



INSTITUTO DE BIOLOGIA  
CURSO DE CIÊNCIAS BIOLÓGICAS

**IS THERE A GAP BETWEEN MICROBIAL ECOLOGY AND GENERAL  
ECOLOGY? AN ANALYSIS BASED ON THE EQUILIBRIUM THEORY OF  
ISLAND BIOGEOGRAPHY**

(Há uma lacuna entre a ecologia microbiana e a ecologia geral? Uma análise baseada na teoria do equilíbrio de biogeografia de ilhas)

por

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## **BANCA EXAMINADORA**

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3 **ISLAND BIOGEOGRAPHY**

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9 **ABSTRACT**

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11 Some authors argue that the field of microbiology is undergoing a revolution due mostly to the  
12 recent advances in the molecular procedures. Even so, there are claims that microbial ecology  
13 development is compromised by scarcely accessing theories from general ecology. Two general  
14 reasons have been pointed to explain the distance between these two areas: First, distinct  
15 developmental trajectories based on their distinct interest areas, resulting on the production of  
16 independent literature bodies. Second, the great differences of microorganisms in relation to larger  
17 organisms, such as microscopic sizes, high rates of population growth, dispersal and population  
18 abundances, fast evolution speed and unique reproduction features. Such differences would prevent  
19 theories developed for one group to be applied to the other, since the functioning of systems  
20 composed by each group should differ significantly, being incompatible with each other. No concrete  
21 evidence nor further analysis of both of these statements have been presented, however. Here we  
22 appraise these claims by evaluating if the literature of microbial ecology fails in accessing the  
23 developments of general ecology (through historical pattern of citation analysis). We also evaluate if  
24 the theoretical structure developed by the general ecology (i.e., its domain and conceptual and

25 empirical constructs) is suited to deal with phenomena investigated by microbial ecology. We based  
26 our analysis on the equilibrium theory of island biogeography (ETIB). Our findings suggested that  
27 microbial ecology fails in accessing the most influential and current articles from general ecology. Only  
28 MacArthur and Wilson's seminal book of ETIB was greatly cited, as already expected. However,  
29 theoretical structure of ETIB proved to be quite adequate to microorganisms, demonstrating that  
30 interchangeability is possible with minor adjustments. We hence believe that there is not a full gap  
31 between microbial and general ecology.

## INTRODUCTION

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Some authors argue that the field of microbiology is undergoing a revolution due mostly to the recent improvements in the methodological procedures of molecular and bioinformatics nature [1–3] that allow the production and evaluation of huge amounts of information, as multi-omic data. The emergence of Big Data has stimulated debates on an alleged obsolescence of theory in science [4,5], but, according to Hey *et al.* [6], it rather seems to have added a new approach (i.e., data-intensive scientific discovery) to the three traditional ones is science, namely theory, experiment, and simulation. In fact, several authors continue to stress the centrality of theory for the development of the fields of biology [7], ecology [8] and microbiology [9] and the need to establish fruitful dialogues between Big Data e traditional approaches [10].

Not long ago it has been stated that the development of the field of microbial ecology would be compromised due to its scarcity in accessing theories from general ecology [11]: if such issue were not overcome, microbial ecology would become an encyclopedia of simple accumulated data, unable to offer broader mechanistic understanding of microbial ecological systems and bearing low predictive power [11]. Previous discussions on this gap between microbial ecology and *general ecology* (herein used to designate the ecological science developed based mainly on macroscopic organisms) has received little attention [12] until recently [11,13–16], when attempts to connect both areas started to show in the literature [17–19].

Two general reasons have been suggested to explain the gap between microbial and general ecology. The first involves the historical process of the rising and development of both disciplines [14]. The study of microorganisms started in the mid-17<sup>th</sup> century [20]. The term “ecology” was coined only in mid-1860s, but the “ecological thought”, or the questionings of ecological nature, existed long before that [21,22]. However, while the about to come ecologists were focused on the spatial patterns of distribution of species or the relationship between organisms and their surrounding environment, the interests of the about to come microbiologists were mainly directed to public health and medicine

58 [23–25]. Those distinct developments of each discipline based on their distinct areas of interest would  
59 promote idiosyncratic research developments leading to the production of quite independent  
60 literature bodies [14].

61 The second reason stresses the differences between macro- and microorganisms both in terms  
62 of their biological features and of the technical difficulties they impose to be studied [11,14–16].  
63 Microorganisms differ from macroscopic organisms due to their microscopic sizes, their high rates of  
64 population growth and dispersal, their high abundances, their fast evolution speed, and due to unique  
65 aspects of their reproduction biology, among others. Such differences would prevent that theories  
66 developed using one group of organisms could be promptly used to explain or predict responses of the  
67 other group since the functioning of systems composed by each group should differ and the access to  
68 its components would present distinct difficulties.

69 The literature that claims that these are causes for the gap between microbial and general  
70 ecology, however, does that without presenting hard evidences on the lack of scientific communication  
71 between both areas and without deepening the analysis of the impediments for theoretical  
72 interchangeability between them. Here we evaluate these claims. First, we evaluate if the literature of  
73 microbial ecology fails in accessing the developments of general ecology. Secondly, we evaluate if the  
74 structure of one theory developed by the general ecology is suited to deal with phenomena  
75 investigated by microbial ecology.

76 Microbial ecologists, just as general ecologists, have the interest to understand temporal and  
77 spatial distribution patterns of living organisms, in other words: Biogeography [26–28]. The Equilibrium  
78 Theory of Island Biogeography (ETIB) It was first proposed by MacArthur and Wilson in 1963 [29], and  
79 provides explanation to temporal and spatial distribution patterns of organisms specifically of insular  
80 habitats. It is referred as one of the most important and influential theories in ecology [30]. Indeed,  
81 the theory promoted insights and prompted the development of many fields in ecology, such as in  
82 metapopulation studies [31], conservation biology and natural reserves [32,33] and even other



83 important biogeographical theories such as the Neutral Theory, proposed by Hubbell [34]. Its  
84 framework involves concepts such as extinction, speciation, dispersal among others, to explain the  
85 organisms' distribution patterns, such concepts may exhibit a very particular pattern when concerning  
86 microorganisms. This framework and concepts are well analyzed in Scheiner and Wilig's book "The  
87 Theory of Ecology", providing us a good baseline to contrast them within the microbial scope. Also, the  
88 term "Island Biogeography", which is unequivocally related to the ETIB, would make simpler to access  
89 the bibliographical production from both fields, general and microbial ecology. Taking into account all  
90 those aspects, we considered to use such theory to evaluate the gap between the areas.

91         To evaluate the assumed scarcity of communication between the disciplines, we analyze if and  
92 how the literature of microbial ecology makes reference to relevant papers produced by general and  
93 microbial ecology on ETIB. To evaluate the alleged impediments for theoretical interchangeability  
94 between them we analyze if the structure of the ETIB developed under the scope of general ecology is  
95 suited for understanding phenomena related to microorganisms.

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## MATERIAL AND METHODS

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### 100 **Evaluating “scarcity of communication”:**

101           If the claim that the field of microbial ecology fails to access important theoretical contributions  
102 from general ecology is true, then microbial ecology papers on a given subject either will not make  
103 reference to the most important papers in general ecology that have contributed to it or will make  
104 such reference but in a way, that does not access the theoretical contributions present in the cited  
105 paper. To evaluate this claim we proceeded as follows.

106           First, we sampled the most influential papers on ETIB in the production of general ecology  
107 published after the seminal paper “Equilibrium-theory of insular zoogeography”, by Robert H.  
108 MacArthur and Edward O. Wilson published in 1963 [29]. To do so we used the searching expression  
109 [“island biogeography”] to rescue papers present in the Web of Science™ (WOS) database associated  
110 to the area categories “biodiversity conservation”, “biology”, “ecology”, “entomology”,  
111 “environmental sciences”, “environmental studies”, “evolutionary biology”, “forestry”, “history  
112 philosophy of science”, “limnology”, “marine fresh water biology”, “ornithology”, “philosophy”, “plant  
113 sciences”, and “zoology”. For each period of five years from 1963 to 2016 we picked the three papers  
114 with the highest rate of total number of citations in the WOS database per age of the article. We added  
115 to the sample the 1963 paper and the 1967 book of MacArthur and Wilson [29,35] as they represent  
116 seminal works on the area that would not be rescued in our search in WOS. Only papers not related to  
117 microorganisms and both theoretical and empirical papers were included in this sample (herein named  
118 *general ecology sample*).

119           Then we used the same searching expression to rescue papers from WOS database associated  
120 with the area categories “agriculture multidisciplinary”, “agronomy”, “biotechnology applied  
121 microbiology”, “critical care medical”, “engineering environmental”, “engineering industrial”, “history  
122 philosophy of science”, “microbiology”, “mycology”, “soil sciences”, “virology”, and “water resources”.

123 In order to expand this sample, we searched the Google Scholar™ database using the expression  
124 [microorg\* OR microb\* AND “island biogeography”]. We restrained our search to the 60 first papers  
125 since going further, the results were very unspecific, and we consider the expense of the survey effort  
126 in relation to the possible gains unprofitable. All the papers rescued in WOS and Google Scholar™  
127 search were evaluated in their content, only those approaching ETIB in the context of microorganisms’  
128 studies (either theoretical or empirical studies) were included in this sample (herein named *microbial*  
129 *ecology sample*).

130 Finally, we evaluated the citation occurrence, that is, if the papers in the microbial ecology  
131 sample cited any of the papers included in the general or microbial ecology sample. Within the  
132 occurrences, we classified every citation event as a theoretical citation, if the citation was made to  
133 develop theoretical aspects of ETIB (e.g., by presenting or developing the principles or processes that  
134 would explain the species richness in the context of the theory), or a non-theoretical citation, if the  
135 citation was not made to develop theoretical aspects of ETIB (e.g., for discussing historical aspects of  
136 the development of ETIB or for presenting primary data or other empirical information from  
137 experiments). The resulting historical pattern of citation was then used to evaluate the proposition  
138 that the field of microbial ecology fails to access important theoretical contributions from general  
139 ecology.

#### 140 **Evaluating “impediments for theoretical interchangeability”:**

141 If the claim that there are theoretical impediments for interchangeability between microbial and  
142 general ecology is true, then the structure of theories developed by the general ecology would not be  
143 suited for understanding phenomena related to microorganisms. To evaluate this claim for ETIB, we  
144 proceeded as follows.

145 Pickett et al (2007) defined a theory as “a system of conceptual constructs that organizes and  
146 explains the observable phenomena in a stated domain of interest” [36]. They describe the anatomy  
147 of a theory as a set of basic conceptual contents (assumptions, concepts, and definitions), empirical

148 contents (facts and confirmed generalizations) and derived conceptual contents (laws, models,  
149 theorems, translation modes, and hypotheses) that are connected to each other by a structure  
150 (denominated framework). Based on this scheme and on the hierarchical nature of theories, Scheiner  
151 and Willig [37] presented a general theory of ecology that serves as the supporting framework for the  
152 constitutive theories of ecology, and several authors presented in this same book the structure of some  
153 of these constitutive theories, as did Sax and Gaines [30], in Chapter 10, for ETIB. Here, we considered  
154 this as the structure of ETIB developed by the general ecology (herein *general ecology ETIB*) and we  
155 evaluated, through a series of steps, if it can be applied to the domain of island biogeography in  
156 microbial ecology (herein *microbial ecology ETIB*).

157         First, we examined the domain of general ecology ETIB, in order to see if it was correspondent  
158 with microbial ecology ETIB. As the domain is inferred from the conceptual and empirical constructs  
159 of a theory [36], it was necessary to give an in-depth examination of the ETIB propositions, so we can  
160 confirm if the theory actually supports microorganisms. Accordingly, we evaluated if basic conceptual  
161 and empirical contents of general ecology ETIB (mainly assumptions, concepts, definitions and  
162 confirmed generalizations) are valid for the context of microbial ecology ETIB. In the scheme of  
163 Scheiner and Willig [37], a theory can be described by a series of “propositions”, that represent “broad  
164 statements about empirical patterns and the processes that operate within the domain” of the theory;  
165 propositions are built on concepts, confirmed generalizations and laws. Also, following this scheme,  
166 the background of a theory includes its domain, assumptions and definitions. Sax and Gaines [30]  
167 formulate the propositions of general ecology ETIB and comment them. We detected the basic and  
168 empirical contents of general ecology ETIB by accessing these propositions and comments. We then  
169 evaluated the validity of these contents in the context of microbial ecology ETIB based on arguments  
170 of validity present in the theoretical citation events evaluated in the analysis of scarcity of information  
171 (see above) and also in other relevant papers.

172         To do the analysis described in the previous paragraph we followed the definitions of the

173 contents presented by Pickett et al.[36]: *domain* = the specific phenomena, its concepts and time and  
174 space scales addressed by the theory; *assumptions* = explicit or implicit presumptions about the nature  
175 of the system of interest needed to build the theory; *concepts* = labeled abstractions from objects or  
176 regularities that constitute the phenomena, established from many observations, and that are broad  
177 than the individual elements to which it refers; *definitions* = conventions necessary to structure, clarify,  
178 restrict and determine the use of the terms (usually concepts) in question; *confirmed generalizations*  
179 = condensations and abstractions from a body of facts that have been tested or systematically  
180 observed.

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## RESULTS

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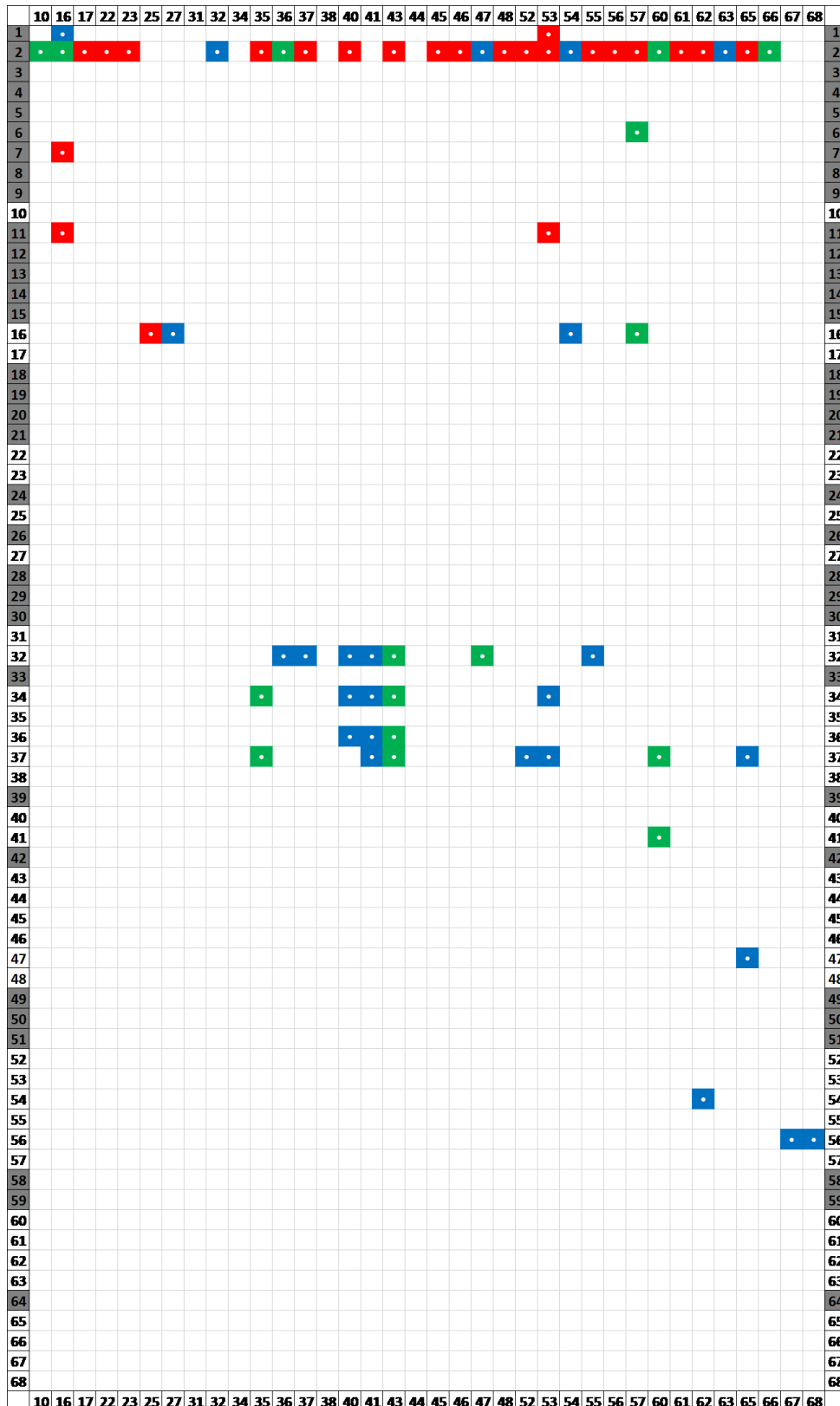
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### 185 **Citation Occurrence and Pattern**

186       The search for “island biogeography” performed for building the general ecology sample  
187 retrieved 1428 entries in the WOS that allowed us to choose 30 papers based on the citation criterion.  
188 The mean number of citations per year in the sample was 16.11, ranging from zero (1968) to 47.5  
189 (2001). Adding the MacArthur and Wilson seminal paper and book the sample totalized 32 documents.  
190 The search for building the microbial ecology sample retrieved 52 entries in the WOS from which 20  
191 were kept after the evaluation of content. The search in Google Scholar™ added other 16 papers to  
192 the sample, resulting in 36 documents in this sample. The list of these 68 documents is available as  
193 supplementary material to the present work (S1 Table).

194       Most of the 36 papers in the microbial ecology sample cited documents from the general  
195 ecological sample: 27 cited the MacArthur and Wilson book and 3 of this subset cited also from 1 to 3  
196 other documents, all of which published in 1980 or before. 27 of the 32 documents in the general  
197 ecology sample were not cited by any paper from the microbial ecology sample (Figure 1). A smaller  
198 group of papers from the microbial ecology sample (19 of 36) cited papers from the microbial ecology  
199 sample that were published from 1987 to 2011 (Figure 1).

200       The historical pattern of citation analysis also detected that 25 of the 36 papers in the microbial  
201 ecology sample made theoretical citations. From these, 24 made theoretical citations from the book  
202 by MacArthur and Wilson and 6 of these made theoretical citations also of other papers from the  
203 general ecology sample, all published in 1980 or before (Figure 1). Only 6 papers presented theoretical  
204 citations from the papers of the microbial ecology sample (Figure 1). The total of citations events  
205 analyzed was 125, 56 of which were theoretical and 44 of which referred to papers from the general  
206 ecology sample, being 39 only to MacArthur and Wilson’s book.



207 **Figure 1: Historical Pattern of Citations.** Citation occurrence and nature are represented by filled cells. Red cells:  
 208 only theoretical citations events; blue cells: only non-theoretical citations events; green cells: both citations  
 209 events. Columns exhibit the documents from the microbial ecology sample, rows exhibit all documents from the  
 210 complete articles samples (grey cells are those from general ecology sample). All documents are ordered  
 211 chronologically. A total of 125 citations events were counted within 64 occurrences. A total of 56 events of  
 212 theoretical nature and 69 non-theoretical. MacArthur and Wilson’s book (second row) accounted for 51 of all  
 213 citations events, 39 of which are theoretical.

214 Therefore, although this pattern reveals that the literature on microbial ecology ETIB accessed  
215 some of the highest impact documents from the correspondent ecological literature, it also  
216 demonstrates that only the oldest documents were accessed, what precludes the incorporation of the  
217 recent developments of the field derived from the ecological literature.

## 218 **Theoretical interchangeability impediments evaluation**

219 In this section, we present the results from our general ecology theoretical contents analysis,  
220 and if they are suited to microorganisms.

221 **ETIB Domain:** Sax and Gaines [31] formulate the domain of the general ecology ETIB as the  
222 *“explanation for variation in patterns of species richness across space and time for island and insular*  
223 *habitats”*.

224 This formulation is broad enough to encompass both macro and microorganisms. By stating that  
225 the theory applies not only to islands but also to insular habitats, the authors attribute to the theory  
226 the necessity to explain phenomena occurring in a wide range of environmental situations and spatial  
227 scales in which patches of potential habitats are isolated of each other by a hostile environment (e.g.,  
228 islands in the ocean and leaves in a tree [38]).

## 229 **ETIB basic conceptual and empirical contents expressed in its propositions:**

230 Here we present the ETIB propositions of both ecological (propositions 1 to 7) and evolutionary  
231 models (propositions 8 to 11) and its components with their definitions. The difference between those  
232 models is the time scale in which the phenomena addressed are explained. We underlined the relevant  
233 concepts to appraise theoretical adequacy and presented their definitions.

234 **Proposition 1:** *“The rate of immigration of species (i.e. the arrival of new species) to an island*  
235 *decreases as the number of species that have arrived on an island increases; the rate reaches zero when*  
236 *all species that could colonize from an available pool of species have done so”*.



237 According to the authors, this proposition is obtained by deductive reasoning. The assumption  
238 underlying such proposition is that the number of new species from a pool of colonists that can arrive  
239 on an island will decrease as these species arrive on the island. The arrival of new species will reach  
240 zero when all species from the colonist pool have already arrived on the island.

241 The concept of *Immigration* is pointed out by MacArthur and Wilson themselves as a difficult  
242 one to define [35]. It is directly related with the concepts of *Arrival* and *Colonize*. The issue here is  
243 whether a species must or not establish itself on the island so that immigration is characterized. More  
244 specifically we could ask “transient individuals from a given species should be counted as  
245 immigrants?”. Sax and Gaines start the proposition with the term “arrive”, which do not necessarily  
246 imply establishment, but simply punctual presence in a location. They latter use the term “colonize”,  
247 which presumes establishment. This may lead to some ambiguity in defining *Immigration*. MacArthur  
248 and Wilson [35] stated that they arbitrarily consider that the *Immigration* of one species occurs when  
249 it has successfully *colonized* a given island, that is, when a reproducing population is settled. We  
250 remark, however, that, as pointed by MacArthur and Wilson, different definitions of immigration will  
251 result in either underestimating or overestimating the immigration rate, but without compromising  
252 the theory.

253 Another concept brought in the proposition is that of *Island*. The concept of an island can be  
254 defined as a discrete habitat circumvented by a surrounding matrix with a certain degree of isolation  
255 [30]. Two important concepts here are (1) habitat and (2) level of isolation, and not surprisingly, they  
256 are linked. Habitat is a concept closely related to species requirements [39]. A given territory or  
257 location can be a habitat to a certain species but not to another. In the context of the ETIB this clarity  
258 in defining habitat is crucial to the predictive power of the theory. A patch of forest that is surrounded  
259 by pasture may not represent an island to a species that can inhabit both physiognomies, but may be  
260 so for a forest specialist species.

261 The last concepts are *Species* and *Number of species* (also referred as diversity or species  
262 richness). Those concepts pose particular difficulties due to the variety of definitions of species [40,41].  
263 In order to measure the number of species of a given location, we must have a clear notion of what a  
264 specie is, and how we are going to identify them.

#### 265 **Fit of Proposition 1 to microbial ecology ETIB**

266 The high dispersal rates of microorganisms led Beijerinck and Baas-Becking to postulate that, for  
267 this group of organisms, "*everything is everywhere, but the environment selects*" [42,43]. Such  
268 proposition is not contradictory to the logical deduction that if all species of a given pool have arrived  
269 to an island, then no new species can do so, and immigration rate would reach zero. Some adjustments  
270 may, however, be needed. The definition of species requires attention, and it must consider the  
271 microorganism under study. This is particularly true for bacteria. In such case, other concepts, such as  
272 Operational Taxonomic Unit (OTU), can be applied as an equivalent to species [44]. New molecular  
273 techniques also allow the survey of bacteria richness [45], indicating that such difference in the species  
274 concept do not hinder the application of the proposition to microorganisms.

275 **Proposition 2:** "*The rate of immigration of species to an island decreases with increasing*  
276 *isolation from a pool of potential colonists*".

277 **Proposition 3:** "*The rate of immigration of species increases with increasing island size*".

278 Propositions 2 and 3 are based on the physical process of diffusion [30]. The assumption  
279 underlying those propositions is that migrating organisms would follow the physical principle which  
280 says that the nearer a given target is from a source of diffusing elements the more frequently such  
281 elements will arrive in it. Similarly, the elements in diffusion arrive in a bigger target more often than  
282 in a small one.

283 Sax and Gaines develops those propositions using "near" and "far" to characterize islands,  
284 indicating an unstated assumption that distance is the criteria of *Isolation*. As the ETIB does not work

285 exclusively with real island, *Isolation* can be anything that interferes in the flux of migratory organisms,  
286 and thus impacting on the immigration rate. This could include physical barriers, distancing from a  
287 *Colonist Pool* and dispersal mechanism presented by the organism, which implies that the *Isolation* has  
288 a species-specific component. The *Colonist Pool* is a given location functioning as a spot source of  
289 organisms. The second concept, *Size*, refers to the dimension of the target. The underlying notion here  
290 is that it is defined by the total surface available for “landing” of the immigrants.

### 291 **Fit of Propositions 2 and 3 to microbial ecology ETIB**

292 Those propositions seem to be adequate to approach microorganisms. It is long known that  
293 microorganisms have long-distance dispersal [46–49], which may imply they can reach any location, as  
294 stated, once again, by the Beijerinck and Baas-Becking’s postulate. This does not deny the proposition,  
295 however, once it deals with *rates*. The deduction that a body with a constant diffusion speed (or  
296 dispersal seep, in the biological context) will reach an isolated target more often than a far one is  
297 preserved. Also, the unlimited dispersal of microorganisms start to be questioned as evidence of  
298 endemism starts to appear [50,51]. One important consideration is that in light of isolation as distance,  
299 it is important to settle the colonists pool, so we can define which habitat is more isolated. As  
300 microorganisms have diffusion sources of immigration [52], evaluate the distance to one specific  
301 source may pose a problem. With respect to the area, it also fits to microorganisms with no special  
302 consideration.

303 **Proposition 4:** “*The rate of extinction of species established on an island (of a given size)*  
304 *increases with increasing number of species*”.

305 **Proposition 5:** “*The rate of extinction of species established on an island decreases with*  
306 *increasing size of an island*”.

307 These propositions are inferred respectively by deductive reasoning and natural history  
308 knowledge [30]. The assumption driving the first proposition is simply that if a higher number of  
309 species is present in a given location, then there are more species to be extinct. The second assumption

310 is that bigger habitats can harbor greater species populations, and under the confirmed generalization  
311 that greater populations are less prone to go extinct, great islands will exhibit lower extinction rates.

312 *Extinction* has a strong link with the concept of *Immigration*, and it is not so easy to define as  
313 well. As we said before, if we consider a transient individual of a new species passing through an island  
314 as an immigrant, its species will be extinct as soon as it leaves it, overestimating extinction rates. More  
315 simply, extinction can be defined as the absence of a given species that has been previously recorded  
316 in a given location.

### 317 **Fit of Propositions 4 e 5 to microbial ecology ETIB**

318 Although the idea that the more species inhabit one area the more species can go extinct may  
319 look undoubtedly logical, it may exhibit some particularities in the microbial field. First, the normally  
320 high population levels could attenuate the extinction rates. Secondly, it is well known that many  
321 microorganisms can go into a state of dormancy [53–55]. It is important to define precisely extinction.  
322 A species must be completely absent from a location or the absence from only the active portion is  
323 enough? As those quiescent states normally confer the organism with resistance, they can still account  
324 for the local diversity [56]. This may lessen the extinction rates, and the expected pattern of species  
325 richness may vary somewhat. It is not well known how important extinction is to natural microbial  
326 populations [57]. Nevertheless, the proposition still can be applied to microorganisms.

327 **Proposition 6:** *“The number of species on an island will be determined by an equilibrium between*  
328 *rates of immigration and extinction”.*

329 **Proposition 7:** *“The rate of species turnover (i.e., change in species composition) will be*  
330 *determined by an equilibrium between rates of immigration and extinction”.*

331 Those propositions are the icing on the cake of ETIB. They rely on the equilibrium processes  
332 observed in chemistry, physics and population biology [30]. It relies on the confirmed generalization  
333 from population biology dynamics, which claims that the total number of individuals of close

334 population is determined by opposing rates of birth and mortality [30]. Herein, it is assumed that the  
335 total number of species in an island can be assessed by evaluating the difference between the  
336 immigration and extinction rates. The assumption is that when immigration is higher than extinction,  
337 the number of species in the island will increase, when extinction is higher, then the number of species  
338 will decrease. The richness will stabilize when both rates reach the same value, and every extinguished  
339 species is replaced by a new one. This leads to the second proposition, which claims that the species  
340 turnover would be defined by such equilibrium in both rates.

341         Sax and Gaines do not precise the definition of *Equilibrium*. This concept has a long history in  
342 ecology development, based on another concept: *Balance of Nature* [58]. Based on the authors'  
343 discussion of the proposition, we conclude that the authors define Equilibrium as the situation in which  
344 immigration and extinction rates are numerically equivalent and their difference equals to zero,  
345 resulting in no addition or loss in the total value of species richness. The *Species Turnover* is defined by  
346 the number of species eliminated and replaced per unit time [59]. An equilibrium turnover will be  
347 defined when both rates, immigration and extinction, are equal, which means that when a given  
348 number  $n$  of species is extinct, the same number will be replaced by new immigrants.

#### 349         **Fit of Propositions 6 and 7 to microbial ecology ETIB**

350         Based on the other propositions, which are necessary to derive the latter two, we can infer that  
351 microorganisms would as well fit in. The changes and particularities of those organisms may result in  
352 different form of the curves or in the intensity of the events, but the main processes and the total  
353 phenomena would be yet assured.

354         **Proposition 8:** *“In addition to immigration, the number of species on an island can be increased*  
355 *by speciation”.*

356         This proposition, according to Sax and Gaines, is based on deductive reasoning [30], although  
357 we would like to complement it with knowledge from evolutionary biology [60]. Its assumption is that  
358 local richness is determined by many factors, and new species do not arise only by immigration, but

359 also by speciation events. Sax and Gaines argued, based on a confirmed generalization, that the  
360 geographical patterns of endemic species exclusive of island habitats, indicates speciation as an  
361 important feature to be considered on ETIB.

362 One of the core concepts of Evolutionary Biology, *Speciation* can be broadly defined as the  
363 phenomenon leading to the specific divergence from one initial population. More precisely it can be  
364 defined as the “accumulation of reproductive isolation and of morphological/genetic differences  
365 through time” [60].

#### 366 **Fit of Proposition 8 to microbial ecology ETIB**

367 Microorganisms do not represent a monophyletic group. The organisms encompassed by the  
368 discipline are greatly diverse, including their reproduction forms. However, microorganisms do exhibit  
369 genetic recombination events and speciate [52,61]. Once these events are not exclusive of  
370 macroscopic organisms, once more, the microorganisms do not seem to reject the proposition, and  
371 new species could count to island diversity through speciation beyond immigration.

372 **Proposition 9:** *“Speciation will only be important to an equilibrium in species number in a*  
373 *“radiation zone” found at the outward limits of species capacity for natural dispersal”.*

374 **Proposition 10:** *“The distance to a “radiation zone” is taxon specific”.*

375 Those propositions are obtained from observation of pattern in the geographic distribution of  
376 endemic species [30]. The propositions are based on the dispersal capacity of each species and the  
377 distance of an island within such capacity. Populations in islands located near the edge of the dispersal  
378 reach of the species are more prone to speciate than those in islands located near the colonist pool.  
379 The assumption here is that lower immigration rates lead to gene flow reduction, what enables  
380 speciation. This is somehow peculiar, considering that the speciation process approached in its  
381 definition considers only gene flow interruption in relation to the colonist pool, and not in the island  
382 site itself. In spite of this, the assumption agrees with the second proposition: islands located far from

383 the colonist pool have lower immigration rates. However, the assumption fails to take into account the  
384 third proposition, which claims that the island size also has implications in the immigration rate. It also  
385 does not consider specific biological aspects, like differences in evolutionary constraints and  
386 evolvability among lineages.

387 A *Radiation Zone* is the spatial area of natural dispersal of a species [30], we refer to it above as  
388 “dispersal reach”. There is an important underlying assumption in this concept. As we discussed above,  
389 the *Radiation Zone* effect is expected to play a role in the speciation in relation to the colonist pool,  
390 which means an allopatric speciation. This model does not take into account sympatric speciation  
391 processes [62], nor local allopatric speciation (allopatry within the island).

#### 392 **Fit of Propositions 9 and 10 to microbial ecology ETIB**

393 Even considering, as we saw before, that microorganisms have high dispersal rates, they are  
394 subject to speciation processes, and there is evidence of the importance that physical isolation has to  
395 speciation processes [61]. This would indicate that those statements would be true to those organisms.  
396 However, to some microorganisms, sympatry can play an important role in speciation, perhaps as  
397 important as allopatry [52,63,64]. Finally, speciation is a complex phenomenon, and occurs in many  
398 ways [65]. As the proposition does not consider such variety of process, and states that speciation  
399 would *only* be important at a gene flow reduction related to the colonist pool condition, we hence  
400 reject it.

401 **Proposition 11:** *“An equilibrium in species number reached ecologically is a “quasi equilibrium”*  
402 *that can be increased over evolutionary time”.*

403 The last proposition of the theory, based on principles of evolutionary biology [30], states that  
404 the equilibrium expected to be observed in the ecological time, is actually not a real equilibrium, as  
405 the number of species can rise when considered the evolutionary time. The basic assumption is that  
406 the immigration can be overestimated when counting the species diversity, once many of the extant

407 species could have raised by evolutionary processes. No novel concepts have been underlined in this  
408 proposition.

#### 409 **Fit of Proposition 11 to microbial ecology ETIBW**

410 We assume this proposition to be also true to microorganisms. However, microbial processes  
411 timescale is very different from that of macro-organisms. A likely result of such microbial characteristic  
412 is a possible overlap between ecological and evolutionary timescales [66]. This would imply that the  
413 evolutionary model of ETIB may play an important role in the description and explanations of microbial  
414 diversity in such theory.

#### 415 **Citation events content and theoretical adequacy**

416 Our analysis of the texts related to the theoretical citation events did not detect an important  
417 amount of statements evaluating the adequacy of the general ecology ETIB to microorganisms. In fact,  
418 from all the 56 theoretical citation events, 40 described basic propositions, as species-area  
419 relationship, predicted by ETIB. Only 16 approached somehow the microbial aspects concerning the  
420 theory functioning and its statements. These 16 citation events were made by a total of 10 papers:  
421 Andrews *et al.*, 1987 [67]; Wilson *et al.*, 1997 [68]; Dolan, 2005 [69]; van der Gast *et al.*, 2005 [70];  
422 Ramette and Tiedje, 2007 [52]; Gray *et al.*, 2007 [71]; Peay *et al.*, 2010 [72]; Locey, 2010 [73]; Tanesaka  
423 2012 [74]; and Lepère *et al.* 2013 [75]. We analyzed these articles to verify whether they develop more  
424 of the microbial aspects regarding the ETIB.

425 Few articles discussed the difficulties related to the unspecific colonist pool. According to  
426 Andrews [67], the imprecision of the source of colonist makes unfeasible the distance-decay analysis.  
427 Ramette and Tiedje [52] also pointed that the “mainland” is not so clear to define, making difficult the  
428 estimations of immigration rates. Often the isolation is measured within island systems, as done by  
429 van der Gast *et al.*, 2005 and Lepère *et al.* 2013 [70,75], in such case community composition is used  
430 to infer distance effects on diversity. Wilson [68], by working with endophytic fungi saw that plant  
431 infections were observed after rainy and cold periods. One could trace a link directly between the



432 dispersal mode of such organism and the isolation degree of it. This could be estimated without the  
433 need of a physical distance reference from a given source location, the environmental condition would  
434 be the main factor controlling dispersal.

435         The species definition problem is quickly overpassed by application of correspondent measures  
436 of diversity as discussed by van der Gast *et al.* and Ramette and Tiedje [52,70].

437         The questions concerning dispersal and immigration are often presented by discussing the  
438 postulate of Beijerinck and Baas-Becking. Actually, testing the veracity of this postulate seems to be  
439 one of the main focus of many articles. Nowadays there is crescent information supporting microbial  
440 endemism, and many articles discuss, even though briefly, this aspect of microorganisms [52,69–  
441 73,75]. Andrews [67] does not approach the ubiquity postulate, but he rapidly comments about the  
442 difficulties of defining immigration and extinction.

443         Speciation, extinction and dormancy are less approached. Gray *et al.* [71] present results in  
444 which environmental selection on divergent populations are decisive in a bacteria genus diversity.  
445 Ramette and Tiedje [52] elaborate a very clarifying review of the speciation role in microorganisms  
446 biogeography. They also approached the extinction processes, stating that natural microbial  
447 population extinction rate information is scarce in literature. Indeed, we do not encounter much  
448 discussion concerning extinction, however it seems to be quite consensual the idea that  
449 microorganisms are resistant to extinction [70,73]. Discussion about dormancy was also rare: it was  
450 briefly commented by Andrews [67], which states that quiescent microorganisms could play an  
451 important role in the diversity processes dynamics. Moreover, Locey [73], realizes a substantial review  
452 about the role of dormancy within the ETIB, considering its impacts on extinction rates.

453         All authors have adapted the concept of island to fit into the microbial context. An interesting  
454 particularity is that van der Gast [70] uses volume as island “area” parameter, and make reference to  
455 other studies that have done so.

456           From all those 10 articles, only three consisted of a theoretical review of ETIB within  
457 microbiology area. They were: Dolan, 2005 [69], Ramette and Tiedje, 2007 [52] and Locey, 2010 [73].  
458 The others approach the theory in an essay to test its applicability to microorganisms.

459

460

## DISCUSSION

461

462

463           The alleged gap between general and microbial ecology is due, as pointed in bibliography [14],  
464 to the different research interests and characteristics of organisms of both areas, which would lead to  
465 a dearth in communication in between them. The first goal of this study was to evaluate such  
466 distancing in the light of this aforesaid aspect, to know: scientific communication. Our historical  
467 pattern of citation results showed an interesting pattern. If microbial ecology articles do access general  
468 ecology papers, we would expect a continuous occurrence of citation of contemporary relevant papers  
469 throughout the analyzed period. However, we also expected a continuous citation of the seminal  
470 document by MacArthur and Wilson [35]. This prediction proved to be only half true. Two clusters of  
471 citation were observed. With almost 41% of all citations occurrence, MacArthur and Wilson was the  
472 most cited document and comprehends the first cluster. As it also accounts for the great majority of  
473 theoretical citations, and considering what is pointed in literature, we can conclude that microbial  
474 ecology theoretical appropriation from general ecology theoretical development is actually lagging  
475 behind [14].

476           This could have seriously implications, once possible theory novelties would have not been  
477 retrieved. Particularly in the ETIB, Whittaker *et al.* [76] general dynamic model proposes enlightening  
478 to the importance of the evolutionary processes in the diversity dynamics in islands. It has great  
479 potential to explain microbial diversity patterns, once speciation and local diversification might have  
480 an important role in those organisms' processes. This article, being surveyed in our analysis and  
481 compounding the general ecology sample, was never cited by any article from microbial ecology  
482 sample. With respect to the citations per area, MacArthur and Wilson represented more than 80% of  
483 the citations of the general ecology sample. No paper from the general ecology sample was cited after  
484 1980. This reinforce the temporal stagnation idea.

485           The second citation cluster represents citations within the microbial ecology area, and it is  
486 mostly composed by non-theoretical citations (44, against only 8 theoretical). Although we found  
487 theoretical review articles in our microbial sample they were never cited by the papers from the  
488 microbial ecology sample.

489           We must emphasize, however, that our methodology considered only the most influential  
490 articles from general ecology, and measured influence with the total citations by publication time rate.  
491 It is possible that those microbial articles were citing less influential ecological papers and this was not  
492 evaluated by us.

493           Concerning the ecological theoretical contributions to microbial articles, our results showed that  
494 there was seemingly no great difference between the number of theoretical and non-theoretical  
495 citation (56 and 69 respectively). The microbial fitting of the theory, however, was not very important  
496 in the citations' content. A majority of theoretical citations were not related to the adequacy of ETIB  
497 to microorganisms. Here we call to attention that this does not mean the adequacy discussion is  
498 completely absent in those documents, and it could have been developed in parts of the text other  
499 than the citation events evaluated by us. Our analysis did not access this.

500           With respect to the second objective of evaluation, namely impediments for theoretical  
501 interchangeability, it seems that the theory fits well enough the microorganisms. The domain  
502 presented by Sax and Gaines is compatible with microorganism even though a microbial ETIB would  
503 have a more restricted domain regarding the organisms studied. Our analysis of the ETIB theoretical  
504 propositions showed that all seven propositions from the ecological model were able to be applied in  
505 microbial systems.

506           Almost all concepts analyzed were compatible with microbial ecology. One exception is the  
507 concept of *Species*, which is particularly problematic to bacteria. In general ecology ETIB species is the  
508 unity used to infer diversity and turnover. As microbiologists have tools to infer microbial diversity,

509 mostly thanks to molecular revolution, a more general concept shall be used. The term species may  
510 still continue to be employed for cultural reasons, but it must be clear what it means.

511 Another concept that would require changes is the one of species number or *Richness*. When  
512 considering the quiescence capacity of many microorganisms, the richness of a given community can  
513 be addressed in many forms. As microbial seed-banks have great importance to the diversity patterns,  
514 we must consider if we should take into count the microbes that are present in the environment,  
515 independently of their activity state, or the partition that functioning plays a role in the environment.  
516 Because of that subdivision of the concept would be useful: *Total richness* for both active and dormant  
517 microorganisms; *effective richness* for the functional partition of microorganism; and attempts to  
518 calculate a possible *potential richness* could be done, in order to measure the approximate amount of  
519 species that potentially could contribute to diversity patterns and maintenance.

520 This lead us to propose, therefore, the inclusion of a new concept to the application of ETIB to  
521 microorganisms: *Dormancy*. The patterns of extinction and immigration might shift significantly when  
522 considering dormancy events [53,73]. The incorporation of such concept to the framework of the  
523 theory, considering the particular aspects of immigration, extinction and richness, is crucial to accurate  
524 analysis. Interestingly, this might be as well true to macroscopic organisms which display such feature,  
525 like plants [77].

526 From the four propositions of the evolutionary model, only two showed application issues.  
527 Those considering the conditions necessary to speciation interfere on the species equilibrium.  
528 However, we assume that this proposition does not fit even to macroscopic organisms, and must be  
529 reformulated for the theory as whole.

530 The claimed gap between the areas was developed under two factors: scarce communication  
531 and theoretical incompatibility. Our results indicate that such a gap between microbial ecology and  
532 general ecology seems to be only partial. Microbial ecology has a poor access to high impact,  
533 contemporary general ecology literature, which demonstrated limited, but not absent,

534 communication. MacArthur and Wilson's book was already expected to be cited, once it is the  
535 proponent of the theory under investigation. Thus, the ecological citations of such document were  
536 inevitable. Microbial ecology rarely cited other high impact articles from general ecology published  
537 after that document. Further investigation would be necessary in order to see if it is a general pattern,  
538 or if it is conditional to ETIB. However, with respect to the theoretical adequacy between both areas,  
539 it seems that ETIB fits well enough to microorganisms, as long as some concepts and definitions are  
540 adapted. Also, as microbiology encompasses a large variety of organisms, it is also very important to  
541 consider the particularities of the group under study [75], which does not imply an interchangeability  
542 impediment. In conclusion, the alleged noxious distance between microbial ecology and general  
543 ecology seem not to be so important when ETIB is taken into account, although improving the dialogue  
544 between both disciplines could help to advance the theory making it more general and its components  
545 better defined. New evaluations similar to ours focusing other theories shared by both disciplines can  
546 help to establish if scarcity of communication and theoretical interchangeability impediments  
547 characterize the relationship between them.

548

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**S1 Table. Complete documents sample**

<b>NB</b>	<b>POOL</b>	<b>AUTHOR(S), YEAR</b>	<b>ARTICLE TITLE</b>
1	ECO	Macarthur & Wilson, 1963	Equilibrium-theory of insular zoogeography
2	ECO	Macarthur & Wilson, 1967	The Theory of Island Biogeography
3	ECO	Hamilton, 1968	Macarthur, rh - theory of island biogeography
4	ECO	Porter, 1969	Tropical island biogeography - missouri botanical gardens sixteenth annual systematics symposium
5	ECO	Straw, 1969	Theory of island biogeography - MacArthur, RH and Wilson, EO
6	ECO	Simberloff & Abele, 1976	Island biogeography theory and conservation practice
7	ECO	Simberloff, 1976	Species turnover and equilibrium island biogeography
8	ECO	Diamond, 1976	Island biogeography and conservation - strategy and limitations
9	ECO	Davis & Glick, 1978	Urban ecosystems and island biogeography
10	MICRO	Henebry & Cairns, 1980	The effect of island size, distance and epicenter maturity on colonization in fresh-water protozoan communities
11	ECO	Gilbert, 1980	The equilibrium-theory of island biogeography - fact or fiction
12	ECO	Higgs, 1981	Island biogeography theory and nature reserve design
13	ECO	Abbott, 1983	The meaning of z in species area regressions and the study of species turnover in island biogeography
14	ECO	Zimmerman & Bierregaard, 1986	Relevance of the equilibrium-theory of island biogeography and species area relations to conservation with a case from amazonia
15	ECO	Case & Cody, 1987	Testing theories of island biogeography
16	ECO	Andrews <i>et al.</i> , 1987	Fungi, leaves, and the theory of island biogeography
17	MICRO	Allen, 1988	Re-establishment of va-mycorrhizas following severe disturbance - comparative patch dynamics of a shrub desert and a subalpine volcano
18	ECO	Hanski & Gilpin, 1991	Metapopulation dynamics - brief-history and conceptual domain
19	ECO	Rorslett, 1991	Principal determinants of aquatic macrophyte richness in northern European lakes
20	ECO	Bierregaard <i>et al.</i> , 1992	The biological dynamics of tropical rain-forest fragments
21	ECO	Wu & Loucks, 1995	From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology
22	MICRO	Marois & Coleman, 1995	Ecological succession and biological-control in the phyllosphere
23	MICRO	Dekesel, A, 1996	Host specificity and habitat preference of <i>Laboulbenia slackensis</i>

24	ECO	Collinge, SK, 1996	Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning
25	MICRO	Wilson <i>et al.</i> , 1997	Ecology and description of a new species of <i>Ophiognomonina</i> endophytic in the leaves of <i>Quercus emoryi</i>
26	ECO	Hubbell, 1997	A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs
27	MICRO	Andrews & Harris, 2000	The ecology and biogeography of microorganisms of plant surfaces
28	ECO	Ricketts, 2001	The matrix matters: Effective isolation in fragmented landscapes
29	ECO	Whittaker <i>et al.</i> , 2001	Scale and species richness: towards a general, hierarchical theory of species diversity
30	ECO	Oertli <i>et al.</i> , 2002	Does size matter? The relationship between pond area and biodiversity
31	MICRO	Lachance <i>et al.</i> , 2003	Geography and niche occupancy as determinants of yeast biodiversity: the yeast-insect-morning glory ecosystem of Kipuka Puauulu, Hawai'i
32	MICRO	Papke <i>et al.</i> , 2003	Geographical isolation in hot spring cyanobacteria
33	ECO	Whittaker <i>et al.</i> , 2005	Conservation Biogeography: assessment and prospect
34	MICRO	Bell <i>et al.</i> , 2005	Larger islands house more bacterial taxa
35	MICRO	Dolan, 2005	An introduction to the biogeography of aquatic microbes
36	MICRO	Van Der Gast <i>et al.</i> , 2005	Island size and bacterial diversity in an archipelago of engineering machines
37	MICRO	Reche <i>et al.</i> , 2005	Does ecosystem size determine aquatic bacterial richness?
38	MICRO	Dobbeler, 2005	Ascospore diversity of bryophilous Hypocreales and two new hepaticolous <i>Nectria</i> species
39	ECO	Lomolino, 2005	Body size evolution in insular vertebrates: generality of the island rule
40	MICRO	Van Der Gast <i>et al.</i> , 2006	Bacterial diversity is determined by volume in membrane bioreactors
41	MICRO	Green & Bohannan, 2006	Spatial scaling of microbial biodiversity
42	ECO	Donald & Evans, 2006	Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes
43	MICRO	Gray <i>et al.</i> , 2007	The biogeographical distribution of closely related freshwater sediment bacteria is determined by environmental selection
44	MICRO	Manfield <i>et al.</i> , 2007	Influence of sustainability and immigration in assembling bacterial populations of known size and function
45	MICRO	Turnbaugh <i>et al.</i> , 2007	The human microbiome project
46	MICRO	Vyverman <i>et al.</i> , 2007	Historical processes constrain patterns in global diatom diversity
47	MICRO	Ramette & Tiedje, 2007	Biogeography: An emerging cornerstone for understanding prokaryotic diversity, ecology, and evolution
48	MICRO	Cockell <i>et al.</i> , 2007	Interplanetary transfer of photosynthesis: An experimental demonstration of a selective dispersal filter in planetary island biogeography



49	ECO	Whittaker <i>et al.</i> , 2008	A general dynamic theory of oceanic island biogeography
50	ECO	Seehausen <i>et al.</i> , 2008	Speciation reversal and biodiversity dynamics with hybridization in changing environments
51	ECO	Laurance, 2008	Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory
52	MICRO	Bisson <i>et al.</i> , 2009	Variation in Plumage Microbiota Depends on Season and Migration
53	MICRO	Lyons <i>et al.</i> , 2010	Theory of island biogeography on a microscopic scale: organic aggregates as islands for aquatic pathogens
54	MICRO	Peay <i>et al.</i> , 2010	Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands
55	MICRO	Locey, 2010	Synthesizing traditional biogeography with microbial ecology: the importance of dormancy
56	MICRO	Johnson & Winquist, 2011	Island biogeography effects on microbial evolution may contribute to Crohn's disease
57	MICRO	Tanesaka, 2012	Colonizing success of saprotrophic and ectomycorrhizal basidiomycetes on islands
58	ECO	Fahrig, 2013	Rethinking patch size and isolation effects: the habitat amount hypothesis
59	ECO	Rybicki & Hanski, 2013	Species area relationships and extinctions caused by habitat loss and fragmentation
60	MICRO	Lepere <i>et al.</i> , 2013	Geographic distance and ecosystem size determine the distribution of smallest protists in lacustrine ecosystems
61	MICRO	Falk <i>et al.</i> , 2013	Partial bioaugmentation to remove 3-chloroaniline slows bacterial species turnover rate in bioreactors
62	MICRO	Bahram <i>et al.</i> , 2013	Ectomycorrhizal fungi of exotic pine plantations in relation to native host trees in Iran: evidence of host range expansion by local symbionts to distantly related host taxa
63	MICRO	Whiteson <i>et al.</i> , 2014	The Upper Respiratory Tract as a Microbial Source for Pulmonary Infections in Cystic Fibrosis: Parallels from Island Biogeography
64	ECO	Fukami, T, 2015	Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects
65	MICRO	Teittinen & Soininen, 2015	Testing the theory of island biogeography for microorganisms-patterns for spring diatoms
66	MICRO	Buosi <i>et al.</i> , 2015	Effects of Seasonality and Dispersal on the Ciliate Community Inhabiting Bromeliad Phytotelmata in Riparian Vegetation of a Large Tropical River
67	MICRO	Loudon <i>et al.</i> , 2016	Vertebrate Hosts as Islands: Dynamics of Selection, Immigration, Loss, Persistence, and Potential Function of Bacteria on Salamander Skin
68	MICRO	Yan <i>et al.</i> , 2016	Environmental filtering decreases with fish development for the assembly of gut microbiota

First column: All articles sampled enumerated chronologically (1 to 68). Second column: Sample group to which the article belongs (microbial ecology sample = MICRO; general ecology sample = ECO).