Insights on nitrogen and phosphorus co-limitation in global croplands from theoretical and modelling fertilization experiments

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Abstract:

20   Crossed fertilization additions are a common tool to assess nutrient interaction in a given ecosystem. Such fertilization experiments lead to the definition of nutrient interaction categories: e.g. simultaneous co-limitation, single resource response, etc. (Harpole et al., 2011). However, the implications of such categories in terms of nutrient interaction modeling are not clear. To this end, we developed a theoretical analysis of

25   nitrogen (N) and phosphorus (P) fertilization experiments based on the computation of ratios between plant demand and soil supply for each nutrient. The theoretical analysis is developed following two mathematical formalisms of interaction: Liebig's law of minimum and multiple limitation hypothesis. As results of the theoretical framework, we defined the corresponding between most Harpole categories and the values of the

30   limitation by each nutrient when considered alone in the control experiment (i.e. without additional nutrient supply). We showed that synergistic co-limitation could occur even using Liebig's formalism under certain conditions as a function of the amount of N and P added in fertilization experiments. We then applied our framework with global maps of soil supply and plant demand for croplands to achieve their potential yield. This allowed

35   us to estimate the global occurrence of each limitation category, for each of the possible interaction formalism. We found that a true co-limitation could affect a large proportion of the global crop area (e.g. ~42% for maize) if multiple limitation hypothesis is assumed. Our work clarifies the conditions required to achieve N and P co-limitation as function of the interaction formalism. Combined with compilation of field trials in cropland, our

40   study would improve our understanding of nutrient limitation in cropland at the global scale.

Keywords: nutrient limitation, nutrient interaction, nitrogen, phosphorus, cropland

1. Introduction

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In global assessments of crop ecosystem productivity limitations by nutrients, nitrogen (N) and phosphorus (P) are sometimes considered independently (Peñuelas et al., 2013); or they are considered together but without focusing on how the interaction modulates the limitation (Mueller et al., 2012). N and P cycles interact strongly with different

50 processes that are key to this coupling (Achat et al., 2016). The most commonly studied interaction is related to the limitation of plant growth by nutrients: an increase in organ biomass (mainly composed of carbon, C) requires a given amount of both N and P, to respect stoichiometrical constraints. The interaction between carbon and nutrients is usually represented by C:nutrient ratios for each organ. Plant growth is assumed to be

55 limited when the demand for nutrients, estimated from C:nutrient ratios and C available for potential growth, is not satisfied by the supply of nutrient taken up by the plant. Due to incomplete knowledge about the mechanisms at the basis of the interaction and how these mechanisms are combined when integrating spatial scales (plant organ, individual, community, ecosystem) (Ågren et al., 2012; Davidson and Howarth, 2007; Sistla and

60 Schimel, 2012; de Wit, 1992) the characterization of multiple element limitation remains an open scientific question. Two formalisms are generally used: Liebig's law of the minimum (LM) or the multiple limitation hypothesis (MH). In LM, plants are assumed to be limited by a single nutrient at a time, while in MH, it is assumed that plants adjust their growth patterns and thus they are co-limited by multiple nutrients simultaneously

65 (Ågren et al., 2012). The MH formalism thus assumes that plants will mine the least available nutrient by using other resources. For instance, plants or groups of species growing in an ecosystem with a P-poor soil will invest C and N in the root system (and potentially to fungal mycorrhizae that form symbioses with plant roots (Ryan and

Graham, 2018)) to access more P (Davidson and Howarth, 2007). Both formalisms could

70   be considered as macro-properties that reflect the same plant adjustments processes

but, depending on the conditions, those adjustments may lead to an emerging behaviour

that verifies one or the other formalism (Ågren et al., 2012). The further the supply of an

essential nutrient deviates from a conceptual optimum stoichiometry of plants, the

more plants will follow the LM formalism (Ågren et al., 2012). LM is commonly assumed

75   in many studies and is for instance used in most large-scale models dealing with multiple

nutrient limitations (Barros et al., 2004; Goll et al., 2012; Mueller et al., 2012).

One way to assess the current nutrient limitation empirically is to provide single

applications of +N, +P and +NP and to measure the increase in ecosystem productivity as

80   compared to a control trial without any application. By definition (Harpole et al., 2011),

there is a *true* NP co-limitation when the ecosystem is observed to respond to combined

N and P addition only, or to both N and P when added separately. The different

categories of nutrient limitation are summarized in Harpole et al. (2011) and in Table 1.

Fertilization experiments are common in natural ecosystems and meta-analysis of these

85   experiments have provided a global picture of nutrient limitation in natural ecosystems

(Augusto et al., 2017; Elser et al., 2007; Harpole et al., 2011). Results from recent meta-

analyses have shown that a true co-limitation is found in 28-42% of the studies (Augusto

et al., 2017; Harpole et al., 2011). This challenges the view that plants are generally

limited by one nutrient at a time (i.e. LM). However, which categories of nutrient

90   limitation are consistent with each interaction formalism (LM and MH) is not clear. For

croplands, experiments with single applications of fertilizer are not as common as those

for natural ecosystems and it is usually difficult to retrieve the application level before

the experiment (e.g. Deguchi et al., 2017; Restelatto et al., 2017), which prevents an

accurate definition of the control in these cases. On the other hand, long-term field

95 experiments are common in croplands (especially for P, e.g. Bai et al., 2013) but for a

given treatment; the same amount of fertilizer is applied each year for decades, which

precludes analysis of current limitation. Crossed fertilization additions are difficult to

decipher from multi-nutrients and repeated fertilizer applications, as usually performed

in croplands. To our knowledge, no meta-analysis of NP limitation in cropland field trials

100 exists, which prevents us from having a global picture of N and P limitation based solely

on observations.

In this work, we provided a theoretical framework of N and P fertilization experiments

based on the computation of ratios between plant demand and soil supply for each of

105 the two nutrients. The theoretical analysis is developed for two mathematical

formalisms of interaction (LM or MH). This allowed us to define the corresponding

between Harpole categories and the values of the limitation by each nutrient when

considered alone. We analytically investigated how the choice of formalism modifies the

NP limitation. Finally, we applied our framework on global spatially explicit

110 computations of soil supply and plant demand of N and P for croplands to achieve their

potential yield, in order to assess the occurrence of co-limitation in croplands for each

interaction formalism.

115 **2. Theoretical framework**

Based on a framework commonly used in global studies (Goll et al., 2012; Kvakić et al., 2018), we defined the limitation of a nutrient considered alone as the ratio of its soil supply (S) and the demand by the plant to achieve its potential biomass (D):

120 $$R_N = min\left(1, \frac{S_N}{D_N}\right)$$ (Eq.1)

$$R_P = min\left(1, \frac{S_P}{D_P}\right)$$ (Eq.2)

where S_X and D_X correspond to the supply and demand of the nutrient X, respectively (in kgX/ha/yr) with X is in {N,P}.

125 Crossed fertilization experiments are a common tool to assess nutrient limitation on a given site. They correspond to changes in nutrient supply in different combinations from the control (E_1): addition of N alone (E_2), P alone (E_3) or N and P together (E_4) (Fig. 1). Based on the above equations defining the limitations of N and P (Eqs 1 and 2, respectively), theses changes in nutrient supply translate into limitations of each

130 nutrient for each experiment E as follows:

E_1: $$R_N(E_1) = min\left(1, \frac{S_N}{D_N}\right) \quad \text{and} \quad R_P(E_1) = min\left(1, \frac{S_P}{D_P}\right)$$ (Eq.3)

E_2: $$R_N(E_2) = min\left(1, \frac{S_N + A_N}{D_N}\right) \quad \text{and} \quad R_P(E_2) = min\left(1, \frac{S_P}{D_P}\right)$$ (Eq.4)

E_3: $$R_N(E_3) = min\left(1, \frac{S_N}{D_N}\right) \quad \text{and} \quad R_P(E_3) = min\left(1, \frac{S_P + A_P}{D_P}\right)$$ (Eq.5)

E_4: $$R_N(E_4) = min\left(1, \frac{S_N + A_N}{D_N}\right) \quad \text{and} \quad R_P(E_4) = min\left(1, \frac{S_P + A_P}{D_P}\right)$$ (Eq.6)

135 with A_N and A_P corresponding to the increase of N and P soil supply following addition of

N and P, respectively.

In the above framework, each nutrient is considered alone while the two nutrients interact. An ecosystem is thus defined by its NP limitation, called R_{NP} in the following.

140 Two formalisms of interaction have been here considered to compute R_{NP} from R_N and R_P: multiple limitation hypothesis (called MH in the following, Eq.7) or Liebig's law of the minimum (LM, Eq.8):

$$R_{NP\_MH}(E_i) = R_N(E_i).R_P(E_i) \qquad \text{(Eq.7)}$$

$$R_{NP\_LM}(E_i) = min(R_N(E_i), R_P(E_i)) \qquad \text{(Eq.8)}$$

145 where E_i is the experiment i.

We analytically investigated to which extent the choice of the formalism has an effect on the value of R_{NP} for a given (R_N, R_P) couple (Fig. 2a-c). We also investigated how the formalism modulates the increases in R_N and R_P required to alleviate the NP limitation

150 (here represented by an increase in R_{NP} to reach an arbitrary value of 0.75) (Fig. 2d-i). Such increases are called ΔR_N and ΔR_P in the following. ΔR_N and ΔR_P corresponds to the smallest increase in R_N and R_P required at the same time to make R_{NP} equal to 0.75 (Fig. 3). We found that the largest differences in R_{NP} between the LM and MH mathematical formulations are obtained for comparable R_N and R_P values ($R_N \sim R_P$) and both within

155 [0.25-0.75] (Fig. 2c). In addition, the largest differences in ΔR_N between LM and MH occur for $R_N < R_P$ and both R_N and R_P lower than 0.75 (Fig. 2f). Symmetric results are obtained for ΔR_P (Fig. 2i).

In fertilization experiments, nutrient limitation is assessed by looking at the change in productivity (Δpro) according to the addition of P alone (Δpro_{+P}), N alone (Δpro_{+N}) or N

160

and P together (Δpro_{+NP}). Δpro is here expressed relatively to the potential productivity (i.e. without any limitation). Harpole et al. (2011) defined different categories of limitation when considering the two nutrients in interaction. Each category is entirely defined by: i) the character null or non-null of Δpro_{+N} and Δpro_{+P} and ii) the relationship

165 between Δpro_{+NP} and ($\Delta pro_{+N}+\Delta pro_{+P}$) (column 3 of Table 1). Following Harpole et al. (2011), co-limitation exists when the increase in productivity following the addition of N and P together is strictly greater than the sum of increases in productivity when each nutrient is added alone (i.e. $\Delta pro_{+NP} > \Delta pro_{+N} + \Delta pro_{+P}$). Any co-limitation is defined as a synergistic relationship. A given co-limitation is in addition considered as true if the

170 responses to +N and +P are either both equal to 0 (i.e. $\Delta pro_{+N}=0$ and $\Delta pro_{+P}=0$, simultaneous co-limitation, category A in Table 1) or both non-null (i.e. $\Delta pro_{+N}\neq0$ and $\Delta pro_{+P}\neq0$, independent co-limitation, category B).

Here, we assumed that the change in productivity following the addition of +N, +P or

175 +NP is equal to the change in R_{NP} following the nutrient addition, i.e.:

$$\Delta pro_{+N}=R_{NP}(E_3)-R_{NP}(E_1) \qquad\qquad \text{(Eq.9)}$$

$$\Delta pro_{+P}=R_{NP}(E_2)-R_{NP}(E_1) \qquad\qquad \text{(Eq.10)}$$

$$\Delta pro_{+NP}=R_{NP}(E_4)-R_{NP}(E_1) \qquad\qquad \text{(Eq.11)}$$

where E_i is the experiment i (Fig. 1). This is a key assumption in our approach. Through

180 these equations, we assumed that the productivity of a given experiment is proportional to R_{NP} and that the slope of this relationship is equal to 1. In fact, a slope equal to 1 is not necessary to develop the theoretical analysis described in Text S1. As mentioned before, Harpole categories are defined through i) the character null or non-null of Δpro_{+N} and Δpro_{+P} and ii) the relationship between Δpro_{+NP} and ($\Delta pro_{+N}+\Delta pro_{+P}$). These definitions are

185   true even if the productivity of each experiment (and thus the different Δpro) is divided

by the same slope. We keep here a slope equal to 1 for the sake of simplicity. Eq.9-11

also imply that the relationship of proportionality between the productivity and R_{NP} is

true for all values of R_{NP}, in the range [0-1]. In reality, the productivity vs. limitation

relationship is very likely asymptotic (e.g. Bai et al., 2013). Here, we may approach this

190   non-linearity by assuming a linear relationship for R_{NP} in [0,*thresh*] where *thresh* is a given

threshold; followed by a plateau for R_{NP} in [*thresh*,1] (which corresponds to assume a

slope of 0 for the productivity vs. limitation relationship). The corresponding between

Harpole categories and the values of R_N and R_P found at the end of our theoretical

analysis are still valid in this more general case, but on the restricted range of R_N and R_P

195   values between 0 and *thresh* (in this case, the value 1 used as boundary for R_N and R_P in

category definitions – columns 4 and 6 of Table 1 – should be replaced by *thresh*). For the

sake of simplicity, we keep in the following 1 as the high boundary and came back on this

point in the Discussion.

200   For each interaction formalism (Eq.7 or 8), we translated the Harpole category definition

(column 3 of Table 1) into conditions on $R_N(E_1)$ and $R_P(E_1)$ thanks to Eq.9-11. This means

that we are able to define most Harpole categories in terms of limitation of each

nutrient considered alone in the control experiment. $R_N(E_1)$ and $R_P(E_1)$ are respectively

called R_N and R_P in the following. The equation manipulation is described in details in

205   Text S1 for both MH and LM.

We showed in particular that to belong to the category "independent co-limitation"

(category B in Table 1) with MH formalism, an ecosystem has to be characterized by both

R_N and R_P in]0,1[(a reversed bracket used in an interval means here that the

corresponding endpoint is excluded from the interval). All other categories (A, C-G)

210   require at least one ratio equal to 0 or 1: e.g. serial limitation N (category C) requires R_N equal to 0 and R_P in $]0,1[$ (Table 1). Categories E,F,G are defined by $\Delta pro_{+NP} = \Delta pro_{+N} + \Delta pro_{+P}$ and we showed that this requires at least one ratio equal to 1 with MH formalism (Text S2).

We showed that the formalism LM cannot represent true co-limitation, except in the

215   very specific category A (i.e. $R_P = R_N \neq 1$). We found that synergistic co-limitation alone (categories C and D) can occur with LM but to be in these categories, the amount of N (if the control is N limited) or P (if the control is P limited) added in the fertilization experiments should be large enough to remove the initial limitation.

Conclusions of this analysis are summarized in Table 1 (columns 4 for MH and column 6

220   for LM).

3. Quantifying co-limitation in croplands at the global scale

225 **3.1. Computation of spatially explicit R_N and R_P**

We computed spatially explicit maps of R_N and R_P in croplands (0.5° latitude x 0.5° longitude) based on the computation of nutrient demand and soil supply. We then applied the above described theoretical framework on these R_N and R_P values to classify

230 each grid-cell according to Harpole categories for the two interaction formalisms.

The computation of supply and demand maps used to estimate R_N and R_P are described below. To summarize, plant nutrient demand is based on nutrient harvest index data from the literature combined with spatially explicit distribution of crop potential yield (Y_{pot}) (Mueller et al., 2012). The soil N supply has been approached by using a soil N

235 budget taking into account fertilizer (mineral and organic), atmospheric deposition, biological fixation, and losses by ammoniac volatilization (Bouwman et al., 2011a), while the soil P supply is assessed by a potential root uptake model that accounts for soil P diffusion and soil P legacy effects. More details can be found in Table S1.

240 Following Kvakić et al. (2018), demands for N and P to reach potential yields (D_N and D_P, in kg(N or P)/ha/yr) were derived from the combination of i) fixed parameters related to distribution of carbon (C) and nutrients between the different plant organs at maturity found in the literature and ii) spatially explicit potential yield (Y_{pot}, in kgC/ha/yr):

$$D_X = Y_{pot}.\left(\frac{X_{\%,grain}}{XHI} + \frac{X_{\%,root}.RSR}{HI}\right) \quad \text{(Eq.12)}.$$

245 XHI corresponds to the nutrient harvest index (i.e. the ratio between the nutrient content of grain and the nutrient content of shoot, no unit), HI is the harvest index (i.e. the ratio between the carbon content of grain and the carbon content of shoot, no unit),

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RSR is the root/shoot ratio (no unit) and $X_{\%,grain}$ and $X_{\%,root}$ are nutrient concentrations (kg(N or P)/kgC) for grain and root, respectively. Kvakić et al. (2018) has shown that a

250   XHI-based method provides similar demand estimates compared with others based on the nutrient concentration of all plant organs or QUEFTS (Sattari et al., 2014). The definition of the parameters used in Eq.12 (XHI, HI, RSR, $X_{\%,grain}$, $X_{\%,root}$) is based on nutrient and C biomass of different plant organs. These definitions as well as values used in the study are given in Table S2. Details about the Eq.12 are given in Text S3.

255   The potential yield (Y_{pot}) is provided by Mueller et al. (2012) in tons of dry matter per hectare. In Mueller et al. (2012), the world grid-cells are divided into climate bins, defined by different combinations of growing degree days and amount of yearly precipitation; and within a climate bin, the potential yield is defined as the area-weighted 95th percentile of the observed yields.

260

The supply of P (S_P, in kgP/ha/yr) corresponds to the sum of a potential root uptake and a prescribed fraction (called α) of the inorganic content of total P fertilizer applied in the year considered Kvakić et al. (2018). The potential root uptake is determined by soil P availability and monthly root length density, following some assumptions about P

265   diffusion in soil (Text S4). Soil P availability is derived from the current global distribution of soil P, as in Kvakić et al. (2018). The global distribution of soil P was determined by combining information on farming practices, soil P dynamics, soil biogeochemical background, climate effect on soil P dynamics, etc., as well as the past variation of some of these drivers (Ringeval et al., 2017). Thus, we explicitly considered the soil P legacy

270   effect, as it has been shown to be an important process (Ringeval et al., 2014; Sattari et al., 2012). Root characteristics parameters, root biomass at harvest (derived from Y_{pot}, RSR and HI) and seasonality in root biomass (computed by 0 and 1 and derived from

simulations of one global gridded crop model, LPJmL (von Bloh et al., 2018)) were combined to compute monthly root length density (Text S4). As in Kvakić et al. (2018),

275   we assumed that a fraction of the applied fertilizer P is directly available to the plant in the same growing season, thus bypassing the P diffusion pathway.

Following Bouwman et al. (2017), the supply of N is approached by the soil N input of the year considered (chemical and organic fertilizer, atmospheric deposition and fixation) minus losses corresponding to NH_3 volatilization. Datasets were provided by Bouwman

280   et al. (2011). Except in few recent studies (e.g. ten Berge et al. (2019) that focuses on sub-Saharan Africa), N applied in previous years is generally neglected due to the higher lability of N than P. We follow the same assumption as it is common in global modelling approaches (Bouwman et al., 2017; Conant et al., 2013; Lassaletta et al., 2014). Mineralization of soil organic N was also neglected as under steady state conditions it is

285   expected to be compensated by N immobilisation in soil microbial biomass.

Each term (S_N, D_N, S_P, D_P) is spatially explicit at half-degree resolution. An uncertainty related to each term has been considered (Text S5). Maize, rice and wheat are considered in this study (see the crop-dependent terms in Table S1) and the ratios computed are

290   representative of the year 2000. Only grid-cells for which R_P and R_N could be computed are considered, which determines the crop area and the global crop production considered in our study (Table S3). In the Main Text, a specific focus is made on maize because it is the most widespread across latitudes. Caveats of our approach are discussed in Section 4.

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3.2. Effects of formalism choice on global NP limitation

Spatial distributions of R_N, R_P as well as R_{NP} computed with both formalisms are described and discussed in Text S6. The relationship between R_{NP} and actual yield gap

300 provided by statistical approaches (Y_{real}/Y_{pot}, with Y_{real} being the actual yield) has been investigated at country scale (Text S7).

The effect of formalism choice on the global values of R_{NP}, ΔR_N and ΔR_P depends on the distribution of grid-cells in the (R_N, R_P) space (grey dots in Fig. 2c,f,i). Even though significant, the difference between LM and MH in global R_{NP} is small (Table 2). This is

305 explained by a small number of grid-cells (~2%) characterized by conditions that maximize the difference between the LM and MH mathematical formulations (i.e. comparable R_N~R_P and both within [0.25-0.75], see above). Finally, ~55% of the grid-cells are characterized by a difference LM − MH which is smaller than the uncertainty computed with a given formalism (LM or MH).

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The global averages of ΔR computed with MH (ΔR_N=0.44±0.00, ΔR_P=0.30±0.01) are larger than those computed with LM (ΔR_N=0.37±0.00, ΔR_P=0.25±0.01). It was analytically shown (Fig. 2) that the LM − MH difference of ΔR_N is maximal for a combination of small R_N and medium R_P, as encountered in the centre of the USA (Text S6 and Fig. S1). Large

315 differences are also noticeable in regions with high limitations of both nutrients, such as the Western Russian Federation and Ukraine.

3.3. Occurrence of Harpole categories

320 We computed the occurrence of each Harpole category by using conditions on R_N and R_P described in Table 1. We checked that these occurrences are equal to the values found when: numerical fertilization experiments are performed, R_{NP} are computed for each

experiment (Eq.7-8) and Eq.9-11 are then applied. Increase of N and P supply (A_N and A_P) in fertilization experiments are here equal to 30kgN/ha/yr and 5kgP/ha/yr, respectively

325 and are spatially homogeneous for all cropland around the World.

With the formalism MH, we found that true co-limitation occurs in 41.7±0.6 % of the global crop area for maize, via independent co-limitation (category B in Table 1). This category is found in the USA, South America, the Western Russian Federation and

330 Ukraine (Fig. 4a). As showed theoretically, to belong to that category a crop has to be characterized by both R_N and R_P in]0,1[. In our simulations, these conditions occur for ~42% of the maize crop area.

Synergistic co-limitation alone (categories C and D) occurs for 6.7±0.3 % of the global

335 maize crop area and this is only explained by serial limitation N (category C, dark blue in Fig. 4a): no serial limitation P was found in our numerical application. This can be explained by the fact that R_P (contrary to R_N) is never null in our simulations because of the soil P legacy taken into account in our approach (Ringeval et al., 2017). This also prevents simultaneous co-limitation (A) from being found. The occurrence of co-

340 limitation at the global scale varies between crops (41.7±0.6 % for maize, 32.5±0.4 % for wheat and 18.7±0.8 % for rice, not shown). Except for few regions (e.g. India), grid-cells where the three crops are grown belong to the same limitation category for all crops (not shown): the difference in occurrence of co-limitation between crops is mainly explained by the crop-specific global distribution.

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As theory shows (Text S1), the formalism LM cannot represent true co-limitation, except in the very specific category A (i.e. $R_P=R_N\neq1$), which is never encountered in our study

(Fig. 4b and Table 1). We found that synergistic co-limitation alone (categories C and D) can occur in more than 15% of the global maize area with LM. However, this number is

350   sensitive to the amount of N and P added in the fertilization experiments (called respectively A_N and A_P in Fig. 1). E.g. a cropland which is initially P-limited is classified in the category D if the amount of P added (A_P) is sufficient to remove the P limitation (i.e. the cropland becomes N limited); otherwise, it belongs to the category F (Table 1).

355

4. Discussion

Previous studies estimating the occurrence of co-limitation in natural ecosystems were based on fertilization experiments performed around the World and provide some

360   insights into the best way to represent the NP interaction (Elser et al., 2007; Harpole et al., 2011). Studies reviewing such experiments (characterized by a single application of nutrient) are not available for cropland, so we chose another strategy by computing the occurrence of co-limitation for each interaction formalism. Our work also clarifies the mathematical conditions in terms of supply/demand ratios required to place an

365   ecosystem into a category of nutrient limitation, as defined by Harpole et al. (2011). In particular, we found that synergistic co-limitation can occur with Liebig's law of the minimum under certain conditions that are functions of the amount of N and P added in fertilization experiments, as already suggested by Ågren et al. (2012). We found that, if multiple limitation hypothesis is the most appropriate way to represent nutrient

370   interaction, co-limitation should occur for ~50% of the maize crop area (42% of true and synergistic co-limitation + 7% for synergistic alone co-limitation). The percentage of true co-limitations found here is higher than those reported for natural ecosystems in Harpole et al. (2011) (28%) but similar to values found in Augusto et al. (2017) (42%). However, these previous figures should be compared with caution as they were not

375   obtained with the same methodology. It is also worth noting that change in the plant community can occur consecutively to fertilizer application in natural ecosystems, which does not happen in cropland systems as they are mostly single crop. Experiments with single increase of fertilizer in cropland have to be selected and then compiled. Such meta-analysis would tell us if co-limitation is really common in croplands, suggesting e.g.

380   that farming practices tend to promote co-limitation. On the contrary, the absence of

such co-limitation would suggest that human perturbation of nutrient cycles pushes the crop plant outside of its adaptation capacity.

The occurrences of different limitation categories are a function of the spatial distribution of R_N and R_P, as posited by our theoretical framework. However, these maps are prone to uncertainty due to simplifications in our modeling approach.

First, we recognize that the use of constant parameters at the global scale in the computation of supply and demand is too simple (Sadras, 2006) in particular with respect to plant adjustments to nutrient limitations (Colomb et al., 2007) which are susceptible to modify nutrient organ concentrations. However, the aim of our study is to assess nutrient limitation and thus, we used organ concentrations derived from field experiments in stressed conditions (Van Duivenbooden (1992) and Table S2). Global changes are also very likely modifying yield and grain composition (e.g. Long et al., 2006; Müller et al., 2014) and this effect was not considered in our study which does not simulate temporal changes in nutrient limitation. Besides, it is worth nothing that considering grid-cells independently in our uncertainty analysis (Text S5) made these parameters artificially vary in space.

We used potential yield provided by statistical methods based on maximum attainable yield within climate bins (Mueller et al. 2012) but such approaches have difficulty distinguishing irrigated and rainfed crops and thus, the here used Y_{pot} could be in fact water-limited in some places (van Ittersum et al., 2013b). Updates to the statistical methodology are ongoing to improve the separation between water-limited and irrigated yield potential (Mueller, personal comm.).

We also did not consider some agronomic managements that are susceptible to modulate nutrient limitation. In particular, we did not consider cultivar diversity across

World regions. Such diversity is susceptible to modify parameters (in particular, HI) which are considered constant in space in our approach. However, cultivar diversity is difficult to consider at the global scale and up to now, it was mainly investigated through spatial variability in phenological development (van Bussel et al., 2015). To a much lesser extent,

410 the effect of cultivar diversity on allocation (e.g. through variability in harvest index, susceptible to modify the here compute nutrient demand) was taken into account (Folberth et al., 2016). Also, some effects of crop rotation on nutrient limitation were not considered in our study. E.g. crop rotation can modulate the soil P availability because of difference in the strategies developed for enhancing nutrient acquisition

415 among crops (Redel et al., 2007) and this effect was neglected here. However, N fixation by leguminous that can be incorporated within the crop rotation with cereals was indirectly considered in our study: our computation of N supply was not a function of crop (Table S1) and thus, the N supply budget encompasses an term for N fixation by leguminous occurring in the same grid-cell as cereals (Bouwman et al., 2011).

420 In our approach, the limitation of potential yield is computed by considering current farming practices to derive the supply. Current practices could be influenced by other limiting factors: e.g. if a crop is water limited, farmers can adapt their practices and reduce their nutrient applications accordingly. Sensitivity tests where the demand would be derived from actual yield (instead of potential yield, as in the Main Text) could help in

425 the determination of areas where other limiting factors might play a role (Fig. S2). The next step is to consider more limiting factors together.

Our computation of ΔR_N and ΔR_P, i.e. the increase in R_N and R_P required to increase R_{NP} is based on the minimum "physiological" needs for plants. Behind the multiple limitation's mathematical formalism, an increase in R_{NP} can be achieved for different combinations

430 of increases in N and P (i.e. for different couples (ΔR_N, ΔR_P)): despite non-substitution at

the molecular or cellular level (Sinclair & Park, 1993), one element can partly compensate for the other at the plant scale. Here, we considered only one couple (Fig. 3), while external variables such as the price or the ease of access to fertilizers will also influence the farmer's choice and could make him/her select another NP combination. This should

435   be taken into account in future attempts to make link with scenarios of nutrient management and policy more straightforward. ΔR_N and ΔR_P could be translated to increase in soil supply by considering nutrient demand in each grid-cell. However such change in supply cannot be easily translated into a change in fertilizer, since our supply estimates take into account some processes occurring after the fertilizer application: for

440   P, we take into account the dynamics of P in soil (diffusion and root uptake) while for N, we allow for NH_3 volatilization. Our nutrient requirement calculation is driven solely by nutrient limitation, independently of yield gap, contrary to previous estimates based on: soil quality indicators (with no distinction between N and P) (Fischer et al., 2012; Pradhan et al., 2015), statistical relationships between fertilizer application and yield (Mueller et

445   al., 2012) or "N uptake gaps" based on yield gap and minimal/maximal values of the physiological N efficiency in aboveground biomass derived from the QUEFTS model (ten Berge et al., 2019; Schils et al., 2018). More generally, our nutrient limitation is not straight connected to the yield gap because the actual yield is not used in our computation.

450   Our theoretical analysis has also few caveats. In particular, we assumed a linear relationship between R_{NP} and the productivity of each experiment (Eq. 9-11). As underlined in the method section, our conclusions are still valid if we assumed a linear relationship up to a value *thresh* if *thresh* replaces 1 in the definition categories given in Table 1. The value *thresh* is nevertheless theoretical because the calculated nutrient

455   limitation (R_N, R_P, R_{NP}) has no physical meaning and is disconnected from physical

measure of e.g. soil P content (Olsen P, etc.). The fact that the transition between linear and plateau regimes occurs for the same R_{NP} (1 or *thresh*) globally should be an acceptable assumption as we took into account the spatial variation in soil properties to compute the soil nutrient supply.

460

Two formalisms are usually used to characterize multiple element limitation: in Liebig's law of the minimum, plants are generally limited by one nutrient at a time, while plants are generally co-limited in a multiple limitation hypothesis. Our study reveals that the choice of the formalism has only a marginal effect on the estimate of current global NP

465   limitation (R_{NP}) for the cereals considered. This result is explained by the fraction of grid-cells in our approach that is within the area of the R_N vs R_P space that maximizes the difference between the two formalisms. The formalism choice has a bigger effect on the increases in R_N and R_P required at the same time to alleviate the NP limitation. Because of very different theoretical founding principles behind each formalism, the use of one

470   or other formalism leads to very different estimates of occurrence of co-limitation in cropland. As mentioned earlier, Liebig's law of minimum or multiple limitation hypothesis could be considered as macro-properties that reflect the same processes of plant adjustments but, depending on the context, plant adjustments lead to one or the other formalism (Ågren et al., 2012). It was also stipulated (Farrior et al., 2013) that

475   plants can be limited by only one resource at a time, but that the integration of the different limitations in time makes the plants limited by several resources at the scale of the growing season. In our point of view, the use of mechanistic models, through the representation of dynamic allocation (e.g. through a cost-based approach (Franklin et al., 2012)) and floating C:nutrient ratios (Zaehle and Dalmonech, 2011) would allow the

480   explicit consideration of some plant adjustments, preventing the need to choose

between formalisms.

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Tables

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Table 1 (two pages). Nutrient limitation categories defined in Harpole et al. (2011) and occurrence for each crop in our modelling approach with MH formalism. Δpro_{+X} is the change in productivity following the application of +X (with X=N, P or NP) in fertilization experiments. In the 1st column, the y-axis defines ecosystem productivity and the dots

490 correspond to the different experiments (white: control, blue: after addition of P, red: after addition of N, magenta: after addition of NP). Each category is defined as function of i) the character null or non-null of Δpro_{+N} and Δpro_{+P} and ii) the relationship between Δpro_{+NP} and ($\Delta pro_{+N}+\Delta pro_{+P}$) (3th column). Synergistic co-limitation means that $\Delta pro_{+NP} > \Delta pro_{+N} + \Delta pro_{+P}$. The different categories (columns 1-3) are derived from

495 Harpole et al. (2011) while category B is restricted here to the "super-additive case" (subadditive or additive are neglected because they cannot happen in MH or LM, see Text S1).

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Long name of the category, letter used hereafter and figure	Co-limitation	Definition of the category	Analytic conditions required to be in that category for MH *	Occurrence for MH: % of global crop area (% of grid-cells)	Analytic conditions required to be in that category for LM	Occurrence for LM: % of global maize area (% of grid-cells)
Silmutaneous co-limitation A	True and synergistic	$\Delta pro_{+N}=0$ $\Delta pro_{+P}=0$ $\Delta pro_{+NP}>\Delta pro_{+N}+\Delta pro_{+P}$	$R_N=0$ and $R_P=0$	0.0±0.0 (0.0±0.0)	$R_P=R_N\neq1$	0.0±0.0 (0.0±0.0)
Independent co-limitation; super-additive B	True and synergistic	$\Delta pro_{+N}\neq0$ $\Delta pro_{+P}\neq0$ $\Delta pro_{+NP}>\Delta pro_{+N}+\Delta pro_{+P}$	R_N in]0,1[and R_P in]0,1[	41.7±0.6 (35.9±0.3)	Cannot occur	0.0±0.0 (0.0±0.0)
Serial limitation N C	Synergistic	$\Delta pro_{+N}\neq0$ $\Delta pro_{+P}=0$ $\Delta pro_{+NP}>\Delta pro_{+N}+\Delta pro_{+P}$	$R_N=0$ and R_P in]0,1[	6.7±0.3 (8.9±0.2)	$R_N<R_P$ and $R_P(E_2)<R_N(E_2)$ **	6.3±0.4 (9.4±0.2)
Serial limitation P D	Synergistic	$\Delta pro_{+N}=0$ $\Delta pro_{+P}\neq0$ $\Delta pro_{+NP}>\Delta pro_{+N}+\Delta pro_{+P}$	R_N in]0,1[and $R_P=0$	0.0±0.0 (0.0±0.0)	$R_P<R_N$ and $R_N(E_3)<R_P(E_3)$	9.5±0.5 (10.6±0.3)
Single-resource response N E	No	$\Delta pro_{+N}\neq0$ $\Delta pro_{+P}=0$ $\Delta pro_{+NP}=\Delta pro_{+N}+\Delta pro_{+P}$	R_N in [0,1[and $R_P=1$	37.1±0.6 (46.0±0.4)	$R_N<R_P$ and $R_P(E_2)\geq R_N(E_2)$ ***	48.4±0.8 (60.7±0.5)
Single-resource response P F	No	$\Delta pro_{+N}=0$ $\Delta pro_{+P}\neq0$ $\Delta pro_{+NP}=\Delta pro_{+N}+\Delta pro_{+P}$	$R_N=1$ and R_P in [0,1[	2.7±0.3 (1.3±0.1)	$R_P<R_N$ and $R_N(E_3)\geq R_P(E_3)$	24.0±0.9 (11.5±0.5)

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No response G	No	$\Delta pro_{+N} = 0$ $\Delta pro_{+P} = 0$ $\Delta pro_{+NP} = \Delta pro_{+N} + \Delta pro_{+P}$	$R_N = 1$ and $R_P = 1$	11.8±0.3 (7.8±0.1)	$R_N = 1$ and $R_P = 1$	11.8±0.3 (7.8±0.1)

*a reversed bracket used in an interval means that the corresponding endpoint is excluded
505   from the interval; e.g. R in [0,1[means 0≤R<1.
** corresponds to "E_1: N-limited and E_2: P-limited"
*** corresponds to "E_1: N-limited and (E_2: N-limited or NP-limited or not limited at all)"

510 **Table 2.** Global values (± one standard-deviation) of the supply/demand ratio (R) for N, P or NP.

Nutrient(s)		N	P	NP (formalism LM)	NP (formalism MH)
Ratio (R)	Maize	0.42 ± 0.00	0.62 ± 0.01	0.32 ± 0.00	0.29 ± 0.00
	Wheat	0.49 ± 0.00	0.73 ± 0.00	0.43 ± 0.00	0.40 ± 0.00
	Rice	0.70± 0.00	0.79 ± 0.01	0.60 ± 0.01	0.59 ± 0.01

Figures
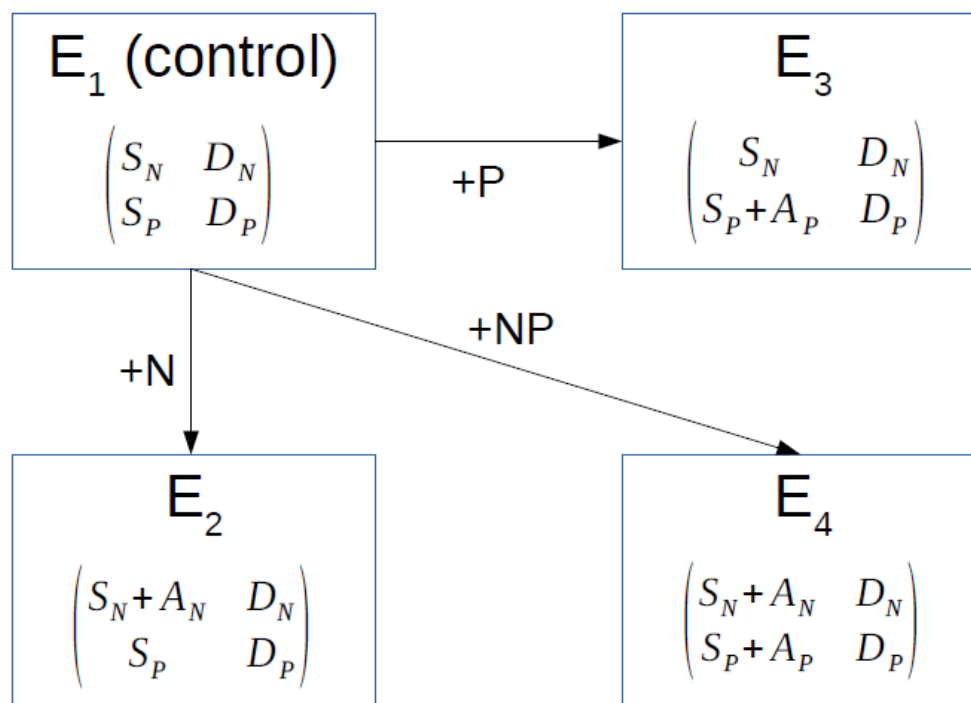
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Figure 1. Fertilization experiments. The different experiments (E_1-E_4) vary as function of their supply of N (S_N or S_N+A_N) and P (S_P or S_P+A_P).

520
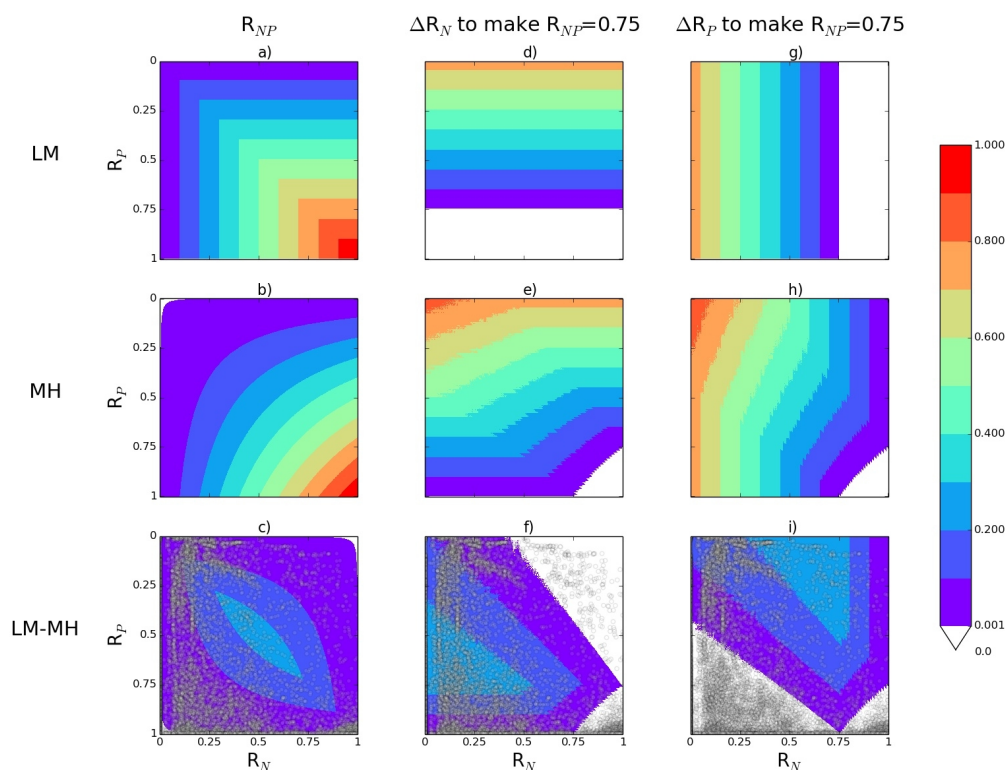
Figure 2. R_{NP}, ΔR_N and ΔR_P for any values of R_P (x-axis) and R_N (y-axis). Each variable is provided for the two formalisms (LM and MH) as well as for the difference LM-MH. Grey
525 transparent dots in panels c,f,i correspond to all grid-cells considered for maize in our modelling approach.
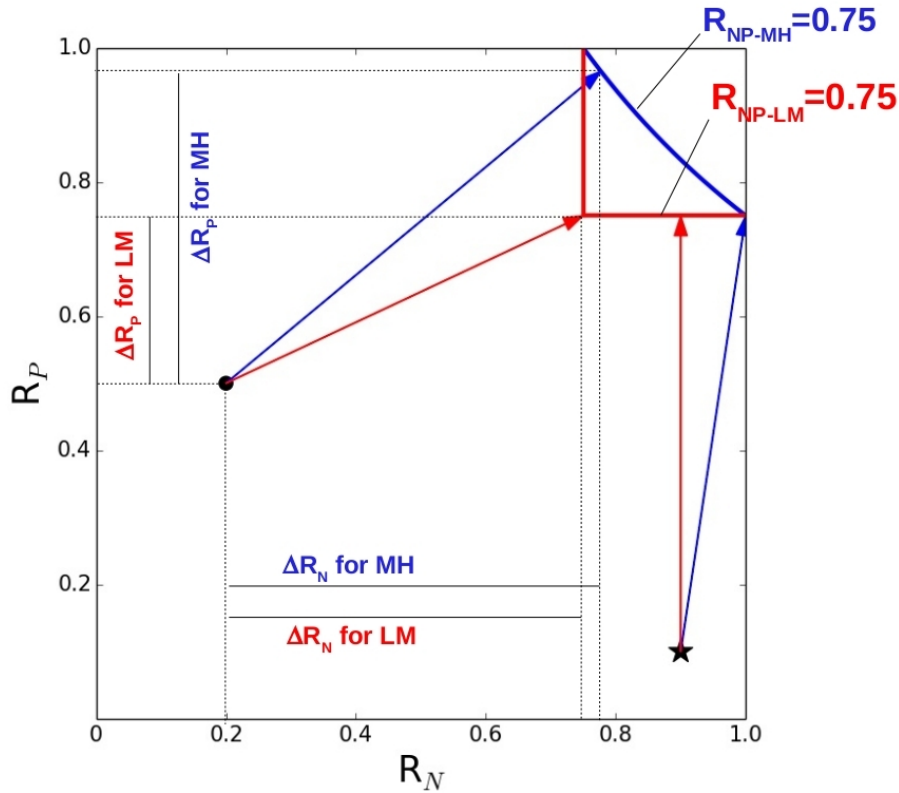
Figure 3. Schematic representation of the computation of (ΔR_N, ΔR_P). A given grid-cell is
defined by its (R_N, R_P) in the plan characterized by the base $(\vec{R}_N, \vec{R}_P)$. For a given grid-
cell and a given formalism, we called $\vec{u}$ the shortest vector linking (R_N, R_P) and the
curve (or segments) defining R_{NP}=0.75. We called x and y the compounds of $\vec{u}$ in the
basis $(\vec{R}_N, \vec{R}_P)$, i.e. $\vec{u}=\begin{pmatrix} x \\ y \end{pmatrix}$. We defined $\Delta R_N = max(0, x)$ and $\Delta R_P = max(0, y)$. In
the above figure, two grid-cells are provided as an example: (R_N=0.2; R_P=0.5) for the black
dot, and (R_N=0.9; R_P=0.1) for the black star. The formalism of interaction defines the
(R_N,R_P) couples that make R_{NP}=0.75: the blue curve defines R_{NP}=0.75 for MH while the two
orthogonal red segments define R_{NP}=0.75 for LM. $\vec{u}$ is provided for each grid-cell and
each formalism (blue arrow for MH ; red arrow for LM). We explicitly plotted the ΔR_N and
ΔR_P for the black dot and the two formalisms (solid black lines). Note that for the grid-
cell symbolized by the black star, $\Delta R_N = 0$ for LM.
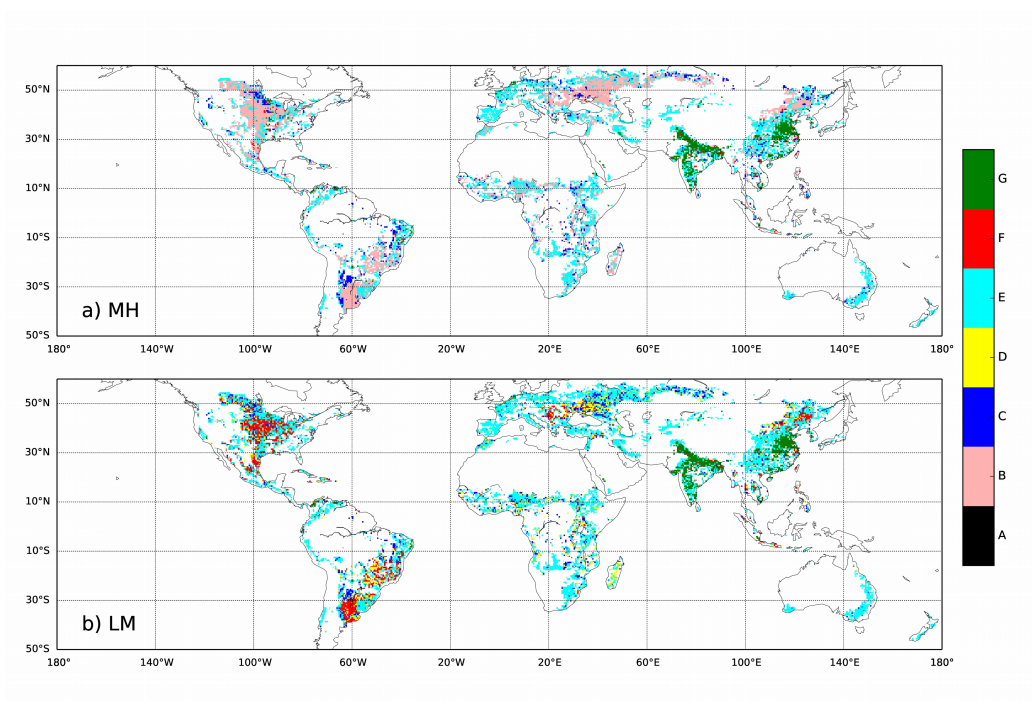
Figure 4. Spatial distribution of the categories defined in Table 1 and in Harpole et al. (2011) for MH (a) and LM (b) for maize. For LM, whether one grid-cell belongs either to category C (dark blue) or to category E (cyan) depends on the value of A_N. The same reasoning applies for categories D (yellow) and F (red) with A_P.

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Data and Code availability:

550 Files corresponding to supply and demand for N and P (variables called S_N, S_P, D_N, D_P in the manuscript) are made available (Ringeval et al. ,2019) on the following link.
Computer scripts written by the authors to generate and manipulate files of supply and demand for N and P are available upon request to the corresponding author.

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Author contribution:

B.R conceived the project; B.R. and M.K. performed the computations; B.R, S.P and L.A analysed the results; N.D.M, C.M, T.A.M.P and X.W. provided datasets and their expertise on these datasets; B.R, M.K, L.A, P.C, D.G, N.D.M, C.M, T.N, T.A.M.P, N.V, S.P wrote the article.

Competing interests:

The authors declare no conflict of interest.