Functional trait effects on ecosystem stability: assembling the jigsaw puzzle

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Abstract

Under global change, how biological diversity and ecosystem services are maintained in time is a fundamental question. Ecologists have long argued about multiple mechanisms by which local biodiversity might control the temporal stability of ecosystem properties. Accumulating theories and empirical evidence suggest that, together with different population and community parameters, these mechanisms largely operate through differences in functional traits among organisms. We review potential trait-stability mechanisms together with underlying tests and associated metrics. We identify different trait-based components, each accounting for different stability mechanisms, that contribute to buffering, or propagating, the effect of environmental fluctuations on ecosystem functioning. This comprehensive picture, obtained by combining different puzzle pieces of trait-stability effects, will guide future empirical and modeling investigations.

Biotic mechanisms of stability: a jigsaw puzzle

As biodiversity is declining at an unprecedented rate, a particularly urgent scientific challenge is to understand and predict the consequences of biodiversity loss on multiple **ecosystem functions** [1–3] (see Glossary). Temporal **stability** of the functioning of ecosystems is critical to both intrinsic and human purposes (Box 1, Fig. 1). Temporal stability can be defined as the ability of a system to maintain, through time, multiple **ecosystem properties** in relation to reference conditions. Key elements of stability (Box 1, Fig. 1) are, for example, inter-annual constancy in ecosystem properties, but also resistance and recovery from environmental change and perturbation. Stability is maintained by populations, communities and ecosystems that can buffer the effects of environmental variation, thus retaining ecosystem functions such as productivity, carbon sequestration, pollination etc. The idea that greater biodiversity stabilizes natural communities and ecosystems [i.e. diversity begets stability, 4,5] has led to a long-running debate on the relationship between species diversity and stability [6,7].

At the same time, the understanding that the functioning of ecosystems depends on species´ **functional traits**, rather than only on species diversity *per se*, is becoming a dominant paradigm [1,8–10]. Trait-based approaches, in combination with classical taxonomic approaches, have been developed to unravel species coexistence mechanisms [11–13] and predict ecosystem functions and services at a given point in time [1,14]. The mechanisms by which biodiversity affects temporal stability (Box 2) also operate through differences between organisms in terms of their functional traits (Fig. 1). However, scattered evidence and diverse methods exploring these links have prevented a more complete view of the complex relationships between traits and stability. One potential limitation is that the concepts of stability and their drivers remain a major source of Babylonian confusion and disagreement among scientists today [15]. Stability, including its underlying mechanisms, is a multifaceted concept (Box 1 and 2), and understanding it requires connecting a wide variety of drivers across various scales. Some seminal works have paved the road for future research [16,17], but connecting these scattered puzzle pieces remains an essential step for developing comprehensive conceptual and quantitative trait-based frameworks. In this review, we analyse the main pieces of the biodiversity- and trait-stability puzzle and explore connections between these pieces that can generate integrative conceptual and quantitative approaches for future research (Fig. 1 and Fig. 2).

Stability components

The term stability is frequently used and misused in ecology [15]. This term is generally associated with either the ability of an ecosystem to minimize the variability over time of one of its elements or recover it quickly after a perturbation. While specific ecosystem functions or services are most often assessed, stability also includes a species' **population size** or community composition. Scholars have either focused on ecosystem fluctuations around some 'equilibrium' condition, under stochastics environmental fluctuations, or ecosystem response to specific perturbations. This distinction underpins the debate on how to classify and quantify different stability components [7,18]. Among multiple approaches, scholars have identified three main types of stability components (Fig. 1), which can be further refined [19–21].

The first component is temporal variability **or constancy**. Constancy describes the extent of natural fluctuations of an ecosystem property when environmental conditions and disturbance levels fluctuate within historical ranges and without the occurrence of extreme events. In these conditions, ecosystem properties fluctuate around a reference condition ('baseline'). Constancy can be measured by the inverse of the **coefficient of variation (CV)** of an ecosystem property. Other approaches avoid the confounding effects of long-term **temporal trends** on CV, which can arise due to directional species **temporal turnover** [22,23]. This is often the case when ecosystems are subjected to long-term environmental change (e.g. increasing drought).

The second component is **resistance**, the ability to maintain a given ecosystem function when subjected to a perturbation by a substantial environmental stress or disturbance. It can be quantified as the (inverse of the) deviation from the reference level of the ecosystem function of interest. Resistance can be also estimated as the ability of an ecosystem to buffer long-term environmental changes [24].

The third component is **recovery**, the ability of an ecosystem property to return to its reference condition after being subjected to a perturbation. This can be quantified in different ways, for instance, as the time required by an ecosystem property to return to a baseline [21] or the extent of recovery at a given time after perturbation. More definitions of stability components exist, together with different quantification methods. For example, **resilience** includes both resistance and recovery, although in some cases it is equated only with recovery [6,16,20,21].

It should be noted that most studies on stability have investigated only one or a few ecosystem properties, especially biomass production [see 10,14 for reviews]. However, the relationship between biodiversity and stability should be relevant to multiple ecosystem functions, such as nutrient cycling or pollination [1,14,25]. An increasing number of studies have demonstrated that biodiversity is playing a role in multifunctionality [26,27].

4

136 ################### BOX 2 ###############

137 **Stability mechanisms**

138 The hypothesis that biodiversity can increase ecosystem stability has generated a great

139 debate in ecology [5,6]. Biotic effects are expected to modulate various components of

140 stability within a given trophic level via several ecological mechanisms. Three distinct

141 mechanisms involve functional traits: (a) dominant species, (b) compensatory dynamics, and

142 (c) insurance. These mechanisms are expected to be differently associated with different

143 components of stability (Fig. 1). The first two mechanisms have been related to constancy

144 [28]. However, the effect dominant species have also been related to resistance and recovery

145 after perturbations, together with the insurance effect [6,16,29]. Other mechanisms operate,

146 for example, at the landscape level [16,30], but local biodiversity effects, addressed here, are

147 arguably the first crucial link.

148 The **dominant species effect** reflects the effect of communities' most abundant

149 species through their overwhelming influence on multiple ecosystem functions. The coefficient

150 of variation (CV) in total community productivity [i.e. inverse of constancy, 28,31], reflects

151 fluctuations of individual species' populations and can be influenced directly by the weighted

152 average of the CVs of individual species' abundances.

153 **Compensatory dynamics** occur when temporal fluctuations in the abundance of

154 some species are offset by fluctuations of others [6,32]. Compensatory dynamics decrease

155 synchrony among species and can be interpreted as the effect of varying species-specific

156 responses to environmental fluctuations, species interactions and stochastic events. The

157 positive effect of species richness on stability, increasing with independent fluctuations and

158 lower synchrony between species, is called the `**averaging**` or `portfolio` effect [6,32].

159 Differing species-specific environmental sensitivities can also underpin the **insurance**

160 **effect**. Various definitions of the insurance effect exist. Here, following McCann [6], we first

161 distinguish the insurance effect from compensatory dynamics by whether pronounced

162 **perturbation** events are considered (Box 1) where an insurance effect characterizes the

163 ability of an ecosystem to resist and recover after a perturbation. A perturbation can cause a

164 decline or loss in some dominant species. The insurance effect implies the presence of some

165 subordinate species being 'redundant' (i.e. with similar ecosystem effects but differing

166 sensitivity to perturbations; see Puzzle piece 5) with the declining dominant species

167 [20,33,34]. These 'redundant' species can replace the formerly dominant species and

168 maintain ecosystem functioning. Note that this directional substitution is distinguishable from

169 a regular fluctuation between dominant species expected under compensatory dynamics,

170 which also do not necessarily follow perturbations. Redundancy can support both higher

171 resistance and recovery. In practice, distinguishing perturbations from historical variability and

172 environmental stochasticity in local conditions can be arbitrary, but the identification of any

173 specific perturbation is essential for assessing mechanisms of resistance and recovery [35].

174 ############ end box 2 ##################

Puzzle Piece 1: effects of dominant species' traits

According to the 'mass-ratio hypothesis' [36], dominant species in a community, through their traits, exert the strongest effect on ecosystem functions at a given time (called 'immediate' effects). Such **dominant species' traits** do not have only immediate effects. One of the two main drivers of constancy is how stable populations are within a community, expressed as average species-level population stability weighted by species' relative abundances [28]. The constancy of species populations has been related to species traits [37–39]. Moreover, resistance and recovery of community biomass after perturbation have been related to the functional traits of the dominant species in a community, rather than to species diversity itself [29]. As such, variation in trait values of dominant species in a community can bridge the gap between temporal population dynamics, community properties and ecosystem stability.

Recent studies have shown that key **trade-offs in functional traits** between species, such as the **leaf economics spectrum** [10], or dormancy [39–41] in plants, can help predict both community and population stability [37,42]. One extreme of the leaf economics spectrum trade-off comprises species with faster relative growth rate and faster acquisition of resources (**acquisitive** species). The other extreme defines species with slower growth but, potentially, a greater ability to store resources and thus better withstand extreme events and stressful periods (**conservative** species). It remains unclear, however, whether above-ground trade-offs such as the leaf economics spectrum are mirrored by dormancy or below-ground trade-offs [43]. Below-ground storage organs, including non-structural carbohydrate reserves [44], could help buffer population growth (i.e. where species accumulate resources in more favorable years and use them to compensate growth in less favorable years [12]). Similarly, seed dormancy, as a bet-hedging strategy, increases population constancy by reducing short-term reproductive success in favor of longer-term risk reduction [40]. Expanding trade-off mechanisms to various organisms, the classic r/K selection theory [45] already predicted a general differentiation between r-type species, with higher relative growth rate, colonization and dispersion but with lower temporal population stability, and K-type species, with lower relative growth rate but more stable populations.

Based on these trade-offs, it is expected that communities dominated by slow-growing, conservative species are more stable over time and will be more resistant to extreme events [7,46,47]. First, the few existing results generally confirm the expectations that more conservative species have more stable populations [41,48], e.g. characterized by higher leaf dry matter content (LDMC) and lower relative growth rates [37]. Second, communities dominated by plant species with greater LDMC are more stable, in terms of both composition and overall biomass [49,50]. A global meta-analysis on sown biodiversity experiments showed that the increase in fast-growing species (with an acquisitive leaf economy) destabilizes community biomass through time [17]. These studies showed the relevance of **Community Weighted Mean (CWM)** traits (i.e. average of trait values weighted by species abundance), and hence of dominant species [51].

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Puzzle Piece 2: compensatory dynamics through species dissimilarity

Constancy is also influenced by the synchrony in the fluctuations of different populations within communities [28]. While it is generally accepted that a decrease in species synchrony increases stability of ecosystem properties, the mechanisms generating synchrony, or a lack thereof, are more controversial. **Synchrony** between species is generally attributed to similar species responses to environmental fluctuations [52,53]. Hence, species with similar adaptations to the environment (i.e. similar response traits; see Puzzle Piece 5) should fluctuate synchronously, and species with different adaptations can fluctuate independently or compensate for each other [3,11]. Note that compensatory dynamics are sometimes broadly associated with any deviation from a perfect synchrony between species due to independent fluctuations (sometimes called **asynchrony**), while compensation exceeding averaging effects arises from negative (sum of) covariance between species (**anti-synchrony**).

A pattern of compensatory dynamics could result also from biotic interactions, a hypothesis that has caused controversy. For example, **competition** among functionally similar species could create a pattern where two species prevail over each other in alternating fashion species can alternatively prevail over the other [54]. This effect could destabilize individual populations (e.g. increasing community CV). However, the potentially negative covariance between species due to competition could compensate this effect and even result in an increased constancy at the community level [12,55]. Competition might also generate compensatory dynamics through environment–species interactions; for example, environmental conditions that shift species' competitive abilities will decrease synchrony among functionally dissimilar species [56]. **Facilitation**, especially in severe environments, can increase constancy when some plants buffer microhabitat environmental fluctuations for other plants [57]; however, its role in synchrony between populations remains to be clarified. Compensatory dynamics could be also driven by other biotic interactions such as **intransitive competition** [58], i.e. in a rock–paper–scissors game between species with different traits.

The relationship between species synchrony and species **pairwise trait dissimilarity**, could provide a mechanistic view on the drivers of compensatory dynamics (Box 2). There is increasing empirical evidence that greater trait similarity between species is associated with greater synchrony [3,59–61]. As such, an increase in community **functional diversity** should lead to greater constancy. Support for a decrease in synchrony with increasing functional diversity has been found in beetle communities [62] and in manipulated plant communities [56,63]. The recent study by Craven et al. [17] failed to detect any marked effect of plant functional diversity, expressed only for the leaf economics spectrum, on synchrony, but detected an effect of **phylogenetic diversity**, as in Cadotte et al. [64]. This is possibly because the relationship between pairs of species and their synchrony is better appreciated on the basis of **multiple traits** [3,62]. Phylogenetic diversity can be considered as a proxy of multi-trait diversity and unmeasured traits [65]. It should be noted that classic species coexistence theories, like limiting similarity and niche complementarity, also predict

255   that multi-trait dissimilarity could allow species coexistence by decreasing competition for

256   similar resources, and improve ecosystem multifunctionality [13]. In a temporal context, multi-

257   trait dissimilarity could cause, beside these effects, compensatory dynamics.

258

259

260   **Puzzle Piece 3: redundancy and the insurance effect**

261   The 'insurance effect' requires the presence of multiple species with a similar effect on

262   ecosystem functioning but different sensitivities to specific perturbations. Authors have thus

263   stressed the importance of **functional redundancy**, i.e. the presence of multiple species with

264   a similar effect on a given ecosystem function, as an important recovery and resistance

265   mechanism [16]. A quick recovery can be obtained, for example, when a subordinate species,

266   with similar effects on ecosystem functioning, but different environmental sensitivity, rapidly

267   replaces lost dominant species [33]. For instance, a conservative stress-tolerant species

268   could replace a more acquisitive species during an extreme drought event, thus maintaining

269   equal ground cover and soil stabilization. Likewise, a generalist pollinator species could

270   maintain pollination, usually realized by a specialist species, after an unusually early spring or

271   a fire [66]. These species replacements would not count as regular alternation of dominant

272   species (compensatory dynamics), but long-term compositional changes following a given

273   perturbation, including extinction events. Another important difference between insurance and

274   compensatory dynamics is the selection of relevant functional traits. While, as we saw above,

275   compensatory dynamics reflect adaptation to both multiple abiotic and biotic conditions, for

276   which a multivariate trait dissimilarity (or phylogenetic distance) between species is important,

277   insurance can be ideally tested by selecting species' adaptation to a specific perturbation.

278   There is evidence that low functional redundancy in fish communities increases

279   ecosystem vulnerability to environmental changes [67]. It is also expected that greater

280   diversity in resource use between species lowers the requirement for multiple species in order

281   to maintain stability in each ecological function [68], i.e. a lower number of species is required

282   to maintain redundancy if these species have sufficiently different environmental sensitivities.

283   Although these effects seem very promising, there are methodological difficulties in

284   quantifying functional redundancy. Functional redundancy should ideally reflect how many

285   different species there are for a given functional role in a community, and it is thus not fully

286   covered by measures of functional diversity alone [69–71]. Measures of the functional role of

287   rare species, in this sense, are increasingly getting attention [72]. A common approach is to

288   define the number of species within functional groups [e.g. 16,33]. However this depends on

289   the definition of functional groups in a community [34,67]. While in some cases, e.g. nitrogen-

290   fixing species, their delineation is rather straightforward, assigning species to separate groups

291   is often unfeasible or context-dependent since traits often vary continuously rather than

292   supporting any division into clear-cut groups [73,74]. New approaches have therefore been

293   proposed to quantify functional redundancy without defining functional groups. However,

294   problems remain with existing metrics as they correlate too tightly with measures of species

295   diversity or functional diversity, raising doubts on their actual value [69–71]. Future

296   developments for quantifying functional redundancy are thus required, especially to account

297   for the potential of subordinate species to replace dominant species in a community in the

298   face of specific perturbations.
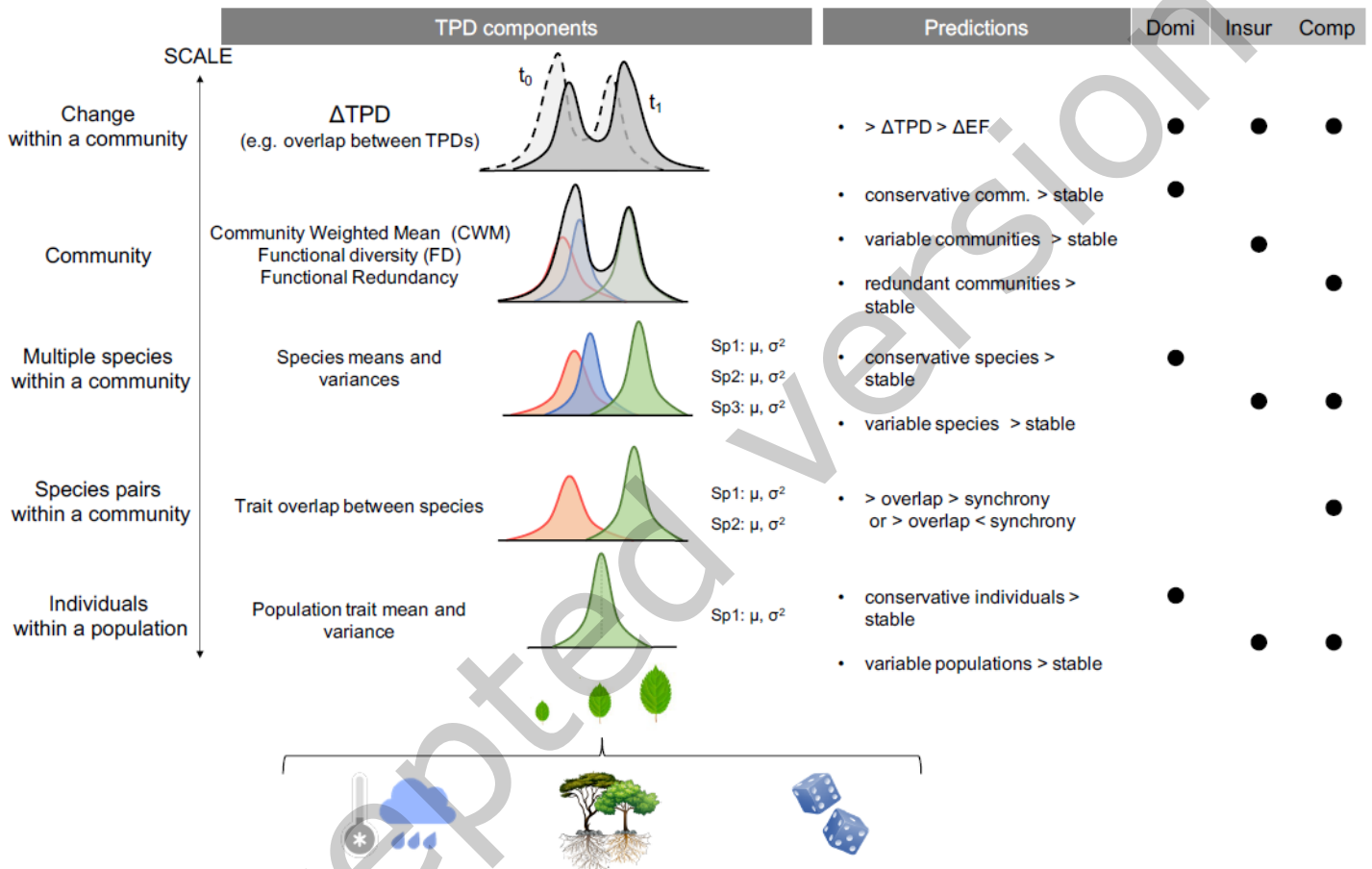
################ Box 3################

Trait Probability Density

Trait-related stability mechanisms can be assessed by using different facets of trait-abundance distributions within and across species. Trait-abundance distributions are broadly referred to as **Trait Probability Density** (**TPD).** The TPD reflects the relative abundance of trait values at a given study scale. It can be described by the different statistical 'moments' of trait distributions (e.g. mean, variance, skewness, kurtosis) on multiple scales, from individuals to ecosystems. A great variety of measures exist to characterize multiple TPD components, which is not bound to given mathematical approaches [69,75,76].

By integrating species abundances and traits, TPD has the potential for connecting population and community dynamics, and thus scaling up temporal variations in species populations to ecosystem functioning and its stability (Fig. 1). TPD in a local community is the result of both random and deterministic processes governing changes in species' relative abundances from the local **species pool** [77; Fig. 1] and trait variability within species (Box 4). Temporal changes in TPD components can thus affect stability and can be assessed together with taxonomy-based measures such as species richness and evenness or synchrony between species, which are also known to influence stability [28,31] (see 'Connecting pieces with TPD: data analysis considerations'). Changes in TPD build up from population to community trait structure and different tests can be run, at different scales, to track the effect of these changes on stability (Box 3 Figure I).

[[see Figure I for Box 3 in the specific file]]

Figure I. Different components of Trait Probability Density (TPD), at different scales, with
323 reference to their potential test and possible stability mechanisms (Domi = dominant species
324 effect; Insur = insurance effect; Comp = compensatory dynamics effect). Note that spatial
325 TPD changes within a site or landscape can be also visualized similarly to the case of
326 'Change within a community'; in that case, however, spatial heterogeneity in TPD (ΔTPD)
327 should result in an overall more stable ecosystem functioning [16,30].

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331   ############# end box 3 ##################

Puzzle Piece 4: response and effect traits

A decisive puzzle piece modulating different trait-stability mechanisms is the trait **response–effect framework** [78], as originally suggested by Oliver et al. [16]. Which species will increase or decrease in response to both environmental fluctuations, including disturbances, and biotic interactions depends on their '**response traits**', i.e. traits that affect the fitness of species for given ecological conditions, including prevailing interactions [10]. For example, plant traits related to drought tolerance, such as succulence [74], or the ability to retain water in isopods [79], are traits associated with greater fitness of species in drier conditions [80,81]. Similarly, species with traits associated with a higher intrinsic relative growth rate will recover more quickly from environmental perturbations [16] but will also be less constant in abundance over time [29,37].

Some functional traits also have the potential to affect other trophic levels and multiple ecosystem functions [10,14,25]. **Effect traits** are therefore those traits of an organism that impact prevailing ecosystem processes and functions. For example, mandible strength will determine the extent and type of food consumed in grasshoppers [82]. Flammability traits in plants modify the fire regime and generate eco-evolutionary feedback [83]. Secondary compounds in leaves not only offer defense against herbivory but might slow down litter decomposition [84], while floral traits will affect pollination [25].

The covariation, or the overlap, between response and effect traits has been identified as the key mechanism by which environmental changes can be translated into ecosystem function changes [78,85]. The response–effect framework, however, has been only rarely assessed in the context of stability [16]. For example, accounting for both response and effect traits has been advocated as an important aspect in estimating functional redundancy [34]; however empirical tests are scarce [but see 86]. More broadly, with greater trait overlap between response and effect traits, changes in environmental conditions will more likely propagate into ecosystem functions, thus decreasing stability. This effect, however, will depend on the stability mechanisms under consideration and the TPD components considered (Fig. 2 and below).

It should be noted that it can be difficult to understand to what extent a trait is purely a response or an effect trait, or both. Whether a given trait operates as a response or effect trait depends on the environmental context and ecosystem functions of interest. Traits that are related to the processing of resources (e.g. gas exchange, water and nutrient uptake in plants, or body size in animals) will be likely both response and effects traits for corresponding functions of biogeochemical cycling. But these traits will not affect, at least directly, some other ecosystem functions. For example, leaf traits associated with several functions of resource use do not directly affect pollination, which depends on flower traits, although they might be correlated through phylogeny [25].

The puzzle comes together: buffering vs. propagating

Oliver et al. [16] already stressed the central importance of the interplay between response and effect traits for the insurance effect. Here, by expanding this, we illustrate how this interplay represents the centerpiece for translating, via TPD, population and community changes to ecosystem functioning, integrating different stability components and their underlying mechanisms. The central concept bringing this puzzle together is that environmental fluctuations and perturbations cause changes in population abundances, and possibly intraspecific phenotypic variation (Box 4), modifying the local TPD for response traits (ΔTPD_R; Fig. 1).

To what extent do these changes cause a modification in ecosystem functioning (ΔEF)? For the sake of simplicity, we will distinguish two extreme situations (Fig. 2): (i) communities '**buffering**' the effect of environmental change (i.e. with very small consequences for ecosystem functions, small ΔEF, greater stability) vs. (ii) communities '**propagating**' environmental change effects on ecosystem functions, (a large ΔEF, lower stability). In general terms, a community will be buffering, or conversely propagating, a given environmental change depending on the extent of change in response traits. A small change in TPD for response traits (ΔTPD_R) will likely result in small changes in ecosystem functions (small ΔEF) because of limited changes in effect traits. The larger the ΔTPD_R, the greater the chance that some effect traits will change as well and, hence, increase the change in 'propagation' effects (marked ΔEF). Further, this propagation will be stronger with a tighter overlap between response and effect traits, i.e. a high $\rho(R_T, E_T)$. Let us consider now a few scenarios as examples of the flow from population abundances to ΔEF, depending on the magnitude of ΔTPD_R and $\rho(R_T, E_T)$. In the following we unpack how these scenarios determine how much communities buffer or propagate effects of environmental changes on ecosystem functions, and thus how the different puzzle pieces can come together.

a) Stable dominants

The first scenario is when small changes in composition within a local community follow a given environmental change (scenario 1, Fig. 2). This could happen both under natural environmental variability in an ecosystem at equilibrium or following a perturbation. An example of this pattern was observed in plant communities dominated by conservative species after an extreme drought event [29]. These communities were able to buffer (i.e. high resistance) environmental variations [87], likely because of the buffered population growth of the dominant species. Buffered population growth is a key mechanism of coexistence in fluctuating environments, also described as the 'storage effect' [12], where conservative species can withstand unfavorable years, for example, due to resource storage [88]. We can thus expect small changes in all facets of TPD, and thus stability in multiple ecosystem functions (low ΔEF), independently of whether species have overlapping response and effect traits.

b) Compensatory dynamics

Compensatory effects are usually considered to be a key mechanism of constancy [6] but may also destabilize ecosystem functioning. Constancy in ecosystem functioning can be obtained when 'inconstant' populations of species with similar effect traits periodically (for example, on a yearly basis) 'compensate' for each other (scenario 2, in Fig. 2), i.e. they negatively covary in time (**anti-synchrony**). As we discussed above, theoretical [11] and empirical evidence [3,59–62] suggests that anti-synchrony will occur between species with different response traits (moderate to high ΔTPD_R, and overall high FD in a community; case 1 in Fig. 2), reflecting different environmental preferences. Constancy in ecosystem functioning will then occur only if effect traits and response traits are dissociated (high FD in response traits, low in effect traits). Otherwise changes in species composition will propagate into changes in effect traits and cause ΔEF. Imagine a case where the ecosystem function of interest is pollination, and two anti-synchronous species have different response traits (e.g. different LDMC) and also different effect traits (e.g. flower types with access to different pollinators; case 2 Fig. 2), i.e. high $\rho(R_T, E_T)$. In this case we can expect a periodic change in ΔEF both in decomposability and pollination. Anti-synchrony could also occur between functionally similar species (low ΔTPD_R) after temporal changes in the competition hierarchy [3,11; case 2 in scenario 2, Fig. 2,58]. In this case, buffering is more likely, especially if effect and response traits overlap.

c) Insurance effect

The insurance effect can be particularly important in the case of replacement of a dominant species by an otherwise subordinate species following some exceptional perturbation [e.g. fire or drought, 89]. Such directional species replacements (different from periodic replacement in compensatory effects above) are expected between species with different adaptations to given perturbations (and, likely, a high ΔTPD_R in specific traits; a replacement between species with similar response traits following an extreme climatic or disturbance event is not likely). An insurance effect is again possible only if response and effect traits are dissociated (case 1, scenario 3, Fig. 2). It should be noted that greater species diversity should increase the odds that more species will have different adaptations to perturbations [53]. At the same time the greater the diversity in ΔTPD_R, the lower the species richness needed to buffer an ecosystem process [68]. For this reason, functional redundancy between dominant species and subordinate species, key for the insurance effect, is expected to reflect the interplay of both species diversity and functional diversity across species. Note also that in scenario 3, Fig. 2, it can happen that some functional traits may exert some insurance effects, but the total population abundance can still decrease. Some ecosystem functions, such as soil stability and formation, could be thus affected by the perturbation, simply as a consequence of reduced plant cover (see next section).

Connecting the pieces with TPD: data analysis considerations

Connecting different biotic drivers of stability is a tall challenge and remains a critical gap in our understanding of trait effects on ecosystem stability. Approaches similar to **path analysis** can provide a way forward for testing causal and cascading connections among the functional make-up of populations and communities and those of communities and ecosystem properties [17,31,56,62,90]. Existing studies have already considered a selection of TPD components to explain specific components of stability [3,17,31,56,62,90]. It is thus important to select predictors and tests based on the mechanism(s) of stability considered (Fig. 1) and the specific scale of interest (Box 3 for specific tests). As discussed above, trait selection is also a key step that depends on the stability mechanism under evaluation (response traits) and the ecosystem function considered (effect traits). A useful set of trait-based predictors includes (i) CWM for studies on dominant species and insurance effects, (ii) functional dissimilarity between dominant species (i.e. for functional diversity) for compensatory dynamics and (iii) functional redundancy between sets of dominant and subordinate species for an insurance effect.

In these approaches it is important to connect TPD components with key predictors that are usually considered when assessing the biodiversity–stability puzzle [17,28,31,62]; this also depends on the biotic mechanisms of stability being tested (Box 1 and 2). As we saw above, key measures are synchrony between species for compensatory dynamics, and population CV for dominant species effects. The overall community CV is the most frequently used measure for compensatory dynamics. For compensatory dynamics, under certain conditions, the number of species in a community is mathematically associated with the CV of total community abundance [averaging/portfolio effect, 6]. Evenness in species' abundances, or the relationship between species abundances and their variability (mean-variance scaling), can both indirectly affect the CV of total community abundance in different ways [28]. Total community abundance and overyielding (i.e. species in mixtures being more productive than in monocultures, thus increasing total abundance) both affect CV. These, and other predictors and interdependencies, are essential for appropriately modeling biodiversity effects on constancy, even if they do not reflect ecological mechanisms per se [28].

In biodiversity experiments that manipulating species number, species richness can appear as an important direct driver of multiple components of TPD and stability [17]. In natural conditions, however, both species richness and TPD can be rather seen as a result of assembly mechanisms determined by local conditions. In these cases, compensatory dynamics is related to synchrony, and underlying trait dissimilarity [3], rather than to species richness itself [32,91]. On the contrary, the case of the insurance effect shows the relevance of directly considering indices such as species richness together with TPD dimensions [71]. Combining species richness and functional diversity can thus be useful to estimate functional redundancy while new indices of functional redundancy are being developed.

Different parameters of population abundances are other important drivers in the causal relationships between biodiversity and stability of ecosystem functions. For example,

492 either mean population variability or total abundance, and sometimes both, are considered in
493 causal relationships. Both the ranking in population abundances and average population
494 stability vary depending on species' response traits within the local species pool and these
495 traits directly affect indices such as CWM and functional diversity. Moreover, some ecosystem
496 functions will also depend directly on the total abundance of local populations, for example,
497 through its effect on the denominator of CV. Two communities with identical distributions of
498 trait values could have very different total abundances of individuals, especially since TPD is
499 generally based on species relative abundances [69]. A greater absolute abundance in one
500 community, while keeping all other TPD components fixed, could imply direct effects on
501 ecosystem functions, for instance greater resource use, greater productivity etc. Total
502 population abundance can thus modulate ecosystem stability directly, or even indirectly via
503 changes in TPD components.

504 Environmental conditions might also modulate ecosystem functioning directly, not
505 only indirectly through changes in TPD components. For example, in their meta-analysis
506 across biodiversity experiments manipulating sowing species diversity, Craven et al. [17]
507 showed the direct effects of environmental conditions (both their mean and heterogeneity) on
508 stability of productivity, independently of the biotic predictors considered. Additionally, within
509 given locations, environmental effects may primarily operate indirectly through changes in
510 TPD components.

511 An important practical decision when using taxonomic or functional components of
512 diversity as predictors of stability is at what point in time they should be computed. Authors
513 usually consider an average species richness, or an average FD, across the studied period
514 when assessing constancy through CV [3,17,62]. The accumulated species richness, or
515 overall FD, across the whole period, has also been considered, although they tend to be
516 correlated with average values [3]. These correlations, however, might be weak when
517 communities undergo gradual species turnover, or after a strong perturbation, which would
518 change species composition and species richness over time [92]. In these cases, detrending
519 methods should be considered [23,93]. For resistance and recovery, the optimal approach is
520 to compute biodiversity indices before and at various stages after the perturbation under
521 study.

522

523   ###### BOX 4 ######

524   **Future puzzle pieces: intraspecific trait variability**

525   Most of the examples and studies reviewed so far refer to the effect of species diversity and

526   trait dissimilarity between species, including trait trade-offs between species. However, most

527   of the mechanisms act first on the variability of local populations, and therefore cause

528   phenotypic differences within and between populations of a species. **Intraspecific trait**

529   **variability** (ITV) could theoretically affect stability [16]. At the same time, it is important to

530   differentiate between ´spatial´ intraspecific trait variability (among individuals) and ´temporal´

531   intraspecific trait variability (between seasons or years, including plasticity and micro-

532   evolutionary processes). Both these expressions of ITV are components of TPD [69].

533   Changes in time, or space, in TPD can be caused by ITV and species turnover, or more

534   frequently by both [94].

535   ITV caused by **genetic variation within the population** can affect its stability

536   [95,96]. For example, individuals within a population with more conservative traits could have

537   more stable growth or reproduction over time while individuals with less conservative

538   strategies would be less resistant, but exhibit faster recovery [97]. Hence a population with

539   both 'types' could be maintained, overall more constantly in time, in fluctuating conditions.

540   Wright et al. [98] hypothesized that higher intraspecific trait variability could confer greater

541   stability within species, possibly through an insurance mechanism, although compensatory

542   mechanisms between different genotypes could also occur [99].

543   Another mechanism concerning the effect of intraspecific trait variability on stability is

544   phenotypic variation across generations. This can be caused by either **selection** of different

545   phenotypes over time or **transgenerational plasticity**. Zuppinger-Dingley et al. [100] and

546   Latzel et al. [101] highlighted the importance of within-species trait variability and year-to-year

547   trait-adjustment effects on ecosystem stability and the influence of both selection and

548   transgenerational plasticity on ITV. Ultimately, selection across generations can increase

549   functional diversity in a community [100]. Interactions between species within a given season

550   can stabilize communities via transgenerational effects in plant traits in the following growing

551   seasons [102]. Thus, these within-species adjustments seem to be an important, yet largely

552   unexplored, component of the stability of communities. However, the empirical testing of

553   intraspecific trait variability effects on stability will be challenging, particularly if we are not

554   able to separate the cause of phenotypic variation. We should be also aware that high

555   intraspecific trait variability might be a consequence, instead of the cause, of population

556   instability. For example, seasonal drought will probably have a spatially non-homogenous

557   effect on plants, causing high levels of intraspecific variability in some traits, and, at the same

558   time, this will also affect the population size, causing temporal variability.

559   ############## end box 4 ###############

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Concluding remarks

Several biotic mechanisms affect the different components of ecosystem stability. Theoretical and empirical evidence is accumulating suggesting that these biotic mechanisms are affected by different components of the trait-probability distributions within local species pools. Future studies therefore need to consider differences in trait values within and between species when assessing how different biotic mechanisms affect stability (see Outstanding Questions). We argue that conceptual and terminological clarity would provide a more complete picture of the effects of biodiversity on stability by connecting the pieces of the trait-stability puzzle.

Different tests are possible depending on the ecological scale considered (Box 3), and the interplay between population dynamics and community properties (Fig. 2) is key in determining biodiversity effects on the stability of ecosystem functioning. Comprehensive frameworks testing biodiversity effects on ecosystem properties need to combine multiple types of metrics (Fig. 1), not necessarily trait-based, which are also selected depending on the stability mechanisms under scrutiny. Variation in the local populations can result in overall changes in community structure, which may, or may not, propagate into changes in ecosystem functioning. The strength of this propagation depends on the extent of trait changes and the degree of overlap between response and effect traits – an idea which has, so far, not been fully incorporated in analyses linking biodiversity and stability. Including response and effect trait analyses can also help to improve the quantification of functional redundancy, which is essential for testing the insurance effect. In the future, attention should also be paid to the potential for intraspecific trait variability in affecting local population stability, via intraspecific adjustments (Box 4). While here we have reviewed mechanisms of stability within given trophic levels, trait mechanisms acting across trophic levels will be central to future developments for assessing the stability of multi-trophic ecosystem functions. Finally, the framework and concepts synthetized in this review should be applicable to different types of environments, and under different global-change scenarios. This will enable us to assess to what degree the effects of different biotic mechanisms of stability vary along gradients of habitat severity and habitat heterogeneity and in response to different types of perturbations.
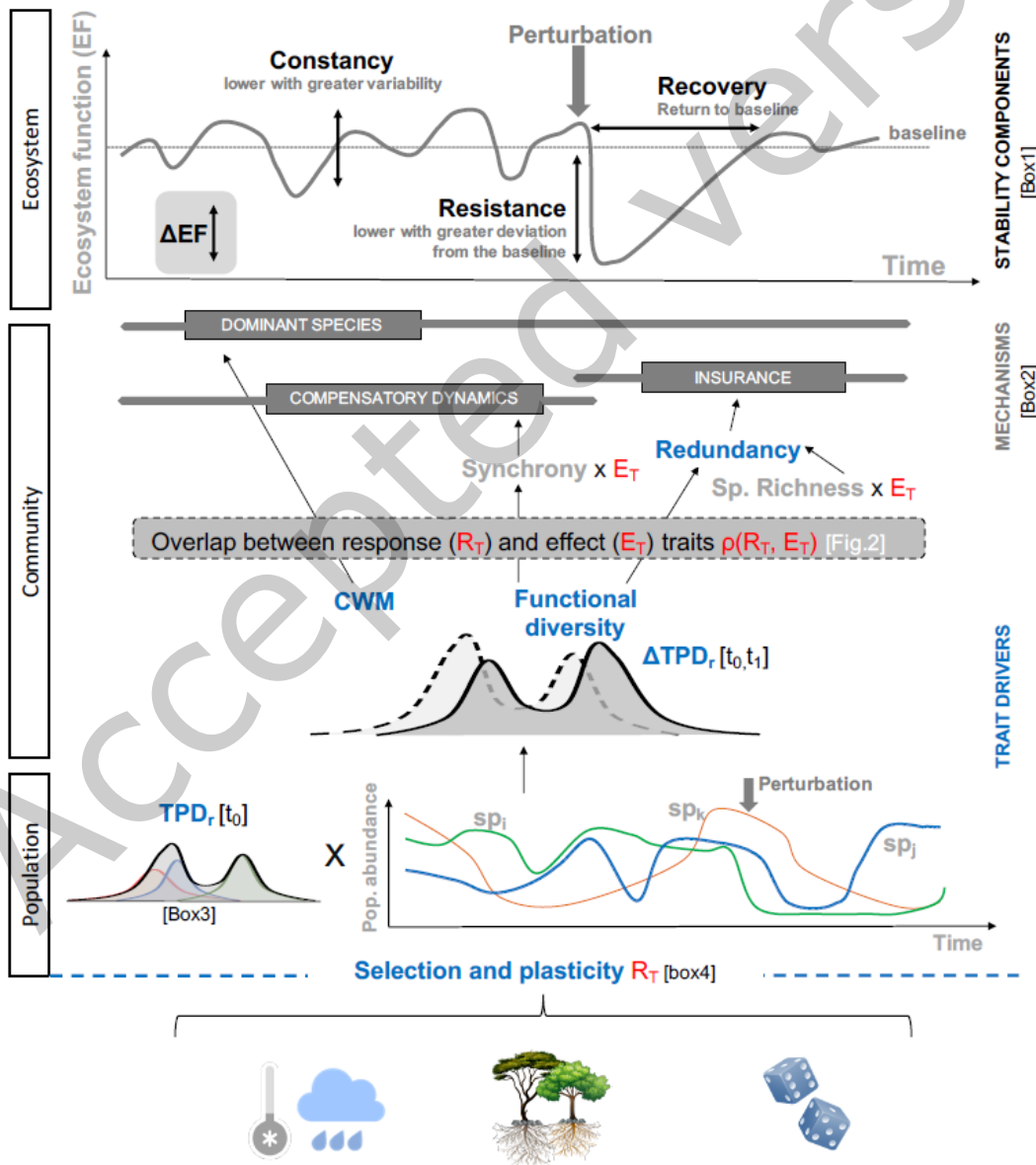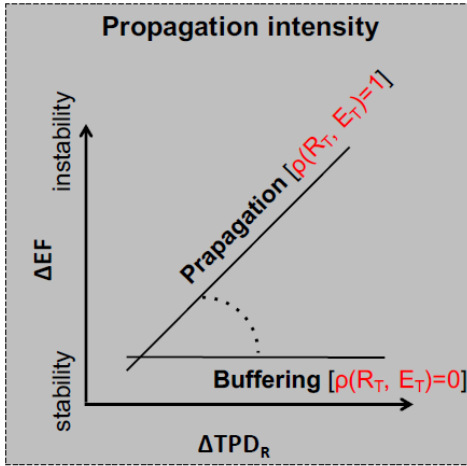
603 **Figure 1. Changes in population abundance, in response to deterministic and**
604 **stochastic events, build up into different changes at the community level (e.g. TPD,**
605 **species richness, synchrony) and affect different components of ecosystem stability**
606 (variation of a given ecosystem function in time, i.e. ΔEF, with higher ΔEF implying lower
607 stability). The effects of biodiversity can be summarized as three main biotic mechanisms
608 together with their corresponding set of trait-related measures. The response to deterministic
609 and stochastic events can be expressed in terms of response traits (R_T) and translates into
610 changes in community traits structure (broadly defined as ΄ΔTPD_R΄, i.e. community Trait
611 Probability Density in terms of response traits). The overlap between response and effect
612 traits (E_T) will result in changes in different stability components and in changes in different
613 biotic stability mechanisms. Details about several elements of the figures can be found in
614 specific sections of the manuscript (e.g. Box 1 etc.). Drawings at the bottom of the figure are
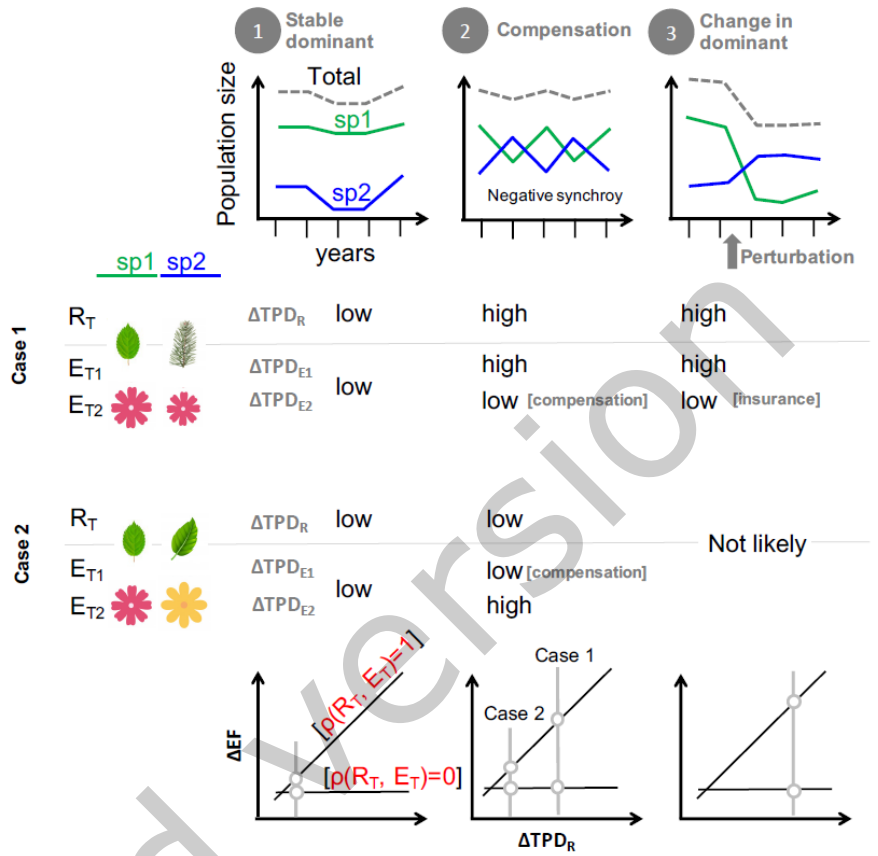615 from freepik.com.

616

617 **Figure 2. Effect of the overlap between response and effect traits, expressed as their**

618 **covariation [i.e. $\rho(R_T, E_T)$], on the modulation of different biotic effects that control**

619 **ecosystem function stability.** Variation in response traits at the community level (ΔTPD_R

620 changes in community Trait Probability Distribution in terms of response traits) may or may

621 not result (propagating vs. buffering respectively) in changes in ecosystem function (ΔEF),

622 increasing the chance of greater ΔEF. Three scenarios are considered (see section ´The

623 puzzle comes together: buffering vs. propagating´ for details), and each one results in

624 different species composition changes, i.e. fluctuations of two species in time (sp1 and sp2),

625 and their sum (Total). In the 'stable dominant' scenario (scenario 1) the dominant species

626 remains stable after some environmental change or perturbation, while the subordinate

627 species decreases and then recovers. In the 'compensation' scenario (scenario 2) the two

628 species alternate regularly in dominance. In the 'change of dominant' scenario (scenario 3),

629 related to an insurance effect, the subordinate species replaces the dominant species after a

630 perturbation causing long-term compositional changes. Within each scenario we consider two

631 cases: (1) one in which the two species have different response traits (R_T, e.g. one species

632 has high leaf dry matter content, LDMC, and another has low LDMC), and (2) one in which

633 the two species in a community have similar response traits. Within each of these two cases,

634 species can have both similar or different effect traits (E_T) for different ecosystem functions,

635 referring to the example in figure, leaf type and flower would be traits associated with different

636 functions, e.g. decomposition rate and pollination rate. For each scenario, a specific

637 projection of the propagation intensity scheme is reported in the lower part of the figure

638 (vertical lines in panels at the bottom of the figure indicate how Case 1 and 2 affect stability;

639 Case 1 and 2 have different effects only in scenario 2). The labels 'low' and 'high' summarize

640 the extent of ΔTPD components. See details in the main text. Drawings of leaves and flowers

641 are from freepik.com.

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Glossary

649

Asynchrony: deviation from a perfect synchrony in species' fluctuations.

Anti-synchrony: prevailing negative covariance between species' fluctuations (e.g. negative synchrony).

Averaging/portfolio effect: Link between an increase in species number and the decrease in the coefficient of variation (CV) of community abundance in the case of independent species fluctuations.

Buffering: the ability of a system to maintain given ecosystem functions despite species turnover. It is the opposite of propagation.

Community weighted mean (CWM): The average of trait values weighted by the relative abundance of each species in a community.

Compensatory dynamics: The changes in the relative abundance of some species that are offset, or compensated for, by changes in the relative abundance of other species.

Constancy: A stability component describing how invariable (i.e. as inverse of temporal variability) ecosystem properties are in a given period without particularly extreme events.

Dominant trait effect: The effect exerted by the dominance of species with particular traits, which governs how a community as a whole responds to environmental fluctuations and affects ecosystem functioning. It is linked to the mass-ratio-hypothesis. It can be quantified by the community weighted mean (CWM).

Ecosystem property: Broadly defined as any measurable component of an ecosystem or its constituent components, including ecosystem functioning, population abundances, species composition, species diversity etc.

Effect traits: Any characteristic of an organism that has repercussions for environmental conditions, community properties, ecosystem processes or functions.

Functional diversity: The extent of trait differences among a set of organisms. It is commonly quantified with multiple indices reflecting, for example, average trait dissimilarity or the volume of trait space occupied by a set of species.

Insurance effect: A system's ability to buffer the effect of perturbations on community or ecosystem processes by the replacement of species by others with similar effect traits. It depends on functional redundancy.

Intransitivity competition: Interactions among species in a community in which they do not follow a linear hierarchy but a 'stone–scissor–paper' game without a single best competitor.

681 Pairwise trait dissimilarity: Functional trait differences between pairs of species in terms of

682 given traits or multiple traits. Sometimes a phylogenetic distance (e.g. length of branches

683 connecting two species in a phylogenetic tree) is used as well.

684 Perturbation: A relatively sudden change in environmental conditions or in the disturbance

685 regime beyond the range of the historical variability (e.g. exceptional fire, flood or drought).

686 Propagation: The process by which species turnover is directly translated into changes in

687 ecosystem function.

688 Recovery: The ability for a population, community or ecosystem function to reorganize and

689 return to its reference condition after it has been affected by a perturbation.

690 Redundancy: The degree to which species perform similar functions. Communities with high

691 redundancy are expected to be able to lose species without great changes in ecosystem

692 functions due to replacement of dominant species by subordinate species with similar effect

693 traits.

694 Resilience: The degree to which an ecosystem function can resist or recover rapidly from

695 perturbations.

696 Resistance: The ability of an ecosystem to remain unchanged when being subjected to a

697 perturbation. It is inversely proportional to *vulnerability*.

698 Synchrony: The pattern that occurs when most of the species in a community respond in the

699 same manner to variation in abiotic and biotic conditions, leading to concordant species

700 fluctuations.

701 Trait Probability Density (TPD): Distribution of trait values of an ecological unit, from the

702 individual to ecosystem level, in a given functional space. Such trait distributions can be the

703 basis of multiple indices and components.

704 Turnover: The rate or magnitude of change in species composition, e.g. replacement of

705 species and their abundances in space or time.

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