

BG3.25 vPICO display materials

Carbon storage in phosphorus limited grasslands may decline in response to elevated nitrogen deposition: a long-term field manipulation and modelling study

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Manuscript details

- The following work is freely and openly available as a preprint manuscript in Biogeosciences:
 - Taylor, C.R., Janes-Bassett, V., Phoenix, G., Keane, B., Hartley, I.P., Davies, J.A.C., (2020). Carbon storage in phosphorus limited grasslands may decline in response to elevated nitrogen deposition: a long-term field manipulation and modelling study. *Biogeosci. Discuss*, 1–37, DOI: 10.5194/bg-2020-392
- This manuscript is currently under review and has received some changes since initial submission:
 - More focus on organic P cycling rather than consequences for carbon storage
 - Title updated to: ‘Organic phosphorus cycling may control grassland responses to nitrogen deposition: a long-term field manipulation and modelling study’
 - We highlight that the two grasslands are both P-limited and the key contrasts are in their soil conditions rather than limiting nutrient
- Data will be deposited and made publicly available through NERC’s EIDC when (or if) the final manuscript is published – currently it is available in the supplementary info document

Introduction – Nitrogen deposition

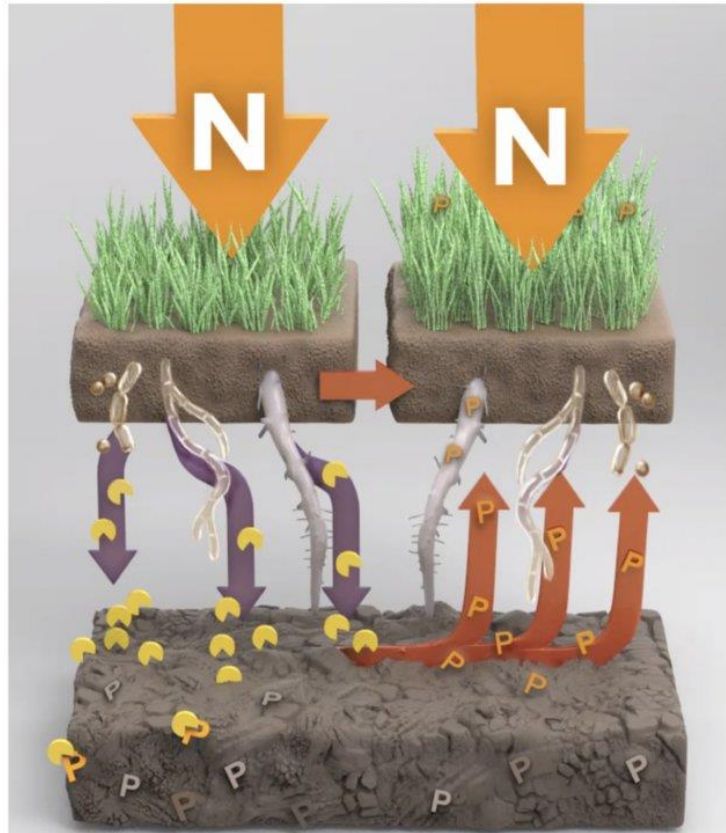
- Many ecosystems around the world, particularly those in young soils, are limited by nitrogen (N)
- Much of these N-limited ecosystems occur in regions experiencing high rates of anthropogenic N deposition, such as North America and North West Europe
- N deposition has a wide range of negative impacts on ecosystems, but when it occurs on N-limited systems, it can stimulate productivity and enhance ecosystem carbon stocks¹
 - It can do so by increasing carbon input belowground^{1,2}, combined with reducing the rate at which soil organic matter decomposes³

Introduction – Phosphorus limitation

- However, many ecosystems in temperate regions aren't N-limited, instead being co-limited by N and phosphorus (P) or solely limited by P^4
- Such forms of nutrient limitation are globally widespread and may be increasing in prevalence and severity as N availability increases but P does not, increasing the stoichiometric demand for P^5

Introduction – Organic P and N deposition

- Recent research⁶ has suggested that in systems that have experienced prolonged periods of N deposition, plants may be able to utilise additional N resources to acquire P
- They may do so by investing N into phosphorus-acquiring enzymes that cleave P from organic forms within the soil⁶
- We know much less about how P-limited ecosystems may respond to N deposition and how it may affect soil C, N and P cycling, or what determines a P-limited ecosystem's response



Chen *et al.* (2020), *Global Change Biology*,
26, <https://doi.org/10.1111/gcb.15218>

- This figure from Chen *et al.*'s recent meta-analysis summarises this very nicely
- Increased N availability from prolonged deposition allows plants to invest more in P cycling enzymes that cleave P from organic sources
- Over time, accumulated acquisition of organic P is sufficient to overcome P limitation and stimulate productivity
- We wanted to examine this process within the N14CP model

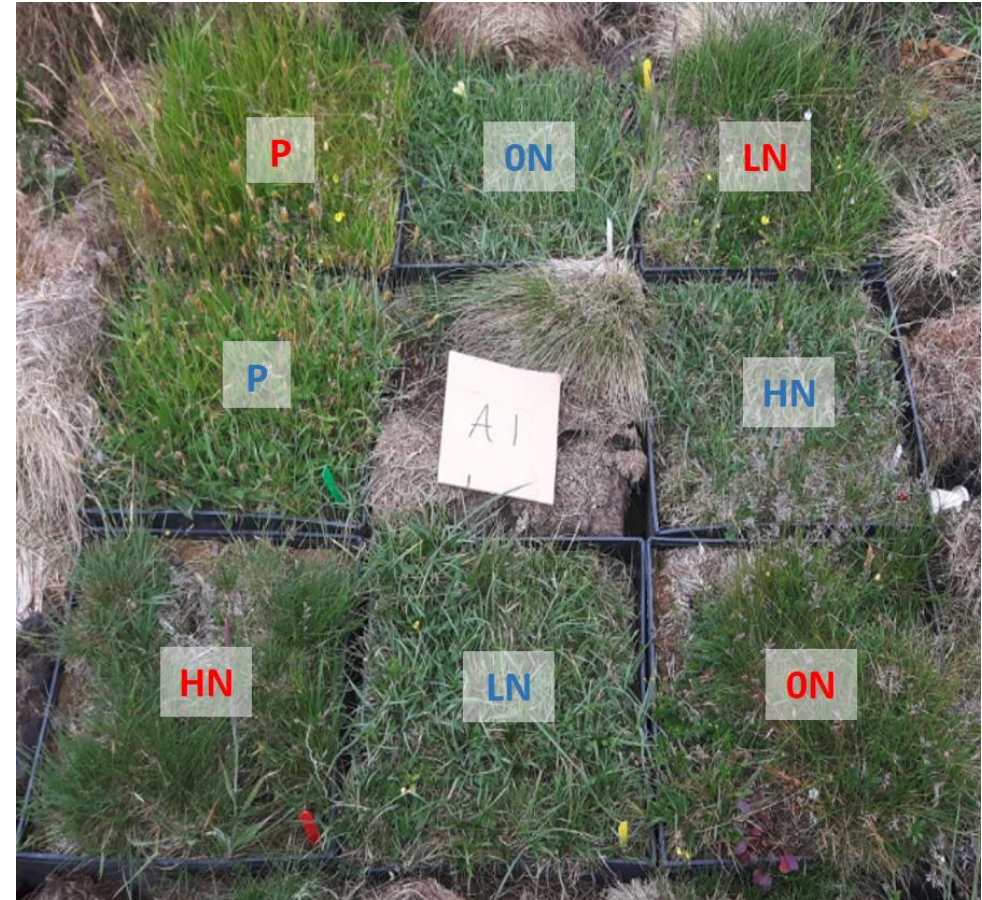
Aims

- In this work, we aimed to investigate how two P-limited ecosystems may have responded to chronic N deposition and experimental nutrient manipulation
 - What may the consequences have been for ecosystem C, N and P stocks?
 - What role may organic P access have in determining these responses?
 - How might this response differ between grasslands?
- We do so by combining data from a long-term nutrient manipulation experiment with an integrated C-N-P cycling model (N14CP)
- We use the experimental data to drive the model and to calibrate two P cycling conditions, including organic P uptake by plants, to investigate the potential role of organic P cycling under conditions of elevated N availability

Methods – Wardlow grasslands (field site description)

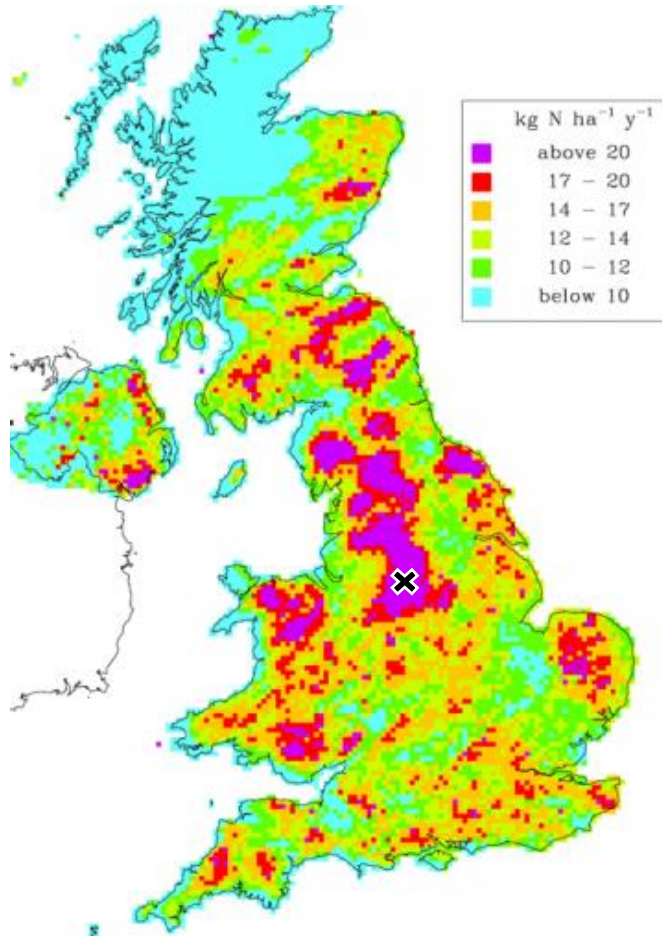
- The two grasslands (one acidic, the other limestone) are from the Wardlow Hay Cop long-term experiment which has been running continually since 1995:
 - <https://www.ecologicalcontinuitytrust.org/wardlow>
- The grasslands are predominantly P-limited though other forms of nutrient limitation are occasionally observed
- The grasslands are located in the Peak District National Park and have been exposed to some of the highest rates of background N deposition in the UK – at the onset of the experiment, this was in excess of $3 \text{ g N m}^{-2} \text{ yr}^{-1}$
- These grasslands have been experimentally manipulated to investigate the consequences of additional N loading from deposition (with two N treatments), and the alleviation of P limitation with a single P treatment
- These treatments are coded as such:
 - ON – distilled water control – background N deposition only
 - LN – ‘low nitrogen’ – $3.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ – an approximate doubling of background deposition
 - HN – ‘high nitrogen’ – $14 \text{ g N m}^{-2} \text{ yr}^{-1}$ – N loading equivalent to agricultural treatment
 - P – ‘phosphorus’ – $3.5 \text{ g P m}^{-2} \text{ yr}^{-1}$ – sufficient to alleviate P limitation

- An example of both grasslands and all nutrient treatments side-by-side in a separate experiment (PLACE*)
 - Blue are limestone and red acidic plots
 - In this work we use the original plots at Wardlow
- *Phosphorus limitation and carbon dioxide enrichment project:
- <https://www.researchgate.net/project/Phosphorus-limitation-and-ecosystem-responses-to-carbon-dioxide-enrichment-PLACE>



- This is the limestone grassland at Wardlow in the summer of 2018 during a prolonged drought period
- The benefits of the P treatment are highly visible despite the drought, where the treated plot is much greener and more productive





- Wardlow (marked by the X) is located in one of the most N-polluted parts of the UK and has been exposed to chronic and high levels of N deposition
- Map source: Centre for Ecology and Hydrology
<http://www.pollutantdeposition.ceh.ac.uk/pollutant-views>

- Nutrient treatments have been applied via a backpack sprayer monthly since 1995 and bimonthly since 2017
- The nutrient solutions are dissolved in distilled water as most deposition on these upland grasslands is in wet form
- The picture shows me applying nutrients to the acidic grassland at Wardlow



Methods – empirical data

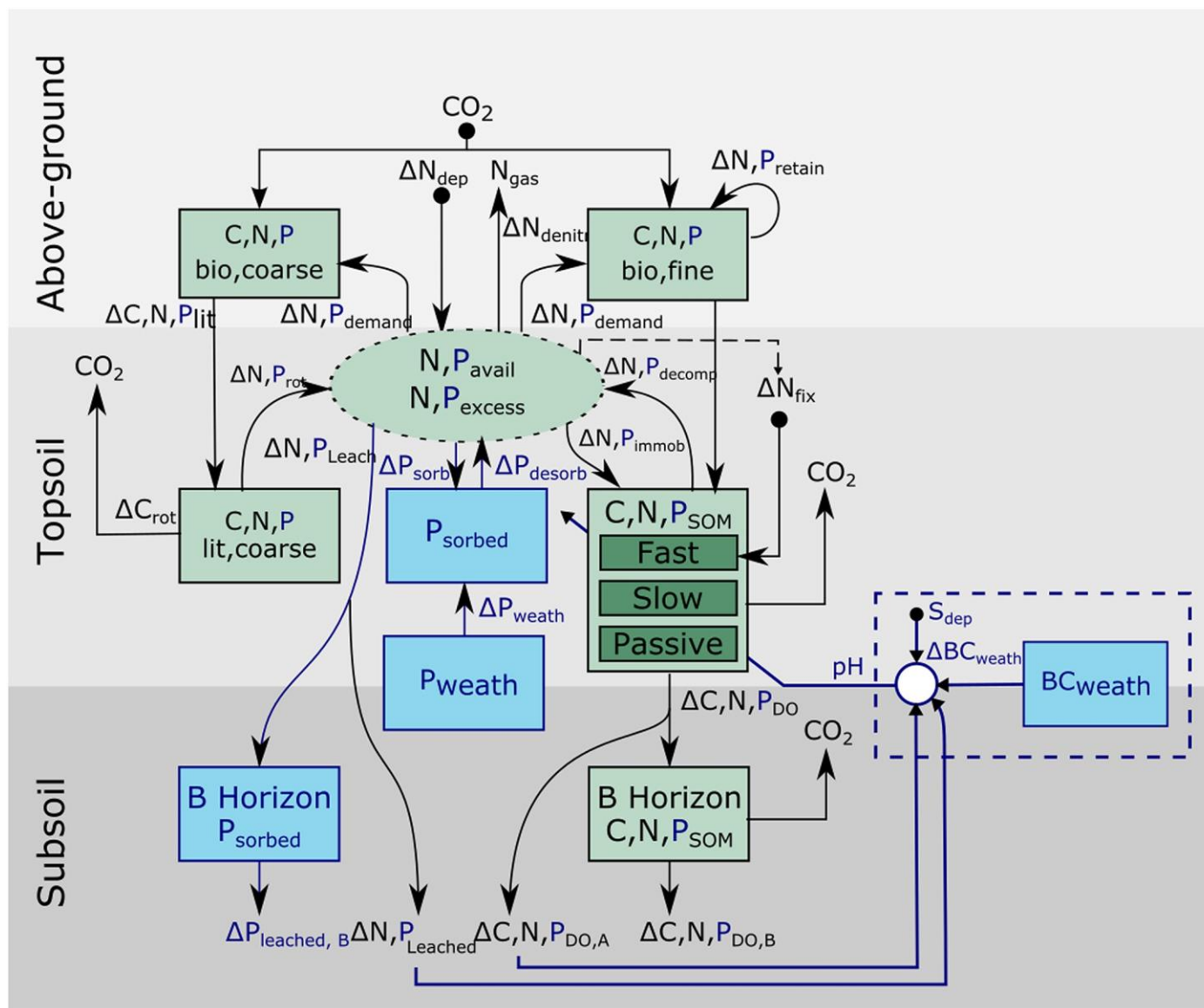
- We used data from these grasslands to simulate a similar nutrient manipulation experiment within N14CP, to better our understanding of P-limited ecosystems in high N environments, and to explore the function of organic P cleaving within the model
- In order to calibrate and later test the N14CP model, we needed to collect (or collate) empirical data from Wardlow
- Data were all converted into model-compatible stocks in g m^{-2} :
 - Calibration data:
 - Soil organic C – acid stripped soil samples, ran through mass spectrometer
 - Total soil N (assumed equivalent to organic N in the model) – collected alongside SOC
 - Total soil P (organic + sorbed P in model) – acquired from previous work⁷
 - Testing data:
 - Biomass carbon – assumed 50% of dry biomass harvest as carbon content⁸ – kept separate for assessment of model performance

- Soil organic C and soil total N were collected from all four nutrient treatments
- Soil samples were dried, ground, acid stripped (to remove inorganic C) and analysed in an isotope-ratio mass spectrometer to determine C and N content
- Bulk density was also collected to convert SOC and total N to stocks
- Total P data was used from a previous study at Wardlow by Horswill *et al.*
- Biomass data was used from the first year's harvest of the aforementioned PLACE project, prior to any CO₂ fumigation
 - It was assumed that half of the dry plant biomass was carbon content as in Chapin *et al.*



Methods – The N14CP model (in brief)

- N14CP is a mechanistic biogeochemical cycling model that simulates the flows and stocks (or pools) of C, N and P within temperate semi-natural ecosystems
- The model simulates the cycling between the atmosphere (including human nutrient input), biomass, topsoil, subsoil and leachate
- Movement of C, N and P is largely governed by stoichiometric demand which is determined on the basis of Liebig's law of the minimum for nutrient limitation
- The model spins up from the onset of the Holocene
- For the full model description, refer to Davies *et al.* (2016) (in reference list)
- The model schematic is presented on the next slide showing the different pools, and parameters that govern movement of C, N and P within the model



Methods – Simulating the experiment

- We collected input driver data from, or as close to Wardlow as possible, to run the model
 - N deposition data
 - Climate – temperature and precipitation
 - Land use / plant functional type history
 - Experimental nutrient manipulations – added to model in this work
- We then used the empirical soil C, N and P data to calibrate P cycling processes / conditions for each grassland
 - P_{Weath0}
 - An initial condition that determines the initially available weatherable inorganic P at soil formation – very important for simulating at the site scale with N14CP²
 - $P_{\text{CleaveMax}}$
 - The maximum amount of newly-cleaved organic P that can be taken up by plants – previous work with N14CP has suggested organic P cycling may be an important aspect of simulating low-P ecosystems⁹

- We used a cost function to determine which values to use
- Scaled by number of observations (no. of treatments for which data is available) to reduce weighting bias
- Combination of $P_{\text{CleaveMax}}$ and P_{Weath0} that reduced the F value the most for each grassland, while maintaining the general pattern in responses was used

$$F = \left(\frac{SAE[C_{SOM}]}{\bar{C}_{SOM,Obs}} \right) / C_n + \left(\frac{SAE[N_{SOM}]}{\bar{N}_{SOM,Obs}} \right) / N_n + \left(\frac{SAE[P_{Total}]}{\bar{P}_{Total,Obs}} \right) / P_n$$

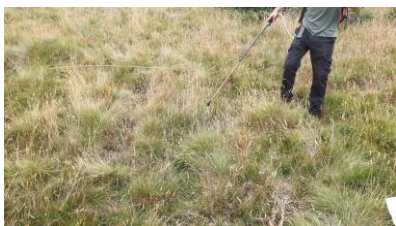
PFT history



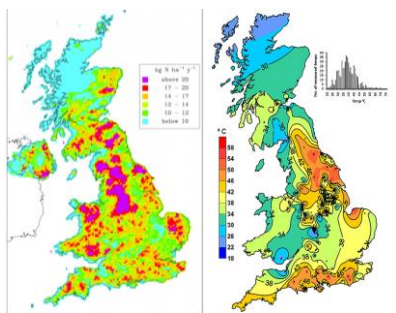
Land use (e.g. grazing)



Fertiliser application



Climate and deposition data

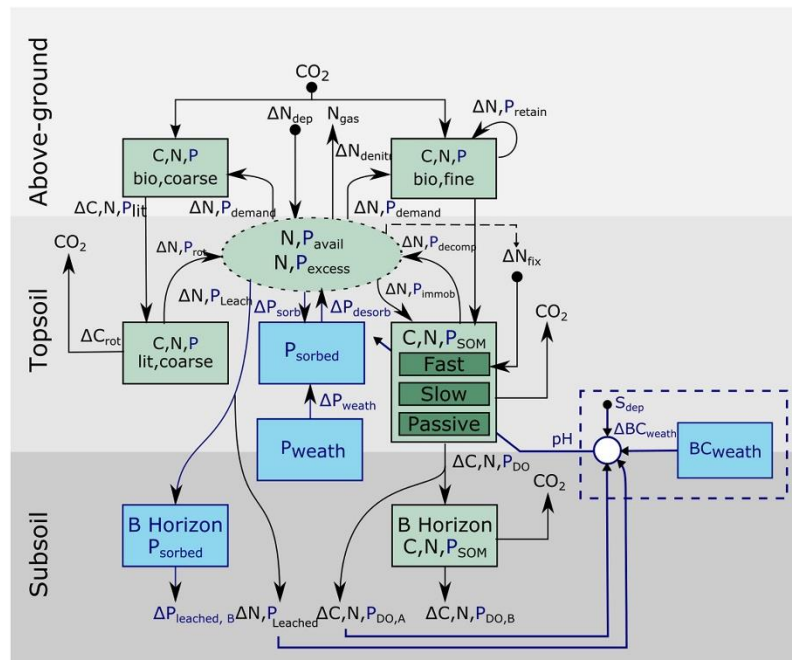


3

Grassland simulations

1

Input drivers



Calibrate initial conditions

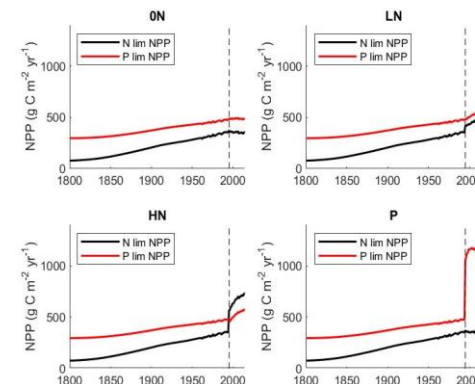
2

Weatherable P
supply - P_{weath0}

Organic P access -
 $P_{CleaveMax}$

4

Model outputs



5

Compare to observations

6

Model experiments

Results - content

- Model parameter selection
 - Results of the calibration to empirical data
- Model performance
 - An assessment of the model's ability to simulate the magnitude of empirical stocks and their pattern of responses to nutrient treatment
- Limiting nutrient through time
 - Nutrient-limited productivity through time (helps explain / contextualise responses)
- Time-series of C, N and P
 - How biomass C, SOC, SON and SOP have changed through time with N deposition and nutrient manipulation
- Grassland C, N and P budgets
 - A small mechanistic section to explore what pools have changed

Results – Model parameter selection



Grassland	$P_{\text{CleaveMax}}$ ($\text{g m}^{-2} \text{ season}^{-1}$)	P_{Weath0} (g m^{-2})
Acidic	0.316	150

- High $P_{\text{CleaveMax}}$ suggests that in order to simulate the acidic grassland, the model required access to large amounts of organic P
- Combined with a low P_{Weath0} value, which indicates low availability of inorganic forms of P, this suggests that organic P uptake is important for the modelled acidic grassland

Results – Model parameter selection

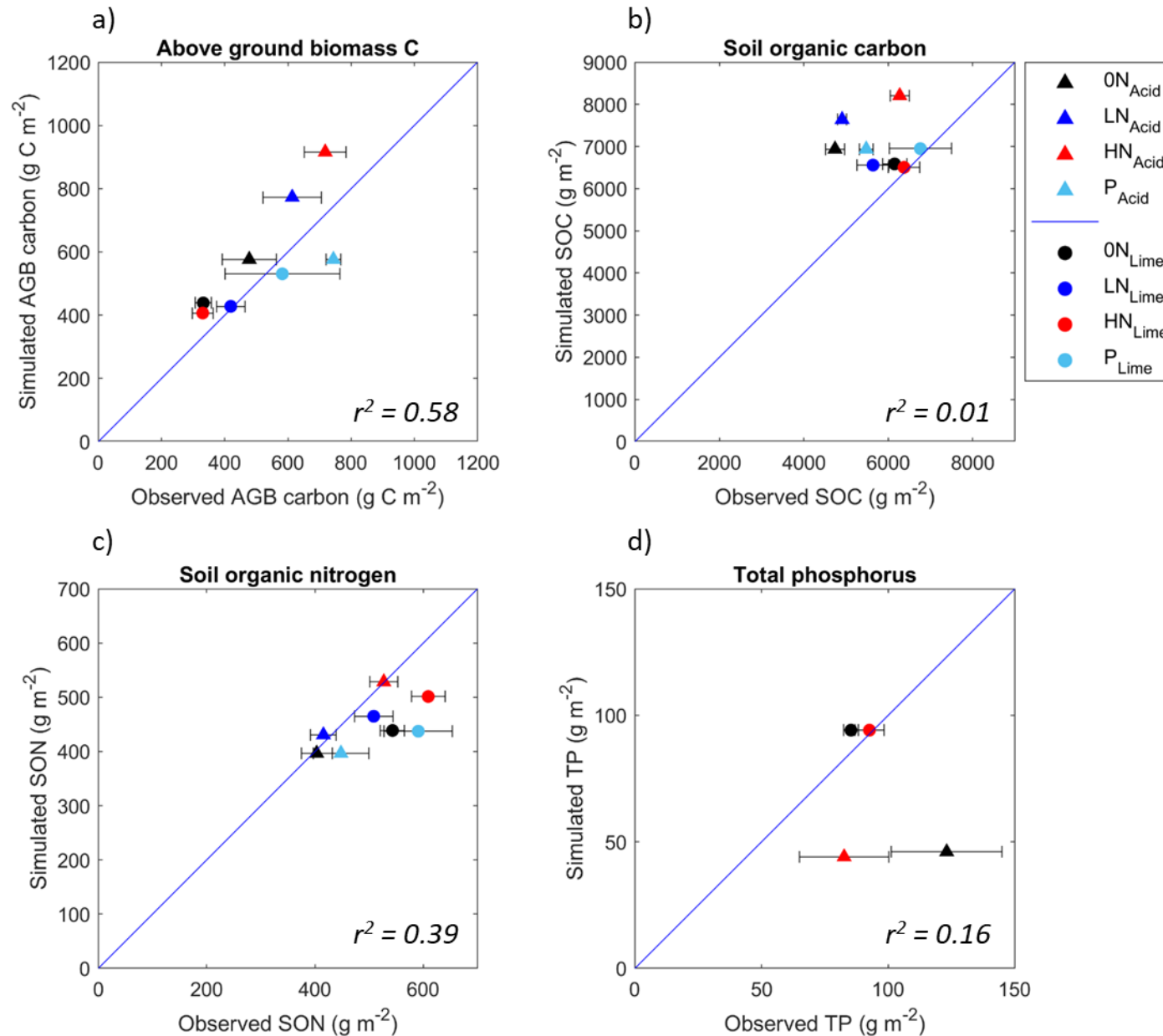


Grassland	$P_{\text{CleaveMax}}$ ($\text{g m}^{-2} \text{ season}^{-1}$)	P_{Weath0} (g m^{-2})
Acidic	0.316	150
Limestone	0.032	300

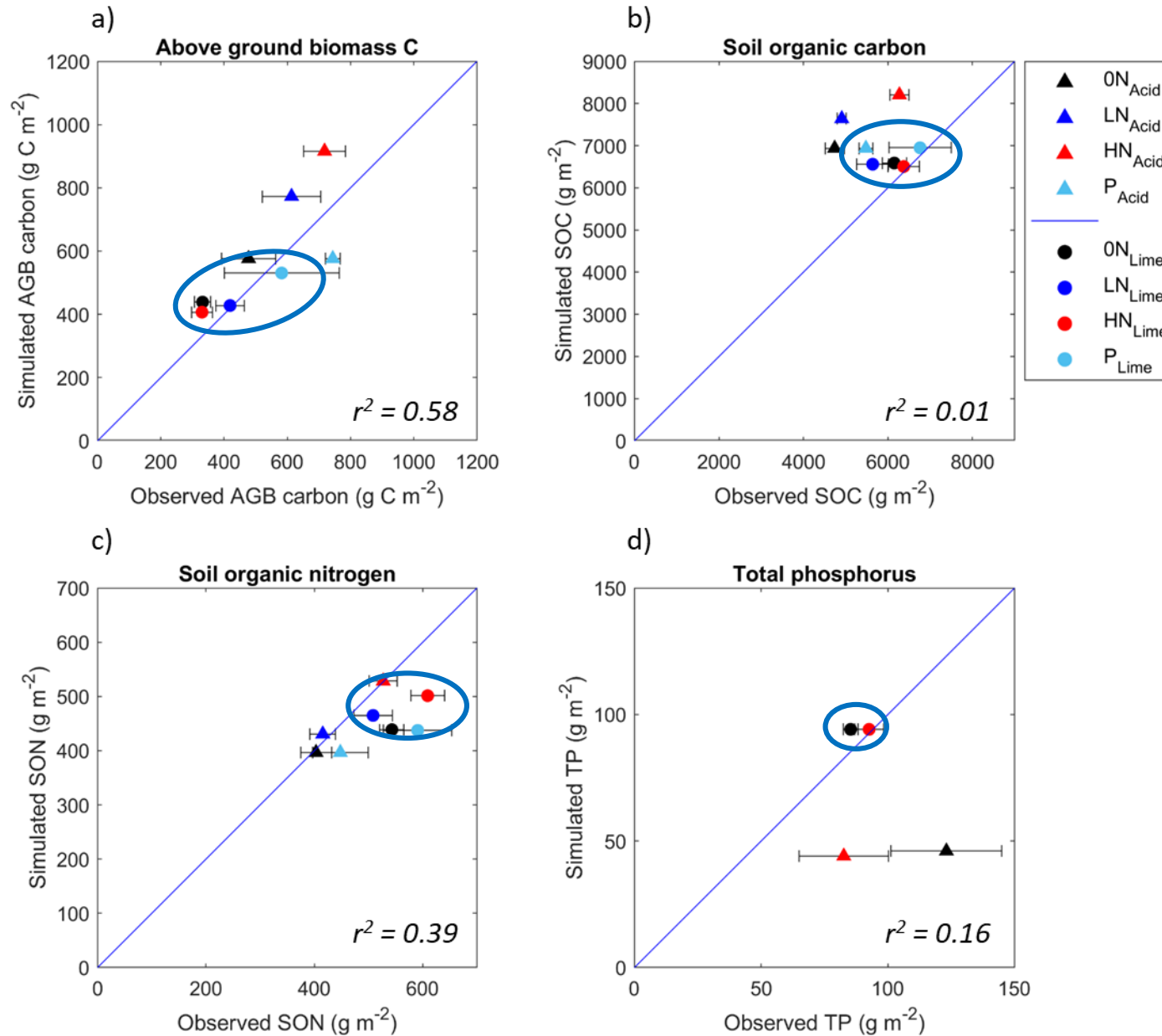
- The limestone grassland was less able to access P from the soil organic P pool
- Inorganic P formed a larger proportion of total soil P than in the acidic grassland

Results – Model performance

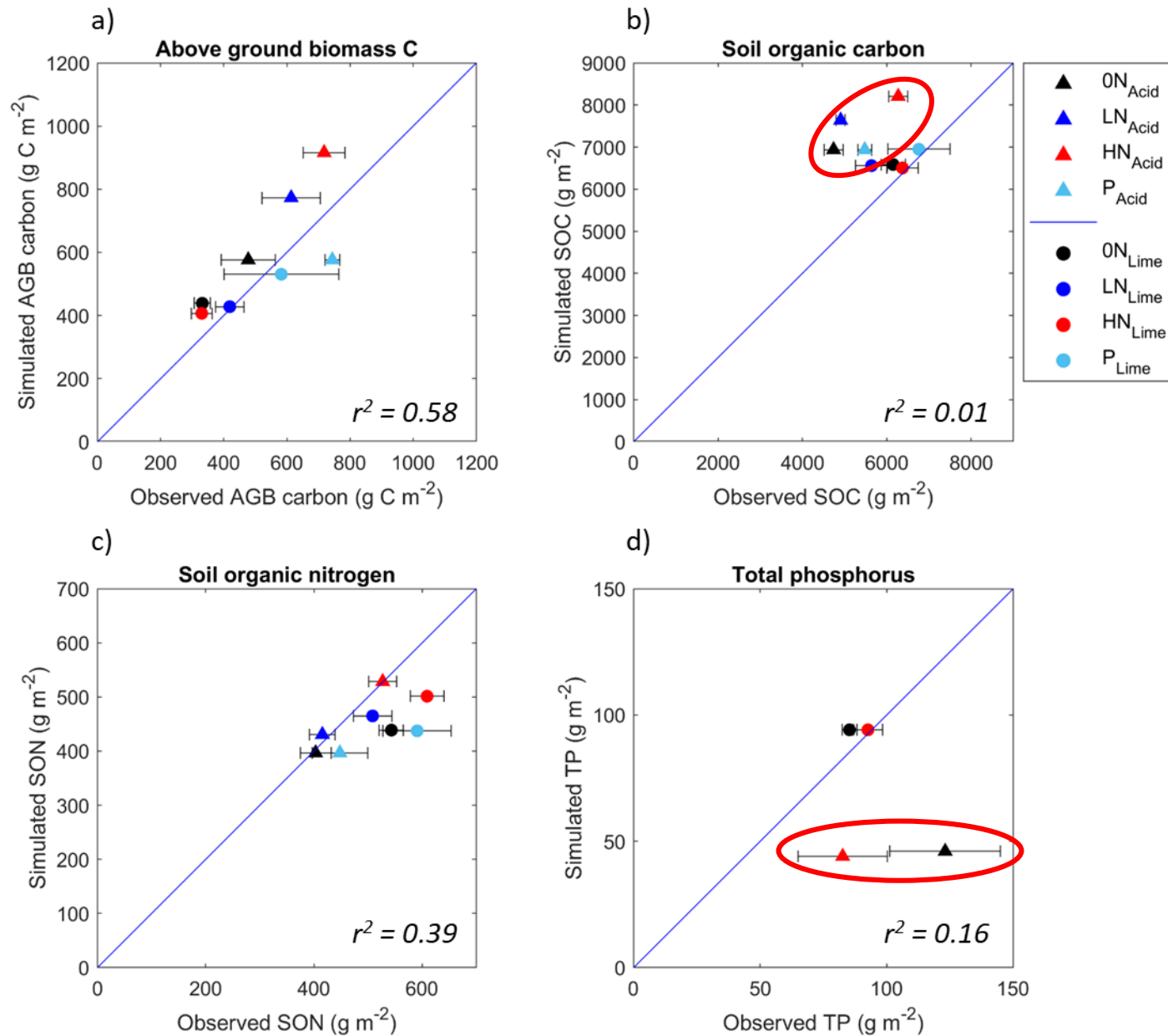
- Simulated biomass C, and soil C, N and P were compared to empirical observations for the same variables
- How well the model captured the sizes of the empirical pools is represented by the distance to the blue 1:1 line
 - The closer data points are to this line, the more similar the modelled and empirical estimates of C, N and P pools are
- The ‘pattern’ of responses reflects how the model’s estimates of responses to nutrient treatment compare to empirical responses
 - For instance, does the response appear N or P limited?
- Together, these give an indication of how well the model’s parameter selections may reflect the Wardlow grasslands



- Overall good performance, the average discrepancy between observed and simulated data is only 6.6% ($SE \pm 9.1$) and 1.2% ($SE \pm 4.4$) for the acidic and limestone grasslands respectively across all variables
- Empirical patterns in data are broadly captured too, limestone grassland is clearly P-limited, though acidic grassland appears N-limited in behavior
- Some notable differences exist that warrant further attention



- The model has simulated a limestone grassland with very similar pool sizes to the empirical estimates
- It has also captured the P-limited nature of the grassland, with biomass increasing with only P addition
- Where organic access to P is fairly modest, the model appears capable of effectively simulating the dynamics of a P-limited grassland

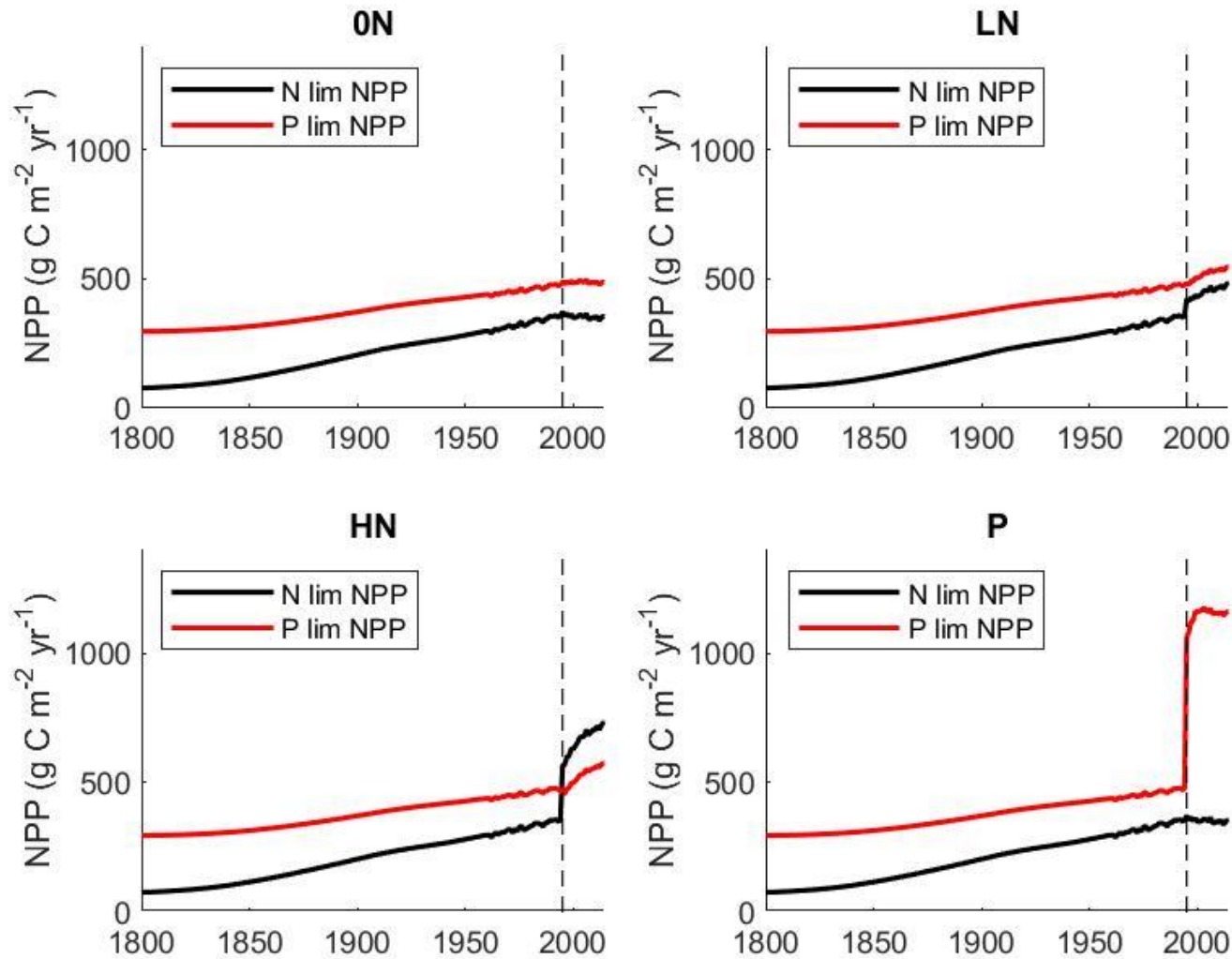


- However, the model is less effective at simulating the C and P pools of the acidic grassland, where it underestimates total P and overestimates SOC
- This suggests that the model may struggle to simulate the grassland C, N and P stocks when their formation relies more on organic forms of P
- Calibrating $P_{\text{CleaveMax}}$ in such a way likely makes it too easy for plants to take up newly available P from organic sources and therefore biomass and soil carbon increase at the expense of the SOP pool

Results – Limiting nutrient through time

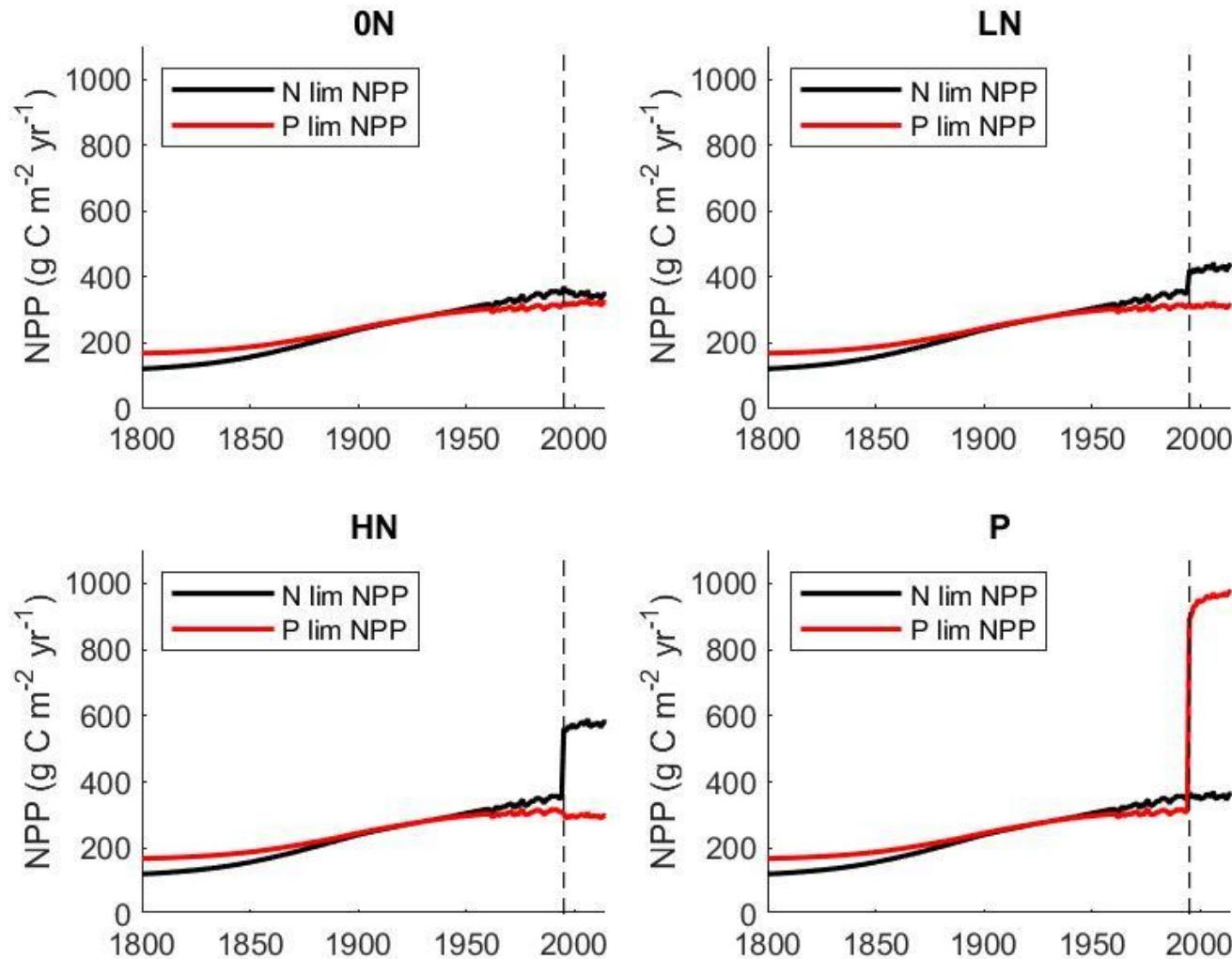
- The following plots highlight which nutrient (N or P) is most limiting to NPP in each nutrient treatment scenario
- N14CP utilises a law-of-the-minimum approach to nutrient limitation, hence the lowest of the two lines dictates the actual productivity of the site
 - Temperature and precipitation are omitted from the plots as the modelled grasslands are all limited by nutrients not climate
- Experimental treatments within the model begin in 1995 at the vertical dashed line

Simulated **acidic** grassland



- The modelled acidic grassland is N limited in the control group
- LN treatment increases N-limited productivity but the grassland remains limited by N
- LN and HN treatment increase the P-limited NPP and the grassland becomes P-limited in the HN treatment
- However, it is a more productive P-limited grassland, hence HN still stimulates productivity
- P treatment has no effect on N-limited productivity

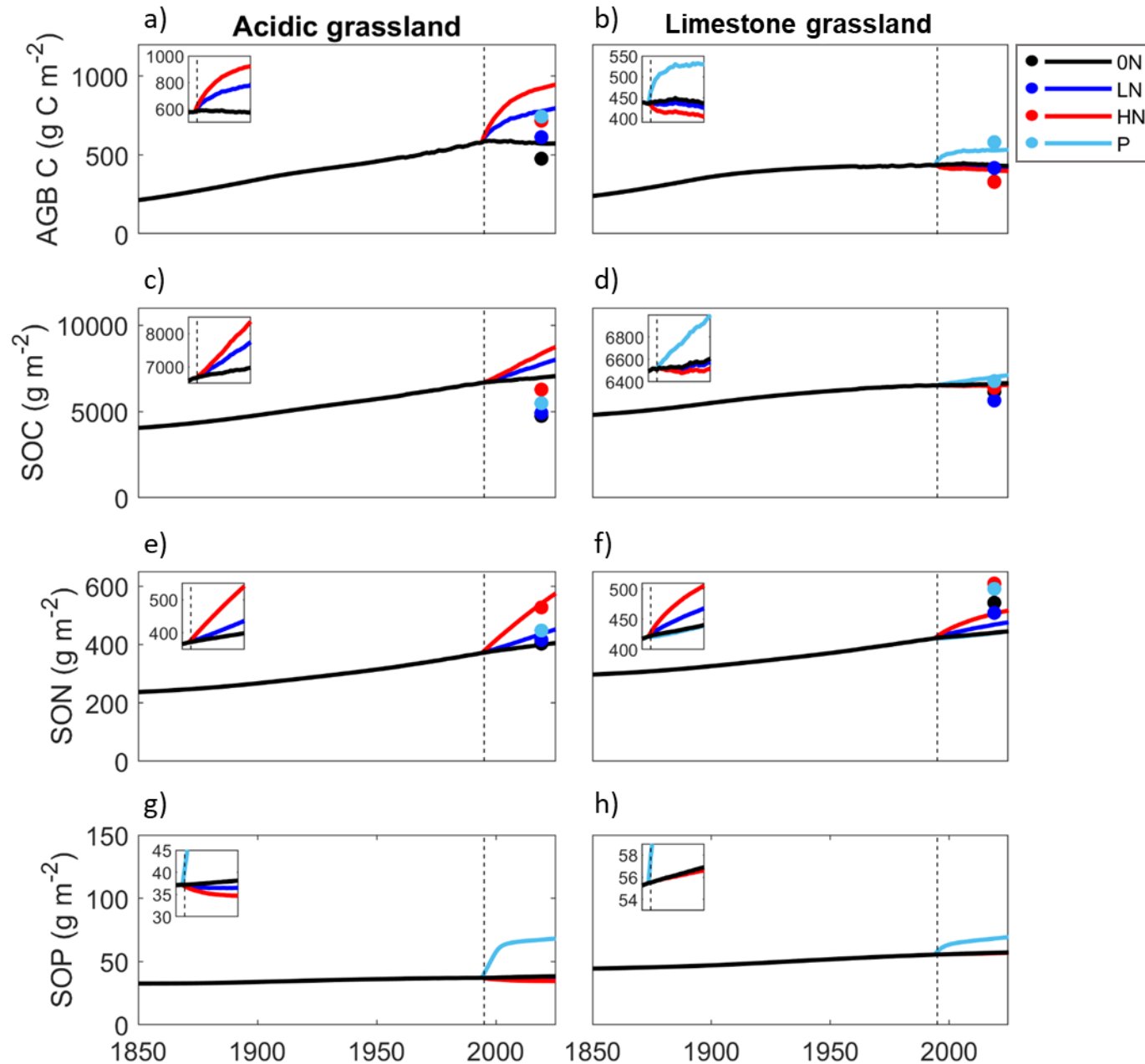
Simulated **limestone** grassland



- The modelled limestone grassland is P-limited in the control group
- In contrast to the acidic grassland, LN and HN treatment reduce P-limited productivity
- This suggests the N treatments are worsening P limitation
- P treatment results in a more productive N-limited grassland, hence we see a positive growth response to P

Results – Time-series of C, N and P

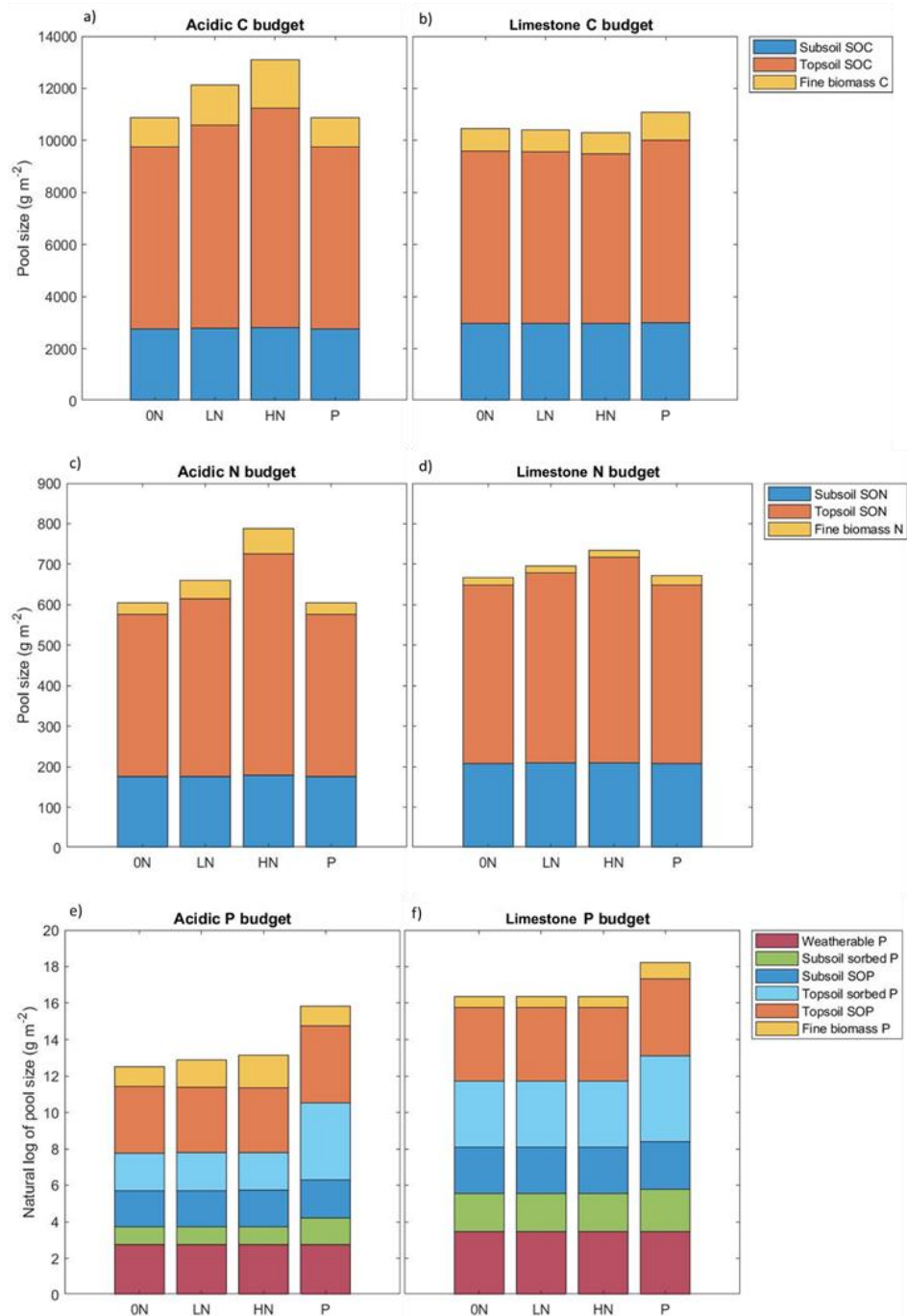
- The following are time series plots showing the development of ecosystem C, N and P stocks since the onset of widespread N deposition in the 1800s
- The black line shows the model's estimate for the effects of N deposition on it's own, which post 1995 (at the vertical line again), becomes the 0N treatment
- Empirical estimates are overlain to provide some context for the modelled changes in C, N and P stocks
- Note that empirical P data was for total not organic P, so the SOP time series has no associated empirical data



- Acidic grassland
 - Rapid growth of biomass and SOC pools with N deposition
 - Biomass C and SOC increase with N but not P addition
 - Size of the SOP pool declines markedly with N treatment
- Limestone grassland
 - Smaller growth in C pools resulting from N deposition
 - Biomass C and SOC declines with N treatment but increases with P treatment
 - SOP pool is accessed in N treatments but is not heavily degraded

Results – Grassland C, N and P budgets

- Modelled C, N and P budgets for the acidic and limestone grasslands for the year 2020
- Modelled sizes of C and N pools are in grams per metre squared, and P pools are presented as $\log_n$ grams per metre squared
- Temporary pools such as available N and P and fixed N are not presented here to avoid 'double counting' in other pools



- Acidic

- Total ecosystem C and N increases with N treatment but not P
- Responses of the SOP pool are in contrast to those of C and N, declining with N addition
- Nitrogen treatments facilitated access to SOP from both subsoil and topsoil
- This increased plant available P and facilitated its uptake into biomass material

- Limestone

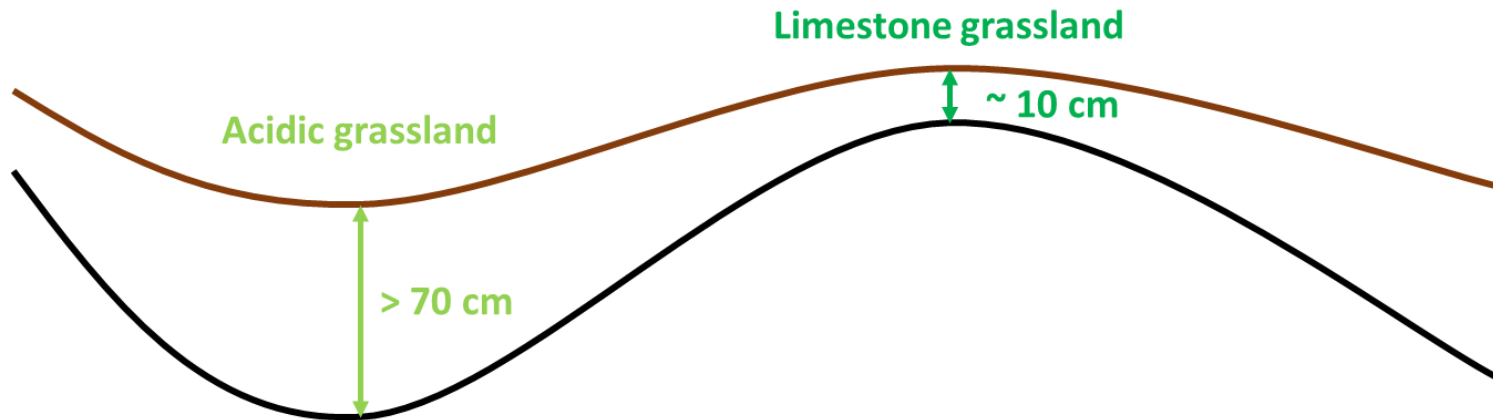
- Ecosystem C (but not N) declined with N addition
- This response was ubiquitous to all C pools, with declines in subsoil, topsoil and biomass C
- The response of the limestone P pools mirrors that of carbon, with declines in subsoil SOP, topsoil SOP, available P and biomass P with LN and HN addition

Discussion

- Model parameter selection – reflective of Wardlow soil conditions, but also reflects how the model ‘decided’ to choose values based on empirical data
- Model performance – okay overall, good for limestone grassland but struggled with acidic where organic P was more important – potentially misses P protection in secondary mineral compounds
- Time series – contrasting effects of the same treatments on the two grasslands, with consequences for ecosystem C, N and P cycling
- Budgets – more mechanistic insight into what is happening within the simulated grasslands

Discussion – Model parameter selection

- The limestone grassland occurs on the hill brow atop a limestone bedrock and consequently has a shallow soil, often no more than 10 cm away from the limestone
- As a result, plant roots can be in contact with the bedrock, making inorganic weatherable forms of P such as calcium phosphate, more accessible
- The acidic grassland however, occurs in the hill trough, allowing loess to accumulate and resulting in a deeper soil profile
- Plant roots rarely reach bedrock here, hence organic P sources are in relatively greater supply than for the limestone grassland – model parameters appear to reflect this



Discussion – Model performance

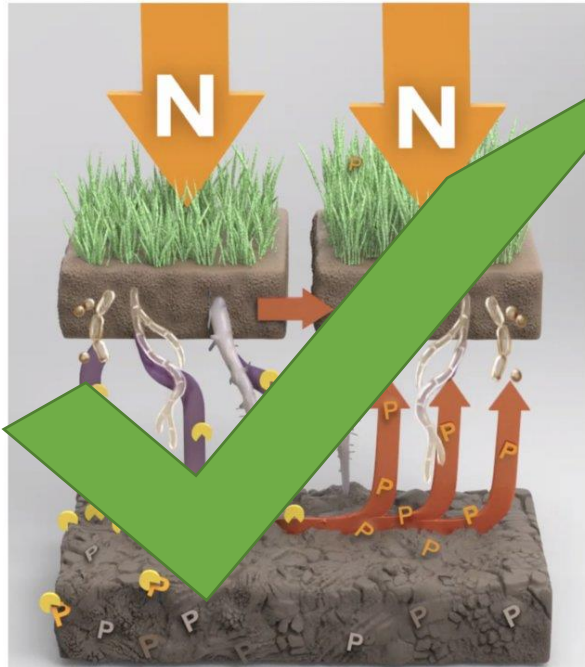
- When access to organic P was more important, as with the acidic grassland, model performance was weaker
- In particular, plant and soil C was overestimated and total P underestimated
 - Our simplistic representation of plant access to newly-cleaved P probably underestimates the ability of the soil to rapidly immobilise P, making it too easy for plants to utilise organic P
 - In the acidic grassland, much of the P cleaved from the organic pool is likely to be immobilised by microbes or bound in aluminium and iron based complexes, reducing its accessibility to plants
 - This is something our representation of organic P uptake misses and may explain why P is transferred from soil to plants in such quantities

Grassland	Biomass response	Stock estimates		
		<i>SOC</i>	<i>SON</i>	<i>Total P</i>
Limestone	P-limited			
Acidic	N-limited	↑		↓

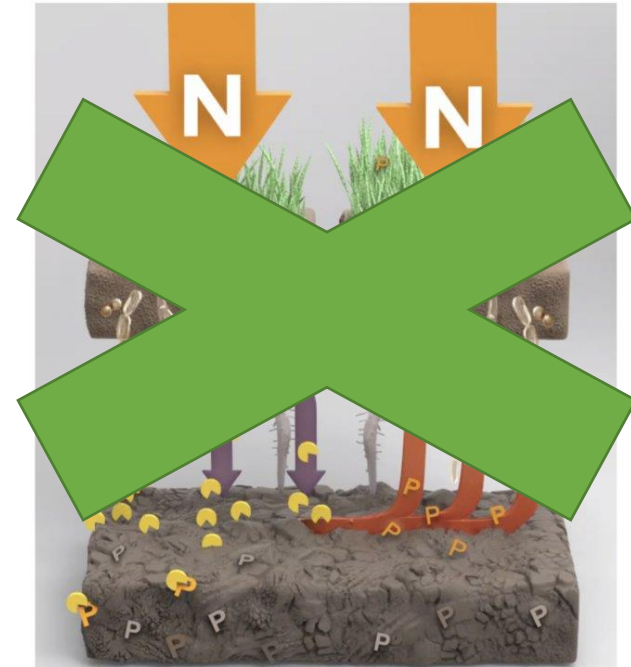
Discussion – Time series / nutrient limitation / budgets

- The response of the modelled acidic grassland to long term N treatment suggests that it is accessing sufficient organic P forms to alleviate resulting P limitation
 - This is at the expense of the SOP pool which is rapidly degraded
- The same treatments in the limestone grassland that lacks such an ability leads to worsening P limitation
 - N treatment increases the demand for P while reducing the size of the bioavailable P pool, leading to less biomass replacing that which senesced in the previous growing season
 - Biomass C input to the SOC pool declines, and more SOC is respired than is produced
 - Ecosystem C stocks reduce as a consequence

Acidic



Limestone



Chen *et al.* (2020), *Global Change Biology*,
26, <https://doi.org/10.1111/gcb.15218>

Conclusions

- N14CP can simulate P-limited ecosystems, particularly if organic P access is fairly low
 - Some caveats to our particular approach
- Access to different phosphorus forms is a key determinant of ecosystem nutrient limitation and their responses to changes in nutrient availability
- Organic P cleaving may prevent the onset of 'anthropogenic P limitation' in grasslands
- Prolonged N deposition in ecosystems that lack this ability may lose carbon

References

1. Tipping, E., J. A. C. Davies, P. A. Henrys, G. J. D. Kirk, A. Lilly, U. Dragosits, E. J. Carnell, A. J. Dore, M. A. Sutton, and S. J. Tomlinson, (2017), Long-term increases in soil carbon due to ecosystem fertilization by atmospheric nitrogen deposition demonstrated by regional-scale modelling and observations, Scientific Reports, 7, 11. <https://doi.org/10.1038/s41598-017-02002-w>
2. Davies, J. A. C., E. Tipping, E. C. Rowe, J. F. Boyle, E. G. Pannatier, and V. Martinsen: Long-term P weathering and recent N deposition control contemporary plant-soil C, N, and P, (2016), Global Biogeochemical Cycles, 30(2), 231-249. <https://doi.org/10.1002/2015GB005167>
3. Zhai, D., Jin, W., Shao, J., He, Y., Zhang, G., Li, M., Huang, H., & Zhou, X. (2017). Different response patterns of soil respiration to a nitrogen addition gradient in four types of land-use on an alluvial island in China. Ecosystems, 20(5), 904–916. <https://doi.org/10.1007/s10021-016-0079-7>
4. Du E, C. Terrer, A. F. A. Pellegrini, A. Ahlström, C. J. van Lissa, X. Zhao, N. Xia, X. Wu, (2020), Global patterns of terrestrial nitrogen and phosphorus limitation, nature geoscience, <https://doi.org/10.1038/s41561-019-0530-4>
5. Goll, D. S., V. Brovkin, B. R. Parida, C. H. Reick, J. Kattge, P. B. Reich, P. M. van Bodegom, and U. Niinemets, (2012), Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling, Biogeosciences, 9(9), 3547-3569. <https://doi.org/10.5194/bg-9-3547-2012>
6. Chen, J., Groenigen, K.J. van, Hungate, B.A., Terrer, C., Groenigen, J.-W. van, Maestre, F.T., Ying, S.C., Luo, Y., Jørgensen, U., Sinsabaugh, R.L., Olesen, J.E., Elsgaard, L. (2020), Long-term nitrogen loading alleviates phosphorus limitation in terrestrial ecosystems. Global Change Biology 26, 5077–5086. <https://doi.org/10.1111/gcb.15218>
7. Horswill, P., O. O'Sullivan, G. K. Phoenix, J. A. Lee, and J. R. Leake, (2008), Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition, Environmental Pollution, 155(2), 336-349. <https://doi.org/10.1016/j.envpol.2007.11.006>,
8. Chapin FS, Matson PA, Mooney HA (2011) Principles of terrestrial ecosystem ecology. Springer, New York
9. Janes-Bassett, V, J. Davies, E. C. Rowe, E. Tipping, (2020), Simulating long-term carbon nitrogen and phosphorus biogeochemical cycling in agricultural environments, Science of The Total Environment, 714, <https://doi.org/10.1016/j.scitotenv.2020.136599>

Acknowledgements

- Technical assistance (empirical data collection)
 - Irene Johnson
 - Heather Walker
 - Gemma Newsome
- Advice and interpretation
 - Jonathan Leake
- Manuscript co-authors and the PLACE team
- Funding
 - NERC ACCE DTP - <https://acce.shef.ac.uk/>
 - NERC PLACE grant

Empirical



Iain Hartley



Gareth Phoenix



Ben Keane



Jonathan Leake



Chris Taylor

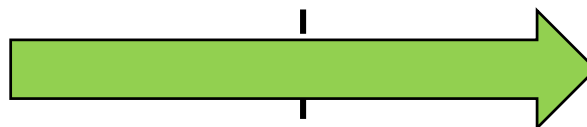
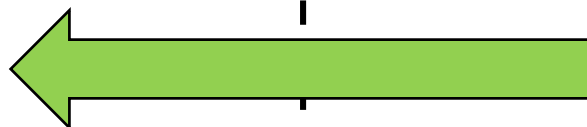
Modelling



Jessica Davies



Victoria Janes-Bassett



Contact info

Please feel free to get in touch if this work (or other PLACE or Wardlow related work) interests you or you have any questions!

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- Researchgate: <https://www.researchgate.net/profile/Christopher-Taylor-19>
- Phoenix lab website: <https://sites.google.com/a/sheffield.ac.uk/phoenix-ecology-global-change-lab/about-us>