

Assessing species saturation: conceptual and methodological challenges

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ABSTRACT

Is there a maximum number of species that can coexist? Intuitively, we assume an upper limit to the number of species in a given assemblage, or that a lineage can produce, but defining and testing this limit has proven problematic. Herein, we first outline seven general challenges of studies on species saturation, most of which are independent of the actual method used to assess saturation. Among these are the challenge of defining saturation conceptually and operationally, the importance of setting an appropriate referential system, and the need to discriminate among patterns, processes and mechanisms. Second, we list and discuss the methodological approaches that have been used to study species saturation. These approaches vary in time and spatial scales, and in the variables and assumptions needed to assess saturation. We argue that assessing species saturation is possible, but that many studies conducted to date have conceptual and methodological flaws that prevent us from currently attaining a good idea of the occurrence of species saturation.

Key words: biodiversity, niche, community assembly, carrying capacity, equilibrium, species–area, stability, immigration–extinction, species pool.

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I. INTRODUCTION

Is there a maximum number of species that can coexist in a given assemblage? And is there a maximum number of species that a lineage can produce? These questions have puzzled biologists for decades because they have important implications for understanding how biological diversity is spatially distributed and evolutionarily regulated. In effect, ecological and evolutionary theory predicts that an upper limit must exist (Schluter, 2000; Ricklefs, 2006; Phillimore & Price, 2008; Gascuel *et al.*, 2015; Rabosky & Hurlbert, 2015). However, the question is not so much about whether a limit as such exists, but rather whether it has been reached. Numerous studies have attempted to address this question, but their answers differ: many studies support the idea of saturation (e.g. Terborgh & Faaborg, 1980; Sepkoski, 1984; Alroy, 2008; Rabosky & Lovette, 2008; Rabosky & Hurlbert, 2015) while many others reject it (e.g. Benton, 1995; Cornell, 1999; Stohlgren *et al.*, 2008a; Harmon & Harrison,

2015), and some others explain its relativity with regard to different factors like spatial scale (Shurin *et al.*, 2000), seasonality (Starzomski, Parker & Srivastava, 2008), and species interactions (Cornell & Lawton, 1992; Stachowicz & Tilman, 2004). Often, answers are based on different definitions of saturation or the same definitions are tested at different spatial or temporal scales, which prevents reaching any definite conclusion about the prevalence of saturation. The lack of a standard definition or classification limits our ability to test appropriately for saturation in ecological and evolutionary contexts. Thus, despite the apparent simplicity and intuitive appeal of the concept, testing for saturation has proved problematic, to the degree that its appropriateness as a concept has been questioned by some researchers who claimed that it might lead to confusing ideas in ecology (Whittaker, 1977). Terborgh & Faaborg (1980, p. 178) wrote “... no author has proposed a set of operational criteria by which a saturated community could be distinguished from an unsaturated one”. Nearly 40 years later we still lack them.

Herein, we review the literature associated with the concept of saturation. We searched *Web of Science* and *Google Scholar* for combinations of terms related to saturation (community, niche and species saturation) and found 42 matching studies. Almost no study provided a conceptual definition of the term. Furthermore, these studies supported the comments of numerous authors that our understanding of the topic is hampered by misconceptions (Loreau, 2000), lack of a clear analytical framework (Cornell & Lawton, 1992; Cornell, 1999; Russell *et al.*, 2006), and lack of robust methodological approaches (Cresswell, Vidal Martinez & Crichton, 1995; Palmer & van der Maarel, 1995; Mateo, Mokany & Guisan, 2017), for which the cited studies suggest relevant solutions. In addition, it became evident that saturation is a phenomenon that has been assessed at different scales, from local assemblages at ecological timescales (e.g. Fox, McGrady-Steed & Petchey, 2000; Krasnov *et al.*, 2006), to entire lineages over geological periods (e.g. Brayard *et al.*, 2009; Benson *et al.*, 2014), or a combination of both (e.g. Jousset *et al.*, 2008; Pinto-Sanchez, Crawford & Wiens, 2014; Gascuel *et al.*, 2015). Thus, in addition to the 42 matching studies, we reviewed another 101 publications that did not appear in our initial search but whose results are relevant to this review. These include studies on bounded–unbounded diversity and ecological equilibria.

Based on the conceptual background from our survey, we propose the following definition of saturation: *Saturation is the dynamic equilibrium of species richness due to niche limitation within a given group of organisms and within an environmental and temporal reference frame.*

Based on this definition, and as we explain further below, saturation can be demonstrated when we have evidence for stability and/or equilibrium of species numbers as well as evidence for niche limitation. While the restrictions of this definition might appear narrow, we argue that this avoids the interchangeable and misleading use of the terms stability and equilibrium as synonyms of saturation. According to this definition, the context matters, making it impossible to provide a more detailed definition that applies to all relevant situations because as illustrated in this review, the maximum number of species that can coexist depends on where, when, and of whom. This does not mean that for a specific study this definition should not be detailed to fit the purpose of the study.

The insights gained from our survey are presented in two parts. First, we outline seven general challenges of studies on saturation. Second, we provide a list of methodological approaches that have been used to study different aspects of saturation. These are classified in terms of what they actually test for: stability, equilibrium, or niche limitation. We explain the rationale, provide examples, and discuss the approach in the light of the seven main challenges outlined and in relation to method-specific challenges. We place special emphasis on assessing stability because this is mainly addressed in the context of studying saturation, whereas equilibrium and especially niche limitation are widely considered in ecological and evolutionary studies.

While this review is not intended to be the final word on the topic, we hope that we can add some clarity to the discussion by addressing the often-underestimated challenges of studying species saturation and summarizing the ways in which the topic has been approached.

II. SEVEN CHALLENGES IN ASSESSING SATURATION

We now address seven central issues that emerged from our review of the literature and that we consider to be of crucial importance when assessing species saturation.

(1) Conceptual and operational definitions of saturation

The use of the term saturation has varied over time and with different authors. It has its origin in chemistry, where it describes the maximum amount of solute that can possibly be dissolved in a solvent under certain conditions of temperature and pressure (Encyclopaedia Britannica, 2011). The concept of saturation as a maximum amount of species coexisting in a given region dates back to the early 20th century. Grinnell (1914, pp. 98–99) in his study of the animals and birds of the lower Colorado Valley asks: “is the Colorado fauna full? Are all the ecological niches, which are available in this area and which have occupants in other regions, occupied here?”. Although Grinnell pioneered this concept, he did not coin the word saturation, and it was not until the mid-20th century that the term saturation reached a broader application in the field of ecology (Schoener, 1989).

Elton (1950, p. 20) compared the number of animal species at different sites and argued that “the number of animal [species] that can live together in an area of uniform type rapidly reaches a saturation point”. He went on to generalize the idea (p. 22) as “in any fairly limited area only a fraction of the forms that could theoretically do so form a community at any one time.” Elton (p. 17) warned about the difficulty of defining the “area of uniform type”, as he explained, “a study carried out on the animal community of a single major habitat creates, for working purposes, an arbitrary boundary that does not exist in nature”. Finally, he also explicitly stated that it was the total number of species in a certain guild that has an upper limit, but that composition could be highly variable among assemblages (or communities as he called them) and also within assemblages through time.

A decade later, the mathematical concepts provided by the theory of island biogeography (MacArthur & Wilson, 1967) further contributed to understanding the differences in the number of species among assemblages. MacArthur & Wilson (1967, p. 176) defined saturation as the “equilibrium state”. They proposed that as an area accumulates species the immigration rate falls, and the extinction of the species already present rises. When the extinction rate equals the immigration rate, the number of species is at equilibrium or

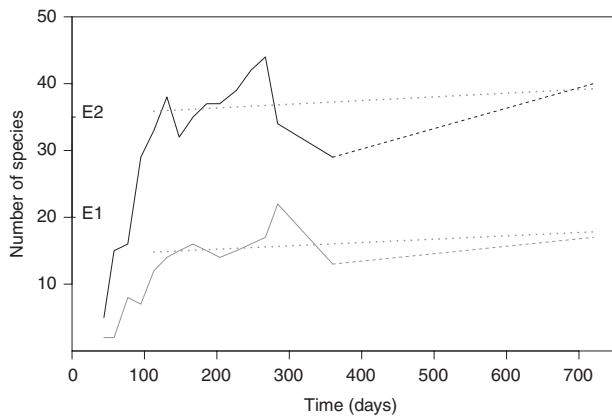


Fig. 1. A classic example of an experimental test of saturation (modified from Simberloff & Wilson, 1970). In this study, small islands (E1, E2) were defaunated and the recovery of insect richness was monitored for 2 years. Pre-defaunation number of species are indicated for each island at time zero. Linear regression (dotted grey lines) indicate no significant change in the number of species after 113 days (E1: $r^2 = 0.01$, $F = 1.14$, $P = 0.31$; E2: $r^2 = -0.05$, $F = 0.45$, $P = 0.52$). The fact that insect richness returned to pre-defaunation levels and that it then remained stable over time was taken as indication of saturation. The trajectory between years 1 and 2 is represented by a dashed line because no intermediate censuses were made.

saturated. It is important to note that the authors treated the terms equilibrium and saturation as equivalent. Later, Simberloff & Wilson (1969, 1970) carried out empirical tests of this theory, in which all insects were removed from small mangrove islands in the Florida Keys. They found that over time insect species richness returned to pre-defaunation levels on most of the islands (Fig. 1).

These examples already exemplify one of the main challenges in assessing saturation. Whereas some authors (in fact, very few) define saturation in a conceptual way, the majority of definitions are operational, in the sense that they claim that saturation can be detected when a certain number of conditions are met, such as in the above example by MacArthur & Wilson (1967). It is important, however, to realize that an operational definition is always based on a conceptual definition, even if the latter is not explicitly stated. Because the validity of any conclusions drawn from a study can only be evaluated against a set of definitions, we consider it imperative for authors to provide both conceptual and operational definitions of saturation, as they apply to their study system.

(2) Pattern, process and mechanism: stability, equilibrium and niche limitation

A major limitation to our understanding of saturation is the challenge of differentiating between the patterns resulting from saturation from the processes and mechanisms that cause it. Thus, applying a consistent terminology to each of these levels is crucial for clarity of communication and we suggest the following differentiation.

Stability is a condition where the number of species does not show a significant change in relation to a period of time or in relation to an increasing species pool. Stability represents a pattern of no directional change (but see Section II.3) and it is the first indicator that saturation might occur (Terborgh & Faaborg, 1980; Cornell & Lawton, 1992; Srivastava, 1999; Loreau, 2000; Stohlgren *et al.*, 2008a; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). However, by itself stability is not sufficient to demonstrate saturation because species numbers can remain stable simply because there is no immigration or extinction in a study system (Section II.3). Hence, stability is only a pattern and we need to address the underlying processes and mechanisms to be able to document saturation.

Equilibrium in the context of saturation refers to the dynamic process whereby there is a balance of species additions (*via* immigration or speciation) and losses (*via* emigration or extinction) in a given system. As a result of this dynamic equilibrium, we observe stability in the number of species. Stability and equilibrium constitute indicators that saturation might occur. However, it is only possible to determine if saturation occurs when in addition there is also an indication that stability or equilibrium are reached by means of niche limitation and not through stochastic mechanisms.

Niche-limitation mechanisms originate from a wide range of ecological and evolutionary reasons, including, e.g. minimum population sizes, limits to the similarity of species, species interactions, and niche characteristics set by the environment. Accordingly, a full assessment of saturation requires an assessment of some of these mechanisms.

(3) How stable is stability?

That the number of species in an assemblage or lineage remains stable over time or in space provides an indication that the assemblage or lineage has reached its ecologically determined upper limit of coexisting species. However, no ecological system is totally invariable in time and space (Simberloff, 1974; Chisholm *et al.*, 2014). For example, Simberloff & Wilson (1970) interpreted their data as representing a pattern of stability (despite not using this term), but their results also show some degree of variation (Fig. 1). For example, in Fig. 1 we observe that the pre-defaunation level for island E2 was 35 species, and that following the initial recovery phase after defaunation, there was a period when species richness values varied between 30 and 40. In the context of saturation, stability then implies that species additions and losses may not necessarily be simultaneous, thus leading to a certain fluctuation of species numbers around the equilibrium level. The challenge then is defining the saturation level. Is it at the maximum (40 species), in which case the points in time with 30–39 species would indicate undersaturated assemblages? Or would it lie at the mean value (35 species) in which case those with 36–40 species would be oversaturated? Or would the saturation level be defined better as a range between 30 and 40 species, in which case the assemblage would be considered to be

continuously saturated? And in the latter case, would we still consider the assemblage to be continuously saturated if its richness fluctuates between 20 and 40 species, or even 10 and 40 species?

The complexity of the study systems, and the vast amount of potential predictors, make it hard to distinguish if these fluctuations are changes in degrees of saturation, random variations (Ricklefs, 1987; Cornell & Lawton, 1992; Cornell, 1999; Loreau, 2000), or responses to fluctuations among the ecological factors determining the upper limit of species that can co-exist. From an ecological viewpoint, these fluctuations occur as part of the colonization process. For example, oversaturation might occur when a habitat is colonized within a short time span by a large number of species and it takes some time before competitive exclusion reduces the number of species to its saturation level (MacArthur & Wilson, 1967; Heatwole & Levins, 1972; MacArthur, 1972; Gilbert & Levine, 2013). In turn, local extinction may drive species numbers below saturation levels (MacArthur & Wilson, 1967; MacArthur, 1972). Saturation thus cannot simply be defined as the maximum number of species found over the time of a study.

A comparable challenge arises when examining saturation at evolutionary timescales (Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). Is saturation only accepted if the rate of diversification (i.e. origination minus extinction) through time reaches a slope of zero, or can we already speak of saturation when the slope of the relationship decreases? In this regard, Cornell (2013, p. 158) argued that there might be a need for a new hypothesis, the “damped increase hypothesis”, which would predict that “diversity generally increases through time but that its rate of increase may sometimes be slowed in a diversity-dependent fashion reflective of ecological constraints”. However, it is left open whether this damped increase would eventually lead to a saturation level or continue indefinitely.

Finally, given the dynamic nature of species assemblages (Simberloff, 1974), a concept that might be useful for the assessment of saturation is that of multistability, i.e. the possibility that a system has multiple stable states as the result of its non-linear dynamics (Feudel, 2008). Under this scenario, the question of saturation as an absolute upper limit might become less relevant and turn instead towards the assessment of these ‘stable’ states.

We conclude that it is crucial for authors to define *a priori* how they expect their study system to fluctuate under stable conditions, which sets the stage for assessing saturation.

(4) How to assess equilibrium?

A dynamic equilibrium occurs when species additions are compensated by losses. This is a fundamental characteristic of a saturated system. Thus, one of the essential conditions to demonstrate equilibrium is that the number of species remains stable despite its potential to increase. This is important, because if for some reason no new species were to arrive or emerge in an assemblage, then the number of species would remain stable (assuming no extinction), and this could

then erroneously be taken as an indication of equilibrium or even saturation. Indeed, species assemblages or lineages might reach a state of equilibrium without compensation of additions and losses (Alroy, 2008).

In addition, as already discussed above for stability, the balance between gains and losses is time-dependent and it may take decades to millennia for equilibrium states to become established (Diamond, 1972; Cornell & Lawton, 1992; Loreau & Mouquet, 1999). For example, invasive species might initially increase the species number of an assemblage (Stohlgren *et al.*, 2008a), but this does not automatically imply that the original assemblages were not saturated, because it might take centuries before competitive exclusion reduces species numbers to their original level (Gilbert & Levine, 2013).

In addition, Simberloff (1974) reviewed the concepts and evidence for different equilibrium scenarios. He reflected on different kinds of equilibrium (e.g. taxon cycle and dynamic equilibrium) which differ in the timescales at which they manifest and in their influence on the rates of immigration and extinction over ecological and evolutionary timescales. In this same review, the author discussed the concept of relaxation time developed by Diamond (1972), which is the time required for a system to reach equilibrium after the immigration rates have been altered by means of geological or environmental changes or by species introductions.

(5) Are there degrees of saturation?

As previously discussed, based on the example in Fig. 1 and assuming it as an indication of saturation in those islands, we observe that even saturated assemblages show certain levels of variability (which may be stochastic or ecologically driven), but it is striking that in the ecological literature, stability is generally dealt with as a binary state: an assemblage is either stable or it is not (Cornell, 1999; Srivastava, 1999; Loreau, 2000; Stohlgren *et al.*, 2008a). This contrasts with the literature on evolutionary processes, where reaching stability is often considered as a gradual process (Rabosky & Lovette, 2008; Rabosky & Glor, 2010; Etienne *et al.*, 2011; Gascuel *et al.*, 2015). For example, Cornell (2013) argued that diversity may already be considered to approach its upper limit when the rate of diversification decreases. He proposed the term ‘damped increase’ to account for such a situation. However, it is not clear whether Cornell hypothesized a damped increase with no upper limit, in which case we could not interpret slowdowns as evidence for a limit, but further diversification studies could elucidate this possibility.

Taking this line of thought a step further, one could express the degree of saturation in relation to the species richness value at which an assemblage is saturated (if this is known). For instance, in the example of Fig. 1, if one were to define saturation to be at 35 species, then at a point in time when this assemblage only has 32 species, it could be considered to be 91% saturated (or 9% under-saturated), and with 39 species, it would be 110% saturated (or 10% over-saturated). Of course, the major challenge here remains how to define the saturation limit. Partly, this is a conceptual issue, but

partly it is also a practical issue when the assemblages under consideration are not saturated and hence it is not possible to define such a limit empirically. However, even if the saturation level is unknown, certain patterns such as a deceleration of species immigration may be taken as an indication that an assemblage or a lineage is approaching saturation. Thus, it is more saturated (or less under-saturated, as one prefers) when the immigration rate is low than when it is high. The same argument is valid for saturation at the evolutionary timescale, although obviously at vastly different timescales and with different underlying processes and mechanisms.

Thus, a further conclusion is that it may be more meaningful to consider saturation not as a binary concept but rather as a ratio.

(6) The importance of the referential system

Saturation in chemistry is defined in relation to certain conditions of temperature and pressure (Encyclopaedia Britannica, 2011). Accordingly, in ecology and evolution saturation defined as the maximum number of species that can coexist depends on where, when, and of whom. Because biological systems change over time, a system can or cannot be saturated or can reach a different degree of saturation according to the area and energy available for the organisms, and the evolutionary dynamics of the taxonomic group (Ricklefs, 1987; Cornell & Lawton, 1992; Lawton, 1999; Fine & Ree, 2006; Cornell, 2013).

Once again, we can take Fig. 1 as an indication of saturation in that species richness remained stable over time and rebounded after a major disturbance. However, this does not imply that this is the maximum upper limit of insect species that can co-occur on these islands over evolutionary timescales. What if a completely new insect group were to evolve and use currently unexploited niche space on these islands (as e.g. Fordyce, 2010)? It is likely that overall species richness would increase, just as, e.g. local mammal diversity increased after the exploitation of the aerial niche space following the evolution of bats (Wilson & Reeder, 2005; Simmons *et al.*, 2008), marine fauna diversified after the massive extinction events of the early Ordovician and late Permian (Fig. 2; Raup & Sepkoski, 1982; Sepkoski, 1984; Benton, 1995; Brayard *et al.*, 2009), and feathered dinosaurs “evaded the effects of niche saturation” and prompted the radiation of birds (Benson *et al.*, 2014). Alternatively, and returning to the hypothetical case of the insect fauna, let us suppose that a major global extinction event decreases world-wide insect richness below today’s levels. A local defaunation experiment might then still find evidence for saturation in that species richness would reach stable pre-defaunation levels after some time. Still, this level would be lower than today’s saturation level. Based on our current knowledge, we would know that the island habitats have the capability to support more insect species or have a different level of saturation under different circumstances.

The issue here is that the maximum number of species that can co-occur in an assemblage at a certain point in time is

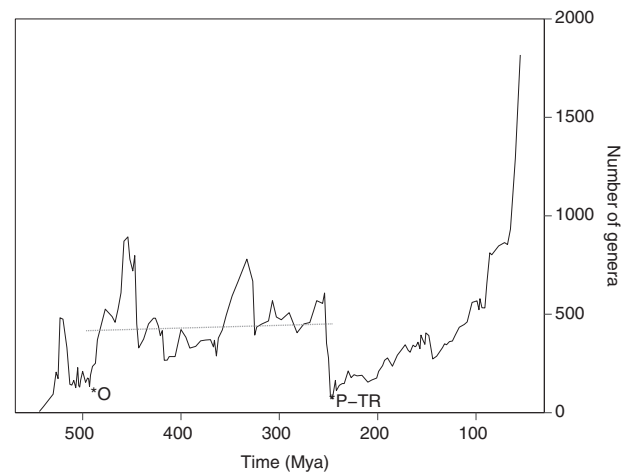


Fig. 2. Diversity of marine animal genera through the Phanerozoic (modified from Sepkoski, 1984). Two major extinction events are indicated by asterisks. Note that after the Ordovician extinction (*O), a strong initial increase occurs and that then the number of genera stabilized for almost 250 million years, suggesting saturation (dashed grey line, $r^2 = -0.01$, $F = 0.24$, $P = 0.62$). However, after the Permian–Triassic extinction event (*P–TR), diversity increased beyond the original saturation level ($r^2 = 0.53$, $F = 77.35$, $P = 1.0e^{-12}$) possibly as a result of major evolutionary innovations that opened new niche space. Mya, million years ago.

not only determined by the habitat conditions (the carrying capacity), but also by the number of species available to colonize the habitat (Cornell, 1999; Srivastava, 1999; Alroy, 2008; Cornell & Harrison, 2014). This regional species pool, from which a local assemblage results, varies in time and space, and accordingly, so will the level of saturation (Terborgh & Faaborg, 1980; Srivastava, 1999; Cornell & Harrison, 2014; Karger *et al.*, 2015).

Furthermore, saturation of a given assemblage may be assessed both in space and in time. This may be exemplified by contrasting two classical studies, that of Elton (1950) and that of Simberloff & Wilson (1969). Elton (1950) examined animal species richness by comparing several assemblages at the same point in time, finding that in similar habitats, species richness was roughly constant, and interpreting this as an indication of saturation. By contrast, Simberloff & Wilson (1969) studied the temporal change in species richness for a single assemblage. What is crucial to consider here is that the same assemblage may be assessed as being saturated under one referential system but not under another.

As an example, we could consider three approaches to studying the biota of an island, which after defaunation is in the process of being recolonized and still has increasing species richness. If we study this island in (i) a temporal framework following Simberloff & Wilson’s (1969) approach, we will find that species richness is still increasing, and conclude that the assemblages are unsaturated. However, if (ii) we compare the assemblages at different sites within the island, following Elton’s (1950) approach, we might find similar richness in comparable habitats and deduce that the

assemblages may be saturated (pending evidence for niche limitation). Yet, if (iii) we compare the island assemblages to those on the mainland, we would find lower richness on the island and conclude that the assemblages are unsaturated. Note that in these examples the difference is not only one of time *versus* space, but also of our implicit definition of the species pool. In examples (i) and (iii), our species pool is the regional flora and fauna from which the species that colonize the island are drawn. In example (ii), we implicitly restrict the species pool to include those species present on the island at the time of the study. So, are these assemblages saturated or not? We consider that this question cannot be answered in absolute terms, but only with reference to the framework within which we assess saturation. Which framework is appropriate will depend on the biological question being asked. If our question is about whether the island is capable of supporting more species, then approaches (i) and (iii) would be appropriate. But if we wanted to know if the species already present on the island are using the available resources to the maximum that is possible with the present biota, then approach (ii) would be appropriate.

So far, we have discussed the aspects of the referential system related to the spatial and temporal coordinates; these aspects refer to the questions of saturation where and when. A third important aspect is that of saturation of whom. Saturation can be studied in groups that share a common ancestor (e.g. a taxon or a lineage) or those that do not (e.g. an assemblage or guild), but the fundamental aspect to be considered is if the targeted species potentially interact or not. This is important because it is the base for niche-limitation mechanisms and sets the stage to defining the appropriate space and timescales and the respective species pool (Section III.3), and in the case of equilibrium, if saturation will be defined in terms of immigration/emigration (Section III.4) or in terms of speciation/extinction rates (Section III.5).

We highlight that careful consideration needs to be given to defining the appropriate referential system for the questions at hand. This applies to all methodological approaches outlined in Section III.

(7) What to measure: diversity, species or traits?

A factor that may also affect the conclusions drawn about saturation is whether the diversity of the studied assemblages is evaluated only based on species richness or whether some index of diversity is used which weights species based on their abundances (Magurran & McGill, 2011). Both approaches have their justification based on the specific questions asked, but it must be clearly stated which of them is used and why. As an example, Fig. 3 shows a data set for fish species recorded over 25 years in the Bristol Channel, and analysed using two different methodological approaches. The first study focused on raw species richness, where a marked increase was found (Henderson, 2007). The second study used a diversity index instead of raw data resulting in a less steep relationship (Magurran & McGill, 2011). In the context of the stability debate, these two approaches may thus lead to different conclusions.

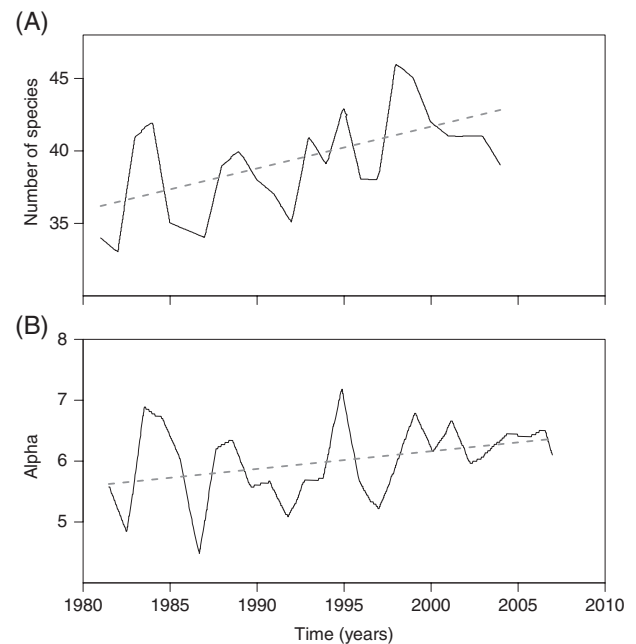


Fig. 3. Fish species richness through time in the Bristol Channel Estuary, UK. (A) Using the number of species observed against time (modified from Henderson, 2007), an increasing trend is detected ($r^2 = 0.39$, $F = 1347$, $P < 2.2e^{-16}$). (B) Fisher's alpha values for the same data (modified from Magurran & McGill, 2011) show a less pronounced relationship ($r^2 = 0.14$, $F = 158.8$, $P < 2.2e^{-16}$).

Another variant is the use of functional richness instead or in addition to taxonomic richness. Functional richness refers to the niche space filled by species in an assemblage (Mason *et al.*, 2005). A functional group is defined as a group of species that share traits linked to ecological functions, in particular those related to the use and competition for resources or to physiological constraints imposed by the environment (Kraft, Godoy & Levine, 2015; Díaz *et al.*, 2016). The idea of assessing functional saturation is to evaluate whether an increase in the number of 'taxonomic entities' translates into an increase in 'ecological entities'. For instance, Canning-Clode *et al.* (2010) used this approach experimentally to evaluate the local–regional richness relationship in artificial marine assemblages. They set bare vinyl panels in analogous marine habitats in different regions of the world and monitored their colonization and succession over 2-month periods for a total of 8 months. Species were classified into functional groups according to traits related to body size, growth form, modularity, motility, and trophic type. The local *versus* regional richness regression analyses demonstrated that for both functional and species richness, assemblages seemed to be saturated at initial and late successional stages. At intermediate stages, however, both types increased with their respective regional richness, indicating under-saturation.

A difficulty in assessing functional saturation is a lack of knowledge on functional biology for most groups of animals and plants; the use of morphological niche volume might

be a way to approach this problem. A morphological niche volume is a 'space' where all key morphological traits of the group of interest occur (Díaz *et al.*, 2016). Hence, saturation would be assessed by comparing the portion of the volume occupied by local assemblages.

In evolutionary terms, we can also think about the evolutionary potential of a specific clade as a reference system, i.e. the potentially limited number of morphological trait combinations that a clade can attain. Using this reference, we can then think of testing saturation of the 'potential morphological volume'. If all of the possible combinations have evolved, this would be indicative of saturation.

III. METHODS TO ASSESS SATURATION

We now summarize methodological approaches for assessing saturation identified in our literature survey. Three general groups were recognized according to the patterns, processes, and mechanisms that define saturation: stability, equilibrium, and niche limitation. We subdivided these groups into subcategories in relation to the temporal timescale, and when needed to the specific aspect assessed by each method.

(1) Stability in ecological time

(a) Species accumulation

(i) *Approach.* This is the approach of Simberloff & Wilson (1969, 1970) in which species numbers are tracked over time after a natural or anthropogenic event has caused an obvious reduction in species numbers (Fig. 1). To be taken as an indication of saturation, it must be shown that (i) the number of species stabilizes, or (ii) reaches the number of species present before the reduction event (if known).

This approach has been used mainly for life forms or ecological guilds, irrespective of their phylogenetic relationships (e.g. Whittaker, 1977). The rationale behind this is the assumption that there is ecological interaction among the species of the selected group.

(ii) *Examples.* Examples of this approach are studies of colonization of the Krakatau Islands (Fig. 4). Periodical plant surveys on the different islands showed that after the volcanic eruption of 1883, there was a continuous increase of species numbers on both the larger island of Rakata and the smaller island of Sertung, although the rate decreased after 1910 (Fig. 4). A decline on Sertung, particularly strong between 1920 and 1940, suggests that its plant assemblages are more saturated than those on Rakata.

(iii) *Evaluation.* Two of the challenges outlined in Section II are particularly relevant here. First, consideration on how to deal with temporal variability is needed (Section II.3). Second, a definition is needed on whether a partial reduction in the accumulation curve is accepted as indicative of saturation or if only a slope of zero is accepted (Section II.5).

Several studies have used species accumulation curves (SACs) over time (Yosef & Tryjanowski, 2002; de Souza,

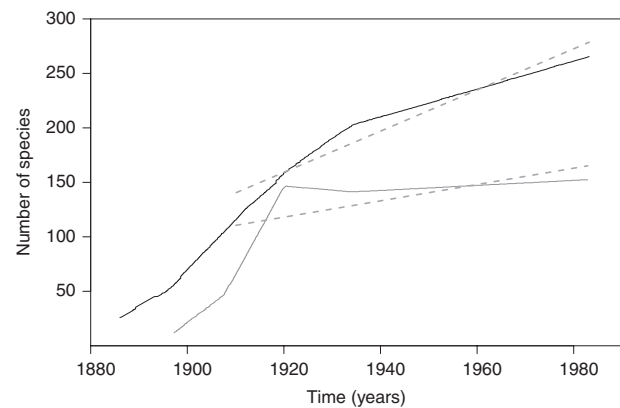


Fig. 4. Number of vascular plant species through time on two of the oldest islands in Krakatau (modified after Whittaker, Bush & Richards, 1989). On Rakata (black solid line), the species number increased continuously despite an accumulation decline after 1910 (top dashed line, $r^2 = 0.94$, $F = 6368$, $P < 2.2e^{-16}$). On Sertung (grey solid line) the number of species increased steadily until about 1920, a subsequent decline followed until about 1940, then it continued increasing but at a lower rate (bottom dashed line, $r^2 = 0.52$, $F = 658.8$, $P < 2.2e^{-16}$). Results on both islands indicate undersaturation, particularly on Rakata.

Marinoni & Marinoni, 2014; Kesting, Petersen & Isselstein, 2015) or in combination with productivity (Guo, Shaffer & Buhl, 2006; Ptacnik *et al.*, 2010; Di Pippo *et al.*, 2014) as tests for saturation. While this may be appropriate in specific cases, we call attention to the risk of confusing sampling completeness with saturation. Assessments of saturation must be based on either complete or equally comprehensive sampling, and to show that the number of species recorded at a site stabilizes over time or with productivity is in no way an indication of saturation at this site.

(b) Number of species

(i) *Approach.* This is comparable to the previous approach, with the difference that there is no initial reduction in species numbers, so that all that is assessed is whether species numbers show a trend in time.

(ii) *Examples.* Long-term monitoring of natural assemblages constitutes the most common example of this kind of assessment of saturation. Figure 5 shows that the number of bird species recorded from Eastern Wood, UK, remained within the range 27–35 species over a 30-year period (Gaston & Blackburn, 2000). Importantly, the total number of species recorded over the years increased over time, showing the ability of additional species to colonize the study region (Section II.3).

(iii) *Evaluation.* One of the important challenges when using this approach is variability (Section II.3). The length of the time record is also important and should consider the natural variation in species numbers because short sampling periods might only show these fluctuations, but in the long term they might be part of a stable trend.

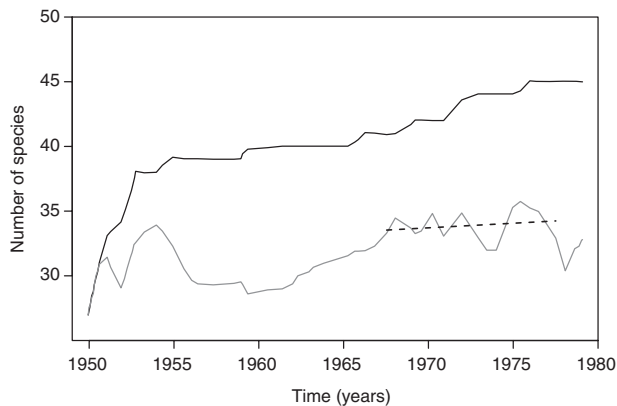


Fig. 5. Number of bird species recorded in Eastern Wood, UK, between 1949 and 1979 (modified after Gaston & Blackburn, 2000). Overall, the number of species per year (grey line) has been increasing over time ($r^2 = 0.34$, $F = 36.46$, $P = 7.60e^{-08}$), albeit with some periods of decline and stability, e.g. between 1967 and 1977 (black dashed line; $r^2 = 0.03$, $F = 0.53$, $P = 0.47$). New species were able to reach the assemblage, increasing the cumulative number of species over time (black line; $r^2 = 0.79$, $F = 257.2$, $P < 2.2e^{-16}$). This is indicative of local saturation coupled with species immigrations and extinctions.

(c) Species introductions

(i) *Approach.* This approach is based on the study of stability of species richness in ecological time, but with the purposeful or unplanned ‘experiment’ of species introductions. The basic assumption is that if assemblages are saturated, then after species introductions they should return to the original level of species richness. Methods included under this approach might be similar to those used in Sections III.1*b*, III.3 or a combination of both.

(ii) *Examples.* The first example is a study of vascular plants in Northwest and Central USA, where Stohlgren *et al.* (2008*a*) assessed local species richness in plots of 100 m² and related it to regional richness. Regional richness was defined as the sum of species richness found in five 1000 m² plots of the same vegetation type. The authors argued that richer local sites should show an asymptotic relation relative to the species pool. They found however a linear relationship between local–regional richness for each vegetation type, and argued against a saturation signal in these assemblages.

In another example, Akatov & Akatova (2010) studied the proportion of native and invasive plant species in open coastal shores of mountain rivers in the western Caucasus. Saturation was assessed by comparing the composition and structure of plant assemblages in plots. The authors assumed that plots located in areas of higher richness should have a higher level of saturation than plots of the same area in poorer assemblages. By doing so, the authors pre-established the level of saturation and then assessed the assemblages ‘resistance’ to invasive species.

(iii) *Evaluation.* Using species introductions to assess saturation is, in principle, a suitable approach but it is riddled with challenges. First, it is known that for a while

following introductions, assemblages may be oversaturated (Sax *et al.*, 2007) and that it may take decades or longer before species numbers stabilize (Gilbert & Levine, 2013). The challenge here is determining whether an assemblage is still in this lag phase or has indeed stabilized at a higher level of species richness.

Second, in the examples above, the authors compared assemblages of originally different species richness. Clearly, there must be biological reasons for these differences, e.g. related to climate or nutrient availability. It is thus hard, if not impossible, to predict the susceptibility of these different assemblages to introduced species (Stachowicz & Tilman, 2004; Fridley *et al.*, 2007).

Third, invasive species may include novel physiological or ecological traits or adaptations not present in the original assemblage (Sax *et al.*, 2007). In such a situation, the original assemblages may have been saturated relative to the original species pools, but not in absolute terms. Here, the issue of the referential system becomes relevant (Section II.6).

Fourth, there is the problem of spatial scale. Numerous studies have shown that locally, invasive species can reduce local species numbers, e.g. when an invasive aquatic species excludes other species (Canonico *et al.*, 2005). However, this rarely leads to total regional extinction of the original species (Gurevitch & Padilla, 2004; Fridley *et al.*, 2007, but see Clavero & García-Berthou, 2005). Thus, at the regional scale, the biota may not be considered saturated, whereas at the local scale it would be.

More generally, if positive effects of introductions on species richness are interpreted as indicative of undersaturation, how do we interpret negative effects of introduced species? If, for example, an invasive species of *Acacia* covers hundreds of km² of fynbos habitat in South Africa and leads to the extirpation of dozens of native species (Richardson, Macdonald & Forsyth, 1989), resulting in both local and regional reductions of species numbers, does this imply that the original assemblages were oversaturated? Obviously not. Clearly, much care should be taken to interpret such cases in terms of the saturation discussion.

(2) Stability in evolutionary time

(a) Species accumulation

(i) *Approach.* The basic approach is equivalent to that in Section III.1*a*, with the difference residing in the temporal and (usually) spatial scales that are covered. Here the number of species is tracked over evolutionary time after an event has caused a significant reduction in species numbers. There are two fundamentally different data sources for this approach: phylogenetic reconstructions derived from molecular analyses of usually extant taxa, and fossil records.

(ii) *Examples.* Basically, any dated phylogeny exemplifies this approach because it documents changes in the number of species of a lineage(s) through time. Figure 6 shows the number of species through time for three different groups using the model developed by Etienne *et al.* (2011). The three groups show a slowdown of diversification

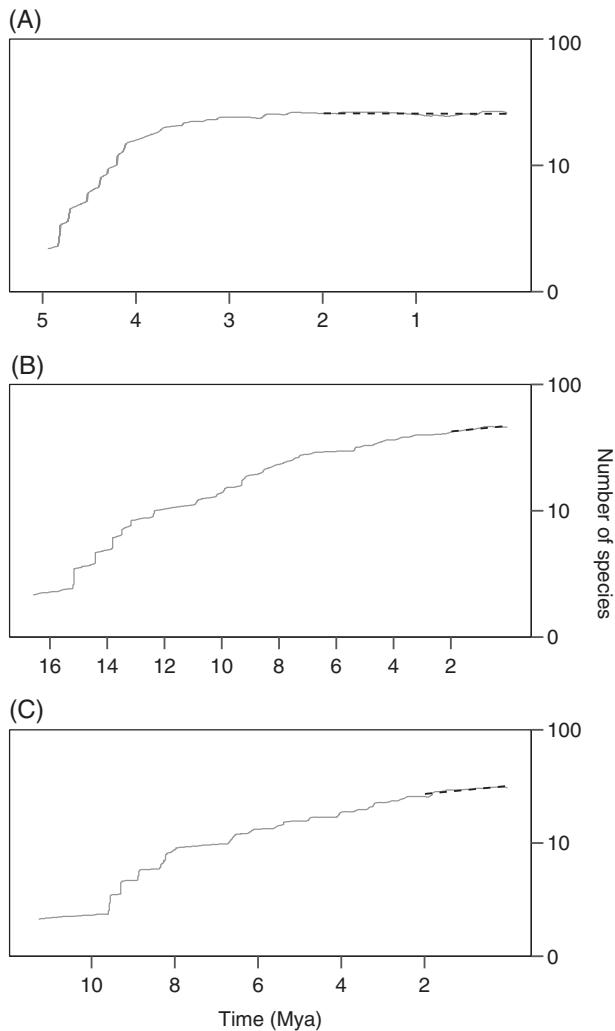


Fig. 6. Number of species through time as predicted only from molecular phylogenies [modified after Etienne *et al.*, 2011, original data from Rabosky & Lovette, 2008 for *Dendroica* (A), Fordyce, 2010 for *Heliconius* (B), and Kozak, Weisrock & Larson, 2006 for *Plethodon* (C)]. Linear models suggest saturation for the warbler genus *Dendroica* which had only a slight increase in the number of species during the last 2 million years (Mya) ($r^2 = 0.016$, $F = 4.434$, $P = 0.04$). The butterfly genus *Heliconius* and the salamander genus *Plethodon* show an ongoing increasing trend during the same period ($r^2 = 0.84$, $F = 308.4$, $P < 2.2e^{-16}$; $r^2 = 0.798$, $F = 357.4$, $P < 2.2e^{-16}$, respectively).

rates, but only North American wood warblers have reached a plateau consistent with saturation (Fig. 6A). Many other studies illustrate this pattern, e.g. on the diversification patterns of marine invertebrates (Rabosky & Hurlbert, 2015), ammonoids after the late Permian mass extinction (Brayard *et al.*, 2009), mammals, in particular for the families Bovidae, Herpestidae, Ziphidae, Ochotonidae and Talpidae (Soria-Carrasco & Castresana, 2011), and the plant genus *Tetralia* (Cyperaceae) from the Cape fynbos (Slingsby, Britton & Verboom, 2014).

(iii) *Evaluation.* When using phylogenetic methods, one of the major challenges is to estimate the past number of

species given that extinction plays a determinant role (Dera *et al.*, 2010; Marshall, 2017). A classic example is that of the diversification of cetaceans, where a phylogeny based only on the extant taxa indicates that species numbers have been increasing, whereas inclusion of the fossil record shows that species numbers were much higher in the past and have been decreasing since the Miocene (Etienne *et al.*, 2011). Thus, while methods with and without fossils are suitable as tests of saturation, by using only the latter, one should be aware that while signs of slowing down or ‘damped’ diversification might be observed (as e.g. in Harvey, May & Nee, 1994), the asymptotic pattern is less likely to be observed.

(b) *Number of species*

(i) *Approach.* Stability here implies that the number of species is constant over geological time periods.

(ii) *Examples.* A first example of this approach was presented in Fig. 2, where the marine fauna record by Sepkoski (1984) suggests a saturated number of genera between the early Ordovician and late Permian. Another example is a study of ammonoid richness after the late Permian extinction event (McGowan, 2005). Figure 7 illustrates the percentage of ammonoid genera in different periods of the early Triassic. Results show that after an initial increase, the percentage of ammonoid genera reached stability. Finally, a fossil record study suggests that several wetland plant assemblages reached a state of stability during the Carboniferous (Cleal *et al.*, 2012).

(iii) *Evaluation.* Large variation in the number of species over geological time is one of the arguments against saturation (Harmon & Harrison, 2015). Hence, again the length of the time record is of major importance in the detection of stability trends, because as Rabosky (2009) explained, the observed trend might vary according to the evolutionary stage of the study group. If only the initial ‘growth’ phase of clades is captured, then a continuous increasing trend will be observed, but this trend might show a decline and further stability in later stages when the growth phase has receded.

(c) *Species introductions*

(i) *Approach.* This approach is analogous to that on species introductions in ecological time (Section III.1c), but at different spatial and temporal scales, with species ‘introductions’ usually the result of long-distance dispersal between continents or biogeographical regions.

(ii) *Examples.* Pinto-Sanchez *et al.* (2014) aimed to find evidence of saturation by studying the impact of the Great American Biotic Interchange (GABI) on patterns of local richness of a group of frogs. They traced the Central or South American origin of each lineage and identified those that dispersed among regions during the GABI. By estimating local species richness in each region before and after the GABI, they assessed the local changes in both invaded assemblages. Since local species richness increased

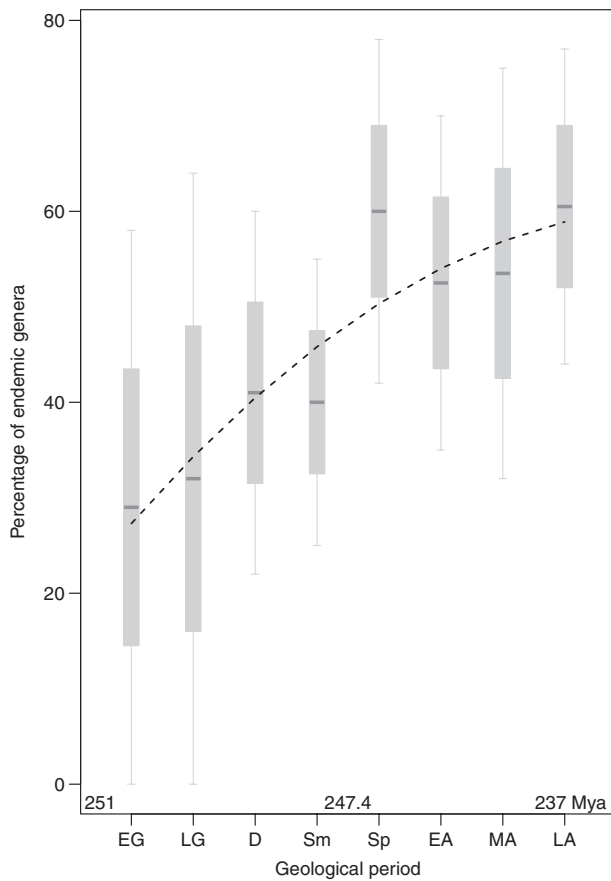


Fig. 7. Patterns in ammonoid endemic genera during the early Triassic (modified after McGowan, 2005). The boxplots show the range (boxes and whiskers) and median (midlines) values of the percentage of endemic ammonoids in each geological period. These values describe an asymptotic curve ($r^2 = 0.37$, $F = 102.9$, $P < 2.2e^{-16}$) with no significant change during the last four periods ($r^2 = 0.006$, $F = 0.01$, $P = 0.92$). EG = Early Griesbachian; LG = Late Griesbachian; D = Dienerian; Sm = Smithian; Sp = Spathian; EA = Early Anisian; MA = Middle Anisian; LA = Late Anisian. Mya, million years ago.

in both assemblages, they concluded that assemblages must have been unsaturated before the GABI.

(iii) *Evaluation.* The challenges of this approach are analogous to those outlined at the ecological timescale (Section III.1c).

(3) Stability relative to the regional species pool

(a) Approach

Under this approach, saturation occurs when the relationship between the local *versus* regional species pool reaches an asymptote (Terborgh & Faaborg, 1980).

(b) Examples

The study of Terborgh & Faaborg (1980) aiming to test saturation of bird assemblages in the West Indies is an early

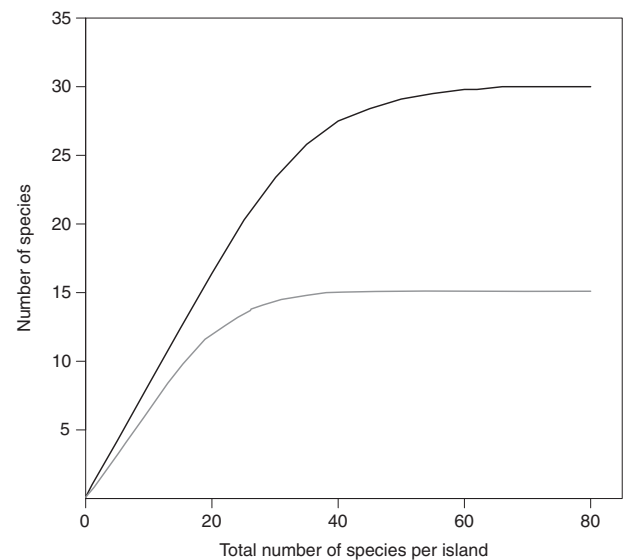


Fig. 8. Number of bird species observed in two habitats (sclerophyll scrub, black; rainforest, grey) against the total number of species on 12 Greater and Lesser Antillean islands (modified after Terborgh & Faaborg, 1980). In this study, the relationship between the total number of bird species on each island and the number of species observed in each habitat had two phases. In an initial linear phase, the number of species in each habitat increased as more species were present in the island; in a second phase the number of species per habitat remained constant despite an increased number of species on the island (scrub: $t = 1.47$, $P = 0.17$; rainforest: $t = 1.64$, $P = 0.11$). The latter phase was interpreted as indicative of saturation.

application of this approach. The authors defined the total number of species present on each island as the insular species pool and then evaluated the local species richness at sites in different habitats on each island. The number of bird species in each habitat increased linearly until it reached a limit, which was interpreted as indicative of saturation on the large islands (Fig. 8).

More recent examples include a survey of local and regional species richness of Collembola in ten grassland types (Winkler & Kampichler, 2000). The regression analyses of local *versus* regional species richness demonstrated a pervasive pattern of stability across all grassland types. In a further study, Patzkowsky & Holland (2003) studied the relationship between local and regional diversity in tropical marine assemblages during 13 million years (Mya) of the Late Ordovician. They concluded that local assemblages did not show stable species numbers but instead that local richness was determined by changes in the regional species pool caused by oceanographic processes. Finally, Krasnov *et al.* (2006) analysed records of flea diversity on 28 small mammal species. In this study, the species pool was defined as all flea species present on a host species, i.e. each host species counted as an independent 'region'. Stability was supported by the asymptote found for all flea assemblages studied.

(c) Evaluation

Despite its apparent simplicity, the local–regional approach to test for saturation is also riddled with challenges (Srivastava, 1999). The first issue deals with adequately defining the scale of the local sampling units (Fox *et al.*, 2000; Shurin *et al.*, 2000). If the local units are so small that there is a limit to the number of individuals that approximates the potential number of co-occurring species, then local richness remains stable due to a sampling effect (Jones, Tuomisto & Olivas, 2008). Take the simple example of a forest assemblage in which local richness is sampled in plots that allow the presence of 100 tree individuals. This size may be adequate if the regional species pool is limited to a few dozen species. However, if there are thousands of tree species in the area, it will be impossible to record more than 100 species in a plot, irrespective of changes in regional species numbers. It is thus crucial to test whether local richness has been sampled in a representative manner, e.g. by using species-richness estimators that estimate the actual number of species in a sample based on subsamples (Gotelli & Colwell, 2001). Only if sampling completeness is equivalent across local sampling units can stability be tested for (Shurin *et al.*, 2000).

The appropriate definition of the regional species pool is even more complex. The local–regional test for saturation is based on the idea that the regional pool includes all species that could potentially occur within our local sampling units at a given period in time (Cornell & Harrison, 2014; Kraft & Ackerly, 2014). The challenge of defining the regional pool becomes evident especially in a mainland situation, where simply using the total number of species recorded at a certain distance around a local sampling unit (regional richness) is likely to include species that will not be able to colonize the local site while at the same time excluding species from further afield that may well make it into our local site (Pärtel *et al.*, 1996; Lessard *et al.*, 2012; Cornell & Harrison, 2014). It is in such a situation where analytical (Eriksson, 1993; Dupre, 2000; Carstensen *et al.*, 2013) and probabilistic species pool approaches may be appropriate (Ewald, 2002; Fukami, 2015; Karger *et al.*, 2016). This does not simply include or exclude a species in the pool based on subjective criteria but assigns a certain probability of a species belonging to the species pool, based on the ecological requirements, distribution, and dispersal ability of the species (Zobel, van der Maarel & Dupré, 1998; Karger *et al.*, 2016). The approach also allows one to incorporate the influence of regional (e.g. dispersal) and local factors (e.g. habitat availability) on local assemblages (Hillebrand, 2005; Harrison & Cornell, 2008).

(4) Equilibrium in ecological time

(a) Approach

This tests the hypothesis that given enough time and under stable environmental conditions, if saturation is present, then the rates of immigration and extinction of a study

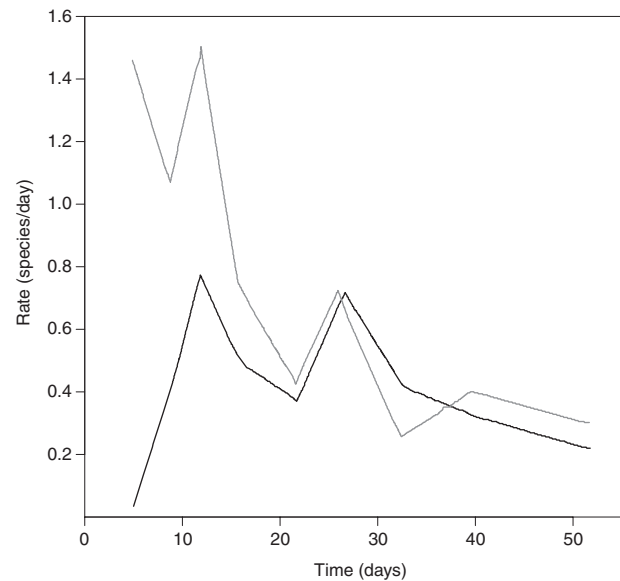


Fig. 9. Average immigration (grey line) and extinction (black line) rates of ciliate species in 42 experimental islands (modified from Have, 1987). After day 20 the rates converged to similar trajectories without significant differences ($t = -0.51$, $P = 0.61$).

group balance each other within an area where the species interact.

(b) Examples

Originally, Simberloff & Wilson (1969, 1970) tried to test this hypothesis in their defaunation experiment, in which they removed all insects from small mangrove islands in Florida, USA, and recorded their recolonization by frequent censuses during a 2-year period. The authors hypothesized that as species richness values rebounded to those before removal, the rates of immigration and extinction should converge towards similar values. However, the observed and simulated curves differed too much from each other and also within themselves, precluding the authors from reaching any conclusion.

Have (1987) created a microcosm experiment to demonstrate the convergence of immigration and extinction in ciliate assemblages. In this study, 42 cylinders of different size were mounted on a platform and immersed in a freshwater pond in Denmark to simulate island habitats for ciliate species. The presence and absence of morphospecies was recorded over time (Fig. 9). As predicted by the island biogeography theory, the rates of immigration and extinction converged after 20 days.

A further example is the equilibrium of bird species in the Channel Islands (Diamond, 1969, 1970). Here, most of the islands were found to be in equilibrium because between 17 and 62% of the resident (breeding) species in 1917 disappeared and were replaced by a similar number by 1968. Finally, Crowell (1973) introduced and monitored populations of different mouse species in small islands

of Penobscot Bay, Maine, USA from 1962 to 1972. He concluded that mice were able to establish and reached equilibrium through a balance of immigration and extinction during this period.

(c) *Evaluation*

Two challenges are of major importance when using this approach. The first is variability in the rates of immigration and extinction, which precluded Simberloff & Wilson (1969, 1970) from demonstrating their convergence. Simberloff (1969) also attempted to demonstrate it by obtaining simulated curves, but without success. The second challenge is the time needed to obtain a data series that captures the trends of immigration and extinction. Using short-living organisms is one way to overcome this challenge (Have, 1987; Fox *et al.*, 2000; Soares, Schoereder & De Souza, 2001), but for many others, long-term experiments and monitoring is the only solution.

(5) Equilibrium in evolutionary time

(a) *Approach*

Here equilibrium is reached when the rates of origination and extinction balance each other. In practice, this implies that an initial increase in the diversification rate of a lineage is compensated by a slowdown that might be caused by a decline in speciation rates or by an increase in extinction rates. As in general for evolutionary-scale studies, this can be studied using phylogenetic or fossil data.

(b) *Examples*

One of the best-known examples of this approach is the diversification of the Caribbean lizards in the Greater Antilles. Rabosky & Glor (2010) argued that while the number of *Anolis* lizards might still be increasing on the largest island Cuba, the number is relatively stable on Hispaniola, Jamaica and Puerto Rico. The reason for this equilibrium is the convergence of speciation and extinction rates towards similarly low values.

The diversification of the wood warbler genus *Dendroica* is another example. Both Rabosky & Lovette (2008) and Etienne *et al.* (2011) found that the number of *Dendroica* species has been stable during the last 2 Mya (Fig. 6A). Also, under a maximum likelihood linear diversity-dependence model, rates of origination and extinction have been at equilibrium since then (Etienne *et al.*, 2011). A further example of equilibrium over evolutionary time is given by Valente *et al.* (2017) for bird species on Atlantic islands.

(c) *Evaluation*

An important aspect to consider here is that equilibrium as an indicator of saturation is specifically defined as the balance between the rates of origination and extinction, because as explained by Alroy (2008) equilibrium in evolutionary time might occur without this condition.

(6) Niche limitation in ecological time

(a) *Approach*

This approach tests the hypothesis that the number of species in a given ecological time and area is constrained by a limited number of available niches.

(b) *Examples*

In a study of birds in the Channel Islands, Jones & Diamond (1976) demonstrated that the lack of a significant change in the total number of breeding birds between 1917 and 1968 (Diamond, 1969) was in many cases the result of competition among species.

Brown (1959) characterized the local distribution of ant assemblages in coconut plantations of the Solomon Islands, finding that different ant species with similar niche preferences would constantly fight and replace each other in the territory they occupied. These fights were more frequent in areas with fewer available niches, i.e. in areas with less diversity of vegetation and habitat heterogeneity. On the contrary, several ant species coexisted in areas with greater heterogeneity.

Levins & Heatwole (1973) also demonstrated niche limitation on a small island near Puerto Rico. Their approach consisted of introducing and monitoring different species of lizards and ants with equivalent niches to the native fauna. The introduced species were able to establish but later became extinct as a result of competition with previously resident species.

Many other studies provide either theoretical, empirical or experimental evidence of niche limitation mechanisms, e.g. studies on minimum population sizes (Cornell, 1999), limits to the similarity of species (MacArthur & Levins, 1967), species interactions (Wilbur, 1972; Shurin & Allen, 2001; Gotelli & Rohde, 2002; Stachowicz & Tilman, 2004; Northfield *et al.*, 2010), niche characteristics set by the area (Rosenzweig, 1995; Ricklefs, 2004; Linder, 2008) and environment (Wiens, 1974; Tilman, 2004; Fierer & Jackson, 2006; Starzomski *et al.*, 2008; Jetz & Fine, 2012).

(c) *Evaluation*

The role of niche limitation in determining community composition covers a huge literature and has been reviewed by various authors (e.g. Elton, 1946; Lawton & Hassell, 1981; Jeffries & Lawton, 1984; Tilman, 2004; Abrams & Cortez, 2015). It would be beyond the scope of this review to explore fully all issues related to this, particularly because most studies on the roles of niche limitation were not concerned with saturation. Indeed, demonstration of niche limitation by itself is not direct evidence of saturation, rather one of several prerequisites necessary to assess it. Nevertheless, one of the crucial aspects is that a profound understanding of the natural history of the interacting species is important because as illustrated in the previous examples, niche-based displacement sometimes only occurs between 'ecological homologues', or in other cases the

effect occurs through indirect competition (Bonsall & Hassell, 1997).

(7) Niche limitation in evolutionary time

(a) Approach

This is an approach rooted in the concept of niche filling (Schluter, 2000; Losos & Miles, 2002), testing the hypothesis that the number of species in a given evolutionary time and area are constrained by a limited number of niches available.

(b) Examples

For *Anolis* lizards in the Caribbean, Mahler *et al.* (2010) demonstrated that the rate of evolution of two important adaptive characters (body size and limb length) decreased in relation to the number of coexisting species on these islands. *Anolis* species on the Greater Antillean islands showed the greatest reduction in the rate of evolution of these traits as a result of a higher density of coexisting species. These results suggest that the number of *Anolis* species is constrained by the limited number of niches that are available.

Another study used the order of trait divergence in the woody plant genus *Ceanothus* to provide evidence of niche limitation (Ackerly, Schwilk & Webb, 2006). The study showed that closely related members of the genus rapidly developed divergence in leaf area, an important adaptive trait, which might in turn have allowed the local coexistence of different species with overlapping distributional ranges.

The niche pre-emption hypothesis (Silvertown, 2004) suggests that niche space is occupied sequentially, and thus taxa arriving earlier to an empty niche would have an advantage over latecomers. Testing this hypothesis, Tanentzap *et al.* (2015) demonstrated that the earlier colonization of plant genera in the alpine assemblages of New Zealand limited the diversification of other genera that arrived later to the same area.

Further studies have documented competitive exclusion based on fossil data, for instance for multituberculate mammals (van Valen & Sloan, 1966; Krause, 1986), bryozoans (Sepkoski, McKinney, & Lidgard, 2000), barnacles (Stanley & Newman, 1980), and bivalves and brachiopods (Liow, Reitan & Harnik, 2015). Importantly, many of these studies come from the marine fauna, where a comprehensive fossil record makes tracking interactions among taxa over evolutionary timescales possible.

(c) Evaluation

Currently, this approach depends heavily on morphological and functional characterization of the study group, and therefore a good knowledge of the adaptive importance of traits is required to assess saturation over evolutionary timescales (Mahler *et al.*, 2010). Still, there are numerous difficulties in demonstrating niche limitation at evolutionary

timescales, for instance if the result of such limitation is a directional trait displacement and this involves not one but many morphological or functional attributes, or if the signal of such displacement is lost over time (Anacker & Strauss, 2014). Another aspect to consider is that detecting niche limitation is plausible for sympatric lineages but much less straightforward for allopatric lineages. The issue here is that for allopatric lineages, niche filling is driven by the interaction among species that are not closely related and hence phylogenetic methods might not be the most appropriate (Mahler *et al.*, 2010).

IV. SYNTHESIS

Historically, many assumptions and hypotheses related to the processes and mechanisms that underlie saturation have been mixed with the study of patterns that result from several ecological phenomena, leading to mixed and inconclusive results (Terborgh & Faaborg, 1980; Srivastava, 1999; Harrison, 2008; Stohlgren *et al.*, 2008a,b; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). Trying to infer the mechanisms by studying the pattern or *vice versa* is fraught with challenges (see e.g., Hillebrand & Blenckner, 2002). We contend that by separating stability, equilibrium, and niche limitation we can achieve a more explicit research agenda in which the hypotheses, sampling design, and results distinguish between assessing the patterns, processes, and mechanisms of saturation, respectively. By often combining them, studies have obtained results that commonly cannot truly demonstrate saturation, nor provide clues for the mechanisms behind it (Cornell, 1999; Lawton, 1999; Loreau, 2000; Shurin & Srivastava, 2005).

To assess saturation, it is thus necessary to demonstrate: (i) stability, under the condition that other species must be able to immigrate or originate *and/or*, (ii) equilibrium, under the same condition than (i), *and* (iii) that such stability and/or equilibrium are the result of a niche-limitation mechanism. Conversely, saturation can be rejected as a hypothesis if the study system can be shown not to meet the criteria of either stability, equilibrium, or niche limitation.

Following these criteria and by gathering information from different sources, we can highlight two study systems in which saturation has been fully assessed, one at an ecological timescale and the other in a more evolutionary context. First, for breeding birds on the Channel Islands it was shown that they had (i) stable species numbers from 1917 to 1968, as a result of (ii) a dynamic equilibrium between immigration and extinction (Diamond, 1969), and (iii) that this equilibrium was the result of competition due to niche limitation (Jones & Diamond, 1976). Second, the lizard genus *Anolis* on the Greater Antillean islands has had (i) a net diversification rate close to zero during the last few million years, with (ii) a balance between speciation and extinction (Rabosky & Glor, 2010), and (iii) a significant decrease in the rates of evolution for adaptive traits, suggesting niche limitation (Mahler *et al.*, 2010).

From these and other examples included herein, it is evident that the different aspects of species saturation have mainly been assessed using insular systems, where studying saturation is easier than in mainland settings because of the well-defined, replicated study units. These examples illustrate further the need for long-term monitoring studies in different mainland and island contexts, and the synergistic advantages of combining results from different data sources in ecology and evolution. Clearly, many more such inclusive studies are necessary before we can reach any general conclusions about the occurrence of saturation in species assemblages.

V. CONCLUSIONS

(1) Studies must provide both conceptual and operational definitions of saturation as it applies to their study.

(2) We propose a conceptual definition of saturation: *saturation is the dynamic equilibrium of species richness due to niche limitation within a given group of organisms and within an environmental and temporal reference frame.*

(3) Operationally, our definition of saturation implies that for saturation to be demonstrated we need to show (i) stability and/or, (ii) equilibrium, both under the condition that other species must be able to immigrate or originate, and (iii) that a niche-limitation mechanism underlies either stability or equilibrium.

(4) In a saturation assessment, the reference system (e.g. spatial and temporal scales) should be clearly defined because saturation might or might not be found in a given system depending on the references considered.

(5) A major unsolved challenge is deciding if fluctuations in the number of species reflect stability or not. Thus, depending on the study system, authors should define *a priori* how stability is defined and how variability is dealt with.

(6) It may be more informative to consider saturation not as a binary concept (saturated or not) but as a ratio (e.g. 80% saturated) as proposed for bounded diversity by Cornell (2013).

(7) Despite a number of publications on the topic of species saturation, most studies conducted to date have ignored one or more of the above challenges, so that our understanding of the prevalence of saturation in natural systems is still very limited.

VI. ACKNOWLEDGEMENTS

We thank R. Cámara Leret, M. Coiro, P. Linder and J. Ringelberg for very helpful comments on early versions of this manuscript. We are also extremely grateful to two anonymous reviewers for outstanding reviews, their insights and highly constructive criticism helped us bring the paper to a new level. This study was funded by the Swiss National Science Foundation (SNSF), grant number CRSII3_147630.

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(Received 9 August 2017; revised 4 April 2018; accepted 10 April 2018)