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Functional trait effects on ecosystem stability: assembling the jigsaw puzzle

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43 **Abstract**

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

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58 **Keywords**

59 compensatory dynamics; community weighted mean; functional diversity and redundancy;
60 insurance effect; trait probability density

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Accepted Version

63 **Biotic mechanisms of stability: a jigsaw puzzle**

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

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

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BOX 1#####

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 stochastic 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].

end BOX 1

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BOX 2

Stability mechanisms

The hypothesis that biodiversity can increase ecosystem stability has generated a great debate in ecology [5,6]. Biotic effects are expected to modulate various components of stability within a given trophic level via several ecological mechanisms. Three distinct mechanisms involve functional traits: (a) dominant species, (b) compensatory dynamics, and (c) insurance. These mechanisms are expected to be differently associated with different components of stability (Fig. 1). The first two mechanisms have been related to constancy [28]. However, the effect dominant species have also been related to resistance and recovery after perturbations, together with the insurance effect [6,16,29]. Other mechanisms operate, for example, at the landscape level [16,30], but local biodiversity effects, addressed here, are arguably the first crucial link.

The **dominant species effect** reflects the effect of communities' most abundant species through their overwhelming influence on multiple ecosystem functions. The coefficient of variation (CV) in total community productivity [i.e. inverse of constancy, 28,31], reflects fluctuations of individual species' populations and can be influenced directly by the weighted average of the CVs of individual species' abundances.

Compensatory dynamics occur when temporal fluctuations in the abundance of some species are offset by fluctuations of others [6,32]. Compensatory dynamics decrease synchrony among species and can be interpreted as the effect of varying species-specific responses to environmental fluctuations, species interactions and stochastic events. The positive effect of species richness on stability, increasing with independent fluctuations and lower synchrony between species, is called the **'averaging'** or **'portfolio'** effect [6,32].

Differing species-specific environmental sensitivities can also underpin the **insurance effect**. Various definitions of the insurance effect exist. Here, following McCann [6], we first distinguish the insurance effect from compensatory dynamics by whether pronounced **perturbation** events are considered (Box 1) where an insurance effect characterizes the ability of an ecosystem to resist and recover after a perturbation. A perturbation can cause a decline or loss in some dominant species. The insurance effect implies the presence of some subordinate species being 'redundant' (i.e. with similar ecosystem effects but differing sensitivity to perturbations; see Puzzle piece 5) with the declining dominant species [20,33,34]. These 'redundant' species can replace the formerly dominant species and maintain ecosystem functioning. Note that this directional substitution is distinguishable from a regular fluctuation between dominant species expected under compensatory dynamics, which also do not necessarily follow perturbations. Redundancy can support both higher resistance and recovery. In practice, distinguishing perturbations from historical variability and environmental stochasticity in local conditions can be arbitrary, but the identification of any specific perturbation is essential for assessing mechanisms of resistance and recovery [35].

end box 2

175 **Puzzle Piece 1: effects of dominant species' traits**

176 According to the 'mass-ratio hypothesis' [36], dominant species in a community, through their
177 traits, exert the strongest effect on ecosystem functions at a given time (called 'immediate'
178 effects). Such **dominant species' traits** do not have only immediate effects. One of the two
179 main drivers of constancy is how stable populations are within a community, expressed as
180 average species-level population stability weighted by species' relative abundances [28]. The
181 constancy of species populations has been related to species traits [37–39]. Moreover,
182 resistance and recovery of community biomass after perturbation have been related to the
183 functional traits of the dominant species in a community, rather than to species diversity itself
184 [29]. As such, variation in trait values of dominant species in a community can bridge the gap
185 between temporal population dynamics, community properties and ecosystem stability.

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

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

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216 **Puzzle Piece 2: compensatory dynamics through species dissimilarity**

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

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

242 The relationship between species synchrony and species **pairwise trait**
243 **dissimilarity**, could provide a mechanistic view on the drivers of compensatory dynamics
244 (Box 2). There is increasing empirical evidence that greater trait similarity between species is
245 associated with greater synchrony [3,59–61]. As such, an increase in community **functional**
246 **diversity** should lead to greater constancy. Support for a decrease in synchrony with
247 increasing functional diversity has been found in beetle communities [62] and in manipulated
248 plant communities [56,63]. The recent study by Craven et al. [17] failed to detect any marked
249 effect of plant functional diversity, expressed only for the leaf economics spectrum, on
250 synchrony, but detected an effect of **phylogenetic diversity**, as in Cadotte et al. [64]. This is
251 possibly because the relationship between pairs of species and their synchrony is better
252 appreciated on the basis of **multiple traits** [3,62]. Phylogenetic diversity can be considered
253 as a proxy of multi-trait diversity and unmeasured traits [65]. It should be noted that classic
254 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.

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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.

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Box 3#####

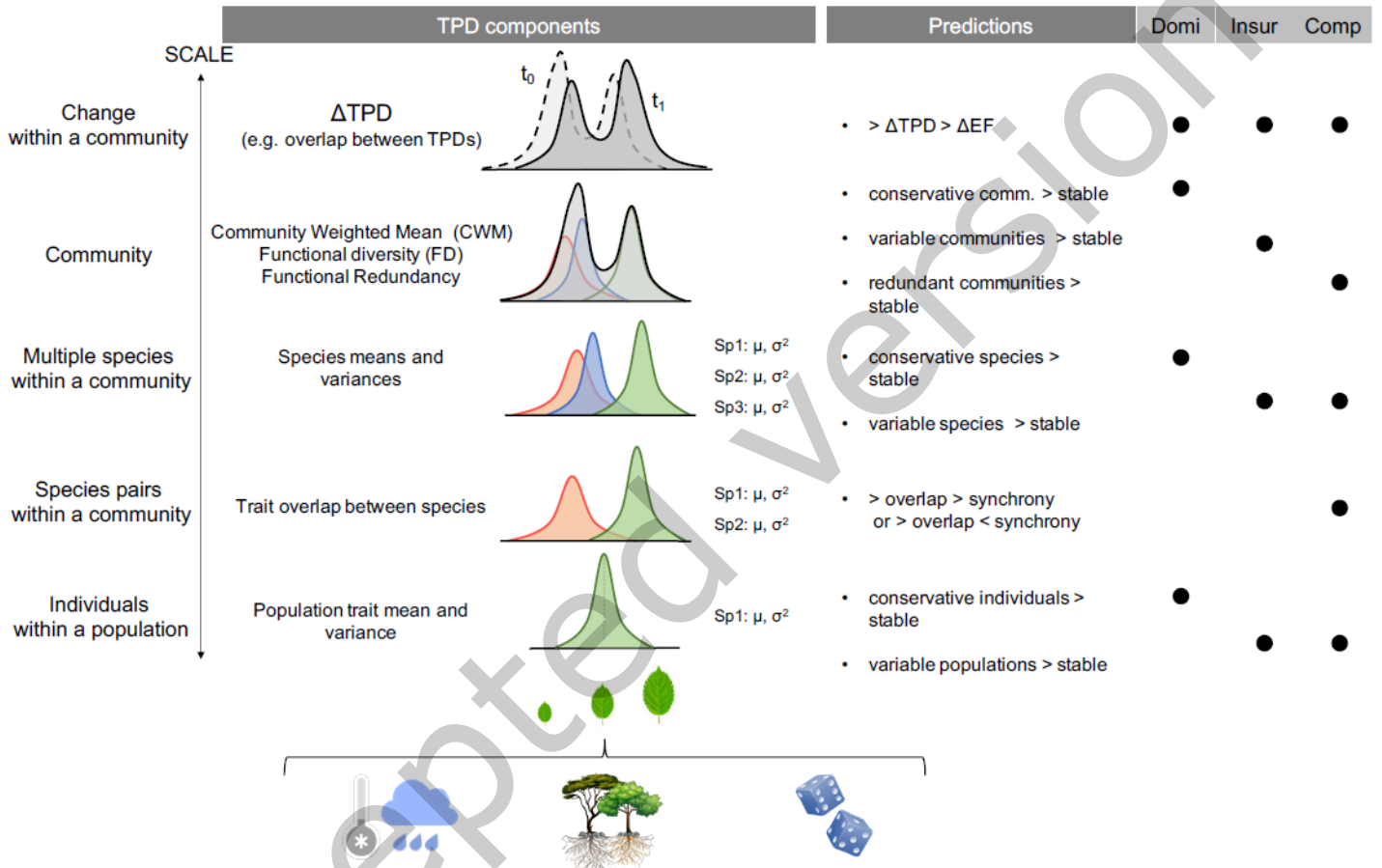
Trait Probability Density

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].

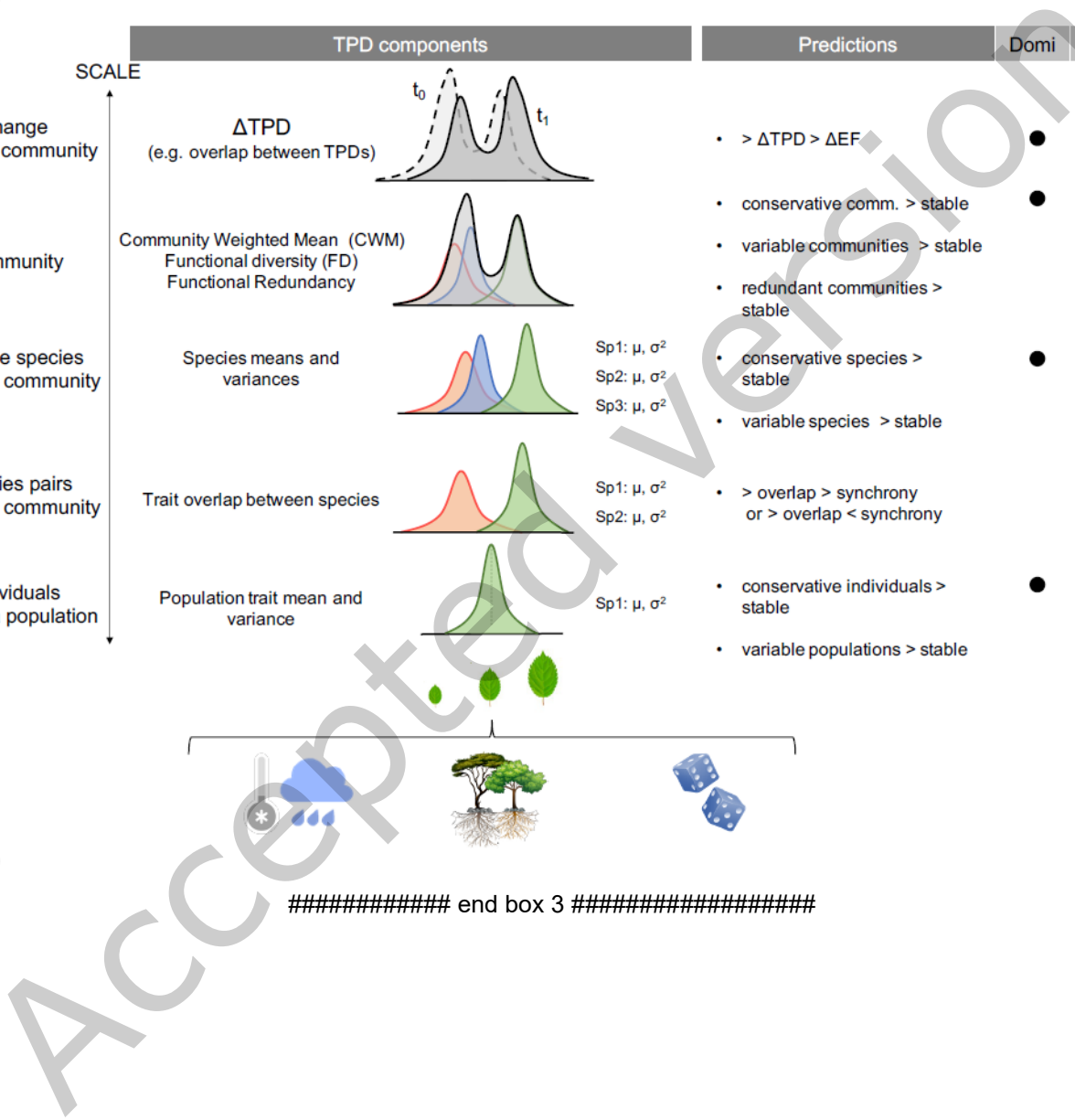
By integrating species abundances and traits, TPD has the potential for connecting population and community dynamics, and thus scaling up temporal variations in species populations to ecosystem functioning and its stability (Fig. 1). TPD in a local community is the result of both random and deterministic 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 1).

[[see Figure 1 for Box 3 in the specific file]]

322 **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 (Δ TPD)
 327 should result in an overall more stable ecosystem functioning [16,30].
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 331 ##### end box 3 #####



332 **Puzzle Piece 4: response and effect traits**

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

343 Some functional traits also have the potential to affect other trophic levels and
344 multiple ecosystem functions [10,14,25]. **Effect traits** are therefore those traits of an
345 organism that impact prevailing ecosystem processes and functions. For example, mandible
346 strength will determine the extent and type of food consumed in grasshoppers [82].
347 Flammability traits in plants modify the fire regime and generate eco-evolutionary feedback
348 [83]. Secondary compounds in leaves not only offer defense against herbivory but might slow
349 down litter decomposition [84], while floral traits will affect pollination [25].

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

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

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372 **The puzzle comes together: buffering vs. propagating**

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

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

397

398 **a) Stable dominants**

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

411

412 **b) Compensatory dynamics**

413 Compensatory effects are usually considered to be a key mechanism of constancy [6] but
414 may also destabilize ecosystem functioning. Constancy in ecosystem functioning can be
415 obtained when 'inconstant' populations of species with similar effect traits periodically (for
416 example, on a yearly basis) 'compensate' for each other (scenario 2, in Fig. 2), i.e. they
417 negatively covary in time (**anti-synchrony**). As we discussed above, theoretical [11] and
418 empirical evidence [3,59–62] suggests that anti-synchrony will occur between species with
419 different response traits (moderate to high ΔTPD_R , and overall high FD in a community; case
420 1 in Fig. 2), reflecting different environmental preferences. Constancy in ecosystem
421 functioning will then occur only if effect traits and response traits are dissociated (high FD in
422 response traits, low in effect traits). Otherwise changes in species composition will propagate
423 into changes in effect traits and cause ΔEF . Imagine a case where the ecosystem function of
424 interest is pollination, and two anti-synchronous species have different response traits (e.g.
425 different LDMC) and also different effect traits (e.g. flower types with access to different
426 pollinators; case 2 Fig. 2), i.e. high $\rho(R_T, E_T)$. In this case we can expect a periodic change in
427 ΔEF both in decomposability and pollination. Anti-synchrony could also occur between
428 functionally similar species (low ΔTPD_R) after temporal changes in the competition hierarchy
429 [3,11; case 2 in scenario 2, Fig. 2,58]. In this case, buffering is more likely, especially if effect
430 and response traits overlap.

431

432 **c) Insurance effect**

433 The insurance effect can be particularly important in the case of replacement of a dominant
434 species by an otherwise subordinate species following some exceptional perturbation [e.g.
435 fire or drought, 89]. Such directional species replacements (different from periodic
436 replacement in compensatory effects above) are expected between species with different
437 adaptations to given perturbations (and, likely, a high ΔTPD_R in specific traits; a replacement
438 between species with similar response traits following an extreme climatic or disturbance
439 event is not likely). An insurance effect is again possible only if response and effect traits are
440 dissociated (case 1, scenario 3, Fig. 2). It should be noted that greater species diversity
441 should increase the odds that more species will have different adaptations to perturbations
442 [53]. At the same time the greater the diversity in ΔTPD_R , the lower the species richness
443 needed to buffer an ecosystem process [68]. For this reason, functional redundancy between
444 dominant species and subordinate species, key for the insurance effect, is expected to reflect
445 the interplay of both species diversity and functional diversity across species. Note also that in
446 scenario 3, Fig. 2, it can happen that some functional traits may exert some insurance effects,
447 but the total population abundance can still decrease. Some ecosystem functions, such as
448 soil stability and formation, could be thus affected by the perturbation, simply as a
449 consequence of reduced plant cover (see next section).

450

451

452 **Connecting the pieces with TPD: data analysis considerations**

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

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

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

490 Different parameters of population abundances are other important drivers in the
491 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.

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BOX 4

Future puzzle pieces: intraspecific trait variability

Most of the examples and studies reviewed so far refer to the effect of species diversity and trait dissimilarity between species, including trait trade-offs between species. However, most of the mechanisms act first on the variability of local populations, and therefore cause phenotypic differences within and between populations of a species. **Intraspecific trait variability** (ITV) could theoretically affect stability [16]. At the same time, it is important to differentiate between ‘spatial’ intraspecific trait variability (among individuals) and ‘temporal’ intraspecific trait variability (between seasons or years, including plasticity and micro-evolutionary processes). Both these expressions of ITV are components of TPD [69]. Changes in time, or space, in TPD can be caused by ITV and species turnover, or more frequently by both [94].

ITV caused by **genetic variation within the population** can affect its stability [95,96]. For example, individuals within a population with more conservative traits could have more stable growth or reproduction over time while individuals with less conservative strategies would be less resistant, but exhibit faster recovery [97]. Hence a population with both ‘types’ could be maintained, overall more constantly in time, in fluctuating conditions. Wright et al. [98] hypothesized that higher intraspecific trait variability could confer greater stability within species, possibly through an insurance mechanism, although compensatory mechanisms between different genotypes could also occur [99].

Another mechanism concerning the effect of intraspecific trait variability on stability is phenotypic variation across generations. This can be caused by either **selection** of different phenotypes over time or **transgenerational plasticity**. Zuppinger-Dingley et al. [100] and Latzel et al. [101] highlighted the importance of within-species trait variability and year-to-year trait-adjustment effects on ecosystem stability and the influence of both selection and transgenerational plasticity on ITV. Ultimately, selection across generations can increase functional diversity in a community [100]. Interactions between species within a given season can stabilize communities via transgenerational effects in plant traits in the following growing seasons [102]. Thus, these within-species adjustments seem to be an important, yet largely unexplored, component of the stability of communities. However, the empirical testing of intraspecific trait variability effects on stability will be challenging, particularly if we are not able to separate the cause of phenotypic variation. We should be also aware that high intraspecific trait variability might be a consequence, instead of the cause, of population instability. For example, seasonal drought will probably have a spatially non-homogenous effect on plants, causing high levels of intraspecific variability in some traits, and, at the same time, this will also affect the population size, causing temporal variability.

end box 4

563 **Concluding remarks**

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

571 Different tests are possible depending on the ecological scale considered (Box 3),
572 and the interplay between population dynamics and community properties (Fig. 2) is key in
573 determining biodiversity effects on the stability of ecosystem functioning. Comprehensive
574 frameworks testing biodiversity effects on ecosystem properties need to combine multiple
575 types of metrics (Fig. 1), not necessarily trait-based, which are also selected depending on
576 the stability mechanisms under scrutiny. Variation in the local populations can result in overall
577 changes in community structure, which may, or may not, propagate into changes in
578 ecosystem functioning. The strength of this propagation depends on the extent of trait
579 changes and the degree of overlap between response and effect traits – an idea which has,
580 so far, not been fully incorporated in analyses linking biodiversity and stability. Including
581 response and effect trait analyses can also help to improve the quantification of functional
582 redundancy, which is essential for testing the insurance effect. In the future, attention should
583 also be paid to the potential for intraspecific trait variability in affecting local population
584 stability, via intraspecific adjustments (Box 4). While here we have reviewed mechanisms of
585 stability within given trophic levels, trait mechanisms acting across trophic levels will be
586 central to future developments for assessing the stability of multi-trophic ecosystem functions.
587 Finally, the framework and concepts synthesized in this review should be applicable to
588 different types of environments, and under different global-change scenarios. This will enable
589 us to assess to what degree the effects of different biotic mechanisms of stability vary along
590 gradients of habitat severity and habitat heterogeneity and in response to different types of
591 perturbations.

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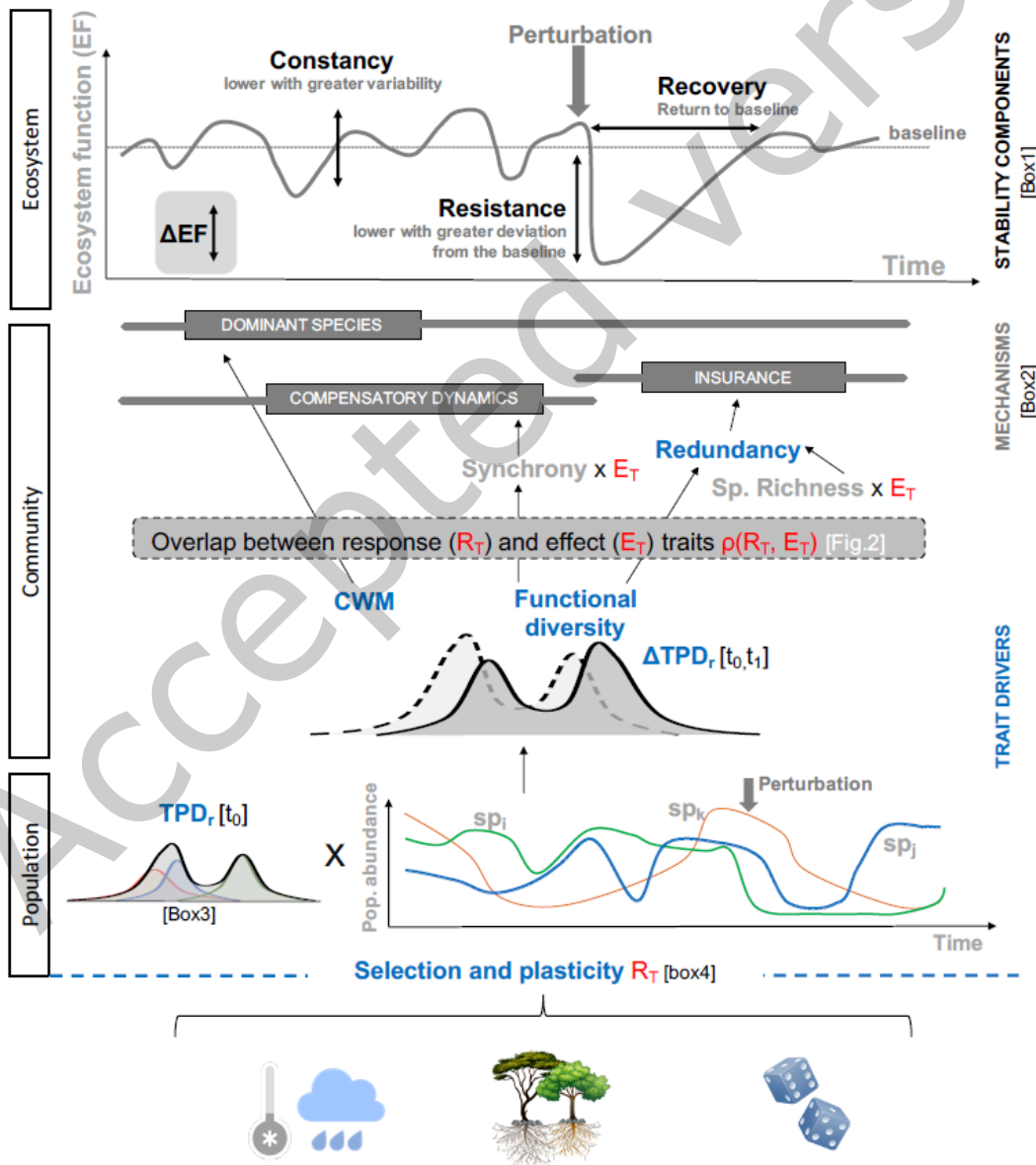
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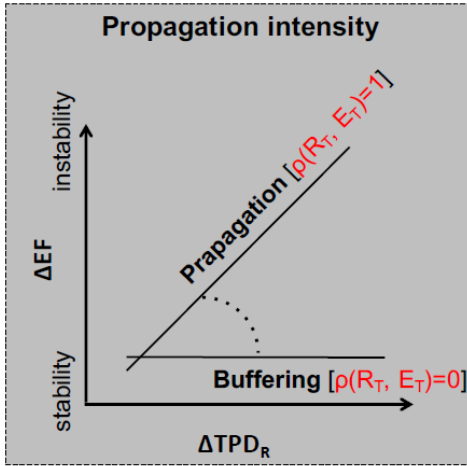
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603 **Figure 1. Changes in population abundance, in response to deterministic and**
 604 **stochastic events, build up into different changes at the community level (e.g. TPD,**
 605 **species richness, synchrony) and affect different components of 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.

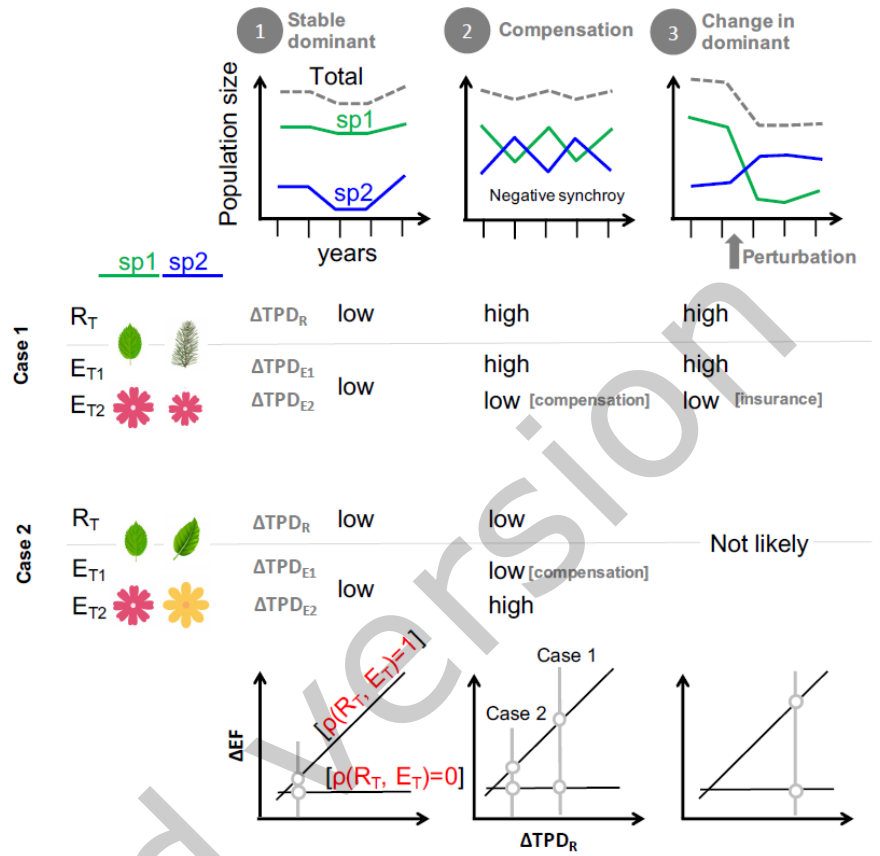


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617 **Figure 2. Effect of the overlap between response and effect traits, expressed as their**
618 **covariation [i.e. $\rho(R_T, E_T)$], on the modulation of different biotic effects that control**
619 **ecosystem function stability.** Variation in 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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648 **Glossary**

649

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

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

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

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

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

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

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

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

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

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

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

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

679 Intransitivity competition: Interactions among species in a community in which they do not
680 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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