Comments

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Not even wrong: Comment by Wagg et al.

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A recent paper by Pillai and Gouhier (2019) (PG) in Ecology argues that biodiversity–ecosystem functioning (BEF) effects calculated by the additive partitioning approach introduced by Loreau and Hector (2001) (LH) are flawed and overestimate biodiversity effects. Biodiversity effects are based on the null expectation that the addition of more species has no effect on function and on "average" species affect functioning the same in mixture as in monoculture assuming no intraor interspecific density effects on performance. However, PG claim that such a null hypothesis is flawed as it is an extension of the neutral theory of species coexistence thus overinflating biodiversity effects (overyielding) because "species in mixtures coexist and by some

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form of niche partitioning overyield," therefore as richness increases inherently species must coexist by occupying different niches based on coexistence theory (CT). Although CT is based on predicting long-term interspecific population outcomes that maintain diversity and predict invasiveness and BEF concepts are based on static richness-function observations, PG state that a more reasonable null expectation for BEF research should be based on CT. Based on these assertions, PG conclude that "overyielding of ecosystem properties should be a natural outcome of coexistence." Although BEF and CT share related ecological concepts surrounding the niche, their different goals, origins, and intended uses prevent us from directly substituting their applications and inferences. Here, we comment on some fundamental concepts that underpin BEF research to elucidate potential misconceptions that may have led PG to conclude that, based on CT, the null expectation of BEF research used by LH is flawed. Specifically, we comment that their logic is flawed because (1) BEF research has originated from fundamentally different null hypotheses and goals than CT, (2) coexistence can occur without positive biodiversity effects (overyielding), and (3) overyielding occurs without stable coexistence. Despite the differences between BEF and CT research origins and approaches, their commonalities have been recognized early on (Harper 1977, Mouquet et al. 2002, Loreau 2004) and requires further empirical investigation that may lead to novel opportunities to theoretically predict, and empirically measure, how dynamic coexistence mechanisms predict static observed biodiversity-ecosystem-functioning relationships in nature.

The Null Hypotheses of BEF is Not Defined by CT

Many early BEF experiments focusing on plant communities found that plant species richness-yield relationships were positive but with declining increases as more and more species were assembled (e.g. Tilman et al. 1996, Hector et al. 1999). Such seminal early BEF research asked simple questions about whether species loss reduced ecosystem functioning and was quantified by varying species richness while holding total sowing or planting density constant to avoid confounding species richness with density (Schmid et al. 2002a). Observed positive saturating richness-productivity curves generated debate at the time as to whether this relationship was simply due to the increasing probability of including one, or a few, highly productive species in more diverse systems (e.g., Huston 1997). This would require the so-called rule of constant final yield (the first law of plant population biology according to Harper 1977), where highly productive species may approach the same

biomass in mixtures as in monoculture, even if sown at lower densities in mixture. The initial skepticism against positive BEF relationships was in part due to theory that predicted negative relationships between ecosystem complexity and stability (May 1972). A further rational for skepticism was the expectation of early agricultural botanists that the best-performing monoculture should always be more productive under ideal conditions than the best mixture (no transgressive overyielding of mixtures, Harper 1977). Assuming that BEF relationships must be positive due to niche partitioning according to CT, and misunderstood by PG, is thus counter to these historical expectations and overlooks the rich history of research on the effects of species mixing and its purpose, which is independent of CT.

De Wit (de Wit 1960, de Wit et al. 1966) introduced the replacement series experimental design, where total density is constant but the mixing ratio of two species is varied. Monocultures of species were used as a reference for identifying the optimal sward-mixing ratio along a replacement series for forage cropping. This design is based on the null expectation that if there are no effects of mixing, individuals of different species are competitively equivalent and thus mixtures should yield as predicted by adding the monocultures in the proportions given by the frequency of the species in mixture. This classic experimental design assesses the effect of increasing the sown density of a species *i*, while equally reducing the sown density of a species *j* to maintain a constant sowing density (Appendix S1: Fig. S1a). If the null expectation is that the yield per individual of a species is constant in constant community density, then a species contribution to yield is its monoculture yield weighted by its sown proportion (Appendix S1: Fig. S1b). The sum of the species relative yields is the relative yield total (RYT), and if species are in mixture with a constant community density, then the null hypothesis is that the RYT = 1. According to this first scenario in Appendix S1, if all species were identical and density was constant between mixtures and monocultures, then increasing species richness should have no effect on yield and no overyielding should occur (RYT = 1 for all species richness levels).

Of course, RYT = 1 is almost never the observed result in field trials, as various ecological mechanisms can be at play. Some of these ecological mechanisms may be related to CT and the limiting-similarity and competitive-exclusion hypotheses (MacArthur and Levins 1967, Chesson 2000). For instance, by reducing the density of species *i* in mixture, it may become released from intraspecific competition, which could lead to increased yield per individual of species *i*. If the other species *j* does not suffer more from *i* than *i* gains from *j*, or if both species behave in the described manner in mixture, i.e., if overall intraspecific competition is stronger than interspecific competition, then RYT > 1 (Appendix S1, scenarios two and three). As long as there is no facilitation between the two species, a maximum RYT = 2 can be achieved in two-species mixtures according to the rule of constant final yield (Appendix S1, scenario two; Schmid et al. 2002*b*). If one or both species facilitates the other and no interspecific competition occurs at all, then RYT > 2 would theoretically be possible.

Whatever the species richness, according to scenario two, the null expectation for mixture yield is the sum of all the component species' monoculture yields (instead of the average). Such a situation with no niche overlap and no interspecific competition between species is of course highly unrealistic but important to consider in the context of PG's new null expectation for biodiversity effects, because it reflects this null expectation in its most extreme form. They argue that the null expectation of BEF research should be that mixtures are overvielding to the degree to which species niches do not overlap and thus do not compete for the same resources. In this case, niche overlap between species under the null expectation could be measured via the classic RYT and by doing this in all possible two-species mixtures, for which null expectations for mixtures of more than two species could be derived. However, to tease apart the two-way interactions from the higher-order interactions would require new experiments that include replicate monocultures, replicate two-species mixtures with all pairs of species and replicated mixtures with higher levels of diversity, a heroic effort that has not been done thus far. Not surprisingly, the real biodiversity effect of interest calculated by PG is generally negative, because they use no correction for multiple niche overlap in mixtures of three or more species. Thus, their null expectation is fundamentally different from the common null expectation used in LH, which corresponds to the first scenario in Appendix S1: Fig. S1. Here, the expected mixture yield is not the sum, but the average of all the component species' monoculture yields and thus increasing species richness does not change vield.

The additive partitioning of biodiversity effects introduced by LH allowed us for the first time to quantify different ways in which relative yields of species could combine to total yield, something that previously was done in more qualitative ways, e.g., by the replacementseries approach of de Wit (1960). Additive partitioning works with relative yields to separate the net biodiversity effect (difference between mixture yield and the average of monoculture yields) into two additive components called the complementarity effect (CE) and the selection effect (SE). The additive partitioning was developed to assess early BEF debates as to whether positive net effects (NE = CE + SE) of biodiversity were driven more or less by particularly productive species (SE) or by a generally increased species performance in mixture (CE). It was not intended to tease apart intra and interspecific density-dependent competitive effects between

species pairs used in CT or to provide direct evidence of any one particular ecological mechanism underpinning BEF relationships as PG incorrectly assume. It was already known prior to the development of the additive partitioning that the use of relative yields confounds intraspecific and interspecific density effects (see Connolly 1986, Jolliffe 2000).

Originally, the aim of the RYT was to compare species of similar monoculture performance in a replacement series. This similarity in monoculture yield simplifies the interpretation of RYT > 1, because if species monocultures are identical, a RYT > 1 will always require a contribution of both species. In this case, the overyielding of the mixture is mostly or fully due to the CE from the additive partitioning method. However, if a more productive species is mixed with a less productive species, RYT > 1 can occur but does not have to be achieved with the SE alone. Here, the additive partitioning approach can be used as it distinguishes this case by assigning the NE of RYT > 1 to SE, where the mixture becomes essentially a monoculture of the more productive species, from other cases where both species contribute to the biodiversity effect. In fact, if two species differ in monoculture yields, there is a large range of possible contributions of SE and CE that lead to NE > 0and RYT > 1 (Appendix S1). Similar arguments apply to cases with RYT < 1 (Loreau and Hector 2001).

Overyielding in mixtures originates from assessing the optimal sward mixing in managed grasslands and whether it is better to plant the best monoculture vs. a mixture (e.g., de Wit 1960). The use of the additive partitioning of biodiversity effects to tease apart the relative contributions of species in mixtures to explain why mixtures perform differently than the average monoculture is fundamental for BEF experiments. The arguments of PG have overlooked this initial intention of BEF studies for assessing yield that does not need to be directly connected to the long-term coexistence of species. Further, the additive partitioning method not only applies to two-species mixtures but can be applied to any species richness level provided that species yields in mixture can be separated and that all species occur in monoculture.

THERE CAN BE COEXISTENCE WITHOUT OVERYIELDING

The fact that CEs and SEs do not have a direct mechanistic explanation in terms of coexistence or niche theory may be one of the frustrations of PG. Indeed, a common misconception is that complementarity effects should be directly equivalent to resource complementarity or spatial complementarity (Barry et al. 2019). While this is an interesting hypothesis, there is little empirical support so far. For example, in a forest experiment, physical crown complementarity was actually more closely related to SEs than to CEs (Williams et al. 2017), perhaps reflecting a competitive trait hierarchy (Kunstler et al. 2012). Disconnects between species coexistence and the mechanisms by which species contribute to overyielding reveal the difficulty in logically substituting the concepts of one into the other and may be based on misconceptions of the origins and objectives of BEF research.

First, although positive effects of biodiversity are commonly observed in both experimental and natural contexts and across different ecosystems (Balvanera et al. 2006, Duffy et al. 2017), the experimental mixing of species does not always result in overyielding. In rare cases, antagonistic interactions among species have also been observed in biodiversity experiments leading to mixtures having RYT < 1. This occurs if overall interspecific competition is stronger than intraspecific competition in a mixture (Appendix S1, scenario four). This result has occurred in bacterial communities, where species increase the production of allelopathic toxins in mixtures, thus leading to a strongly negative biodiversity effect without the competitive exclusion of species during the course of an experiment (Jousset et al. 2011, Becker et al. 2012). Other situations resulting in RYT < 1 can result from positive density dependence. For example, attracting mutualists required by a species becomes limiting at lower densities, such as in the case where the performance of a species is dependent on positive plant-soil feedback effects (van der Putten et al. 2013). While in these cases, both species may suffer in a two-species mixture, RYT < 1 can also result in situations where an unproductive species *j* suppresses a more productive species *i*, even though *j* may be less suppressed by *i* than by itself (Loreau and Hector 2001).

Second, if similar species are expected to compete more strongly for common resources, then it may also be expected that due to their similarity the species also have relatively equal competitive effects on each other (Ebeling et al. 2014). Thus, in mixtures of highly similar species, neither will have a large enough competitive advantage to exclude the other due to their similar fitness (Aarssen 1983, Hubbell 2001, Adler et al. 2007). The consequence of species being competitively equivalent with a high level of niche overlap could again result in species coexisting without overyielding. In such cases, it is clear that statements such as "overyielding of ecosystem properties should be a natural outcome of coexistence" by PG have overlooked the fact that species in mixture can interact and coexist in a way that does not result in overyielding (Turnbull et al. 2013).

THERE CAN BE OVERYIELDING WITHOUT STABLE COEXISTENCE

The hypothesized mechanisms that underpin the empirical static observation of positive BEF relationships and the hypothesized drivers of coexistence run parallel to each other (Mouquet et al. 2002, Loreau 2004, Carroll et al. 2011, Turnbull et al. 2013, 2016). Such parallels may have given PG the impression that the approaches are aimed at achieving the same objective and are readily intermixed. However, CT and BEF relationships are not completely comparable, and longterm stable coexistence is not a necessary condition for enhanced ecosystem functioning in more diverse systems as implied by PG.

First, CT and the additive partitioning method are used at different temporal scales. Additive partitioning is applied to a state variable, usually within a single growing season. In contrast, classic coexistence models are based on per capita growth rates modeled over many demographic turnover events in a community to achieve a stable equilibrium and are therefore process variables. Commonalities between overvielding in BEF research and competitive interactions from CT may be more easily drawn in biodiversity experiments involving trees, where the yearly growth of individuals can be followed (Huang et al. 2018), or in experiments involving perennial herbaceous plants if we replace "per capita growth rate" with "species biomass accumulation rate" within a single growing season, and if we also assume that the species monoculture yield is an indication of species carrying capacity K. The use of monoculture yields to infer K is not unreasonable because according to the law of constant final yield (monocultures sown at a very high density undergo self-thinning until the constant final yield is met; Weiner and Freckleton 2010). This constant final yield can also be reached with a much lower density, where individual plants grow to be larger (Harper 1977). The concept of constant final yield in monocultures may be akin to the concept of a species carrying capacity (K) used in species competition-coexistence frameworks (Westoby 1981). Thus, plants may "adjust" their per capita growth rate within a single cohort to compensate for density variations to achieve the constant final yield (K). This observed phenomenon in plant species populations, where individual plants at lower intraspecific densities grow larger, is likely due to greater resource availability per individual (Bazzaz and Harper 1976, Roscher and Schumacher 2016). Yet, effects of species richness on self-thinning and constant final yield in mixtures have barely been explored (Roscher et al. 2007).

CEs and SEs often change over time in long-term biodiversity experiments (Cardinale et al. 2007, Marquard et al. 2009, Reich et al. 2012, Huang et al. 2018). Temporal changes in CEs (and RYT) can be generated from coexistence models (Turnbull et al. 2013). However, these theoretical models demonstrate that enhanced ecosystem functioning can occur even when long-term stable coexistence is not possible. Turnbull et al. (2013) found that communities can overyield even when stabilizing niche differences (sensu Chesson 2000) cannot overcome fitness differences and therefore allow for stable coexistence. This "transient" overyielding may occur frequently in natural communities, where environmental conditions change and may lead to long-term unstable persistence rather than long-term stable coexistence (Wagg et al. 2017). Nutrient addition can also increase overyielding and simultaneously decrease the number of species that are able to coexist, indicating that enhanced ecosystem functioning with increased species richness and coexistence in these systems may be driven by different mechanisms (Harpole et al. 2016). Therefore, the application of coexistence models to diverse perennial grasslands, where much of BEF research (including the additive partitioning method) has originated, is extremely challenging both for the above reasons and because of largely varying demographic turnover rates. There is no constant per capita growth rate, considering that plant yield-density relationships follow the law of constant final yield and that plant communities can be highly diverse (more than species pairs), resulting in complex higher-order interactions that are difficult, if not impossible, to parameterize.

CONCLUSIONS

Coexistence mechanisms based on niche partitioning and fitness differences are important ecological mechanisms that can relate to positive effects of biodiversity and are useful for deriving empirically testable hypotheses for future studies on the mechanisms underlying BEF relationships. However, the proposed redefining of the null hypothesis by PG, claiming that coexistence always implies "trivial" positive biodiversity effects against which "true" biodiversity effects would have to be evaluated is "circular" in its own way as indicated by the use of the trivial component of biodiversity effects as a measure of coexistence. What PG propose for a null hypothesis corresponds to what Connolly et al. (2013) uses as an estimation of the diversity effect, the sum of all the pairwise interaction effects, and is actually just a special case of diversity-interaction models, which are already much further developed than what PG propose and already address the issues PG raise (Kirwan et al. 2007, Kirwan et al. 2009, Connolly et al. 2011, 2013, Dooley et al. 2015, Brophy et al. 2017).

These are effects of diversity, even if they also are consequences of processes leading to coexistence and should not be downplayed for that. In other words, the null hypothesis of PG is circular as it defines a biodiversity effect as proof of no effect. Furthermore, the use of classic coexistence models for empirically predicting species competitive outcomes at naturally occurring higher levels of diversity (with more than two species) is limited due to higher-order interactions that become more complex across increasing levels of species richness (Levine et al. 2017, Barabás et al. 2018). The additive partitioning of biodiversity effects is also not theoretically limited by first having to parameterize all species' pairwise and higher order interactions in diverse plant mixtures. While the use of CT indeed provides many insights for understanding ecological mechanisms that support biodiversity in nature, its use in practical and applied settings, such as in agricultural ecosystems, where species mixtures are sown at predefined densities and responses are quantified within a single growing season, may not be as useful as relative yields and the additive partitioning method.

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