517 have undergone major developments with parametric methodologies (Ree & Sanmartín, 2009; Landis *et*
518 *al.*, 2013; Matzke, 2014). The explosion of molecular phylogenetics and molecular dating analyses
519 allowed inference of time-calibrated trees, where branch lengths are measured as units of time or rates of
520 molecular evolution. The integration of time-calibrated trees into biogeographic analyses allowed the
521 establishment of links with external sources of temporal information such as landscape evolution,
522 geological history, fossil record, and climate history.

523

524 Typical biogeographic analyses currently use time-trees and parametric models of biogeographic
525 evolution to reconstruct ancestral ranges at speciation nodes, and to infer rates of biogeographic processes
526 (e.g., dispersal, speciation, and extinction). Parametric biogeographic models are based on Continuous-
527 Time Markov chains (CTMC). These are stochastic, memoryless processes in which transition rates
528 between discrete states (i.e., geographic ranges) are governed by an instantaneous Q matrix, with
529 transition probabilities obtained after exponentiating the matrix as a function of time (i.e., branch lengths)
530 (Ronquist & Sanmartín, 2011). Transition rates are defined in terms of biogeographic processes

531 describing the evolution of geographic ranges, such as range expansion, jump dispersal, range contraction
532 and local extinction.

533

534 Biogeographic hypotheses or models about the relative role of these processes in a the geographic
535 evolution of particular groups can be compared statistically using methods for model selection in
536 phylogenetics, such as Likelihood Ratio Tests (LRT) or Bayes Factors (Sanmartín & Meseguer, 2016).
537 Moreover, the rates of these processes may be modified (scaled) to reflect the changing connectivity
538 among the areas of analysis over time (Ree & Smith, 2008). These advances have contributed to the
539 integration of landscape dynamics and geological history into taxon biogeography in the Neotropics (e.g.,
540 Perret *et al.*, 2013; Givnish *et al.*, 2014; Chazot *et al.*, 2016 ;Bacon *et al.*, In press). Dispersal-Extinction-
541 Cladogenesis (DEC), a likelihood-based method derived from CTMC models, is likely the most popular
542 parametric biogeographic method. This method infers anagenetic evolution (i.e., along branch internodes)
543 as a function of two rate parameters: range expansion (dispersal) and range contraction (local extinction).
544 Cladogenetic evolution (i.e., at speciation nodes) is modeled as the likelihood of alternative range
545 inheritance scenarios that describe the division of ancestral ranges into descendant nodes: sympatric
546 speciation, allopatric (vicariance) speciation, and peripheral isolate speciation in the case of widespread
547 ranges (Ree & Smith, 2008).

548

549 The popularity of DEC is based on the fact that, given a time tree and associated terminal distributions, it
550 can provide detailed biogeographic reconstructions of the ancestral origin of a clade and the history of
551 dispersal and extinction events that helped model its spatial evolution (Sanmartín & Meseguer, 2016). A
552 potential drawback of DEC is, however, the number of areas that it can implement. Because widespread
553 geographic ranges (comprising two or more areas) are possible states in the Q matrix, a large number of
554 unit areas rapidly leads to computational and convergence issues. Constraining the number of states based
555 on biological or geological criteria, is a way to decrease model complexity (Ree & Sanmartín, 2009).

556

557 Bay-Area, a data augmentation approach based on stochastic mapping and which extends the DEC model
558 to deal with a large number of unit areas, has been proposed to tackle the limited number of areas allowed
559 in DEC (Landis *et al.*, 2013). Furthermore, the parameter (“J”) was introduced to model “jump dispersal”
560 or founder-event speciation (Matzke, 2014). This extra parameter effectively reduces the contribution of
561 range expansion, and therefore of widespread range evolution, in biogeographic likelihood estimations
562 (Matos-Maraví *et al.*, 2013; Matzke, 2014; Ree & Sanmartin, in prep.). The DEC+J model is
563 implemented in the package BioGeoBEARS (Matzke, 2013) implemented in R (R Development Core
564 Team, 2017), and is now widely used in Neotropical biogeography (e.g., Matos-Maraví *et al.*, 2014;
565 Espeland *et al.*, 2015; Chomicki & Renner, 2016).

566

567 *Cross-taxonomic (multi-clade) approaches.* Unlike single taxon biogeographic approaches, cross-
568 taxonomic approaches aim to extract generalities on the evolution of a biogeographic region or a whole
569 biota, or generalities on the relationships among biogeographic regions or biotas, by reconstructing the
570 history of their individual components. The focus of this approach is not on obtaining detailed
571 reconstructions of each individual lineage (although these reconstructions inform the model), but on
572 inferring shared biogeographic histories, such as general patterns of colonization and diversification or a
573 common response to extinction events. This approach was traditionally known as “area biogeography”
574 and was the focus of the cladistic biogeographic school for decades (Nelson & Platnick, 1980b;
575 Humphries & Parenti, 1999b).

576

577 The first methods used for cross-taxonomic biogeographic approaches were based on parsimony, which
578 does not allow the integration of a temporal dimension (Crisci *et al.*, 1991; Marshall & Liebherr, 2000;
579 Sanmartín, 2016). Further approaches attempted to solve this issue by adopting an event-based approach
580 to recover the relative sequence of biogeographic events (Sanmartín, 2007). However, these methods are
581 subject to “biogeographic pseudo-congruence,” when the same biogeographic pattern originates in two
582 clades at different times and therefore, not as a result of a shared biogeographic history (Donoghue &

583 Moore, 2003). *Ad hoc* introduction of time into event-based methods allow the identification of reticulate
584 history or the cyclical formation and disappearance of dispersal corridors and barriers. This is the case of
585 the North Atlantic and Beringian Land Bridges in the migration of Holarctic faunas and floras (e.g.,
586 Sanmartín, Enghoff & Ronquist, 2001; Donoghue & Smith, 2004). Parametric approaches such as the
587 biogeographic CTMC models (Ronquist & Sanmartín, 2011) offer a more powerful way to obtain
588 generalities about patterns of dispersal and diversification in biotas, allowing us to test between
589 alternative geological or spatial scenarios. One such example is the Bayesian Island Biogeographic (BIB)
590 model of Sanmartín *et al.* (2008), which uses a hierarchical Bayesian model to infer common rates of
591 colonization and area carrying capacities from phylogenetic and distribution data across multiple clades.
592 Because phylogenies are co-estimated with the model (and not fixed as in DEC), and each clade is
593 allowed to evolve under its own molecular rate, BIB can be used across different, unrelated organisms
594 that differ in biological traits such as the age of origin or dispersal ability, but which inhabit the same set
595 of oceanic (Sanmartín, van der Mark & Ronquist, 2008) or continental islands (Sanmartín *et al.*, 2010).

596

597 *Landscape evolution models (LEMs) and biotic diversification.* A potential problem with single-taxon and
598 cross-taxonomic parametric analyses is that areas are treated as traits of organisms evolving along
599 phylogenetic trees. Geology is often used to inform the model but does not form its core. For instance,
600 area connectivity is often used in parametric methods to constrain or scale migration rates but not as an
601 actual part of the model.

602

603 At first, the explanatory power of vicariance biogeography was the ability to predict biogeographic
604 distributions of individual taxa and that of whole biotas from knowledge of how landscapes changed
605 through time (Rosen, 1978). The paradigmatic example is the geological fragmentation of the Gondwana
606 supercontinent, and the resulting fragmentation of the resident Gondwanan biotas. The vicariance
607 biogeography approach satisfies the scientific impulse of systematists and biogeographers for general
608 explanations of organismal distributions, rather than ascribing each distribution to the vagaries of

609 idiosyncratic dispersal and extinction events (Humphries & Parenti, 1999a). However, ecologists have
610 long understood dispersal to be a perennial and pervasive process influencing biogeographic distributions
611 (Cowie & Holland, 2006), and evidence for the action of long-distance, overseas dispersal has now been
612 documented in the formation of many biotas worldwide (Bell *et al.*, 2015) including those in the
613 Neotropics (Smith *et al.*, 2014; Tagliacollo *et al.*, 2015a; Hawlitschek, Ramírez Garrido & Glaw, 2017).
614 Similarly, palaeontologists have long understood extinction as an important driver of patterns in
615 biodiversity and biogeography (Jablonski, 2008). The challenge to vicariance biogeography as a general
616 theory is the commonplace observation that vicariant cladogenesis (i.e., speciation) is only one of three
617 general macroevolutionary processes, along with dispersal and extinction (Ree & Smith, 2008).

618

619 A new generation of methods is now being developed using the power of landscape evolution models to
620 study the full panoply of evolutionary processes, at both microevolutionary (population) level (Byrne &
621 Hopper, 2008; Morlon, 2014) and macroevolutionary (interspecific) scales (e.g., Tagliacollo *et al.*, 2015b;
622 Badgley *et al.*, 2017). For example, uplift of a dissected landscape and river capture are two landscape
623 evolution processes with great power to generate high species richness. Both of these processes
624 simultaneously and continuously merge and separate portions of adjacent landscape areas, allowing biotic
625 dispersal and larger geographic ranges, vicariant speciation and smaller geographic ranges, and extinction
626 when range sizes are subdivided below a minimum persistence threshold (Albert *et al.*, 2017).

627

628 *Integrating fossils into biogeography.* One important shortcoming of molecular-based biogeographic
629 analyses in general, and parametric models of range evolution in particular, is the fact that it is almost
630 always based on extant data alone. Because of the effects of extinction, the pattern of geographic
631 distribution we observe today may be a poor representation of the actual biogeographic history, especially
632 if extinction rates have been unequal among areas (Meseguer *et al.*, 2015) and taxa (Silvestro *et al.*,
633 2016). One way to solve this is to include extinct lineages in biogeographic analyses (Mao *et al.*, 2012),
634 or to use their distribution (the fossil record) to constrain inferences of ancestral ranges (Meseguer *et al.*,

635 2015). This has in many cases revealed a new, different biogeographic history for the study group (Mao *et*
636 *al.*, 2012; Meseguer *et al.*, 2015). An alternative approach is a modification of DEC, termed DES
637 (Dispersal-Extinction-Sampling), to infer rates of dispersal and area extinction exclusively from fossil
638 data (Silvestro *et al.*, 2014; 2015). An additional sampling parameter is used to account for the
639 unevenness of the fossil record both spatially and temporally. Advantages of this approach are that the
640 fossil record provides a more accurate measuring of changes in rates of geographic evolution and
641 unbiased extinction rates, than if only extant taxa are used (Silvestro *et al.*, 2015).

642

643

644 **III. FROM LARGE TO FINE SCALES: BIOGEOGRAPHY MEETS COMMUNITY ECOLOGY**

645

646 While biogeographic studies are key to identify large-scale patterns and processes, different processes
647 operate at regional and local levels. A major question in tropical biodiversity is how ecological
648 communities have been assembled over time and how abiotic factors and species' interactions have
649 influenced this process. Approaches for the study of tropical communities have employed a wide range of
650 models with diverse conceptual roots. Over the last 20 years, there has been an expansion from studies
651 focusing on contemporary community structure and spatial patterns of physical properties of ecosystems,
652 to studies focusing on historical aspects of community structure and evolution (Leite & Rogers, 2013;
653 Smith *et al.*, 2017). Early approaches (e.g., Margalef, 2015) focused on indexes of diversity, descriptions
654 of community membership, as well as flow charts of energy and nutrients through the community. Key
655 variables influencing community structure consistently emphasized classic Hutchinsonian processes such
656 as resource use, competition, and niche partitioning. However, as ecologists adopted new techniques, the
657 resolution of the niche increased from simple variables exclusively to also include high-resolution data on
658 climate, soil chemistry, microbiomes and other physical and biological properties. These approaches have
659 guided several recent analyses of tropical groups, including micro-organisms and palms (Costa *et al.*,
660 2009a; Mendes *et al.*, 2015). Additionally, the availability of spatially explicit online global datasets of

661 climate and environmental parameters has helped spawn a generation of studies using large-scale spatial
662 biodiversity surveys and inventories, analyzed with statistical approaches, allowing the interpolation
663 between sampled sites and estimated diversity in unsampled areas (Costa *et al.*, 2007; 2009b; Steege *et*
664 *al.*, 2010; 2013). Such studies yield important data for interpreting community processes. However,
665 progress in this area is often based on the important assumption that ecosystems and community
666 structures are at equilibrium, or nearly so. Analyzing such data sets under non-equilibrium assumptions is
667 an important challenge for the future.

668

669 The theory of island biogeography (TIB) (MacArthur & Wilson, 2016) introduced parameters such as
670 colonization, immigration, and extinction within a mathematical framework, allowing the prediction of
671 community structure, dynamics, and diversity (Losos & Ricklefs, 2009; Warren *et al.*, 2015). The TIB has
672 inspired models that attempted to integrate additional parameters, such as speciation and island ontogeny
673 (Whittaker, Triantis & Ladle, 2008), abundance (Rosindell & Harmon, 2013), and trophic interactions
674 (Gravel *et al.*, 2011). Whereas the TIB maintained a focus on species as the unit of analyses, another
675 strand of theory introduced individual-based models that assumed ecological or functional equivalence of
676 individuals in communities inspired by Hubbell's neutral theory of biodiversity (NTB) (Hubbell, 1997).
677 In the ecological sense, both the TIB and NTB are not-equilibrium models, however they are often
678 invoked as equilibrium models in macroevolutionary perspectives. Their predictions are based on
679 conditions of systems states (i.e., values of parameters such as dispersal, colonization, speciation,
680 extinction, and the strength of species interactions) in which all competing influences are balanced
681 (dynamic equilibrium), or have not changed over time (static equilibrium).

682

683 Alternatively, other models have dynamic equilibria in which the parameter values balance one another,
684 giving a constant result, such as the number of species. In the last 15 years, community ecology, and an
685 expanded TIB, have adopted a more historical approach by integrating phylogenetic data to the study of
686 community assembly and dynamics, including the role of *in situ* adaptation or speciation versus dispersal

687 in community assembly, the temporal sequence of species interactions, or the role of abiotic and biotic
688 factors in diversification of specific lineages (Webb *et al.*, 2003; Sanmartín, van der Mark & Ronquist,
689 2008; Valente, Etienne & Phillimore, 2014; Valente, Phillimore & Etienne, 2015; Cabral, Valente &
690 Hartig, 2017). By adopting a more historical focus, these methods get around the equilibrium assumption
691 by explicitly attempting to reconstruct the sequence of events leading to modern-day communities. These
692 approaches relax the assumption of ecological neutrality, and focus on the uniqueness of individual
693 lineages, historical contingency, and particularities of present-day outcomes (Emerson & Kolm, 2005;
694 Sanmartín, van der Mark & Ronquist, 2008). In their most recent forms, these models incorporate
695 ecological parameters such as competition and species interactions (Clarke, Thomas & Freckleton, 2016)
696 or landscape dynamics (Aguilée, Claessen & Lambert, 2013).

697

698 The diversity of theoretical approaches has enriched the field of tropical biology, particularly in the
699 Neotropics. Below we provide some examples of how different approaches to community ecology have
700 been applied to (Neo)tropical systems.

701

702 *Island biogeography studies.* The Amazon basin is highly heterogeneous although this heterogeneity is
703 rarely structured in ways that are amenable to the application of island biogeography theory. However,
704 ‘white-sand’ habitats in the interior of the Amazon seem to represent ‘islands’ with savanna-like
705 vegetation and distinctive plants and animals, that often achieve differentiation or endemism due to their
706 isolation and environmental uniqueness compared to the surrounding lowland rainforest (Anderson, 1981;
707 Alonso, Metz & Fine, 2013). Although a similar situation is found for the fragmented and understudied
708 Amazonian savannas (de Carvalho & Mustin, 2017), open areas are characterized by lower richness for
709 some taxa (e.g., amphibians and reptiles) that may harbor species with restricted distributions missing
710 from adjacent Amazonian mainland forests (Borges *et al.*, 2016). These islands are known as “*campinas*”
711 and are the focus of active research programs (see Fine & Bruna, 2016). Bird diversity in these white
712 sands islands has been shown to conform well to the predictions of TIB, with larger and more connected

713 islands including a higher number of species than smaller and more isolated patches (Oren, 1982).
714 Furthermore, assembly studies at the regional scale have shown that lizard local richness is explained by
715 patch size, degree of isolation, and stochastic extinction following isolation (Gainsbury & Colli, 2009).
716 However, Alonso *et al.* (2013) and Borges *et al.* (2016) suggested that more regional effects, perhaps
717 overshadowing patch size, also seem to be at play. For instance, patches south of the Marañón/Amazon
718 region seem to be depauperate when compared to northerly patches (Alonso, Metz & Fine, 2013; Borges
719 *et al.*, 2016). Nonetheless, white sands provide a compelling example of island biogeography theory in
720 the context of a continental biota.

721

722 *Niche-based studies.* The general idea that species are adapted to their environment (i.e., have different
723 niches) has two important consequences. First, species distributions are expected to reflect the distribution
724 of suitable habitats. Second, species composition in local communities should reflect the environmental
725 characteristics of the site, as unsuitable environmental characteristics or biotic interactions make it
726 impossible for a species to establish and/or survive. Along these lines, many studies have aimed to
727 characterize the edaphic associations of tropical plant species (Tuomisto & Poulsen, 1996; Tuomisto *et*
728 *al.*, 2003; Phillips *et al.*, 2003; Costa, Magnusson & Luizao, 2005; Roncal, 2006; Zuquim *et al.*, 2009;
729 Kristiansen *et al.*, 2012; Cámara Leret *et al.*, 2017) and the elevational ranges of many taxa (Kluge, Bach
730 & Kessler, 2008). If there are more species adapted to some environmental conditions than others and
731 dispersal limitations are unimportant, a species richness gradient should result. However, it is also
732 possible that some environmental conditions may allow more species to coexist than others. Several
733 studies have analyzed species richness gradients along environmental gradients such as elevation (Kluge,
734 Kessler & Dunn, 2006; Brehm, Colwell & Kluge, 2007), rainfall (Clinebell *et al.*, 1995; Esquivel
735 Muelbert *et al.*, 2017), and soil fertility (Costa, Magnusson & Luizao, 2005; Steege *et al.*, 2006;
736 Tuomisto, Zuquim & Cárdenas, 2014). In general, these studies have shown that Neotropical species
737 richness tends to be highest in warm, humid, and aseasonal environmental niches at low to middle
738 elevations.

739

740 *Neutral and non-neutral perspectives.* In contrast to niche-based processes, spatial patterns in abundance
741 in communities of anurans from Central Amazonia have been shown to follow Hubbell's neutral
742 biodiversity theory (Diniz-Filho *et al.*, 2011). However, Manceau *et al.* (2015) demonstrated that, the
743 incorporation of population genetic dynamics into NBT supported the hypothesis that biodiversity
744 dynamics are out of equilibrium, and that these types of models can predict macroevolutionary patterns
745 (Manceau, Lambert & Morlon, 2015). Additional research is still needed to assess the relative roles of
746 niche constraints, neutral, and non-neutral processes in explaining and predicting Neotropical
747 biodiversity.

748

749 *Ecological interactions.* It is now evident that species interactions (mutualistic or antagonistic) play a
750 major role in the spatial distribution of taxa, the evolution of communities (Wiens, 2011), and species
751 boundaries (Pigot & Tobias, 2013). Biotic interactions can be a source of ecological divergent selection,
752 with interspecific competition representing a major contributor to ecological character displacement
753 (Rundle & Nosil, 2005). In turn, this suggests that competition may play an important role in shaping
754 ecological speciation at meta-community scale. Geography can also affect gene flow among populations,
755 and the ecological sources of divergent selection (Räsänen *et al.*, 2012). Large-scale biogeographical
756 studies based on interspecies interactions are still lacking, reflecting a general paucity of interaction data
757 as well as difficulties in estimating past interactions and processes. However, speciation resulting from
758 species interactions may represent a main driver of biotic radiations (Elias *et al.*, 2012; Correa Restrepo *et*
759 *al.*, 2016). Such a model seems to apply to both plants (Xu, Schlüter & Schiestl, 2012) and animals, such
760 as the South American opossums, where biotic interactions may have led to allopatric speciation
761 (Gutiérrez, Boria & Anderson, 2014).

762

763 Exploring ecological interactions among species can help improve our understanding of the evolution of
764 biotic associations. For arboreal ants (*Pseudomyrmex*) and their host plant *Vachellia* (Mimosoidae),

765 historical associations and new colonizations (*Platymiscium*, *Tachigali*, and *Vachellia*) have been
766 documented (Chomicki, Ward & Renner, 2015). This study highlights how new interactions, formed by a
767 group of ants colonizing a new plant, can contribute to an interaction shift (from parasitic to mutualistic).
768 The macroevolutionary assembly of ant-plant symbiosis in the Neotropics seems to be highly dynamic
769 and underlines convergent evolution of complex multispecies interactions.

770

771 The integration of phylogenetic inference coupled with network theory has shed light on the importance
772 of interaction dependence (mutual dependence vs. asymmetric dependence) in the radiation of interacting
773 species. For instance, Ramirez *et al.* (2011) unraveled the evolutionary processes involved in the
774 specialized association between Neotropical stingless bees (Euglossini) and Euglossinni-pollinated
775 Orchids using this approach (Ramírez *et al.*, 2011). More specifically, through a combination of
776 phylogenetic inference, network analysis, and chemical data, this study revealed that selection on orchids
777 for their specialized pollinators triggered their radiation, whereas a similar radiation was not observed for
778 the bees.

779

780 *Phylogenetic approaches.* Community phylogenetic approaches have been used to test hypotheses
781 involving multiple historical and ecological factors controlling phylogenetic diversity over time. Kissling
782 *et al.*, (2011) showed that global diversity in palms (Arecaceae) has strong phylogenetic clustering on
783 islands and in the Neotropics (Kissling *et al.*, 2012). Recently, a “Historical Assembly Analysis” was
784 proposed (Weeks, Claramunt & Cracraft, 2016) as a conceptual framework for integrating evolutionary
785 history and ecological processes into studies of biotic assembly. Using this approach, the assembly
786 history of Amazonian *Pteroglossus* toucans was reconstructed through time and space using a
787 combination of phylogenetic and biogeographical tools (Weeks, Claramunt & Cracraft, 2016).

788

789 Thus far, most community phylogenetics approaches have been applied to single lineages, within which
790 competition and other ecological processes are thought to dominate. Because it is unlikely that ecological

791 and community processes operate within individual lineages, cross-taxonomic community assembly
792 analyses would be especially relevant. For instance, important insights were gained from a study on the
793 phylogenetic assembly of Amazonian tree communities within a comparative framework (Dexter *et al.*,
794 2017).

795

796 **Scaling up community ecology approaches**

797 The original goals of community ecology, as established in the early 20th century, were to predict species
798 distributions and abundances, species richness and equitability, community productivity, food web
799 structure, predator-prey dynamics, succession, and community assembly. However, as noted by leaders in
800 this field, this discipline has not yet succeeded in meeting most of these goals (Ricklefs, 2008; Ritchie,
801 2009; Vellend, 2010; Ricklefs & Jenkins, 2011; Weber & Strauss, 2016). The reasons are many, but may
802 be especially associated to the non-equilibrium of most local assemblages, in which the effects of
803 historical contingencies of dispersal, extirpations, and other stochastic processes override the equilibrium
804 expectations generated by local functional processes such as predation and competition (Fig. 4). In other
805 words, the species composition and equitability of most local assemblages are more strongly governed by
806 regional and historical factors than by local ecological interactions (Mittelbach & Schemske, 2015;
807 Manceau, Lambert & Morlon, 2015; Fukami, 2015; Weeks, Claramunt & Cracraft, 2016). This crisis in
808 community ecology has fueled the rise of alternative functionally-neutral theories, like the TIB
809 (MacArthur & Wilson, 2016), the NTB (Hubbell, 2011), and the metacommunity theory (Leibold *et al.*,
810 2004). However, neutral theories have been criticized for their simplistic assumptions and lack of
811 predictive power under the non-neutral conditions frequently observed in nature (e.g., McGill *et al.*,
812 2006). In general, the field of community ecology appears to be ripe for a paradigm shift (DeAngelis &
813 Grimm, 2017).

814

815 While many studies conducted at the global scale aim to test broad hypotheses about drivers of
816 biodiversity gradients (Fine, 2015), others rely on analyses of region-wide field data collected over

817 decades. For example, Amazonian tree diversity catalogued across 1170 forest plots has been used to
818 estimate tree populations across one-degree cells (Steege *et al.*, 2013). In addition to documenting
819 hyperdominance of Amazon tree communities by only 227 species, tree diversity was also shown to be
820 highly heterogeneous across the Amazonian landscape and at local scales (Steege *et al.*, 2013). These
821 surveys set the stage for analyses of the environmental correlates of diversity (e.g., Benavides *et al.*, 2005;
822 Steege *et al.*, 2013). Detailed explanations of the heterogeneity found at multiple scales remains as a
823 major challenge for Neotropical biodiversity research.

824

825 **IV. PHYLOGENY (OUR PRIMARY EVOLUTIONARY TOOL), AND ITS CAVEATS**

826

827 The power of phylogenies to inform evolutionary processes is large and not fully realized (Eiserhardt *et al.*
828 *et al.*, 2011). Phylogenetic data from different organisms are commonly applied in community and
829 evolutionary analyses (Forest *et al.*, 2007; Rull, 2008; Verboom *et al.*, 2009; Pokorny *et al.*, 2015; Bacon
830 *et al.*, 2015). For community analyses, researchers often rely on smaller scale phylogenies (rather than
831 one ‘super tree’), due to denser taxon sampling and more appropriate computational models. An inherent
832 challenge of this approach is that different trees are often based on different priors and models, making it
833 difficult to directly compare them, especially in terms of the distribution of node heights (ages). Several
834 approaches have been developed to address this issue, including Supersmart (Antonelli *et al.*, 2016) and
835 msBayes (Hickerson, Stahl & Takebayashi, 2007). The Supersmart approach reconstruct large calibrated-
836 species phylogenies in a comparable tree framework by allowing the assemblage of vast molecular data
837 with fossil data in three major steps. First, a backbone calibrated-tree is built using sequences from known
838 species and fossils. Then, the backbone tree is partitioned into subclades which in a second step,
839 descendent taxa with well coverage of genetic markers are integrated to infer a calibrated tree under an
840 appropriate model, such as the multispecies-multilocus coalescent model (Edwards, 2009). Third, the
841 resulting species-calibrated trees are implanted to the backbone tree. The msBayes approach, on the other
842 hand, employs a hierarchical Approximate Bayesian Computation algorithm (hABC) to estimate

843 individual phylogenies and shared patterns such as the proportion of simultaneous change in a
844 community, or the time of divergence among co-distributed species pairs across a barrier. This framework
845 has been successfully applied to study the Neotropical biota (Carnaval *et al.*, 2009; Werneck *et al.*, 2012a;
846 Thomé *et al.*, 2016 ; Gehara *et al.*, in press). Furthermore, the BIB model (Sanmartín, van der Mark &
847 Ronquist, 2008) also draws generalities on the evolution of communities by taking the idiosyncrasies of
848 individual clades into account.

849

850 Many large phylogenies were published in recent years at higher taxonomic levels, ranging from
851 phylogenies of complete classes (Jetz *et al.*, 2012; Faurby & Svenning, 2015a; Figueroa *et al.*, 2016) to
852 attempt to build the complete Tree of Life (Hinchliff *et al.*, 2015). Other studies have focused on
853 reconstructing the phylogeny of complete regions such as the Cape of South Africa (Forest *et al.*, 2007),
854 the Californian Floristic Province (Baldwin *et al.*, 2017), the Australian flora (Thornhill *et al.*, 2016). In
855 contrast, we lack well-sampled phylogenies for most Neotropical groups. In addition, many researchers
856 have expressed their justified concerns about too simplistic assumptions and problematic data
857 downloaded from public databases. A common challenge is the compromise between taxon sampling,
858 character sampling (i.e., the number of loci; Edwards, 2009), and computational capacity. Additionally,
859 branch lengths and node-ages in ‘super trees’ are often estimated secondarily, rather than being co-
860 estimated with the phylogeny through the application of appropriate clock and birth-death models. A
861 recently developed analytical platform allows the estimation of large phylogenies through a multi-step
862 process (Antonelli *et al.*, 2016).

863

864 *From single to many loci.* Sequences of only a few loci are available for most Neotropical taxa sequenced
865 to date. Even when multiple loci are available, these loci are often concatenated to enable more time-
866 efficient analyses. Using single locus data to estimate phylogenies is problematic for multiple reasons
867 (e.g., Maddison, 1997; Edwards, 2009; Liu *et al.*, 2015), especially because a single line of evidence is
868 provided by that individual genealogy. Analyzing multilocus sequence data requires more complex

869 computational models that are able to account for expected differences in gene tree topologies under the
870 same species tree.

871

872 Bayesian Multispecies Coalescent (MSC) methods jointly infer topology and node-heights for gene trees
873 and the underlying species tree from multilocus sequence data (Liu *et al.*, 2009; Heled & Drummond,
874 2010; (Xu & Yang, 2016) while taking the stochastic variation of gene genealogies into account. Even
875 though theoretically appropriate, it is often not computationally feasible to co-estimate the species tree
876 and all genealogies, particularly when the number of taxa and loci are high. Instead, many researchers
877 apply summary coalescent methods that split the estimation of gene trees as well as split of the species
878 tree into two consecutive steps. Under this approach, gene trees are estimated separately for each locus
879 and then used in separate analyses that estimate the most likely species trees (Kubatko, Carstens &
880 Knowles, 2009; Liu *et al.*, 2009; Mossel & Roch, 2010; Larget *et al.*, 2010; Mirarab *et al.*, 2014).

881

882 Computation limitations still prevent us from estimating multilocus trees using Bayesian MSC methods.
883 There is high demand for removing this computational bottleneck, which would provide an excellent data
884 source for many downstream analyses. Recent improvements of existing Bayesian MSC methods with
885 more streamlined tree searching algorithms are a step in the right direction (e.g., STACEY; Jones, 2017).
886 Nonetheless, species divergence times based on the molecular clock model infers the original population
887 split rather than the last stage of the speciation process, which may not have an effect on tree topologies,
888 but has implications for diversification analyses. In addition, using such methods for molecular species
889 delimitation are not exempt of controversy, as multispecies coalescence has been proposed to delimit
890 populations rather than species (Sukumaran & Knowles, 2017).

891

892 Another promising approach is SDVQuartets, which does not require *a priori* inference of individual gene
893 trees, but uses mathematical shortcuts (singular value decomposition of the matrix of site pattern
894 frequencies) to infer a species tree under the coalescent framework (Chifman & Kubatko, 2014; Kubatko

895 & Chifman, 2015b). This method has been expanded to incorporate horizontal gene transfer or
896 hybridization (Kubatko & Chifman, 2015a).

897

898 Finally, a different family of methods use gene birth-death (BD) processes to model the evolution of gene
899 trees within species trees. These models can incorporate events such as gene paralogy (duplication) and
900 gene loss (Boussau *et al.*, 2013) or horizontal gene transfer HGT (Szöllösi *et al.*, 2013), or a combination
901 of both (Szöllösi *et al.*, 2015). Coalescent methods of phylogenetic analysis are only slowly making
902 inroads into Neotropical biology, despite the demonstrated superiority over concatenation in handling
903 large-scale multilocus data (Liu *et al.*, 2009).

904

905 **V. CONCLUSIONS AND PROSPECTS**

906

907 **Are we living in a unique time?**

908 A long-standing question is the time of origin of the outstanding biodiversity we encounter today in the
909 Neotropics. The answer to this question is inevitably linked to the search of so-called ‘special periods of
910 time’ and ‘overarching theories’ for Neotropical diversification. The present day era likely is distinct from
911 previous time periods, as manifested in the myriad geological and ecological footprints of the
912 Anthropocene. However, there are often mixed definitions and questions related to the timing and mode
913 of biotic evolution. Indeed, the origin of the Neotropical biodiversity encapsulates two contrasting
914 subjects, the timing of origin of the hyperdiversity and the actual age of extant species (Hoorn *et al.*,
915 2011). It is clear there have been extraordinary periods of time throughout the geological history, both in
916 terms of biodiversity and abiotic aspects (i.e., geology, climate) (e.g., Jaramillo, 2006; Hoorn *et al.*, 2010;
917 Jaramillo *et al.*, 2010). However, all periods of time have contributed to the current biodiversity, and it
918 seems unlikely that all species have entered the scene in a very ‘special’ time for Neotropical
919 diversification. Instead, current diversity has deep origins in geological time, with different events (e.g.,
920 Neogene rise of the northern Andes, formation of the modern Amazon drainage system, rise of the

921 Isthmus of Panama, and Cenozoic cooling culminating in Pleistocene glacial-interglacial cycles) playing
922 different roles at different times.
923
924 Examples of meta-analyses that seek for ‘special’ periods of time often come from time-calibrated
925 molecular phylogenies. For instance, butterfly species-pairs seem to be relatively young in origin (i.e., < 2
926 Ma), suggesting that the Pleistocene and Holocene may have represented ‘extraordinary times’ for
927 Neotropical butterfly speciation (Garzón-Orduña, Benetti Longhini & Brower, 2014). However, time-
928 calibrated phylogenies may not fully address the potential impact of extinction and species duration
929 (Hoorn *et al.*, 2011). In other words, if we were able to travel back in time to any period and sequence
930 species around us, the odds are that most species alive would also be around 2 Ma old. This potential
931 intrinsic bias of these types of studies remains as a challenge to be addressed in the future.
932
933 Incorporating fossil taxa in molecular diversification analyses could help resolve those issues. However,
934 the fossil record is still limited for most Neotropical clades. In simulated phylogenies, the resulting shape
935 of lineage-through-time plots vary significantly when the fossil record is added as compared to
936 phylogenies that incorporate extant taxa exclusively (Matos-Maraví *et al.*, 2014; Xing *et al.*, 2014). The
937 inferred macroevolutionary dynamics estimated from molecular phylogenies may thus be misleading if
938 fossil taxa are neglected, or when macroevolutionary tools do not acknowledge the rare sampling of fossil
939 lineages. New methodological developments to directly integrate fossil (extinct) lineages into phylogeny
940 reconstruction (Ronquist *et al.*, 2012; Heath, Huelsenbeck & Stadler, 2014; Zhang *et al.*, 2016; Silvestro
941 *et al.*, 2016) offer new hope in the quest to retrieve more accurate depictions of evolutionary patterns.
942
943 Variable species concepts and adequate sampling of extant and extinct taxa, represent a serious barrier for
944 our understanding of Neotropical biodiversity. Highly structured populations with considerable genetic
945 divergences may be seen as “incipient species” that have not yet completed the speciation process. For
946 instance, excluding “incipient species” (i.e., highly structured populations that may not have yet

947 completed the speciation process) from phylogenies may incorporate artifacts that may lead to incorrect
948 inferences of a diversification slowdown towards the present (Cusimano & Renner, 2010). Standardized
949 species definitions and broad sampling of taxa are crucial while inferring macroevolutionary dynamics.
950 Indeed, it is very likely that several broadly distributed Neotropical species may be composed of multiple
951 narrowly distributed taxa once studied in further detail.

952

953 **Operational hindrances**

954 Comparative biology has experienced advancements in the theory and practice of biogeography and
955 molecular phylogenetics during the past decades. However, we still need to increase sampling of
956 Neotropical organisms drastically in order to advance our knowledge on the patterns and processes
957 underlying Neotropical biodiversity. Despite this great need, fieldwork in the Neotropics, especially in
958 pristine areas, is time consuming, expensive, and logistically demanding. Research funding for
959 exploratory inventory projects is also becoming increasingly harder to obtain, despite the fact that highly
960 successful projects (i.e., sequencing the first human genome and creating the Amazon Tree Diversity
961 Network) were initially discovery-driven, rather than focused on testing specific hypotheses. Furthermore,
962 obtaining permits to collect and export biological samples is also challenging, involving many differences
963 across national legislations. Finally, fieldwork might be seen as unnecessary given the wealth of
964 specimens already available in biological collections around the world, and their potential for biodiversity
965 and genomic analyses (Buerki & Baker, 2016; Zedane *et al.*, 2016).

966

967

968 Despite all these obstacles, fieldwork remains absolutely essential for data generation and
969 monitoring biodiversity changes (Albert, 2002). Fieldwork also provides students and researchers with a
970 deeper understanding and inspiration of their study systems (often providing new ideas and questions),
971 while facilitates the establishment of new collaborations, enables the exchange of knowledge, fuels the
972 development of new methods, and increases the possibilities of major discoveries (Fleischner *et al.*,

973 2017). We should seriously consider new strategies for the generation of new biodiversity data, as well as
974 for the syntheses of the already available data. Multi-taxon field campaigns could provide unique
975 opportunities for intensive sampling, while optimizing resources, bureaucratic and logistic efforts.
976 Investments on these activities would be mutually beneficial and worthwhile from a global perspective.
977 The future of Neotropical biodiversity research depends on extensive collaborations and coordinated
978 efforts (Baker *et al.*, 2017).

979

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1920

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1943
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1946 A.A. and S.E. initiated and led the project; A.Z. and S.F. compiled the data and carried out the analyses
1947 needed for producing Fig. 2; M.A. formatted references and merged the manuscript revisions; all authors
1948 participated in the discussions held under the ‘Origin of Biodiversity’ Workshop in Göteborg (Sweden) in
1949 the spring of 2017, wrote the paper jointly, read and approved the final version submitted for publication.

1950

1951

1952 **CONFLICT OF INTERESTS**

1953 The authors declare no conflict of interests.

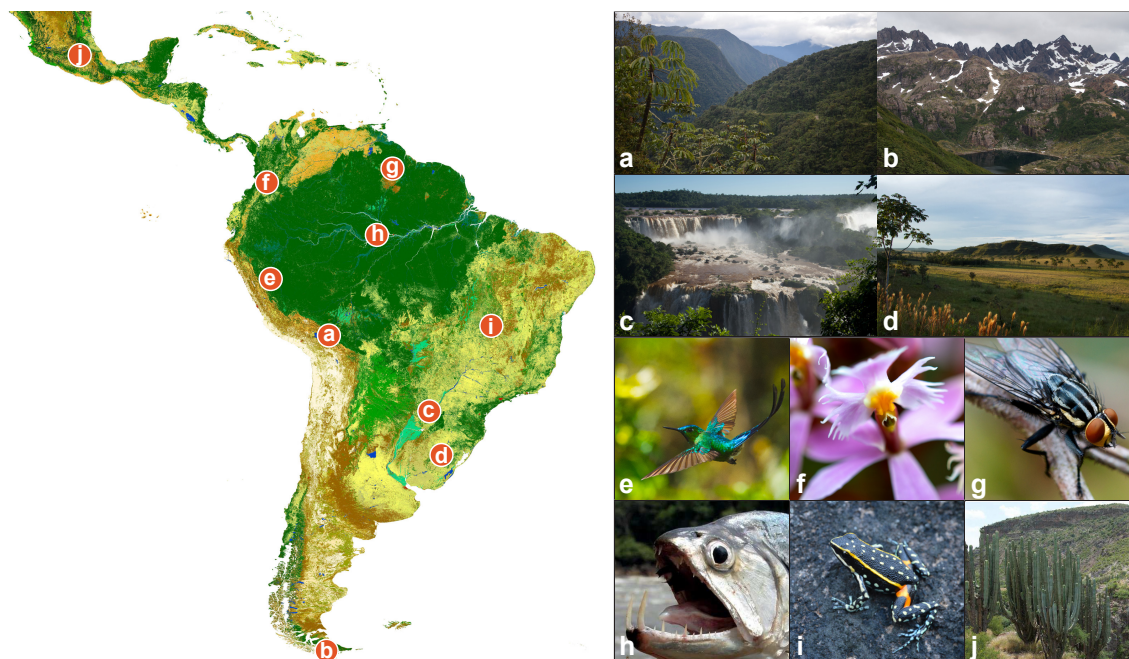
1954

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1957 **FIGURES**

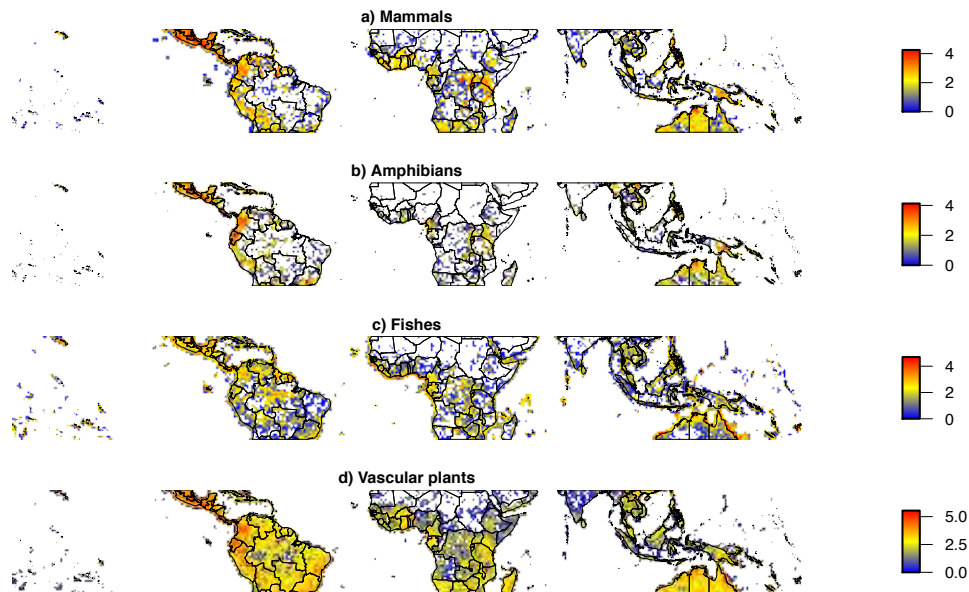
1958



1959

1960 **Fig. 1 The Neotropical region and examples of landscapes and taxa.** Map generated through the
 1961 remote-sensing ESA GlobCover 2009 project and colored by biome assignments (© ESA 2010 and
 1962 UCLouvain; http://due.esrin.esa.int/page_globcover.php). a) Eastern slopes of the Bolivian Andes, where
 1963 the Amazonian and Andean biotas meet; b) Patagonian mountains of southern Chile, which despite being
 1964 in the temperate zone of South America is home to many Neotropical-derived lineages; c) Iguazu
 1965 waterfalls, where increased humidity create gallery forests within the Open Diagonal domain; d) southern
 1966 grasslands of the Pampas, a naturally open habitat now largely influenced by human activity; e) one of the
 1967 ca. 338 known species of hummingbirds, a conspicuous clade currently restricted to the American
 1968 continent and particularly diverse in the Andes; f) *Epidendrum ibaguense*, a widespread species in the
 1969 orchid family in which many new Neotropical species are discovered each year; g) an unidentified fly in

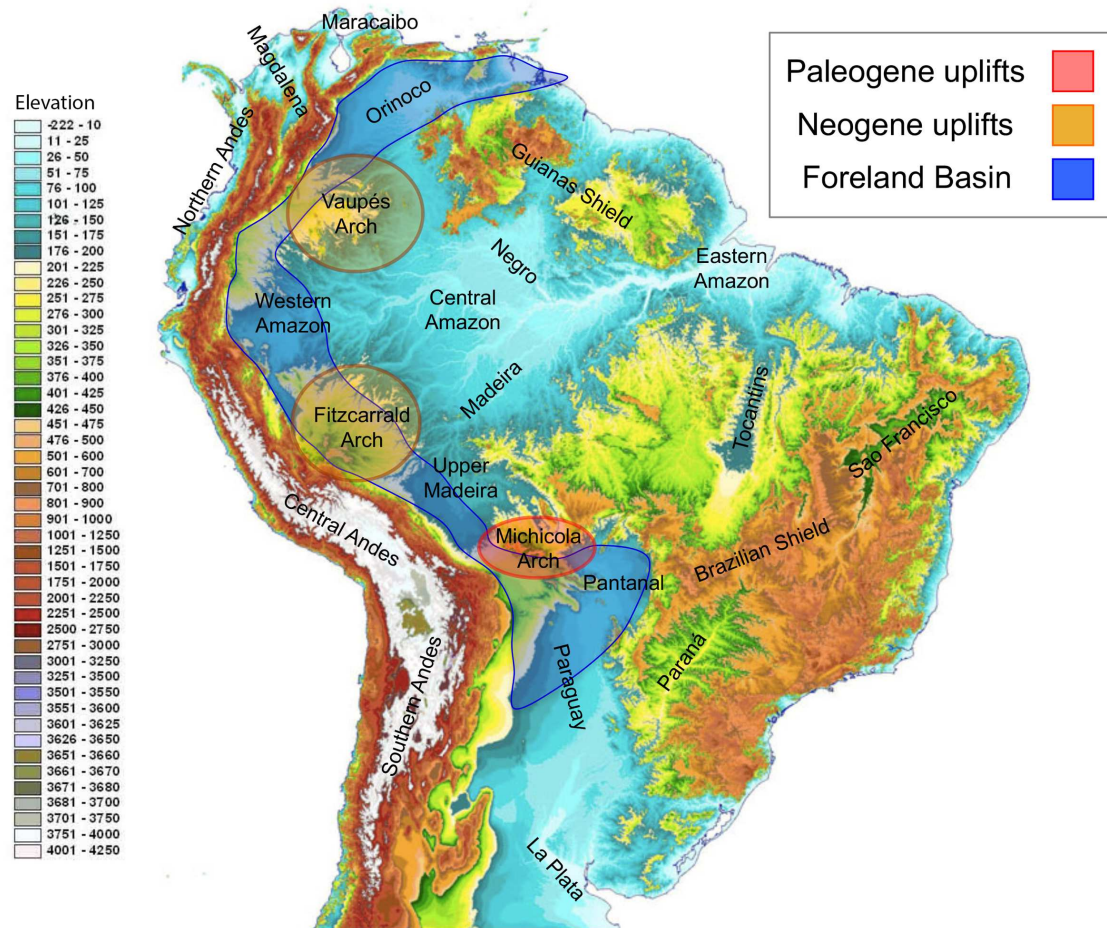
1970 the inselbergs of southern French Guiana, where basaltic rocks emerge several hundred meters above the
1971 surrounding Amazonian rainforest: h) *Hydrolycus scomberoides*, exemplifying the world's richest
1972 ichthyofauna in the Amazon drainage basin; i) *Ameerega flavopicta*, a rock-dwelling frog species adapted
1973 to a region of high seasonality of precipitation; j) a columnar cactus of central Mexico, near the
1974 northwestern limits of the Neotropical region where low-canopy forests and succulent vegetation build
1975 vegetation mosaics across the landscape. [Photo credits: a-g, i-j: A.A.; h: J.A.].
1976



1977

1978 **Fig. 2 Taxonomic sampling across the world's tropics.** Density maps for geo-referenced species
 1979 occurrences available from the Global Biodiversity Information Facility for four organism groups
 1980 between the Tropics of Cancer and Capricorn (23.5 °S to 23.5 °N), showing the main spatial biases of
 1981 taxonomic sampling. All records were cleaned using SpeciesGeoCoder. The figure is shown on a
 1982 cylindrical equal area projection with standard parallels of 11.75 °S and 11.75 °N. The width of each cell
 1983 is consistently 1 degree while the height of each cell is 1 degree at the standard parallels, slightly lower at
 1984 the equator and slightly higher at the Tropics of Cancer and Capricorn. The scale is in log₁₀ number of
 1985 records.

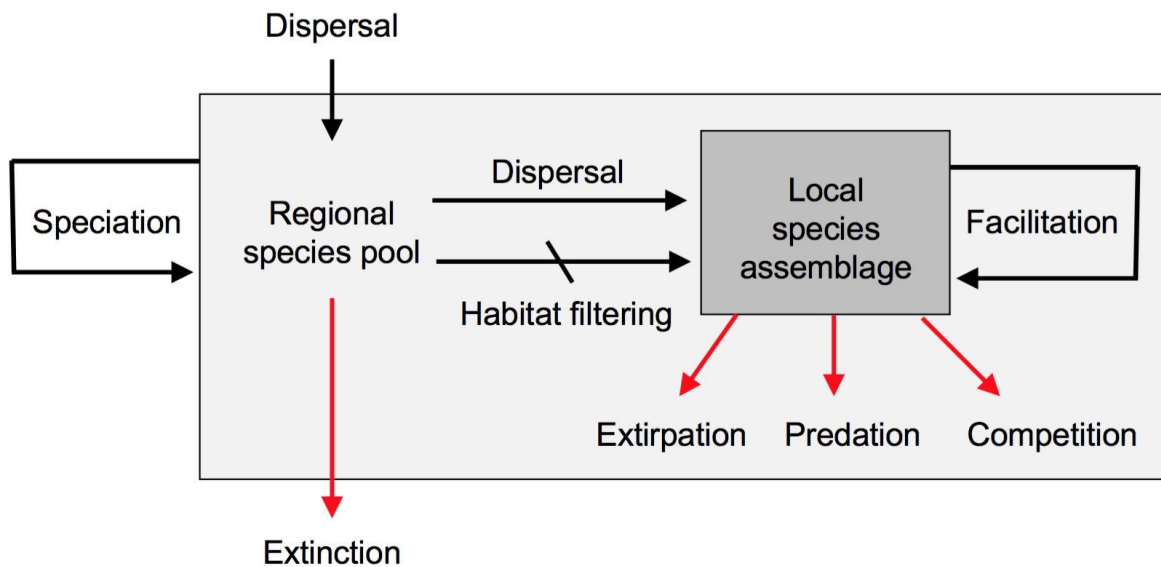
1986



1987

1988 **Fig. 3 The complex topography of South America.** This map highlights the topographic differences
 1989 across the continent, major mountain chains and river basins. Areas colored in blue are sedimentary
 1990 basins in the Andean foreland; areas colored in yellow are topographic barriers (or 'highs') that divide
 1991 these basins and define the Amazon drainage basin in its higher reaches. Base map created by Paulo Petry
 1992 from the Shuttle Radar Topography Mission with elevations in meters. Note that the scale exaggerates
 1993 differences at lower elevations.

1994



1995

1996 **Fig. 4 Main evolutionary and ecological processes contributing to the formation of species richness.**

1997 The regional species pool (light gray box) is defined as the sum of all the local species assemblages
 1998 (darker gray box). Black arrows indicate processes that increase species richness, red arrows processes
 1999 that reduce species richness. Note the hierarchical organization of processes resulting in species richness,
 2000 with evolutionary processes occurring over regional to continental spatiotemporal scales and ecological
 2001 processes occurring over local scales. Speciation and dispersal contribute new species to the regional
 2002 pool, while extinction removes species. Dispersal mediated by abiotic habitat filtering and biotic
 2003 facilitation (Kraft et al., 2014) increase the richness of local assemblages by enhancing establishment of
 2004 species preadapted to local conditions, or aiding in the establishment of other species. Biotic interactions
 2005 such as predation and competition may serve to reduce local richness. Diagram modified from Ricklefs
 2006 and Schluter (1993).

2007 **TABLES**

Biodiversity components	Known knowns	Known unknowns	Unknown unknowns
Taxonomic diversity (i.e., species numbers)	Approximate species numbers for macroscopic organisms; human impact tends to decrease overall diversity	Large portions of biodiversity are unexplored (i.e., microbes, invertebrates, fungi)	Taxonomic units used in biodiversity studies may be unequal
Genetic diversity (within species)	Patterns of genetic diversity for very selected taxa	Overall patterns of genetic diversity	How generalizable are conclusions drawn by such limited patterns of genetic diversity
Phylogenetic diversity	General understanding of the Tree (or Network) of Life	Drivers of diversification	Potential biases in phylogeny reconstruction and time-calibration
Spatial patterns of diversity	Hotspots and general patterns of species richness and diversity; large scale species ranges for charismatic taxa	Areas of endemism; known patterns of biodiversity distributions are biased; ecological preferences of species; drivers of spatial patterns of diversity	Human impact to overall spatial patterns
Functional diversity (traits)	Large scale productivity patterns	Biotic interactions	Relevance of current functional diversity measures; equivalency in functional traits; relationship between current and future functional diversity

2008

2009 **Table 1.** The various components of Neotropical biodiversity, major aspects known about them, and key
 2010 topics that remain to be understood.