Extinction shapes the history of the communities of specialist birds in the white-sand ecosystems of the Amazon.

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Abstract

Understanding how bird species from white sand ecosystems (WSEs) have managed to inhabit and specialize in insular environment in the middle of the Amazon Rainforest is fundamental to understand the evolutionary processes in birds restricted to one type of habitat. We sought to evaluate the diversification processes of the specialist bird species of the white sand ecosystems of the Rio Negro basin by comparing them with the pool of bird species of riparian environments. Many WSEs may be ancient riverbeds, which may favor current riparian species to be potential colonizers and settle within the WSEs. For this, we used an extension of biogeographic evolutionary models to verify state-dependent speciation and extinction models that specifically explain the presence of unmeasured factors that can affect the estimated diversification rates for the states of any observed trait. Thus, it was possible to evaluate the evolutionary processes that most acted in the formation of bird communities of WSEs. The results showed that WSEs specialist bird species have different functional diversity to what was expected on a random basis and evolutionary models have higher extinction and speciation rates in WSEs specialist bird communities. This evidences that source-sink processes maintain WSEs over time, and that they receive generalist and specialist species from riparian ecosystems. According to the models analyzed, once the species have the high degree of adaptation required by an ecosystem with severe conditions, they cannot colonize other ecosystems. Extinction is an important process for the dynamics of biodiversity in the Amazon since, as many species are lost, there is also speciation and high adaptation. This work is one of the first to use local evolutionary analyses in Amazonian ecosystems and was effective in showing that extinction is recurrent, which is a cause for concern due to the severe and rapid ecological changes currently occurring.

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Abstract

Understanding how bird species from white sand ecosystems (WSEs) have managed to inhabit and specialize in an insular environment in the middle of the Amazon Rainforest is fundamental in order to understand the evolutionary processes in birds restricted to one type of habitat. We sought to evaluate the diversification processes of the specialist bird species of the white sand ecosystems of the Rio Negro basin by comparing them with the pool of bird species of riparian environments. Many WSEs may be ancient riverbeds, which may favor current riparian species to be potential colonizers and settle within the WSEs. For this, we used an extension of biogeographic evolutionary models to verify state-dependent speciation and extinction models that specifically explain the presence of unmeasured factors that can affect the estimated diversification rates for the states of any observed trait. Thus, it was possible to evaluate the evolutionary processes that most acted in the formation of bird communities of WSEs. The results showed that WSEs specialist bird species have different functional diversity to what was expected on a random basis and evolutionary models have higher extinction and speciation rates in WSEs specialist bird communities. This evidences that source-sink processes maintain WSEs over time, and that they receive generalist and specialist species from riparian ecosystems. According to the models analyzed, once the species have the high degree of adaptation required by an ecosystem with severe conditions, they cannot colonize other ecosystems. Extinction is an important process for the dynamics of biodiversity in the Amazon since, as many species are lost, there is also speciation and high adaptation. This work is one of the first to use local evolutionary analyses in Amazonian ecosystems and was effective in showing that extinction is recurrent, which is a cause for concern due to the severe and rapid ecological changes currently occurring.

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Introduction

Ecological communities are composed of species that co-occur in a given geographic space and period, which can change in terms of variation in composition and richness (Kreft & Jetz, 2010; Schluter & Pennell, 2017). The composition of these communities is determined by temporal biotic, abiotic and ecological factors (Whittaker et al., 2001; Webb et al., 2002; Cavender-Bares et al., 2009). However, different groups of animals and plants respond differently to eco-evolutionary processes, which creates a puzzle in relation to the history of the formation of communities, both in the composition of their species, and in the ecomorphological adaptation of the species and to what extent they are able manage to disperse . The composition of the species is a reflection of their ecomorphological adaptation and dispersal capacity, which are fundamental for the conquest of new habitats (Weeks et al. 2022). Without abundant sources of evidence or other records showing the past geographic distribution of a lineage, the difference between *in situ* adaptation and colonization is difficult to investigate.

Studying the modifications of the natural history of species is fundamental in order to understand the evolution of the planet's ecosystems (Condamine et al., 2013). Environmental changes and extinctions are part of history, and shape the future of current ecosystems and their species. The past can favor the understanding of what can happen in this current moment of severe and rapid changes in the environment (Barnosky et al., 2011, Naeem et al., 2012). By understanding historical changes and their directions, we can assess the likely consequences in advance. According to ecological modifications, organisms and their characteristics mediate adaptation and dispersal potential (Stroud and Losos, 2016). Intense environmental pressures in certain regions can influence the characteristics of species and pressure them to similar adaptations, even if these are unrelated. Studies show that different families of plants that inhabit equally dry environments in different parts of the Earth, have leaves adapted for the storeage of water (Vicentini, 2004; Eggli & Nyffeler, 2009). The richness of birds, mammals and amphibians is similar, and responds to environmental gradients, but, according to most studies, not to competition between taxa .

Thus, biodiversity patterns need to be studied at spatial and temporal scales, taking into account the multiple forms of variation embedded in the complex concept of biodiversity (Antonelli et al., 2018; Diniz-filho et al., 2009), and should seek to find the specific mechanisms of characteristics (traits) and lineages, with the integration of the idea that ecological and historical biogeographic processes can act strongly in metacommunities (Vellend, 2010). Studying communities and their ecological characteristics is essential in order to understand the paths of diversification and recolonization of species in isolated places, such as islands of ecosystems surrounded by a matrix or forest fragments (Claramunt et al., 2012; Cadotte, 2017; Antonelli et al., 2018). Such transitions between environmentally different areas can allow a species maintain its characteristics and its ancestral ecological niches, which can be explained by the conservatism hypothesis .

In the Neotropics, changes in habitat over time show transitions of the species from ancestral wet and forest habitats to drier environments (Lanna et al., 2022; Tucker et al., 2017). Studies suggest that investigation is essential to generalize these patterns, since one should not just look at a community, but also act in a comparative mode in relation to the diversification processes and the geographical variation of the species. One should also verify the potential to colonize and settle, and compare the species pool of a given region .

Drier environments, with extreme ecological conditions such as high temperatures and water stress, require more specific adaptations for species survival, thus restricting permanence and species richness (Futuyma and Moreno, 1988; Zurita et al., 2017). One example of this type of environment is the white-sand ecosystem (WSE) that is found in the Amazon, which occurs in soils with strong water stress and which are poor in nutrients, and are distributed in isolated patches in the middle of a *terra firme* forest matrix . This ecosystem presents endemic bird species adapted to its specific conditions that are similar to an island, and whose connections between the patches are probably via corridors of riparian ecosystems

Bird communities of WSEs show lower diversity and higher dominance of some species, which is probably due to the limiting pressure of an environment with low habitat complexity (Capurucho et al., 2020). Thus, the distribution of bird communities in WSEs seems to be linked to the adaptation of species to extreme conditions, their dispersal and colonization capabilities, and may be driven by the size and isolation of the spots (Borges et al., 2016). WSEs have two types of formations, i.e., the northern and southern patches of the Amazon, which have different characteristics and evolutionary histories (Matos et al., 2016; Cracraft et al., 2020). Bird communities have species turnover between the patches of WSEs across Amazon

The formation processes of WSEs in the northern Amazon have resulted in greater heterogeneity of environments on the Guiana Shield (Adeney et al., 2016; Rossetti et al., 2012), while the WSEs patches of the southern Amazon feature fewer open areas and appear to be ancient riverbeds (Ritter et al., 2021). Thus, the connectivity of WSE areas with riparian environments are more evident in the north of the Amazon at the present time (Capurucho et al., 2020). Genetic work by WSE bird specialists corroborates a lower connectivity and recent isolation between the populations of the north and south of the Negro River . Herein, we evaluate whether (1) WSEs act as a phylogenetic and functional filter and (2) whether WSE communities are self-sufficient in forming and maintaining their diversity or are maintained by a dispersal of species between WSEs and riparian ecosystems. Lanna et al. (2022) show that forest habitats are older, favoring dispersal to open areas. We thus expect more dispersal events from riparian forest ecosystems to open ones of WSEs. We also expect more speciation events to occur in riparian forest environments and extinction rates to be higher in WSEs due to WSE being a restrictive environment. Knowing the evolutionary processes that play an important role in the formation of WSE specialist bird communities and the evolution of bird characteristics will lead to a better understanding of what happened in the Amazon over time, especially in two important ecosystems that are currently threatened by current climate changes.

Methods

We used two lists, one for the white-sand ecosystem (WSE) and another for the riparian ecosystem. The WSE list has 147 species and 37 families of birds, which were obtained from the work of Borges et al. (2016 (b)), for an area located in the Negro River basin. For the riparian ecosystem, we used the list from the work of Naka et al. (2020) with 439 bird species from 64 families for the Branco River, which is the main tributary of the Negro River.

Based on the species list for white-sand ecosystems and riparian environments, specimens of each of the species was measured. At least three individuals per species were measured in the zoological collections at INPA, the Goeldi Museum and the UFPE collection. Each individual was measured three times and, each time, measurements of the beak (height, length and width), tarsus, total wing length, and length of secondary feathers were otained, and the Kipp index was calculated. Via this, we obtained an average of the functional attribute for the species. All individuals were measured by the same person, always using a digital caliper and a ruler in millimeters. The functional attributes that were measured are all linked to the ecological functions of individuals in the environment (Supplementary Material 1). We ecologically classified the species using the literature of Billerman et al. (2022), Borges et al. (2016a, b) and Naka et al. (2020). Species that are restricted to one type of ecosystem were classified as specialist species, and species that are present in two or more types of Amazonian ecosystems were classified generalists. In our database, the restricted species of riparian ecosystems were represented by "0" (263 species), the restricted ones of white-sand ecosystem environments were represented by "1" (18 species), and those that use the two types of ecosystems represented by "01" (126 species).

Environmental filtration

For the phylogenetic tree, the consensus of 10,000 bird phylogenies published by Jetz et al. (2012) was used. The consensus tree was generated using the Mesquite 3.7 program (Maddison & Maddison, 2021), and maintained the length of the branches. Only the species present in the occurrence database were maintained. Phylogenetic diversity analysis was performed to assess whether WSE communities are composed of a phylogenetic subset of riparian ecosystem communities. The phylogenetic diversity was calculated as the mean phylogenetic diversity of the community (MPD) . The observed MPD was compared to a null model, through a random selection of species from riparian communities, and the observed value for WSE diversity was maintained. The simulation of the null communities was repeated 1,000 times. For each repetition of the data simulation, the average MPD for the community was calculated. The significance of the phylogenetic analysis was assessed by the standardized effect size of the MPD (ses.MPD), with a significance level of 95 %. Positive and significant values of ses.MPD indicate more phylogenetically dispersed communities than what would occur by chance. Negative and significant values indicate phylogenetically grouped communities. The phylogenetic grouping analyses were performed in the*picante* package of the R software .

Filtering of the functional diversity

To evaluate the filtering of the functional attributes in the WSEs, we calculated the diversity of the functional characteristics, such as functional divergence (FDiv), functional dispersion (FDis) and functional richness (Fric) using the *FD* package (Laliberte & Legendre, 2010) do Programa RStudio 2022.07.0. The Gower distance (Gower, 1971) was used as a measure of dissimilarity between the species because it allows the use of different types of traits, whether continuous, ordinal, nominal or binary. The indices of the DAMOCLES model (dynamic assemblage model of colonization, local extinction and speciation) use estimated parameters of colonization (dispersal), local extinction and speciation events. From the generated values, 1,000 null models of community composition were simulated (Pigot and Etienne, 2015). For each simulated community, we calculated the functional diversity metrics and evaluated the significance of functional diversity using the *quantis* of 2.5 and 97.5% of these distributions of null models of functional diversity. Negative and significant values of functional diversity can indicate a grouping of the functional diversity of birds in WSEs in relation to the species pool. Positive and significant values would indicate greater dispersion of the functional attributes of WSE specialist birds.

We evaluated whether WSE communities are comprised and maintained by (1)*in loco* speciation, and have low extinction rates and diversification rates that are higher than the dispersion rates of riparian communities; 2) whether they are comprised of a source-sink dynamic. With the diversity in WSEs being formed by the dispersion of species from riparian communities, and with the extinction rate in WSEs being higher than its speciation rate. The diversification was evaluated using the GeoHiSSE model (Caetano et al., 2018) from the *hisse*v1.9.19 package (Beaulieu and O'Meara, 2016) of the software R. GeoHiSSE allows you to model how the expansion or loss of geographical states (e.g., WSE and riparian communities) (as described below) influences diversification rates. In this way, we can model how the expansion or loss of occurrence of species in WSE and riparian ecosystems can influence the rates of speciation and extinction in these ecosystems.

Geographic states were defined as WSE specialists, riparian ecosystem specialists, and generalists (occur in both ecosystems). A total of six diversification models were constructed to represent the diversification hypotheses. In Model 1, the riparian and WSE ecosystem communities are formed by the dispersion rates between geographical states, with no differences between their speciation and extinction rates. However, direct changes between specialist states are not allowed, and expansion to the generalist state is mandatory, for example specialist WSE species cannot evolve directly to specialists in riparian ecosystems, since they must expand their geographical distribution to generalist and lose the WSE state to become specialists in riparian ecosystems. Model 2 has different dispersion rates between geographic states, with the same dispersion constraints as Model 1, but has different speciation and extinction rates between geographic states. In Model 3, we add a hidden state to the model, dispersion rates are equal to those of Model 1 with the addition of dispersion between the hidden states. Speciation and extinction rates are different between the hidden states, but are equal between the geographic states. In this model, differences in speciation and extinction are caused not by geographic states, but by attributes not included in the model. Model 4 has dispersion rates that are equal to Model 3, but there are no differences in speciation and extinction rates between geographical states nor between hidden ones. In Model 5, the direct change from the status of specialist of riparian environments to WSE specialist is allowed. In Model 6, all events are present, but specialist WSE species do not change to specialists of riparian environments or to generalists. (Table 1). The models were ranked by the weights of the Akaike information criterion corrected for low sampling (wAICc) (Beier et al., 2001) and we calculated speciation, extinction and dispersal rates using the average model of the six diversification models .

Results

We found that the observed phylogenetic diversity was not different from that expected for a random sampling of species from riparian ecosystems (ses.MPD observed = 151.61, P = 0.25). However, WSE species presented lower functional diversity than expected by a neutral diversification and colonization process (Figure 1), thus indicating environmental filtering of species attributes in WSEs.

The best diversification models were Models 5 (wAICc = 0.39), 4 (wAICc = 0.35) and 6 (wAICc = 0.26), respectively (Table 1). In the average diversification model, WSEs had low speciation rates and high extinction rates. On the other hand, riparian ecosystems had low extinction rates and high speciation rates. Generalist species had low rates of speciation and extinction (Figure 2). We also found that there is a hidden state effect on the speciation rates of riparian ecosystems and WSE extinction rates (Figure 2). There are direct transitions between species from riparian ecosystems to WSEs, but not the other way around. In the hidden state A, the rate of transition from riparian ecosystems to WSEs (0.079) was greater than the rate in the opposite flow (0.23). In the hidden state B, the transition was greater between species from WSEs to riparian ecosystems (74.3), than the opposite transition (24.1). Therefore, WSEs are maintained mainly by the colonization of species from riparian ecosystems, since they have a low speciation rate and a high extinction rate. There is also a high flow of WSE species into riparian ecosystems, but these ecosystems are maintained primarily by their high speciation rate and low extinction rate.

Discussion

Specialist bird communities from white-sand ecosystems (WSEs) and riparian environments were examined to try to determine whether there is environmental filter in the WSEs and whether evolutionary processes such as specialization, dispersal and extinction have shaped WSE communities. We found evidence of high extinction in WSE communities, because living in an environment different from the surroundings, with severe conditions, led populations to adapt and specialize, since they either adapt or become extinct. The results show that WSEs communities are composed of species of different evolutionary lineages, and do not differ from a random sample from riparian communities. However, WSEs specialist species are morphologically more similar than species of riparian ecosystem communities.

The models employed in this work were fundamental for answering whether the specialist species of WSEs were filtered mainly by extinction events. High adaptation to an insular environment may have driven the high speciation and endemicity rates of WSEs species. Birds may or may not be present in a given area, and may be affected by the heterogeneity of the local forest, with variation in habitat structure being fundamental in determining the distribution of species . In the GEOHISSE model, more events were added. Including dispersal from riparian environments These modifications made to models 5 and 6 were important to test our hypotheses. WSEs and direct speciation from riparian ecosystems to WSEs (0 to 1). These modifications made to models 5 and 6 were important to test our hypotheses. By increasing the possibility of events, we obtained representative results to explain the composition of the specialist bird communities of the WSEs.Direct speciation could be performed within the models, which allows the possibility of species from open areas to return to riparian forested areas, which did not happen. Perhaps the environmental pressure is so strong that it causes the species to no longer be able to return or not find vacant niches in the riparian forest ecosystems.

With the GeoHISSE analyses, we investigated the dynamics of diversification, with transitions of species over time from riparian forest ecosystems to more open ecosystems such as WSEs. Through this work, we reinforce the potential of riparian areas for the dispersion of species in the landscape with probable corridors. In study by Capurucho et al. (2013), phytogeographic analyses were conducted that showed the expansion of populations of the specialist species black manakin (*Xenopipo atronitens*) that began after the Last Glacial Maximum. This is evidence of a likely rise in local extinctions and subsequent recolonization of patches of white sand ecosystem with species from forest ecosystems. More evidence is found in the study by Azevedo et al. (2020), which shows that open habitats in South America are younger than forest habitats, and favor the colonization of open environments by riparian forest species.

Via the models, the findings in this work show that transitions from forest ecosystems to open areas were more common than the reverse. WSEs could and can provide more empty niches and allow colonization of species from riparian forest environments. This pattern of further transitions from forest to open habitats have been covered in other studies. For example, Antonelli et al. (2018) estimated evolutionary events for six taxonomic groups of species in Neotropical biomes and found that the Amazon was a source of species for all groups of open areas. Zizka et al. (2020) identified more transition events of Bombacoideae plants from evergreen forests (forest habitats) to seasonally dry biomes (open habitats), with multiple colonization events in open habitats. The work of Zizka et al. (2020) follows Antonelli et al. (2018) in their analysis of their data at the biome level, but this can confuse the real differences by contrasting two biomes that have different extents and consequently have distinct biotic influences. Therefore, when performing the inclusion of species that occur within a single biome, we can understand how the environment shapes the dispersal and colonization processes of species within a heterogeneous biome. We therefore propose that future studies should include ecosystems, macro- and micro-habitats of species and not only general biomes in the analyses.

The models used were favorable for this work and sufficient to answer the evolutionary questions regarding the species of WSEs. We were able to show that extinction was the evolutionary process with the highest rates for the WSE. In insular conditions, colonizers experience environmental conditions that were not previously experienced by their ancestors, which cause selective pressures due to new adaptations. Pressures drive speciation rates, but they can be strong and rapid, and extinction is the process that shapes communities since species either adapt or become extinct. According to Barnosky et al. (2011), extinction is very common, but it is usually balanced by speciation. In the Amazon, several events occurred that favored the increase of in extinction and speciation in open areas, such as the fire edaphic factors and seasonal climatic factors that ended up isolating populations and increasing the selective pressure on the species (Els et al., 2021).

Morphological features do not appear to restrict species of WSEs and morphology does not preclude colonization and persistence of species in other Amazonian ecosystems. As such, the evolutionary history of species is more important in order to understand the distribution of species in the various micro- and macro-habitats of Amazonian ecosystems. This restricted association of species results in dependence and high adaptation to be able to disperse in the landscape (Lanna et al., 2022). Little is known about which corridors Amazonian birds use, and how the gene flows of the species are maintained over time. When considering transitions between ecosystems using only the species that are present and their current distributions, it is necessary to consider other factors. Species may have colonized other types of open ecosystems or forest ecosystems from other regions or even from other continents, and not transitioned between these two habitats.

Currently there are analyses with increasingly robust models to evidence evolution and its main drivers. There is still limited understanding about Amazonian communities or about species conservation within a climate change scenario. Accelerated extinction ceases to be a driving force of species selection in the Amazon and could be an unprecedented catastrophe in the history of the planet. For this reason, WSEs are considered increasingly vulnerable and are priority areas for conservation, as they are already limited environments and prone to fire. Wildfires in seasonally flooded riparian environments can abruptly transform forests into a savanna state, thus contributing to climate-induced disturbances and causing ecological transitions .

Conclusion

Via the results obtaining from combining phylogenetic and ecomophological data to evidence the evolutionary history of bird species in white-sand ecosystems and riparian ecosystems of the Amazon, insights about the evolutionary processes that shape communities emerge. As seen for other animal groups, our results demonstrate a predominant pattern of transitions from forests to open habitats. The evolutionary process of extinction in the Amazon seems to be much more common than we imagined, and the WSEs are a species sink that has been important for bird speciation over time. With ecomorphological and phylogeny data we were able to generate more robust tests of evolutionary models. Tropical regions are the regions with the greatest biodiversity on the planet and are under threat, obtaining results with high numbers of extinctions is crucial for further assessments of the populations of specialist species in various ecosystems. We have identified the main drivers and have a small part of the limited understanding of how species will cope, adapt and change their distributions due to climate change. White-sand ecosystems and riparian forest ecosystems are important within the evolutionary process, and include an important tree of life dynamic within the Amazon biome.

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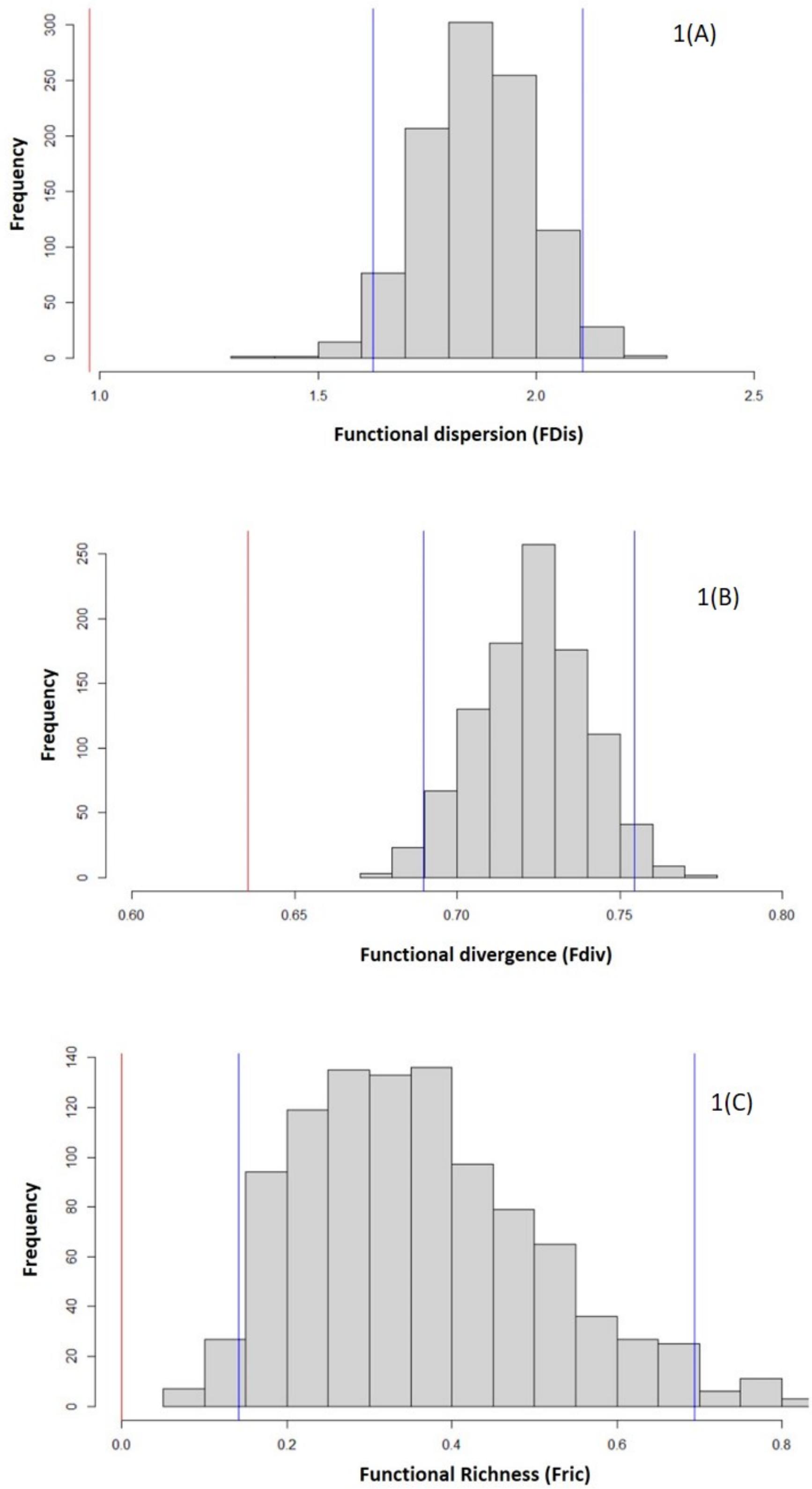
References


1(A)
Frequency
0
50
100
150
200
250
300
1.0
1.5
2.0
2.5
Functional dispersion (FDis)
1(B)
Frequency
0
50
100
150
200
250
0.60
0.65
0.70
0.75
0.80
Functional divergence (Fdiv)
1(C)
Frequency
0
20
40
60
80
100
120
140
0.0
0.2
0.4
0.6
0.8
Functional Richness (Fric)

2(A) 2(B)

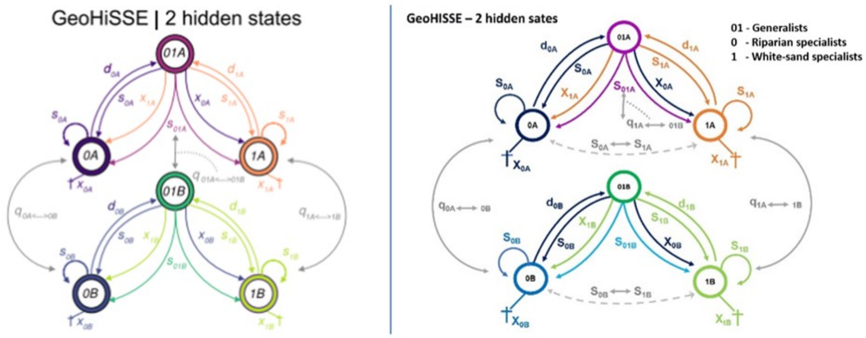
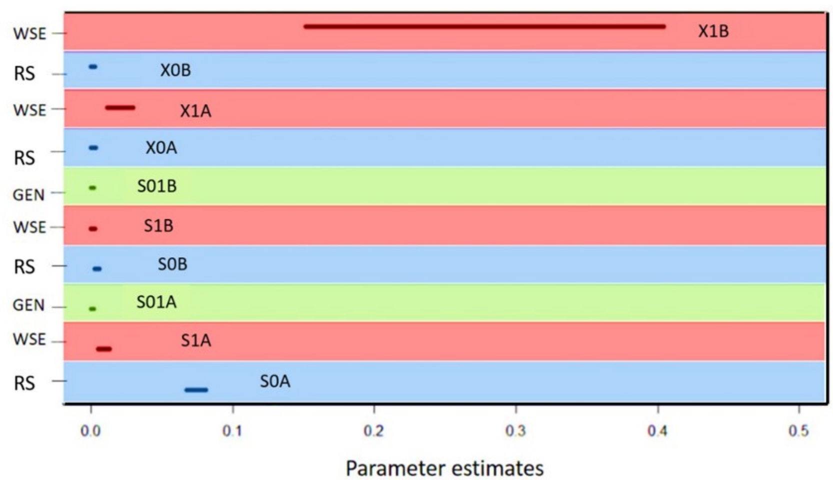


Fig.3



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