

Colonization – persistence trade-offs in natural microbial communities

Vicente J. Ontiveros^a, José A. Capitán^{a,b}, Emilio O. Casamayor^c, and David Alonso^a

^aTheoretical and Computational Ecology, Center for Advanced Studies of Blanes (CEAB-CSIC), Spanish Council for Scientific Research, Accés Cala St. Francesc 14, E-17300 Blanes, Spain

^bComplex Systems Group. Department of Applied Mathematics, Universidad Politécnica de Madrid. Av. Juan de Herrera, 6. E-28040 Madrid, Spain

^cIntegrative Freshwater Ecology Group, Centre of Advanced Studies of Blanes (CEAB-CSIC), Spanish Council for Scientific Research, Accés Cala St. Francesc 14, E-17300 Blanes, Spain

February 19, 2020

Corresponding authors	David Alonso / Emilio O. Casamayor
Address	Centre for Advanced Studies (CEAB-CSIC) C. Accés Cala Sant Francesc, 14 17300 Blanes, Catalunya, Spain
Phone / Fax	+34 972 33 6101 / +34 972 33 7806
E-mail Vicente J. Ontiveros	vicente.jimenez@ceab.csic.es
E-mail José A. Capitán	ja.capitan@upm.es
E-mail Emilio O. Casamayor	casamayor@ceab.csic.es
E-mail David Alonso	dalonso@ceab.csic.es
Type of Article	Letter
Running title	Colonization – persistence trade-offs
Words Abstract	149
Words Main Text	≈4120
Figures / Tables	4 / 2
References	64
Text Boxes	0

Statement of authorship: EOC and DA conceived the study. VJO conducted bioinformatic analyses. VJO and JAC contributed with scripts and analyses. VJO led the analyses of the data and wrote the first draft. All authors carefully edited, revised, corrected, critically contributed to, and approved the final version of the ms. All authors contributed to developing the basic concepts on which this work is based on along several “Bridges” workshops.

Data accessibility statement: The complete genetic datasets are available in GenBank under BioProject record IDs PRJNA566370 (Pyrenean lakes), PRJNA429605 (Monegros), and as supplemental material for the Swiss soils (Hartmann et al., 2014).

Abstract

Fitness equalizing mechanisms, such as trade-offs, are recognized as one of the main factors promoting species coexistence in community ecology. However, they have rarely been explored in microbial communities. Although microbial communities are highly diverse, the coexistence of their multiple taxa is largely attributed to niche differences and high dispersal rates, following the principle “everything is everywhere, but the environment selects”. We use a dynamical stochastic model based on the Theory of Island Biogeography to study highly diverse microbial communities over time across three different systems (soils, alpine lakes, and shallow saline lakes). Here we report for the first time a colonization-persistence trade-off in natural microbial communities. We conclude that this trade-off is mainly driven by rare taxa, which are occasional and more likely to follow independent colonization/extinction dynamics. Our work also emphasizes the fundamental value of dynamical models for understanding temporal patterns and processes in highly diverse communities.

Keywords: Colonization-extinction dynamics Species coexistence Natural microbial communities Species Sorting Neutral Theory Fitness equalization Colonization-Persistence trade-off

14 Introduction

15 Contemporary coexistence theory indicates that there are two major classes of mechanisms that promote coexis-
16 tence: *stabilizing* mechanisms that increase negative frequency-dependent selection, and *equalizing* mechanisms
17 that reduce fitness differences among species (Chesson, 2000). Stabilizing mechanisms comprise resource parti-
18 tioning, disease, or storage effects (Hillerislambers *et al.*, 2012), while equalizing mechanisms such as trade-offs
19 are generally produced by life-history trait evolution in a context of historical contingency (Hubbell, 2001). Al-
20 though many examples of trade-offs can be found in macroscopic communities (e.g., Connell (1961), Siepielski
21 *et al.* (2010), Werner & McPeck (1994)), few have been shown for microbes, usually in experimental metacommun-
22 ities (e.g., Cadotte *et al.* (2006), Livingston *et al.* (2012)). To the best of our knowledge, equalizing mechanisms
23 in natural microbial communities have not been carefully evaluated yet. In this paper, our goal is to examine the
24 role of a colonization – persistence trade-off in promoting coexistence across natural microbial communities in
25 both terrestrial and aquatic ecosystems.

26 The coexistence of a high number of species is a recurring theme in ecology (Hutchinson, 1959). Despite the
27 key insight of Chesson (2000), ecologists are unable to predict species coexistence in an open area (Sutherland
28 *et al.*, 2013). Metacommunity ecology (Holyoak *et al.*, 2005, Leibold & Chase, 2017) tries to understand species
29 coexistence and biodiversity, recognizing the importance of scale and spatio-temporal processes. Metacommunity
30 ecology is characterized by four distinct archetypes: species sorting (SS), which focuses on how local environ-
31 mental conditions enable some species to coexist; neutral theory (NT), which centers on dispersal limitation and
32 demographic stochasticity; patch dynamics (PD), which concentrates on the balance of colonization and extinc-
33 tion processes in relatively homogeneous patches; and mass effects (ME), which emphasizes that dispersal may
34 outweigh competitive forces in a set of heterogeneous patches. Adler *et al.* (2007) relate SS and NT with stabiliz-
35 ing and equalizing mechanisms, respectively. SS is related to niche differences, while in NT, dispersal limitation
36 and stochasticity associated to demographic processes override fitness differences resulting in equalization. In the
37 PD archetype, species diversity is maintained by equalizing mechanisms, such as trade-offs in colonization and
38 competitive ability (Calcagno *et al.*, 2006, Solé *et al.*, 2004, Tilman, 1994), or survival/fecundity and competition
39 (Chave *et al.*, 2002, Muller-Landau, 2010).

40 Microbial communities are highly diverse, and their dynamics have been explained traditionally with the
41 principle "everything is everywhere, but the environment selects" (Barberán *et al.*, 2014, Becking, 1934). Con-
42 sequently, microbial diversity is usually understood appealing to the formation of highly interacting microbial
43 associations maintained by niche differences, thus emphasizing that stabilizing mechanisms underlie microbial
44 coexistence. This interpretation of the principle neglects the effects of dispersal (Barberán *et al.*, 2014, Nemergut
45 *et al.*, 2013), a potential equalizing mechanism. Classical microbial ecology has made almost no mention of
46 coexistence-promoting mechanisms when analyzing microbial communities. However, microbial ecologists have
47 recently started to talk in terms of general theoretical frameworks in ecology, such as community assembly and

metacommunity ecology (Costello *et al.*, 2012, Nemergut *et al.*, 2013). In fact, there has been considerable debate on whether SS or NT dominates as an assembly mechanism in microbial communities, with a somewhat inconclusive result (Lee *et al.*, 2013, Van der Gucht *et al.*, 2007, Woodcock *et al.*, 2007).

Interestingly, it has been conjectured that the relative importance of assembly mechanisms might differ for distinct components of the microbial communities (Langenheder & Székely, 2011, Lindström & Langenheder, 2012). Along similar lines, Hanski 1982 already proposed the *core-satellite hypothesis*, framed within the PD archetype, where stochastic variation in colonization and extinction rates leads to species falling into two distinct categories: core species, abundant and persistent, and satellite species, occasional and rare. Magurran & Henderson (2003) extended the relevance of the core-satellite hypothesis into the temporal domain, finding that core species display a species abundance distribution compatible with a log-normal distribution, while satellite species follow a log-series. These differences were associated with distinct functional roles for these two components. Microbial ecologists have also identified core and satellite species (van der Gast *et al.*, 2011). Thus, the maintenance of species coexistence in highly dynamic communities, such as the microbial ones, should not be constrained to a single dominant mechanism.

Here we suggest that equalizing mechanisms of coexistence in microbial communities are more important than currently acknowledged and that the relative importance of stabilizing vs. equalizing mechanisms is different in core and satellite taxa. In this article, we first validate the use of the simplest stochastic model underlying island biogeography to estimate colonization and extinction rates from temporal series of microbial metacommunities. Then we report a novel colonization – persistence trade-off characterizing these metacommunities coherently at different taxonomical levels. Moreover, we found that this trade-off is mainly driven by satellite species, the rare component of the community. The identification of core and satellite taxa allowed us to conclude that the relative influence of coexistence promoting mechanisms is different for these two components. Recognizing the importance of equalizing mechanisms may render a better understanding of the functioning of highly diverse microbial communities.

Materials and Methods

Data samples

We analyzed temporal samples from (i) the water column of four high altitude lakes in the Spanish Pyrenees, monthly followed during one year (Auguet *et al.*, 2011, 2012), (ii) 12 shallow saline lakes in the Spanish Monegros desert plateau, monthly sampled along three years and covering different dry-wet periods (Triadó-Margarit *et al.*, 2019), and (iii) two sites in Switzerland, after a soil compaction experiment lasting four years (Hartmann *et al.*, 2014). Microbial communities were studied after NGS 16S rRNA amplicons analyses, clustered at 97% OTU

identity, and transformed to presence-absence data. Sequences processing and genetic data analyses were carried out as reported in the original studies where additional ecological and environmental information are also available. The complete genetic datasets are available in GenBank under BioProject record IDs PRJNA566370 (Pyrenean lakes), PRJNA429605 (Monegros), and as supplemental material for the Swiss soils (Hartmann *et al.*, 2014).

Colonization and extinction rates

Throughout this work, we applied the simplest stochastic model underlying TIB (Alonso *et al.*, 2015, Simberloff, 1969, Simberloff & Wilson, 1969). This dynamic model explains the average level of richness and its variation in a study site (or *island*) in terms of colonization and extinction processes, on the one hand, and the total number of potentially colonizing species in the regional pool, or metacommunity richness, on the other hand. As Hanski (2001) showed, this model can be derived from an ensemble of single-species models of presence-absence dynamics, under the assumptions of both species independence and equivalence (Alonso *et al.*, 2015). So, we can estimate the model parameters for the dynamics of the whole community from presence-absence temporal data, and, therefore, we characterize the entire microbial community by a single colonization-extinction pair. Alternatively, we can subdivide the community in guilds, relaxing the equivalence assumption, and estimate a distinct and characteristic colonization-extinction pair for each of them (Alonso *et al.*, 2015, Ontiveros *et al.*, 2019). To calculate colonization (c) and extinction (e) rates from the observed presences and absences, as the microbial communities were sampled following an *irregular sampling scheme* (samples separated by unequal time intervals), we used the functions `irregular_single_dataset` and `irregular_multiple_datasets` from R package ‘*island*’ (Ontiveros *et al.*, 2019).

As a way to assess the applicability of the method to microbial communities, we started estimating colonization-extinction rates for several independent sites. For the Pyrenees dataset, we compared three lakes from the same basin (Lakes Llebreia, Llong and Redó d’Aiguestortes, Auguet *et al.* (2011)) and one in a different basin (Lake Redó, Auguet *et al.* (2012)). We followed a model selection procedure, based on the Akaike Information Criterion and the weight of evidence, w_i (Burnham & Anderson, 2002), to develop a series of models with different sets of partitions of the four lakes, and estimate, for each of these partitions, a pair of colonization and extinction rates. Besides, we used data from the Swiss soils to test the precision of the method when confronted with replicates of the same community. Once we assessed the correct performance of the method, we subdivided whole communities into different taxonomic levels, which we considered as ecologically equivalent guilds, for the three habitats under study. Note that the estimation of colonization-extinction rates for very labile taxa might be biased. Therefore, we excluded, from subsequent analyses, those taxa with an estimated persistence value, defined as the inverse of the extinction rate ($p_i \equiv 1/e_i$), much shorter than the minimal inter-event sampling time (less than approximately a quarter of this time).

Core and satellite members of the community

Multiple methods have been applied to distinguish between core and satellite members of a community. While core species are abundant and persistent, satellite species usually show up at lower abundances and are occasional or even accidental. These two components of ecological communities feature distinct functional characteristics. The fact that persistent members of the community usually follow a log-normal abundance distribution, while accidental species follow the log-series (Magurran & Henderson, 2003), can be potentially used as a method to sort out the community core from the rest. However, when processing sequence data from microbial samples, it is common practice to discard OTU sequences appearing only once to minimize potential errors. Therefore, the log-series is difficult or impossible to assess since it requires to record all real singleton species possibly observed in the sample. Instead of using abundance distributions directly, we have applied Chow tests to identify structural breaks in the relation between logarithmic maximum abundances and occupancy (defined as the probability that a species appears in the community over time). The Chow test (Chow, 1960) aims to identify unexpected changes in the parameters of linear regression models along the range of the independent variable. We first identified the intermediate breakpoint with the highest Chow test's statistic, this leading to two different slopes in the abundance-occupancy relation. Then we estimated the mean occupancy between consecutive ends of the two regression lines. We defined as core members of the community those OTUs with occupancy values higher than the aforementioned mean occupancy. OTUs with occupancy values below this threshold were identified as satellite members of the community. We performed Chow tests using the R package 'strucchange' (Zeileis *et al.*, 2003) and log-normal fits for the core sub-community using the R package 'vegan' (Oksanen *et al.*, 2019).

Results

A colonization - persistence trade-off

Trade-offs in ecology arise due to multiple mechanisms, such as competition, perturbations, or physiological constraints. Trade-offs tend to equalize fitness across species. In the context of colonization-extinction models, the colonization to extinction ratio can be regarded as a good measure of species fitness (Solé *et al.*, 2004). In fact, it represents the number of new colonization events during the average time a species remains present in the system before extinction. If two species share this number, they should reach the same importance in the system, either measured in terms of average abundance or average presence. This is true when species follow Levin's metapopulation dynamics (Solé *et al.*, 2004), or simple colonization-extinction independent dynamics, as we used in this paper. Under the assumption of species dynamics independence, species metacommunity dynamics can be formulated as

$$\frac{d\pi_i}{dt} = c_i(1 - \pi_i) - e_i\pi_i, \quad (1)$$

where (c_i, e_i) stands for the colonization-extinction rate pair for species i belonging to a pool of size S_P ($i = 1, 2, \dots, S_P$), and π_i is the probability that species i is found in a community (i.e., the occupancy of that species). Therefore, the probability of species i being present at equilibrium can be written as

$$\pi_i^* = \frac{k_i}{1 + k_i}, \quad (2)$$

where $k_i = c_i/e_i$ is the colonization to extinction ratio. Now we assume that equalizing mechanisms drive community dynamics, hence we expect that species fitness tends to equalize among species, $k_1 \approx k_2 \approx \dots \approx k_{S_P}$. Therefore, the probability π_i^* , which is also called expected occupancy at stationarity, tends to equalize for those species that share the same dimensionless colonization to extinction ratio, k . Conversely, if steady-state occupancies π_i^* are assumed to be roughly equal across species, then Eq. (2) trivially implies that all colonization to extinction ratios (k_i) will tend to be constant across species. Henceforth, we defined persistence as the inverse of the extinction rate ($p_i \equiv 1/e_i$). Because the hypothesis of equalizing mechanisms implies that all ratios c_i/e_i are approximately constant, $c_i/e_i = c_i p_i \approx k$, we find the following persistence-colonization fitness-equalizing trade-off:

$$p_i = k c_i^{-1}. \quad (3)$$

A generic colonization – persistence trade-off can be conceptualized as

$$p_i = k c_i^\alpha, \quad (4)$$

with exponent $\alpha < 0$. Therefore we conclude that if a community of equivalent species is close to performing colonization-extinction independent dynamics, the exponent α of the generic colonization – persistence trade-off above [Eq. (4)] should be -1. This is our theoretical prediction, the one we have checked across the three different microbial communities. Throughout this work, we have represented colonization and persistence axes on a logarithmic scale. This leads us to conclude that a trade-off between colonization and persistence compatible with independent colonization-extinction dynamics should display a slope equal to -1 on a log scale, as it is deduced from the equation: $\log p_i = K - \log c_i$.

The species equivalence assumption

Under this assumption, all species in the community are described by the same colonization-extinction pair. This approximation allowed us to explore whole community dynamics for microbes in lakes of the Pyrenees and soils in Switzerland. For the lakes in the Pyrenees (Fig. 1A), we found that the dynamics of the three lakes in the same basin were so similar that they accumulated a weight of evidence of 89% (summing over all models considering at least two of the three lakes as having the same colonization and extinction), as opposed to the model with all lakes with different rates, which had only a weight of evidence of 11% (see Tab. S1 in Supporting Information).

169 In the case of the soils in Switzerland (Fig. 1B), the distance among replicas within the same soil type and site in
170 colonization and extinction rates was smaller than between sites, showing that the replicas had similar dynamics
171 on each site.

172 **Relaxing the equivalence assumption**

173 Next, we relaxed this assumption and considered the different taxonomic groups in these two bacterial commu-
174 nities, plus the metacommunity in saline lagoons in the Monegros desert. We found that colonization-persistence
175 patterns were coherent as we descended to lower taxonomic levels. So, the distances of genera and families within
176 phyla, classes, or orders (intra-group) were lower than distances between different higher taxonomic levels (inter-
177 group) in the three communities (Kruskal-Wallis test, all p-values < 0.1 in the Pyrenees and < 0.01 in saline lagoons
178 and soils). Moreover, our estimates of colonization and persistence were negatively related conforming to a generic
179 trade-off. An increase in colonization rates led to decreases in persistence, and this relation was maintained across
180 taxonomic levels for the three communities (Tab. 1). Also, the slope of the linear models relating the logarithms
181 of colonization and persistence was very close to -1 . We recall here that a slope of -1 would correspond to a
182 colonization–persistence trade-off resulting from fitness equalization between different taxonomic groups, under
183 the assumption of colonization-extinction independent dynamics.

184 However, the assumptions underlying a colonization – persistence trade-off with exponent -1 might be too
185 severe to apply to whole communities. It is well-known that core members of a community may display different
186 dynamics from the satellite components of it (Magurran & Henderson, 2003). Satellite species tend to be rare
187 and accidental. Sometimes they are observed, sometimes they are not. These species may be good candidates
188 to show a kind of behavior consistent with colonization-extinction independent dynamics, and, therefore, the
189 satellite subcommunity should tend to show, accordingly, a colonization – persistence trade-off with exponent -1 .
190 Instead, the core members of the community tend to be more abundant, and therefore the relative strength of niche
191 processes, such as interactions and niche segregation, would be higher than in the case of satellite species. Then,
192 core species would not necessarily show a trade-off with exponent -1 if they show any at all.

193 To test this hypothesis, we first identified the core and the satellite members of our communities. As abundance
194 enhances occupancy, following a similar argument as in Magurran & Henderson (2003), we represented the linear
195 relation among maximum abundance and occupancy at the Genus level. However, we used a Chow test analysis
196 instead to separate the core from the satellite members of the community by identifying structural changes in the
197 linear relation among maximum abundance and occupancy. Fig. 2 shows the structural changes found in the three
198 studied communities. The point with the biggest statistic allowed us to infer an occupancy threshold that separated
199 the core from the satellite members of the community. As reported for macroscopic communities, the abundance
200 distribution of the core sub-communities followed a log-normal distribution closely.

201 In sum, the distinction between core and satellite members of the community allowed us to examine the

relationship between colonization and persistence separately for these two components, as shown at the family taxonomic level (Fig. 3). These two components presented significantly different slopes, as shown by testing the hypothesis that satellite and core species share the same slope of the linear model (in logarithmic axes) relating colonization and persistence. Moreover, the satellite component of the communities showed slopes very close to -1, while slopes were lower for the community core, except in the case of soils, where both core and satellite sub-communities showed exponents close to -1 (see Tab. 2). These results were maintained across taxonomic levels, up to the lowest one, the Genus. However, as we go up in the taxonomy, losses in statistical power blur these relationships.

Discussion

In this study, we have shown that occasional and persistent taxa in microbial communities are characterized by colonization – persistence trade-offs. Across the three systems analyzed, we found that microbial taxa conform to an almost perfect colonization – persistence trade-off, especially for the occasional members of the community. The existence of this trade-off is consistent with the satellite component following, in a close approximation, colonization-extinction independent dynamics near to a steady-state. This trade-off also implies the existence of fitness equalization, which may be more important than previously recognized in microbial communities, particularly for the functioning of the satellite sub-community. Satellite members would remain in the community by either evolving higher colonization rates but persisting shorter periods or developing the ability to stay longer in the community along with lower colonization rates. Examples of life-history trade-offs can be found easily among macroorganisms and experimental settings of microbes (Jessup & Bohannan, 2008), but, to the best of our knowledge, this is the first time that such a trade-off is reported in highly diverse natural microbial communities.

We have conceptualized the relationship between persistence and colonization in Fig. 4. This pattern is reminiscent of the one reported by Cadotte *et al.* (2006). However, the main difference with figure 1 from Cadotte *et al.* (2006) is that here we identify core and satellite taxa. The identification of core and satellite species is not new in microbial ecology (van der Gast *et al.*, 2011), although similar terms have arisen to refer to the less abundant component, such as the rare biosphere (Lynch & Neufeld, 2015), or conditionally rare taxa (Shade & Gilbert, 2015, Shade *et al.*, 2014). While satellite taxa would follow the trade-off as a result of fitness equalizing mechanisms, core taxa would be driven by stabilizing mechanisms tending to maintain similar persistence across them, but higher than for satellite taxa. Conversely, within the satellite sub-community, in the presence of equalizing mechanisms, any increase in colonization (or persistence) ability would be followed by decreases in persistence (or colonization) ability. Moreover, core taxa are common, abundant species following a log-normal abundance distribution (Magurran & Henderson, 2003). As Cadotte *et al.* (2006) pointed out, in principle, other kinds of taxa could potentially exist: Hutchinsonian "demons", that would competitively exclude other taxa, and evolutionary "losers", that would not colonize nor persist in the community. The microbial communities we have analyzed ap-

235 pear to be compatible with this conceptual view. The three studied communities showed a log-normal abundance
 236 distribution for the core component, as expected, and our observation of ecological coherence in colonization and
 237 persistence within taxonomic levels might well indicate niche differences (Philippot *et al.*, 2010) produced by sta-
 238 bilizing mechanisms. Furthermore, the satellite component of the aquatic communities under study showed a slope
 239 of approximately -1 compatible with a colonization – persistence trade-off under species colonization-extinction
 240 independent dynamics. Conversely, the soil community showed a similar trade-off (with a slope close to -1) for
 241 both core and satellite taxa. This might be due to the way a soil compaction experiment affected this microbial
 242 community. While the microbial aquatic communities might be considered at a seasonally-driven steady state, the
 243 soil community was intentionally poised out from its natural steady state. For instance, soil compaction may have
 244 led to increased anaerobiosis driving the community out of and far away from a previous natural colonization-
 245 extinction equilibrium. Furthermore, the relaxation time to the new steady-state in response to this disturbance
 246 may have also differed for the different treatments (Hartmann *et al.*, 2014).

247 In the context of metacommunities, stabilizing forces have been associated with SS, while equalizing forces
 248 to NT (Adler *et al.*, 2007). SS and NT have been proposed alternatively as the major mechanisms controlling
 249 microbial community assembly. In fact, the importance of SS has been evaluated against other metacommunity
 250 archetypes as NT (Langenheder & Székely, 2011, Lee *et al.*, 2013) or mass effects (ME) (Souffreau *et al.*, 2014,
 251 Van der Gucht *et al.*, 2007) with contrasting results. Also, NT has been tested and proposed as the dominant force
 252 structuring communities (Ofiteru *et al.*, 2010, Woodcock *et al.*, 2007). The dichotomies niche – neutral (Dumbrell
 253 *et al.*, 2010, Ferrenberg *et al.*, 2013) or stochastic – deterministic (Caruso *et al.*, 2011, Wang *et al.*, 2013, Zhou &
 254 Ning, 2017) are similar to the SS – NT divide, and are often used as synonyms. The most accepted view seems to
 255 be that initial steps in community assembly are dominated by neutral processes, while SS characterizes later stages,
 256 but this view is rarely put in the context of coexistence mechanisms. Our work adds to this discussion the fact that
 257 are precisely satellite species the ones governed by fitness equalization. In the light of our findings, this important
 258 component of natural communities would be integrated by ecologically equivalent, rare species, at the lower end of
 259 the abundance spectrum, undergoing a type of temporal dynamics consistent with simple colonization-extinction
 260 independent dynamics.

261 Equalizing mechanisms can evolve in species-rich communities with strong dispersal and recruitment limita-
 262 tion (Hubbell, 2006), although microbial communities are unlikely affected by these limitations. However, experi-
 263 mental settings have repeatedly shown that microbial trade-offs evolve easily in controlled, species-poor microbial
 264 experiments (Huang *et al.*, 2017, Yawata *et al.*, 2014), and might be key in microbial communities (Litchman
 265 *et al.*, 2015). A potential equalizing mechanism might be horizontal gene transfer, as it has been proposed that
 266 it produces highly flexible gene pools associated with specific habitats (Polz *et al.*, 2013), that would equalize
 267 fitness and increase niche overlap. Also, nonlinear responses to fluctuating environments can act as equalizing
 268 or stabilizing mechanisms (Chesson, 2000). Stabilizing mechanisms are widespread in microbial communities,

269 *e.g.*, resource partitioning, dormancy (Jones & Lennon, 2010), or cross-feeding (Goldford *et al.*, 2018), although
270 the processes underlying these mechanisms are rarely studied or understood at trait or biochemical levels. The
271 strength of these stabilizing mechanisms may well allow the satellite members of the community to coexist in the
272 presence of the core component.

273 The purpose of this study was to examine the importance of equalizing mechanisms for microbial coexistence.
274 Our results rely on a dynamic stochastic model, rooted in classic ecological theory. Although its assumptions are
275 drastically simplifying (*species equivalence* and *species independence*), it should be viewed as an approximation to
276 the actual underlying dynamics of the community or its components (when relaxing the *equivalence* assumption).
277 We used this model to estimate extinction and colonization rates from temporal datasets (Alonso *et al.*, 2015,
278 Ontiveros *et al.*, 2019). However, the accuracy of these estimates should be assessed carefully. First, very rare
279 species may be there, but under detectability levels (MacKenzie *et al.*, 2003, 2006, Ontiveros *et al.*, 2019). Second,
280 when persistence times are too short compared to inter-sampling times, these estimates may not be reliable. If taxa
281 go in and out from the system too rapidly, their estimated rates may be biased. This possible bias is the reason why
282 some labile taxa (less than 13 % in all cases) were removed from our analyses. The exclusion of these taxa did not
283 change the overall patterns reported in this study.

284 The relevance of equalizing mechanisms for coexistence might have been overlooked in natural microbial
285 communities. However, they may be relevant in highly diverse ecosystems, especially acting on occasional taxa,
286 as previously suggested (Langenheder & Székely, 2011). Here we argue that, as a result of fitness equalization,
287 occasional taxa should show a persistence–colonization trade-off with slope -1 in logarithmic axes. For satel-
288 lite species, this pattern may well hold beyond the microbial world, which would be worth exploring in the future.
289 Long-term temporal studies are needed to improve our knowledge of coexistence mechanisms. We hope that fram-
290 ing this discussion in the context of equalizing vs. stabilizing mechanisms would add clarity to current knowledge
291 on the forces maintaining high microbial diversity on Earth ecosystems.

292 **Acknowledgements**

293 This work was funded by the Spanish "Ministerio de Economía y Competitividad" under the projects BRIDGES
294 (CGL2015-69043-P, to EOC and DA), and the Ramón y Cajal Fellowship program (DA). VJO have been sup-
295 ported by a Ph.D. contract funded by the Spanish "Ministerio de Economía y Competitividad" under the projects
296 BRIDGES and SITES (CGL2015-69043-P, CGL2012-39964 to EOC and DA). We thank Joan Cáliz and Martin
297 Hartmann for help in bioinformatic analyses and fruitful discussions. We welcome the facilities and warm and
298 creative atmosphere provided by the "white room" in the Computational Biology Lab (CBL) of the Center for
299 Advanced Studies of Blanes.

References

1.

Adler, P. B., HilleRisLambers, J. & Levine, J. M. (2007). A niche for neutrality. *Ecology Letters*, 10, 95–104.

2.

Alonso, D., Pinyol-Gallemí, A., Alcoverro, T. & Arthur, R. (2015). Fish community reassembly after a coral mass mortality: higher trophic groups are subject to increased rates of extinction. *Ecology letters*, 18, 451–61.

3.

Auguet, J.-C., Nomokonova, N., Camarero, L. & Casamayor, E. O. (2011). Seasonal changes of freshwater ammonia-oxidizing archaeal assemblages and nitrogen species in oligotrophic alpine lakes. *Applied and environmental microbiology*, 77, 1937–45.

4.

Auguet, J.-C., Triadó-Margarit, X., Nomokonova, N., Camarero, L. & Casamayor, E. O. (2012). Vertical segregation and phylogenetic characterization of ammonia-oxidizing Archaea in a deep oligotrophic lake. *The ISME Journal*, 6, 1786–1797.

5.

Barberán, A., Casamayor, E. O. & Fierer, N. (2014). The microbial contribution to macroecology. *Frontiers in Microbiology*, 5, 203.

6.

Becking, L. B. (1934). *Geobiologie of inleiding tot de milieukunde*. No. 18-19. WP Van Stockum & Zoon.

7.

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference : a practical information-theoretic approach*. Springer, New York. ISBN 9780387224565.

8.

Cadotte, M. W., Mai, D. V., Jantz, S., Collins, M. D., Keele, M. & Drake, J. A. (2006). On testing the competition-colonization trade-off in a multispecies assemblage. *The American naturalist*, 168, 704–9.

9.

Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006). Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecology Letters*, 9, 897–907.

10.

Caruso, T., Chan, Y., Lacap, D. C., Lau, M. C. Y., McKay, C. P. & Pointing, S. B. (2011). Stochastic and deter-

- 330 ministic processes interact in the assembly of desert microbial communities on a global scale. *The ISME journal*,
331 5, 1406–13.
- 332 11.
- 333 Chave, J., Muller-Landau, H. C. & Levin, S. a. (2002). Comparing classical community models: theoretical
334 consequences for patterns of diversity. *The American naturalist*, 159, 1–23.
- 335 12.
- 336 Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst*, 31, 343–66.
- 337 13.
- 338 Chow, G. C. (1960). Tests of Equality Between Sets of Coefficients in Two Linear Regressions. *Econometrica*,
339 28, 591.
- 340 14.
- 341 Connell, J. H. (1961). The Influence of Interspecific Competition and Other Factors on the Distribution of the
342 Barnacle *Chthamalus Stellatus*. *Ecology*, 42, 710–723.
- 343 15.
- 344 Costello, E. K., Stagaman, K., Dethlefsen, L., Bohannan, B. J. M. & Relman, D. A. (2012). The application of
345 ecological theory toward an understanding of the human microbiome. *Science (New York, N.Y.)*, 336, 1255–62.
- 346 16.
- 347 Dumbrell, A. J., Nelson, M., Helgason, T., Dytham, C. & Fitter, A. H. (2010). Relative roles of niche and neutral
348 processes in structuring a soil microbial community. *The ISME Journal*, 4, 337–345.
- 349 17.
- 350 Ferrenberg, S., O'Neill, S. P., Knelman, J. E., Todd, B., Duggan, S., Bradley, D., Robinson, T., Schmidt, S. K.,
351 Townsend, A. R., Williams, M. W., Cleveland, C. C., Melbourne, B. A., Jiang, L. & Nemergut, D. R. (2013).
352 Changes in assembly processes in soil bacterial communities following a wildfire disturbance. *The ISME Journal*,
353 7, 1102–1111.
- 354 18.
- 355 Goldford, J. E., Lu, N., Bajić, D., Estrela, S., Tikhonov, M., Sanchez-Gorostiaga, A., Segrè, D., Mehta, P. &
356 Sanchez, A. (2018). Emergent simplicity in microbial community assembly. *Science*, 361, 469–474.
- 357 19.
- 358 Hanski, I. (1982). Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis. *Oikos*, 38,
359 210–221.

- 360 20.
- 361 Hanski, I. (2001). Spatially realistic theory of metapopulation ecology. *Naturwissenschaften*, 88, 372–381.
- 362 21.
- 363 Hartmann, M., Niklaus, P. A., Zimmermann, S., Schmutz, S., Kremer, J., Abarenkov, K., Lüscher, P., Widmer,
364 F. & Frey, B. (2014). Resistance and resilience of the forest soil microbiome to logging-associated compaction.
365 *ISME Journal*, 8, 226–244.
- 366 22.
- 367 Hillerislambers, J., Adler, P. B., Harpole, W. S., Levine, J. M. & Mayfield, M. M. (2012). Rethinking Community
368 Assembly through the Lens of Coexistence Theory. *Annu. Rev. Ecol. Evol. Syst*, 43, 227–48.
- 369 23.
- 370 Holyoak, M., Leibold, M. A. & Holt, R. D., eds. (2005). *Metacommunities: Spatial Dynamics and Ecological*
371 *Communities*. University Of Chicago Press, Chicago.
- 372 24.
- 373 Huang, W., Traulsen, A., Werner, B., Hiltunen, T. & Becks, L. (2017). Dynamical trade-offs arise from antagonistic
374 coevolution and decrease intraspecific diversity. *Nature Communications*, 8, 2059.
- 375 25.
- 376 Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press,
377 Princeton, N.J. ISBN 9780691088228.
- 378 26.
- 379 Hubbell, S. P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology*, 87, 1387–1398.
- 380 27.
- 381 Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *The American*
382 *Naturalist*, 93, 145–159.
- 383 28.
- 384 Jessup, C. M. & Bohannan, B. J. M. (2008). The shape of an ecological trade-off varies with environment.
385 *Ecology Letters*, 11, 947–959.
- 386 29.
- 387 Jones, S. E. & Lennon, J. T. (2010). Dormancy contributes to the maintenance of microbial diversity. *Proceedings*
388 *of the National Academy of Sciences of the United States of America*, 107, 5881–5886.
- 389 30.

390 Langenheder, S. & Székely, A. J. (2011). Species sorting and neutral processes are both important during the
 391 initial assembly of bacterial communities. *The ISME journal*, 5, 1086–1094.

392 31.

393 Lee, J. E., Buckley, H. L., Etienne, R. S. & Lear, G. (2013). Both species sorting and neutral processes drive
 394 assembly of bacterial communities in aquatic microcosms. *FEMS Microbiology Ecology*, 86, 288–302.

395 32.

396 Leibold, M. A. & Chase, J. M. (2017). *Metacommunity Ecology, Volume 59*. Princeton University Press. ISBN
 397 9781400889068. URL <https://www.jstor.org/stable/10.2307/j.ctt1w4d24>.

398 33.

399 Lindström, E. S. & Langenheder, S. (2012). Local and regional factors influencing bacterial community assembly.
 400 *Environmental Microbiology Reports*, 4, 1–9.

401 34.

402 Litchman, E., Edwards, K. F. & Klausmeier, C. A. (2015). Microbial resource utilization traits and trade-offs:
 403 Implications for community structure, functioning, and biogeochemical impacts at present and in the future.
 404 *Frontiers in Microbiology*, 6, 254.

405 35.

406 Livingston, G., Matias, M., Calcagno, V., Barbera, C., Combe, M., Leibold, M. A. & Mouquet, N. (2012). Com-
 407 petition–colonization dynamics in experimental bacterial metacommunities. *Nature Communications*, 3,
 408 1234.

409 36.

410 Lynch, M. D. J. & Neufeld, J. D. (2015). Ecology and exploration of the rare biosphere. *Nature Reviews Microbi-*
 411 *ology*, 13, 217–229.

412 37.

413 MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. & Franklin, A. B. (2003). Estimating site occupancy,
 414 colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84, 2200–2207.

415 38.

416 MacKenzie, D. I., Nichols, J. D., J. A., R., Pollock, K. H., Hines, J. E. & Bailey, L. L. (2006). *Occupancy*
 417 *Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, San Diego, CA.

418 39.

419 Magurran, A. E. & Henderson, P. A. (2003). Explaining the excess of rare species in natural species abundance
 420 distributions. *Nature*, 422, 714–716.

- 421 40.
- 422 Muller-Landau, H. C. (2010). The tolerance-fecundity trade-off and the maintenance of diversity in seed size.
- 423 *Proceedings of the National Academy of Sciences of the United States of America*, 107, 4242–4247.
- 424 41.
- 425 Nemergut, D. R., Schmidt, S. K., Fukami, T., O'Neill, S. P., Bilinski, T. M., Stanish, L. F., Knelman, J. E.,
- 426 Darcy, J. L., Lynch, R. C., Wickey, P. & Ferrenberg, S. (2013). Patterns and Processes of Microbial Community
- 427 Assembly. *Microbiology and Molecular Biology Reviews*, 77, 342–356.
- 428 42.
- 429 Ofiteru, I. D., Lunn, M., Curtis, T. P., Wells, G. F., Criddle, C. S., Francis, C. A. & Sloan, W. T. (2010). Combined
- 430 niche and neutral effects in a microbial wastewater treatment community. *Proceedings of the National Academy*
- 431 *of Sciences of the United States of America*, 107, 15345–50.
- 432 43.
- 433 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B.,
- 434 Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. & Wagner, H. (2019). *vegan: Community Ecology*
- 435 *Package*. URL <https://CRAN.R-project.org/package=vegan>. R package version 2.5-4.
- 436 44.
- 437 Ontiveros, V. J., Capitán, J. A., Arthur, R., Casamayor, E. O. & Alonso, D. (2019). Colonization and extinction
- 438 rates estimated from temporal dynamics of ecological communities: The island R package. *Methods in Ecology*
- 439 *and Evolution*, 10, 1108–1117.
- 440 45.
- 441 Philippot, L., Andersson, S. G. E., Battin, T. J., Prosser, J. I., Schimel, J. P., Whitman, W. B. & Hallin, S. (2010).
- 442 The ecological coherence of high bacterial taxonomic ranks. *Nature Reviews Microbiology*, 8, 523–529.
- 443 46.
- 444 Polz, M. F., Alm, E. J. & Hanage, W. P. (2013). Horizontal gene transfer and the evolution of bacterial and
- 445 archaeal population structure. *Trends in Genetics*, 29, 170–175.
- 446 47.
- 447 Shade, A. & Gilbert, J. A. (2015). Temporal patterns of rarity provide a more complete view of microbial diversity.
- 448 *Trends in Microbiology*, 23, 335–340.
- 449 48.
- 450 Shade, A., Jones, S. E., Gregory Caporaso, J., Handelsman, J., Knight, R., Fierer, N. & Gilbert, J. A. (2014).
- 451 Conditionally rare taxa disproportionately contribute to temporal changes in microbial diversity. *mBio*, 5,
- 452 e01731–14.

453 49.

454 Siepielski, A. M., Hung, K.-L., Bein, E. E. B. & McPeck, M. A. (2010). Experimental evidence for neutral
455 community dynamics governing an insect assemblage. *Ecology*, 91, 847–857.

456 50.

457 Simberloff, D. (1969). Experimental zoogeography on islands: A model for insular colonization. *Ecology*, 50,
458 296–314.

459 51.

460 Simberloff, D. & Wilson, E. O. (1969). Experimental zoogeography on islands: The colonization of empty
461 islands. *Ecology*, 50, 278–296.

462 52.

463 Solé, R. V., Alonso, D. & Saldaña, J. (2004). Habitat fragmentation and biodiversity collapse in neutral commu-
464 nities. *Ecological Complexity*, 1, 65–75.

465 53.

466 Souffreau, C., Pecceu, B., Denis, C., Rummens, K. & De Meester, L. (2014). An experimental analysis of species
467 sorting and mass effects in freshwater bacterioplankton. *Freshwater Biology*, 59, 2081–2095.

468 54.

469 Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel,
470 Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J.,
471 Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., Lambin, X., Lewis, O. T., Malhi, Y.,
472 Mieszkowska, N., Milner-Gulland, E. J., Norris, K., Phillimore, A. B., Purves, D. W., Reid, J. M., Reuman,
473 D. C., Thompson, K., Travis, J. M. J., Turnbull, L. A., Wardle, D. A. & Wiegand, T. (2013). Identification of 100
474 fundamental ecological questions. *Journal of Ecology*, 101, 58–67.

475 55.

476 Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, 75, 2–16.

477 56.

478 Triadó-Margarit, X., Capitán, J. A., Menéndez-Serra, M., Ortiz-Álvarez, R., Ontiveros, V. J., Casamayor, E. O.
479 & Alonso, D. (2019). A Randomized Trait Community Clustering approach to unveil consistent environmental
480 thresholds in community assembly. *ISME Journal*, 13, 2681–2689.

481 57.

482 van der Gast, C. J., Walker, A. W., Stressmann, F. A., Rogers, G. B., Scott, P., Daniels, T. W., Carroll, M. P.,
483 Parkhill, J. & Bruce, K. D. (2011). Partitioning core and satellite taxa from within cystic fibrosis lung bacterial
484 communities. *The ISME Journal*, 5, 780–791.

485 58.

486 Van der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N., Cousin, S., Declerck, S., Jeppesen, E., Conde-
487 Porcuna, J.-M., Schwenk, K., Zwart, G., Degans, H., Vyverman, W. & De Meester, L. (2007). The power
488 of species sorting: local factors drive bacterial community composition over a wide range of spatial scales.
489 *Proceedings of the National Academy of Sciences of the United States of America*, 104, 20404–9.

490 59.

491 Wang, J., Shen, J., Wu, Y., Tu, C., Soininen, J., Stegen, J. C., He, J., Liu, X., Zhang, L. & Zhang, E. (2013).
492 Phylogenetic beta diversity in bacterial assemblages across ecosystems: deterministic versus stochastic processes.
493 *The ISME journal*, 7, 1310–1321.

494 60.

495 Werner, E. E. & McPeck, M. A. (1994). Direct and Indirect Effects of Predators on Two Anuran Species along an
496 Environmental Gradient. *Ecology*, 75, 1368–1382.

497 61.

498 Woodcock, S., Van Der Gast, C. J., Bell, T., Lunn, M., Curtis, T. P., Head, I. M. & Sloan, W. T. (2007). Neutral
499 assembly of bacterial communities. *FEMS Microbiology Ecology*, 62, 171–180.

500 62.

501 Yawata, Y., Cordero, O. X., Menolascina, F., Hehemann, J.-H., Polz, M. F. & Stocker, R. (2014). Competition-
502 dispersal tradeoff ecologically differentiates recently speciated marine bacterioplankton populations. *Proceedings*
503 *of the National Academy of Sciences*, 111, 5622–5627.

504 63.

505 Zeileis, A., Kleiber, C., Krämer, W. & Hornik, K. (2003). Testing and dating of structural changes in practice.
506 *Computational Statistics & Data Analysis*, 44, 109–123.

507 64.

508 Zhou, J. & Ning, D. (2017). Stochastic Community Assembly: Does It Matter in Microbial Ecology? *Microbiol-*
509 *ogy and Molecular Biology Reviews*, 81.

510 **Supporting Information**

511 Supporting Table S1 can be found in file ELEontiverosST1.pdf

Figure Captions and Tables

Figure 1. Colonization and extinction rates precisely differentiate dynamics. In panel A, we pooled the three consecutive Pyrenean lakes from the same basin together while a different colonization-extinction pair characterize the fourth lake from another basin. Lake a, Llebreeta, b, Llong, c, Redó d'Aigüestortes, d, Redó. In panel B, two groups of soil samples cluster together around similar colonization-extinction values. These groups correspond to replicates from the same site. Colonization and extinction rates and their error bars were calculated with function `irregular_single_dataset` from the 'island' R package.

Figure 2. The core members of the community follow a log-normal distribution. A) Lakes in the Pyrenees, B) Soils, C) Shallow saline lakes in Monegros. *Left*, blue dashed lines represent the linear relationship between the highest abundance and occupancy at the Genus level, which presents structural changes, determined by a Chow test with maximum values for the statistic in the grey shaded area. We have considered as core Genus (squares) those that presented values of occupancy higher than the mean occupancy of the point with maximum structural change, while those with a lesser occupancy were considered satellite members (circles). *Right*, the core members of the communities present a log-normal distribution (solid blue line). Pyrenees deviance = 1.063; soils deviance = 0.666; Monegros deviance = 4.042. Log-normal distributions were fitted using function `rad.lognormal` of the R package 'vegan'.

Figure 3. Microbial communities show a colonization–persistence trade-off at the family level. Three different habitats, alpine lakes (A), soils (B), and shallow saline lakes (C), display a linear relationship close to the theoretical expectation under a perfect colonization–persistence trade-off (not shown). The trade-off is maintained throughout the phylogeny, from *Phylum* to Genus. However, core (squares) and satellite (circles) members of the community show different relationships between persistence and colonization, being the satellite members closer to the theoretical expectation. The two legs indicate the -1 slope.

Figure 4. Relationship among colonization and persistence. The relative importance of coexistence promoting mechanisms allows us to distinguish several components in microbial communities. The dotted line indicates a perfect persistence – colonization trade-off, where equalizing mechanisms such as trade-offs lead to similar fitness among groups. Any attempt of the satellite taxa to increase their performance would likely result in a corresponding decrease due to life-history constraints. However, in core taxa stabilizing mechanisms dominate and niche differences are high, due to *e.g.* resource partitioning. Hutchinsonian "demons" would represent very persistent species with great colonization abilities, that would outcompete all other taxa, which is unlikely in microbial communities. Evolutionary "losers" stand for species with low fitness and low colonization abilities that would likely represent accidental dispersers not adapted to the environmental conditions of the community.

Table 1. The logarithms of colonization and persistence in the three communities studied are related. p-values refer to Spearman's ρ .

Community	Level	Slope	Lower C.I.	Upper C.I.	Spearman's ρ	p-value	n
Pyrenees	Phylum	-3.455	-5.288	-1.623	-0.736	0.0058	13
	Class	-2.156	-3.778	-0.533	-0.643	0.0016	22
	Order	-1.906	-3.109	-0.702	-0.548	0.0010	34
	Family	-1.636	-2.678	-0.593	-0.507	0.0008	41
	Genera	-1.619	-2.687	-0.552	-0.516	0.0007	41
Soils	Phylum	-1.402	-2.192	-0.611	-0.468	0.0148	27
	Class	-1.088	-1.582	-0.593	-0.411	0.0009	63
	Order	-1.023	-1.377	-0.669	-0.427	1e-05	100
	Family	-0.815	-1.102	-0.528	-0.441	3e-07	127
	Genera	-0.807	-1.087	-0.527	-0.424	4e-07	136
Monegros	Phylum	-1.072	-1.445	-0.700	-0.709	5e-05	27
	Class	-0.989	-1.300	-0.678	-0.609	3e-06	52
	Order	-0.929	-1.199	-0.660	-0.557	8e-09	95
	Family	-0.907	-1.142	-0.673	-0.480	2e-10	160
	Genera	-0.820	-1.038	-0.602	-0.437	1e-10	202

Table 2. Core and satellite sub-communities show differential relationships for colonization and persistence.

A slope of -1 would correspond to a perfect trade-off between colonization and persistence. We have tested the hypothesis that the slope of the linear model for satellite taxa is equal to the slope obtained for core species (Student's t-test), which was rejected in all cases. Associated p-values and t-scores are shown. Additionally, we report data for fitted slopes and their 95% confidence interval. ^{ns}, p-value higher than 0.1, ^{***}, p-value lower than 0.001.

Community	Tax.	p-value	t-score	Component	Slope	Lower C.I.	Upper C.I.	n
Pyrenees	Family	8e-05	-5.513	Core	-0.168 ^{ns}	-1.651	1.315	25
				Satellite	-1.149 ^{***}	-1.531	-0.767	16
	Genera	3e-05	-5.913	Core	-0.103 ^{ns}	-1.637	1.430	25
				Satellite	-1.148 ^{***}	-1.527	-0.769	16
Soils	Family	0.0012	3.366	Core	-1.038 ^{***}	-1.314	-0.762	49
				Satellite	-0.688 ^{***}	-0.895	-0.482	78
	Genera	0.0004	3.697	Core	-1.056 ^{***}	-1.319	-0.792	51
				Satellite	-0.683 ^{***}	-0.883	-0.482	85
Monegros	Family	2e-05	-4.432	Core	-0.621 ^{***}	-0.905	-0.336	60
				Satellite	-1.081 ^{***}	-1.288	-0.875	100
	Genera	0.0001	-4.032	Core	-0.662 ^{***}	-0.938	-0.385	79
				Satellite	-1.038 ^{***}	-1.223	-0.853	123

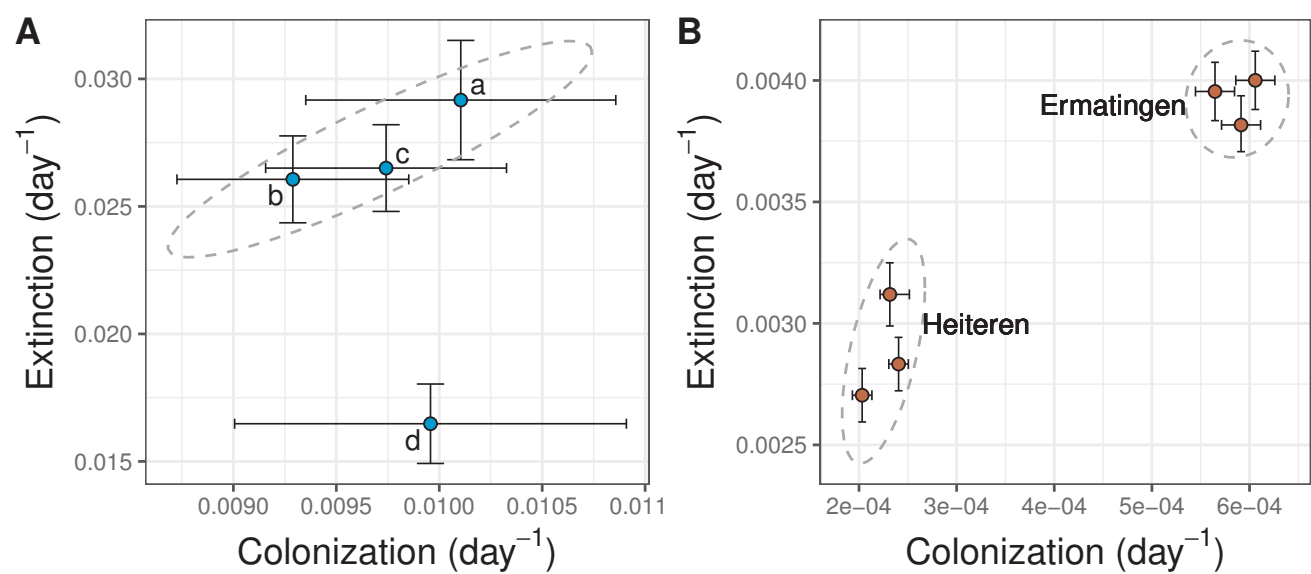


Figure 1

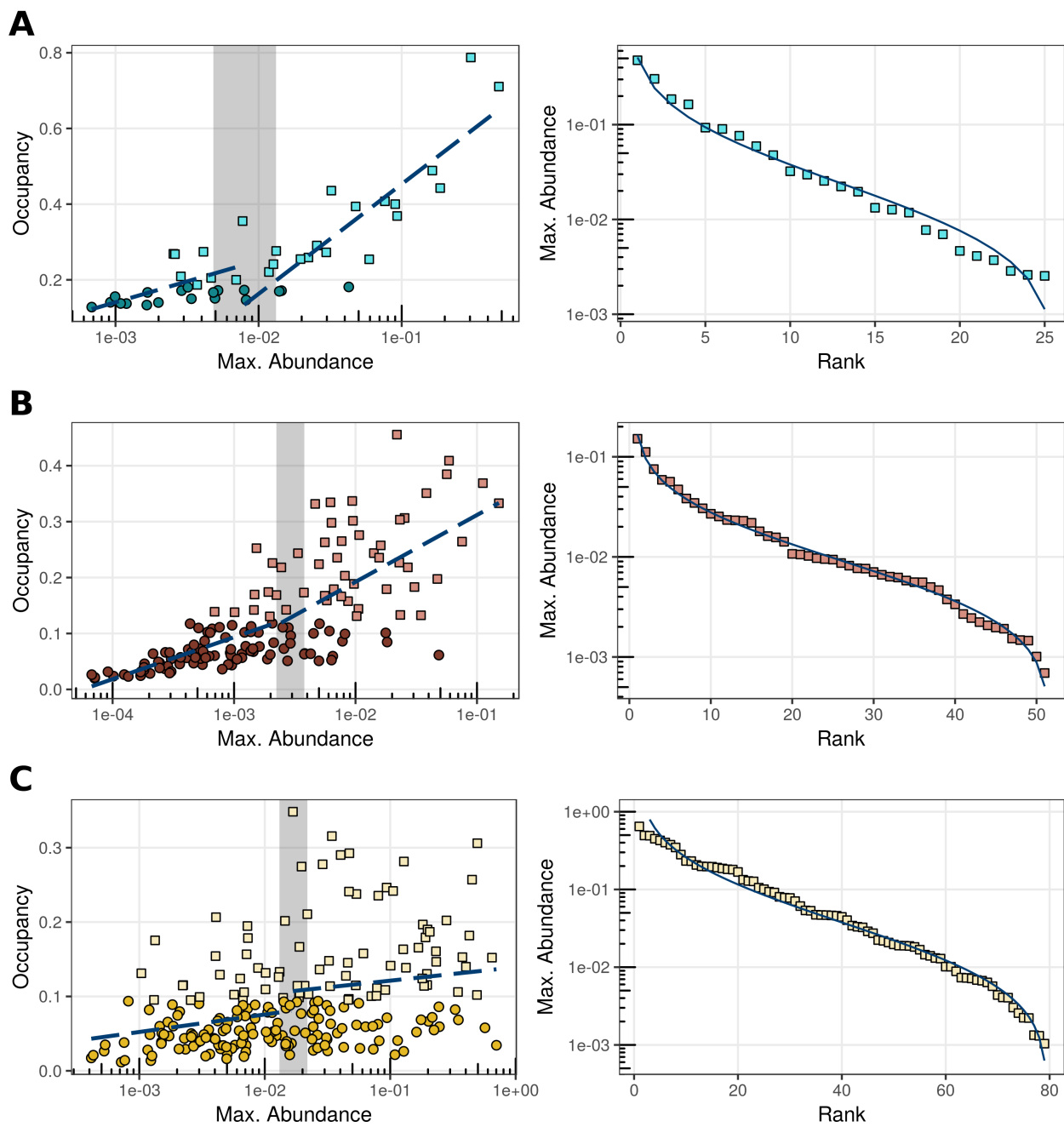
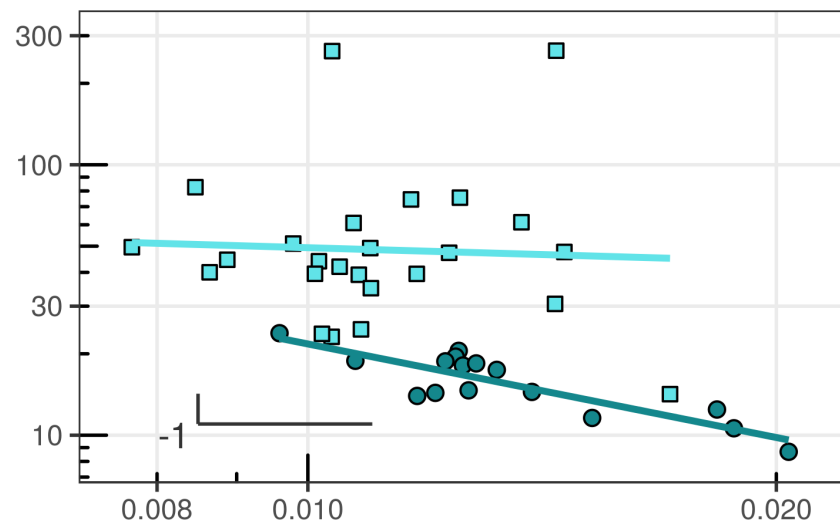
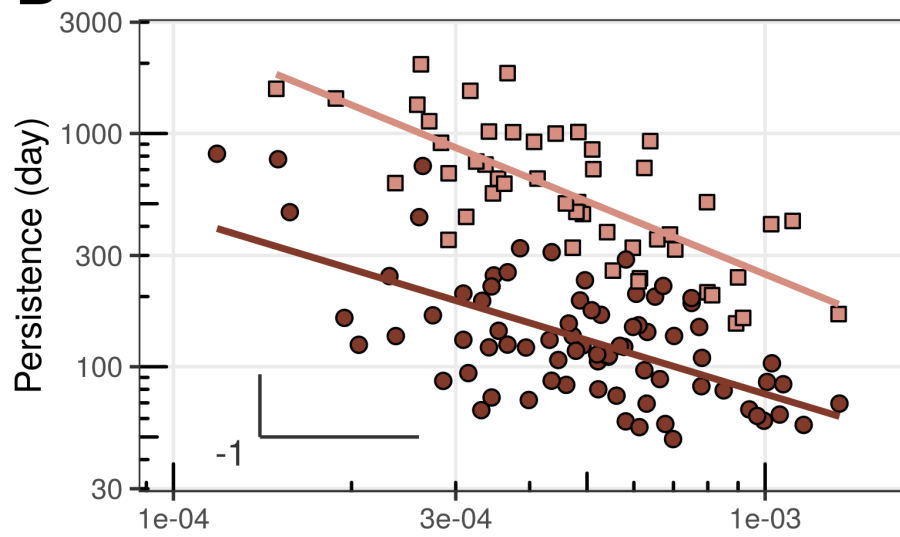
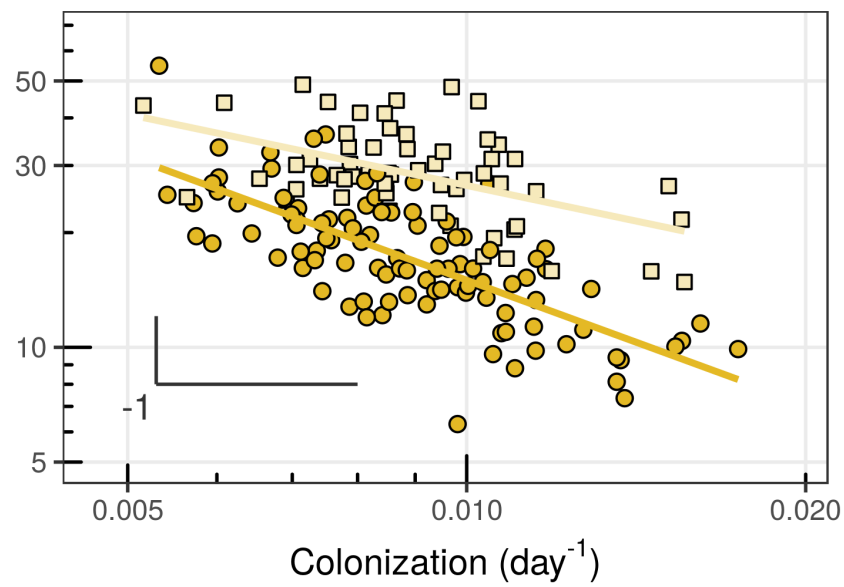


Figure 2

A**B****C****Figure 3**

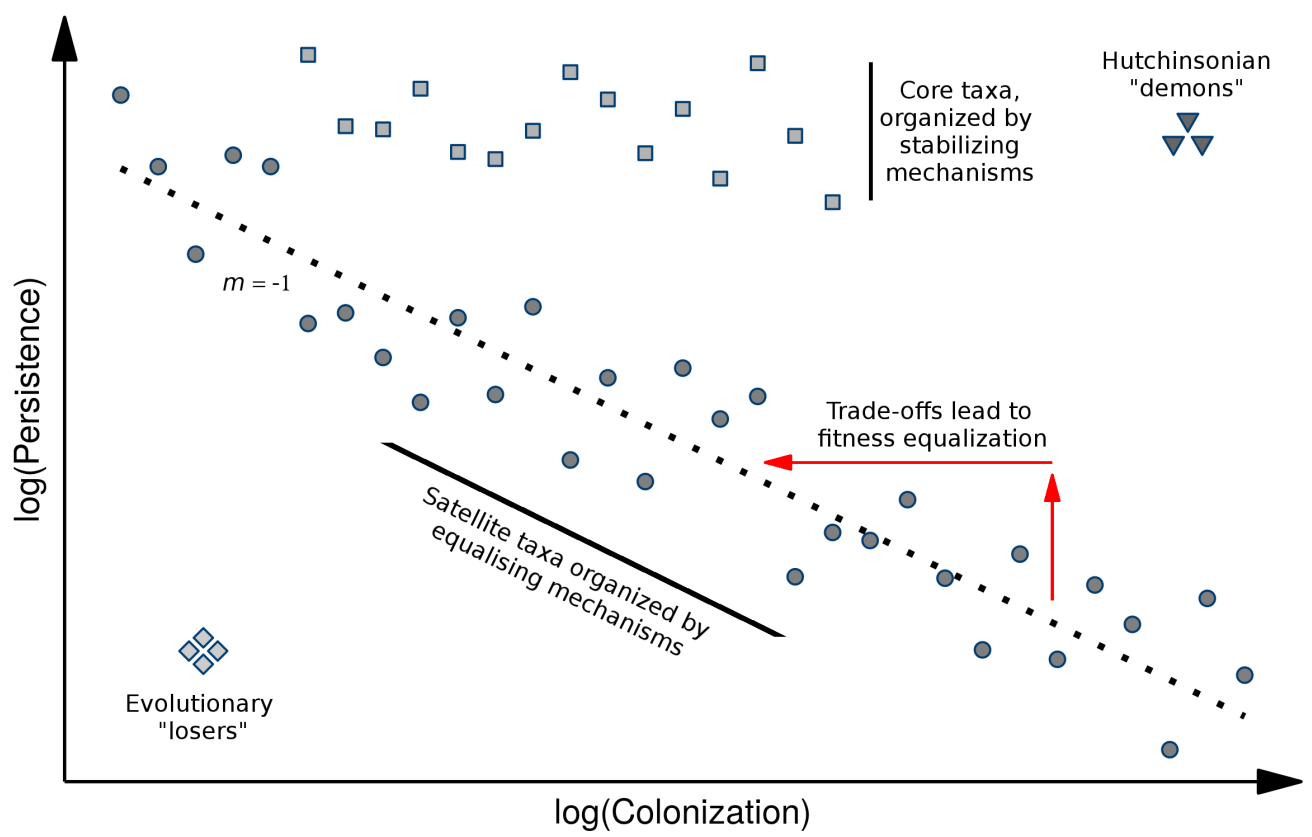


Figure 4