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Isotopic evidence for oligotrophication of terrestrial ecosystems

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Human societies depend on an Earth System that operates within a constrained range of nutrient availability, yet the recent trajectory of terrestrial nitrogen (N) availability is uncertain. Examining patterns of foliar N concentrations ([N]) and isotope ratios ($\delta^{15}\text{N}$) from more than 42,000 samples acquired over 37 years, here we show that foliar [N] declined by 8% and foliar $\delta^{15}\text{N}$ declined by 0.8 – 1.9 ‰. Examining patterns across different climate spaces, foliar $\delta^{15}\text{N}$ declined across the entire range of MAT and MAP tested. These results suggest declines in N supply relative to plant demand at the global scale. In all, there are now multiple lines of evidence of declining N availability in many unfertilized terrestrial ecosystems, including declines in $\delta^{15}\text{N}$ of tree rings and leaves from herbarium samples over the past 75-150 years. These patterns are consistent with the proposed consequences of elevated atmospheric CO_2 and longer growing seasons. These declines will limit future terrestrial C uptake and increase nutritional stress for herbivores.

Human societies depend on a resilient, accommodating Earth System with a constrained range of environmental conditions^{1,2}, yet there is a fundamental uncertainty about the trajectory of nitrogen (N) availability in terrestrial ecosystems. On the one hand, as more and more reactive N has been fixed by humans over time³, planetary boundaries for N fluxes are thought to have been exceeded, generating wide-scale aquatic and terrestrial eutrophication as well as contributing to terrestrial acidification and aquatic anoxia. Exceeding the planetary N boundary is thought to be destabilizing the Earth system^{1,2,4-7}. In contrast, atmospheric CO₂ concentrations have increased by >40% over the past 150 years. Elevated atmospheric CO₂ could be reducing N availability in terrestrial ecosystems as plant N demand increases more than N supplies and/or higher ratios of C to N in plants induce greater microbial N limitation⁸⁻¹¹. Longer growing seasons associated with climate warming could also be increasing plant N demand more than supply in some ecosystems, also reducing N availability¹². With no global databases to directly assess changes in terrestrial N availability, the lack of resolution of the trajectory of terrestrial N cycling constrains our ability to predict future terrestrial C uptake¹³, plant biodiversity¹⁴, and herbivore performance^{15,16}. For example, increasing N availability would generally increase plant productivity in unfertilized ecosystems, reduce plant biodiversity, and increase the growth of herbivores as protein limitation is reduced. Decreasing N availability generally leads to opposite effects. Given the central role of nitrogen in so many ecosystem properties, a basic N trajectory is required to increase the certainty with which regulatory decisions can be made and predict future terrestrial ecosystem function.

To test whether there is evidence of global-scale increases or decreases in terrestrial N availability, we compiled a dataset of 42,822 measurements of foliar N concentrations ([N]) and nitrogen isotope ratios ($\delta^{15}\text{N}$). Measurements were restricted to terrestrial rooted plants that were not directly fertilized and were collected between 1980 and 2017 (Supplementary Figs. 1-3). Similar to foliar [N], foliar $\delta^{15}\text{N}$ scales positively with N availability relative to plant N demand within an ecosystem¹⁷⁻¹⁹ as plants experiencing higher N availability acquire soil N that is more enriched in ^{15}N . When N availability is high, there is a greater relative importance of loss pathways that strongly fractionate against ^{15}N , e.g. denitrification. Also, plants acquire less N from mycorrhizal fungi, which transfer ^{15}N -depleted N to plants. Our dataset is over 30,000 data points larger than previously assembled¹⁷, providing a better representation of global ecosystems and climate space as well as representing an additional 12 years of data to examine temporal trends (Supplementary Fig. 1-2). All samples used in analyses were associated with mean climate data and assigned a mycorrhizal type and N_2 -fixing capacity based on provided data or literature syntheses^{20,21}. Data were then averaged to provide a single foliar $\delta^{15}\text{N}$ value for each species at a given site in a given year before determining relationships between foliar $\delta^{15}\text{N}$ and climate, mycorrhizal type, and foliar [N]. We then tested whether foliar $\delta^{15}\text{N}$ and foliar [N] increased or decreased over time across sites with regression and structural equation modelling.

Results

Examining patterns for 38,451 unsummarized measurements of foliar $\delta^{15}\text{N}$ from non- N_2 -fixing species, mean foliar $\delta^{15}\text{N}$ was 0.4 ‰ and varied by over 40 ‰ across all samples (-20.6 ‰ to +21.4 ‰). As observed in a previous synthesis¹⁷, using data summarized by species at each site

for each year ($n = 10,796$), foliar $\delta^{15}\text{N}$ increased with increasing mean annual temperature (MAT) and decreasing mean annual precipitation (MAP) (Fig 1). With these data, $\delta^{15}\text{N}$ began increasing with increasing MAT above 9.7 ± 1.1 °C which was similar to the 8.5 °C breakpoint observed in the full dataset of the first synthesis¹⁷ and the 9.8 °C breakpoint observed for a global synthesis of soil organic matter $\delta^{15}\text{N}$ ²². As observed previously, in the current synthesis, foliar $\delta^{15}\text{N}$ increases with increasing log-transformed foliar [N] and differed among species with different mycorrhizal associations (Fig 1). Non-mycorrhizal species still had the highest foliar $\delta^{15}\text{N}$, and ericoid species the lowest (Fig 1). Foliar [N] was highest under cold, wet climates and also differed significantly among mycorrhizal types with nonmycorrhizal and arbuscular species having the highest N concentrations (19.2 mg g^{-1}) and ericoid species the lowest (12.4 mg g^{-1}). After accounting for climate, foliar [N], and mycorrhizal type, there were significant differences among continents in foliar $\delta^{15}\text{N}$. For example, samples from Europe were 1.2 ± 0.2 ‰ lower than expected based on climate, mycorrhizal type, and [N] whereas samples from South America were 1.2 ± 0.2 ‰ more than expected (Supplementary Table 1, Supplementary Fig. 4). For foliar [N], leaves from a typical plant with the geometric mean [N] of 17.3 mg g^{-1} would be 11.4 mg g^{-1} if it were from Australia and 20.4 mg g^{-1} from Asia if one held mycorrhizal type and climate constant and only varied the continent of origin (Supplementary Table 1).

After standardizing values for differences in climate, mycorrhizal type, foliar [N], and continent, there was no significant trend in residual $\delta^{15}\text{N}$ over time when comparing at the same foliar [N] over time (-0.004 ± 0.007 ‰ y^{-1} ; $P = 0.51$, $n = 2292$; Supplementary Table 1). However, log-transformed foliar [N] did decline over time (-0.0012 ± 0.0004 y^{-1} ; $P = 0.001$, $n = 2292$; Supplementary Table 1). This rate of decline is the equivalent of a typical plant with the

geometric mean [N] of 17.3 mg g⁻¹ in 1980 declining 8% to 15.6 mg g⁻¹ in 2017. Given this declining foliar [N] over time and the relationship between foliar [N] and $\delta^{15}\text{N}$, we ran additional regression models that standardized foliar $\delta^{15}\text{N}$ for climate, mycorrhizal type, and continent, but did not hold foliar [N] constant over time. Not holding foliar [N] constant over time, residual foliar $\delta^{15}\text{N}$ declined by $1.9 \pm 0.5 \text{ ‰}$ ($P < 0.001$) over 37 years (Fig 2).

To test how changes in foliar [N] were affecting the trend in $\delta^{15}\text{N}$ given that both were changing over time, a structural equation models (SEM) further examined the role of foliar [N] in determining changes in $\delta^{15}\text{N}$ and the changes in $\delta^{15}\text{N}$ that were independent of trends in foliar [N]. Doing so allows partitioning of direct effects of time on foliar $\delta^{15}\text{N}$ from indirect effects that occur through changes in foliar [N]. Working with site-level residual foliar $\delta^{15}\text{N}$ and foliar [N] for non-N₂-fixing species after standardizing for climate, mycorrhizal type, and continent, taking into account [N]-dependent and independent pathways, the SEM resulted in a lower estimate of the decline in foliar $\delta^{15}\text{N}$ in non-N₂-fixing species than the regression with the sums of effects via the two pathways generating an estimated decline of $0.8 \pm 0.5 \text{ ‰}$ over 37 years (Supplementary Fig. 5, Supplementary Table 2). With this approach, 82% of the decline occurred independent of changes in [N], while the remainder was due to the decline in [N].

To explore patterns of changes in foliar $\delta^{15}\text{N}$ and [N] over time across climates for non-N₂-fixing species, we ran a series of SEMs using subsets of the data created by serially adjusting the minimum and maximum MAT for inclusion in the SEM. Examining the coefficients for SEMs across ranges of MAT, plants in hot regions have been more likely to increase in foliar [N] over time than plants from cold regions (Supplementary Fig. 6). Yet, the [N]-independent changes in foliar $\delta^{15}\text{N}$ were consistently negative across the entire range of MAT tested (Supplementary Fig.

6). As a result, after calculating [N]-dependent and [N]-independent pathways of changes in foliar $\delta^{15}\text{N}$, foliar $\delta^{15}\text{N}$ declined across the entire range of MAT tested and the decline was likely of the highest magnitude in hotter regions. Employing a similar approach for MAP, regions with intermediate MAP were most likely to experience increased [N] (Supplementary Fig. 7), but the strength of the [N]-independent declines in foliar $\delta^{15}\text{N}$ led to declines in foliar $\delta^{15}\text{N}$ across the entire range of MAP examined (Supplementary Fig. 7).

N_2 -fixing plants showed similar patterns over time in site-level foliar $\delta^{15}\text{N}$ as non- N_2 -fixers, although it is uncertain whether these patterns result from increasing N_2 fixation or reduced $\delta^{15}\text{N}$ of acquired N due to declining N availability. Across 4,363 samples (Supplementary Fig. 8), mean foliar $\delta^{15}\text{N}$ for N_2 -fixers was 2.0 ‰ and varied by over 24 ‰. Likely reflecting their greater access to N, the geometric mean foliar [N] for N_2 -fixing species was 25.8 mg g⁻¹ as opposed to just 17.3 mg g⁻¹ for non- N_2 -fixers. Foliar $\delta^{15}\text{N}$ increased with increasing MAT, decreasing MAP, and increasing foliar [N] (Supplementary Fig. 9). Potentially signifying greater N_2 -fixation, [N] was increasing for N_2 -fixers between 1980 and 2017 (Supplementary Table 1). However, leaf $\delta^{15}\text{N}$ still declined by 1.5 ‰ over the 37 years. Using the same SEM used for non- N_2 -fixers, taking into account the increases in N as well as N-independent decline, foliar $\delta^{15}\text{N}$ declined by 0.8 ‰. This decline is similar to the rate for non- N_2 -fixers (Supplementary Fig. 10, Supplementary Table 3), but it should be noted that sample size was lower for non- N_2 -fixers (n=377 for data averaged by site and year).

Discussion

Based on evidence that foliar $\delta^{15}\text{N}$ reflects soil N availability to plants in non- N_2 -fixing species, the most parsimonious interpretation of the decline in foliar [N] and foliar $\delta^{15}\text{N}$ for non- N_2 -fixing species is that the ratio of plant N demand to soil N supply is increasing in unfertilized ecosystems across the Earth, i.e. N availability to plants is declining. Within this general global pattern, there are individual examples of local to regional increases in N availability occurring²³⁻²⁵. We also reveal evidence that some climatic regions might be experiencing complicated responses with foliar [N] increasing while foliar $\delta^{15}\text{N}$ decreased. Yet, patterns consistent with broad-scale oligotrophication in unfertilized terrestrial ecosystems are documented in numerous other studies. Evidence of oligotrophication includes regional declines in grass and tree foliar N concentrations^{26,27}, reduced dietary protein in cattle on rangelands¹⁵, reduced pollen protein concentrations²⁸, increased soil C:N²⁹, reduced N mineralization rates in forests³⁰, and reductions in NO_3^- in forest streams³¹⁻³⁴. In addition, declines in $\delta^{15}\text{N}$ of tree rings and leaves from herbarium samples indicate reduction of plant N availability in forests and grasslands over the past 75-150 years^{12,25,27}. It should be noted that these corroborating patterns have been quantified for North America and Europe. Similar research has yet to be conducted to begin to examine other lines of evidence on other continents.

The mechanism behind terrestrial oligotrophication cannot be directly tested here, but progressive nitrogen limitation associated with elevated atmospheric CO_2 and/or longer growing seasons due to climate change are likely candidates due to the global extent of the oligotrophication. Although N deposition does affect terrestrial ecosystem N cycling, North American tree ring and herbarium studies support the timing of the initiation of the decline in N

availability to predate broad-scale increases in N deposition^{25,27} and declines in foliar [N] are unlikely to be explained by greater N deposition rates globally. Further N isotope research on tree rings and herbarium specimens as well as more extensive syntheses of foliar [N] data could elucidate regional variation in changes in N availability over time as well as further explore the timing of declines prior to the years examined here.

Considered alongside these other lines of evidence, our results suggest that most terrestrial ecosystems are undergoing oligotrophication, even while other ecosystems—particularly intensively fertilized terrestrial ecosystems, urban areas, and their downstream receiving waters—are eutrophying. This global bifurcation of N availability raises questions about whether humanity has exceeded a true planetary boundary for nitrogen availability³⁵. Broad-scale reductions of anthropogenic N fixation would certainly reduce impacts on aquatic ecosystems, but at the same time could also further constrain terrestrial C uptake as atmospheric CO₂ concentrations continue to increase and N deposition rates fall¹³. Given projected increases in atmospheric CO₂ concentrations and global temperatures over the next century, it is likely that this oligotrophication will continue and the C:N stoichiometry of most terrestrial ecosystems will continue to increase. It remains to be tested whether reduced plant protein accompanying oligotrophication can explain reductions in production in herbivores³⁶, but declining N availability to plants should cascade up to herbivores^{15,16}. Even if atmospheric CO₂ is eventually stabilized at low enough levels to mitigate the most serious impacts of climate change³⁷, many terrestrial ecosystems will increasingly display signs of too little reactive N as opposed to too much. Preventing these declines in N availability further emphasizes the need to reduce anthropogenic CO₂ emissions.

Data and code availability. The datasets generated during and/or analysed during the current study are available in the Dryad repository [link to be generated upon acceptance]. All code used for statistical analyses and figure generation are available on Dryad (XXX).

- 1 Rockström, J. *et al.* A safe operating space for humanity. *Nature* **461**, 472-475, doi:10.1038/461472a (2009).
- 2 Steffen, W. *et al.* Sustainability. Planetary boundaries: guiding human development on a changing planet. *Science* **347**, 1259855, doi:10.1126/science.1259855 (2015).
- 3 Fowler, D. *et al.* The global nitrogen cycle in the twenty-first century. *Philos Trans R Soc Lond B Biol Sci* **368**, 20130164, doi:10.1098/rstb.2013.0164 (2013).
- 4 Clark, C. M., Morefield, P. E., Gilliam, F. S. & Pardo, L. H. Estimated losses of plant biodiversity in the United States from historical N deposition (1985–2010). *Ecology* **94**, 1441-1448 (2013).
- 5 de Vries, W., Kros, J., Kroeze, C. & Seitzinger, S. P. Assessing planetary and regional nitrogen boundaries related to food security and adverse environmental impacts. *Current Opinion in Environmental Sustainability* **5**, 392-402, doi:10.1016/j.cosust.2013.07.004 (2013).
- 6 Sinha, E., Michalak, A. & Balaji, V. Eutrophication will increase during the 21st century as a result of precipitation changes. *Science* **357**, 405-408 (2017).
- 7 Vitousek, P. M. Human Domination of Earth's Ecosystems. *Science* **277**, 494-499, doi:10.1126/science.277.5325.494 (1997).
- 8 Luo, Y. *et al.* Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* **54**, 731-739 (2004).

262 9 Gill, R. A. *et al.* Nonlinear grassland responses to past and future atmospheric CO₂.
263 *Nature* **417**, 279-282 (2002).

264 10 Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E. & McMurtrie, R. E. CO₂
265 enhancement of forest productivity constrained by limited nitrogen availability. *Proc Natl*
266 *Acad Sci U S A* **107**, 19368-19373, doi:10.1073/pnas.1006463107 (2010).

267 11 Feng, Z. *et al.* Constraints to nitrogen acquisition of terrestrial plants under elevated CO₂.
268 *Glob Chang Biol* **21**, 3152-3168, doi:10.1111/gcb.12938 (2015).

269 12 Elmore, A. J., Nelson, D. M. & Craine, J. M. Earlier springs are causing reduced nitrogen
270 availability in North American eastern deciduous forests. *Nat Plants* **2**, 16133,
271 doi:10.1038/nplants.2016.133 (2016).

272 13 Smith, B. *et al.* Implications of incorporating N cycling and N limitations on primary
273 production in an individual-based dynamic vegetation model. *Biogeosciences* **11**, 2027-
274 2054 (2014).

275 14 Bobbink, R. *et al.* Global assessment of nitrogen deposition effects on terrestrial plant
276 diversity: a synthesis. *Ecol Appl* **20**, 30-59 (2010).

277 15 Craine, J. M., Elmore, A. & Angerer, J. P. Long-term declines in dietary nutritional
278 quality for North American cattle. *Environmental Research Letters* **12**, 044019,
279 doi:10.1088/1748-9326/aa67a4 (2017).

280 16 Stiling, P. & Cornelissen, T. How does elevated carbon dioxide (CO₂) affect plant–
281 herbivore interactions? A field experiment and meta-analysis of CO₂-mediated changes
282 on plant chemistry and herbivore performance. *Glob Change Biol* **13**, 1823-1842,
283 doi:10.1111/j.1365-2486.2007.01392.x (2007).

284 17 Craine, J. M. *et al.* Global patterns of foliar nitrogen isotopes and their relationships with
285 climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New*
286 *Phytol* **183**, 980-992 (2009).

287 18 Craine, J. M. *et al.* Ecological interpretations of nitrogen isotope ratios of terrestrial
288 plants and soils. *Plant Soil* **1**, 1-26 (2015).

289 19 Garten, C. T. Variation in foliar N-15 abundance and the availability of soil-nitrogen on
290 Walker Branch watershed. *Ecology* **74**, 2098-2113, doi:10.2307/1940855 (1993).

291 20 Werner, G. D., Cornwell, W. K., Sprent, J. I., Kattge, J. & Kiers, E. T. A single
292 evolutionary innovation drives the deep evolution of symbiotic N₂-fixation in
293 angiosperms. *Nature communications* **5**, 4087 (2014).

294 21 Brundrett, M. C. Mycorrhizal associations and other means of nutrition of vascular
295 plants: understanding the global diversity of host plants by resolving conflicting
296 information and developing reliable means of diagnosis. *Plant Soil* **320**, 37-77 (2009).

297 22 Craine, J. M. *et al.* Convergence of soil nitrogen isotopes across global climate gradients.
298 *Scientific Reports* **5**, 8280, doi:DOI:10.1038/srep08280 (2015).

299 23 Hietz, P. *et al.* Long-Term Change in the Nitrogen Cycle of Tropical Forests. *Science*
300 **334**, 664-666, doi:10.1126/science.1211979 (2011).

301 24 Decina, S. M., Templer, P. H., Hutya, L. R., Gately, C. K. & Rao, P. Variability, drivers,
302 and effects of atmospheric nitrogen inputs across an urban area: Emerging patterns
303 among human activities, the atmosphere, and soils. *Sci Total Environ* **609**, 1524-1534,
304 doi:10.1016/j.scitotenv.2017.07.166 (2017).

305 25 McLauchlan, K. K. *et al.* Centennial-scale reductions in nitrogen availability in temperate
306 forests of the United States. *Scientific Reports* **7**, 7856, doi:10.1038/s41598-017-08170-z
307 (2017).

308 26 Jonard, M. *et al.* Tree mineral nutrition is deteriorating in Europe. *Glob Chang Biol* **21**,
309 418-430, doi:10.1111/gcb.12657 (2015).

310 27 McLauchlan, K. K., Ferguson, C. J., Wilson, I. E., Ocheltree, T. W. & Craine, J. M.
311 Thirteen decades of foliar isotopes indicate declining nitrogen availability in central
312 North American grasslands. *New Phytol* **187**, 1135-1145 (2010).

313 28 Ziska, L. H. *et al.* Rising atmospheric CO₂ is reducing the protein concentration of a
314 floral pollen source essential for North American bees. *Proceedings. Biological sciences /*
315 *The Royal Society* **283**, doi:10.1098/rspb.2016.0414 (2016).

316 29 Gruneberg, E., Ziche, D. & Wellbrock, N. Organic carbon stocks and sequestration rates
317 of forest soils in Germany. *Glob Chang Biol* **20**, 2644-2662, doi:10.1111/gcb.12558
318 (2014).

319 30 Durán, J. *et al.* Climate change decreases nitrogen pools and mineralization rates in
320 northern hardwood forests. *Ecosphere* **7**, e01251-n/a, doi:10.1002/ecs2.1251 (2016).

321 31 Eshleman, K. N., Sabo, R. D. & Kline, K. M. Surface water quality is improving due to
322 declining atmospheric N deposition. *Environ Sci Technol* **47**, 12193-12200,
323 doi:10.1021/es4028748 (2013).

324 32 Sabo, R. D. *et al.* Watershed-scale changes in terrestrial nitrogen cycling during a period
325 of decreased atmospheric nitrate and sulfur deposition. *Atmos Environ* **146**, 271-279,
326 doi:10.1016/j.atmosenv.2016.08.055 (2016).

327 33 Lucas, R. W. *et al.* Long-term declines in stream and river inorganic nitrogen (N) export
328 correspond to forest change. *Ecol Appl* **26**, 545-556 (2016).

329 34 Bernal, S., Hedin, L. O., Likens, G. E., Gerber, S. & Buso, D. C. Complex response of
330 the forest nitrogen cycle to climate change. *Proc Natl Acad Sci U S A* **109**, 3406-3411,
331 doi:10.1073/pnas.1121448109 (2012).

332 35 Nordhaus, T., Shellenberger, M. & Blomqvist, L. The planetary boundaries hypothesis. A
333 *Review of the Evidence Breakthrough Institute, Oakland, CA* (2012).

334 36 Hallmann, C. A. *et al.* More than 75 percent decline over 27 years in total flying insect
335 biomass in protected areas. *PloS one* **12**, e0185809, doi:10.1371/journal.pone.0185809
336 (2017).

337 37 Pachauri, R. K. *et al.* *Climate change 2014: synthesis report. Contribution of Working*
338 *Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on*
339 *Climate Change.* (IPCC, 2014).

340 38 Rosseel, Y. lavaan: An R Package for Structural Equation Modeling. *Journal of*
341 *Statistical Software* **48**, 1-36 (2012).

342 39 Grace, J. B. *Structural equation modeling and natural systems.* (Cambridge University
343 Press, 2006).

344 40 Eldridge, D. J., Wang, L. & Ruiz-Colmenero, M. Shrub encroachment alters the spatial
345 patterns of infiltration. *Ecohydrology* **8**, 83-93, doi:10.1002/eco.1490 (2015).

346 41 Lu, X., Wang, L. & McCabe, M. F. Elevated CO₂ as a driver of global dryland
347 greening. *Scientific reports* **6**, 20716, doi:10.1038/srep20716 (2016).

348 42 Anderson, J. T. & Gezon, Z. J. Plasticity in functional traits in the context of climate
349 change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). *Global*
350 *Change Biology* **21**, 1689-1703, doi:10.1111/gcb.12770 (2015).

351 43 Aranibar, J. N., Goiran, S. B., Guevara, A. & Villagra, P. E. Carbon and nitrogen
352 dynamics in a sandy groundwater-coupled ecosystem in the Monte Desert, indicated by
353 plant stable isotopes. *Journal of Arid Environments* **102**, 58-67,
354 doi:10.1016/j.jaridenv.2013.11.005 (2014).

355 44 Averill, C. & Finzi, A. C. Increasing plant use of organic nitrogen with elevation is
356 reflected in nitrogen uptake rates and ecosystem delta N-15. *Ecology* **92**, 883-891,
357 doi:10.1890/10-0746.1 (2011).

358 45 Bai, E., Boutton, T. W., Liu, F., Ben Wu, X. & Archer, S. R. Variation in woody plant
359 delta(13)C along a topoedaphic gradient in a subtropical savanna parkland. *Oecologia*
360 **156**, 479-489, doi:10.1007/s00442-008-1003-4 (2008).

361 46 Bai, E. *et al.* Spatial variation of the stable nitrogen isotope ratio of woody plants along a
362 topoedaphic gradient in a subtropical savanna. *Oecologia* **159**, 493-503,
363 doi:10.1007/s00442-008-1246-0 (2009).

364 47 Bai, S. H., Sun, F., Xu, Z. & Blumfield, T. J. Ecophysiological status of different growth
365 stage of understorey *Acacia leiocalyx* and *Acacia disparrima* in an Australian dry
366 sclerophyll forest subjected to prescribed burning. *Journal of Soils and Sediments* **13**,
367 1378-1385, doi:10.1007/s11368-013-0747-6 (2013).

368 48 Bansal, S., Nilsson, M.-C. & Wardle, D. A. Response of photosynthetic carbon gain to
369 ecosystem retrogression of vascular plants and mosses in the boreal forest. *Oecologia*
370 **169**, 661-672, doi:10.1007/s00442-011-2246-z (2012).

371 49 Baptist, F. *et al.* C-13 and N-15 allocations of two alpine species from early and late
372 snowmelt locations reflect their different growth strategies. *Journal of Experimental*
373 *Botany* **60**, 2725-2735, doi:10.1093/jxb/erp128 (2009).

374 50 Baraloto, C. *et al.* Decoupled leaf and stem economics in rain forest trees. *Ecology letters*
375 **13**, 1338-1347 (2010).

376 51 Bauer, G. A. *et al.* in *Carbon and Nitrogen Cycling in European Forest Ecosystems* (ed
377 Ernst-Detlef Schulze) 189-214 (Springer Berlin Heidelberg, 2000).

378 52 Bauters, M. *et al.* Parallel functional and stoichiometric trait shifts in South-American
379 and African forest communities with elevation. *Biogeosciences Discuss.* **2017**, 1-27,
380 doi:10.5194/bg-2017-136 (2017).

381 53 Bazot, S., Fresneau, C., Damesin, C. & Barthes, L. Contribution of previous year's leaf N
382 and soil N uptake to current year's leaf growth in sessile oak. *Biogeosciences* **13**, 3475-
383 3484, doi:10.5194/bg-13-3475-2016 (2016).

384 54 Beyschlag, W., Hanisch, S., Friedrich, S., Jentsch, A. & Werner, C. 15N natural
385 abundance during early and late succession in a middle-European dry acidic grassland.
386 *Plant Biol (Stuttg)* **11**, 713-724, doi:10.1111/j.1438-8677.2008.00173.x (2009).

387 55 Blonder, B., Baldwin, B. G., Enquist, B. J. & Robichaux, R. H. Variation and
388 macroevolution in leaf functional traits in the Hawaiian silversword alliance
389 (Asteraceae). *Journal of Ecology* **104**, 219-228 (2016).

390 56 Blumenthal, S. A., Chritz, K. L., Rothman, J. M. & Cerling, T. E. Detecting intraannual
391 dietary variability in wild mountain gorillas by stable isotope analysis of feces.
392 *Proceedings of the National Academy of Sciences of the United States of America* **109**,
393 21277-21282, doi:10.1073/pnas.1215782109 (2012).

394 57 Blumenthal, S. A., Rothman, J. M., Chritz, K. L. & Cerling, T. E. Stable Isotopic
395 Variation in Tropical Forest Plants for Applications in Primatology. *American Journal of*
396 *Primatology* **78**, doi:10.1002/ajp.22488 (2016).

397 58 Boeckx, P., Paulino, L., Oyarzun, C., van Cleemput, O. & Godoy, R. Soil delta N-15
398 patterns in old-growth forests of southern Chile as integrator for N-cycling. *Isotopes In*
399 *Environmental And Health Studies* **41**, 249-259 (2005).

400 59 Brearley, F. Q. Nitrogen stable isotopes indicate differences in nitrogen cycling between
401 two contrasting Jamaican montane forests. *Plant and Soil* **367**, 465-476,
402 doi:10.1007/s11104-012-1469-z (2013).

403 60 Brearley, F. Q., Fine, P. V. A. & Perreijn, K. Does nitrogen availability have greater
404 control over the formation of tropical heath forests than water stress? A hypothesis based
405 on nitrogen isotope ratios. *Acta Amazonica* **41**, 589-592, doi:10.1590/s0044-
406 59672011000400017 (2011).

407 61 Burton, J. I., Perakis, S. S., McKenzie, S. C., Lawrence, C. E. & Puettmann, K. J.
408 Intraspecific variability and reaction norms of forest understory plant species traits.
409 *Functional Ecology* **31**, 1881–1893 (2017).

410 62 Cardon, Z. G., Stark, J. M., Herron, P. M. & Rasmussen, J. A. Sagebrush carrying out
411 hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into
412 inflorescences. *Proceedings of the National Academy of Sciences of the United States of*
413 *America* **110**, 18988-18993, doi:10.1073/pnas.1311314110 (2013).

414 63 Carr, A. S., Chase, B. M., Boom, A. & Medina-Sanchez, J. Stable isotope analyses of
415 rock hyrax faecal pellets, hyraceum and associated vegetation in southern Africa:

416 Implications for dietary ecology and palaeoenvironmental reconstructions. *Journal of*
417 *Arid Environments* **134**, 33-48, doi:10.1016/j.jaridenv.2016.06.013 (2016).

418 64 Chen, C., Li, J., Wang, G. & Shi, M. Accounting for the effect of temperature in
419 clarifying the response of foliar nitrogen isotope ratios to atmospheric nitrogen
420 deposition. *Science of The Total Environment* **609**, 1295-1302,
421 doi:<https://doi.org/10.1016/j.scitotenv.2017.06.088> (2017).

422 65 Compton, J. E., Hooker, T. D. & Perakis, S. S. Ecosystem N distribution and delta N-15
423 during a century of forest regrowth after agricultural abandonment. *Ecosystems* **10**, 1197-
424 1208, doi:10.1007/s10021-007-9087-y (2007).

425 66 Correa, S. B., Winemiller, K. & Cardenas, D. Isotopic variation among Amazonian
426 floodplain woody plants and implications for food-web research. *Biota Neotropica* **16**,
427 doi:10.1590/1676-0611-bn-2015-0078 (2016).

428 67 Courty, P.-E. *et al.* Carbon and Nitrogen Metabolism in Mycorrhizal Networks and
429 Mycoheterotrophic Plants of Tropical Forests: A Stable Isotope Analysis. *Plant*
430 *Physiology* **156**, 952-961, doi:10.1104/pp.111.177618 (2011).

431 68 Couto-Vazquez, A. & Gonzalez-Prieto, S. J. Effects of biotic and abiotic factors on delta
432 N-15 in young *Pinus radiata*. *European Journal of Forest Research* **133**, 631-637,
433 doi:10.1007/s10342-014-0791-9 (2014).

434 69 Couto-Vázquez, A. & González-Prieto, S. J. Effects of climate, tree age, dominance and
435 growth on $\delta^{15}\text{N}$ in young pinewoods. *Trees* **24**, 507-514, doi:10.1007/s00468-010-0420-
436 2 (2010).

437 70 Craine, J. M. *et al.* Grazing and landscape controls on nitrogen availability across 330
438 South African savanna sites. *Austral Ecology* **34**, 731-740, doi:10.1111/j.1442-
439 9993.2009.01978.x (2009).

440 71 Craine, J. M., Towne, E. G., Ocheltree, T. W. & Nippert, J. B. Community traitscape of
441 foliar nitrogen isotopes reveals N availability patterns in a tallgrass prairie. *Plant and Soil*
442 **356**, 395-403, doi:10.1007/s11104-012-1141-7 (2012).

443 72 Crowley, B. E., McGoogan, K. C. & Lehman, S. M. Edge Effects on Foliar Stable
444 Isotope Values in a Madagascan Tropical Dry Forest. *Plos One* **7**,
445 doi:10.1371/journal.pone.0044538 (2012).

446 73 Crowley, B. E., Rasoazanabary, E. & Godfrey, L. R. Stable isotopes complement focal
447 individual observations and confirm dietary variability in reddish-gray mouse lemurs
448 (*Microcebus griseorufus*) from southwestern Madagascar. *American Journal of Physical*
449 *Anthropology* **155**, 77-90 (2014).

450 74 Crowley, B. E. *et al.* Explaining geographical variation in the isotope composition of
451 mouse lemurs (*Microcebus*). *Journal of Biogeography* **38**, 2106-2121 (2011).

452 75 Dahlin, K. M., Asner, G. P. & Field, C. B. Environmental and community controls on
453 plant canopy chemistry in a Mediterranean-type ecosystem. *Proceedings of the National*
454 *Academy of Sciences* **110**, 6895-6900 (2013).

455 76 Dawes, M. A., Schleppi, P., Hattenschwiler, S., Rixen, C. & Hagedorn, F. Soil warming
456 opens the nitrogen cycle at the alpine treeline. *Global Change Biology* **23**, 421-434,
457 doi:10.1111/gcb.13365 (2017).

458 77 Diaz, F. P., Frugone, M., Gutierrez, R. A. & Latorre, C. Nitrogen cycling in an extreme
459 hyperarid environment inferred from delta N-15 analyses of plants, soils and herbivore
460 diet. *Scientific Reports* **6**, doi:10.1038/srep22226 (2016).

461 78 Domingues, T. F., Martinelli, L. A. & Ehleringer, J. R. Ecophysiological traits of plant
462 functional groups in forest and pasture ecosystems from eastern Amazonia, Brazil. *Plant*
463 *Ecology* **193**, 101-112 (2007).

464 79 Dominguez, M. T. *et al.* Relationships between leaf morphological traits, nutrient
465 concentrations and isotopic signatures for Mediterranean woody plant species and
466 communities. *Plant and Soil* **357**, 407-424, doi:10.1007/s11104-012-1214-7 (2012).

467 80 Elmore, A. J., Craine, J. M., Nelson, D. M. & Guinn, S. M. Continental scale variability
468 of foliar nitrogen and carbon isotopes in *Populus balsamifera* and their relationships with
469 climate. *Scientific Reports* **7**, doi:10.1038/s41598-017-08156-x (2017).

470 81 Ens, E., Hutley, L. B., Rossiter-Rachor, N. A., Douglas, M. M. & Setterfield, S. A.
471 Resource-use efficiency explains grassy weed invasion in a low-resource savanna in
472 north Australia. *Frontiers in Plant Science* **6**, doi:10.3389/fpls.2015.00560 (2015).

473 82 Evaristo, J. & McDonnell, J. J. Carbon, nitrogen, and water stable isotopes in plant tissue
474 and soils across a moisture gradient in Puerto Rico. *Hydrological Processes* **31**,
475 doi:10.1002/hyp.11041 (2017).

476 83 Fajardo, A. & Gundale, M. J. Combined effects of anthropogenic fires and land-use
477 change on soil properties and processes in Patagonia, Chile. *Forest Ecology and*
478 *Management* **357**, 60-67 (2015).

479 84 Falxa-Raymond, N., Palmer, M. I., McPhearson, T. & Griffin, K. L. Foliar nitrogen
 480 characteristics of four tree species planted in New York City forest restoration sites.
 481 *Urban Ecosystems* **17**, 807-824, doi:10.1007/s11252-014-0346-3 (2014).
 482 85 Falxa-Raymond, N., Patterson, A. E., Schuster, W. S. F. & Griffin, K. L. Oak loss
 483 increases foliar nitrogen, delta N-15 and growth rates of *Betula lenta* in a northern
 484 temperate deciduous forest. *Tree Physiology* **32**, 1092-1101, doi:10.1093/treephys/tps068
 485 (2012).
 486 86 Fang, Y. *et al.* Nitrogen deposition and forest nitrogen cycling along an urban-rural
 487 transect in southern China. *Global Change Biology* **17**, 872-885, doi:10.1111/j.1365-
 488 2486.2010.02283.x (2011).
 489 87 Feng, Z., Brumme, R., Xu, Y. J. & Lamersdorf, N. Tracing the fate of mineral N
 490 compounds under high ambient N deposition in a Norway spruce forest at
 491 Solling/Germany. *Forest Ecology and Management* **255**, 2061-2073,
 492 doi:10.1016/j.foreco.2007.12.049 (2008).
 493 88 Finger, R. A. *et al.* Effects of permafrost thaw on nitrogen availability and plant-soil
 494 interactions in a boreal Alaskan lowland. *Journal of Ecology* **104**, 1542-1554,
 495 doi:10.1111/1365-2745.12639 (2016).
 496 89 Frenette-Dussault, C., Shipley, B., Léger, J. F., Meziane, D. & Hingrat, Y. Functional
 497 structure of an arid steppe plant community reveals similarities with Grime's C-S-R
 498 theory. *Journal of Vegetation Science* **23**, 208-222 (2012).
 499 90 Fujiyoshi, L. *et al.* Spatial variations in larch needle and soil N-15 at a forest-grassland
 500 boundary in northern Mongolia. *Isotopes in Environmental and Health Studies* **53**, 54-69,
 501 doi:10.1080/10256016.2016.1206093 (2017).

502 91 Gao, J., Zhao, P., Shen, W., Rao, X. & Hu, Y. Physiological homeostasis and
503 morphological plasticity of two tree species subjected to precipitation seasonal
504 distribution changes. *Perspectives in Plant Ecology, Evolution and Systematics* **25**, 1-19
505 (2017).

506 92 Gao, J., Zhao, P., Shen, W., Rao, X. & Hu, Y. Physiological homeostasis and
507 morphological plasticity of two tree species subjected to precipitation seasonal
508 distribution changes. *Perspectives in Plant Ecology, Evolution and Systematics* **25**, 1-19,
509 doi:<https://doi.org/10.1016/j.ppees.2017.01.002> (2017).

510 93 Gao, J. *et al.* Suppression of nighttime sap flux with lower stem photosynthesis in
511 Eucalyptus trees. *International Journal of Biometeorology* **60**, 545-556,
512 doi:10.1007/s00484-015-1050-6 (2016).

513 94 Godfrey, L. R. *et al.* What did Hadropithecus eat, and why should paleoanthropologists
514 care? *American journal of primatology* **78**, 1098-1112 (2016).

515 95 Golluscio, R., Faigon, A. & Tanke, M. Spatial distribution of roots and nodules, and delta
516 N-15 evidence of nitrogen fixation in *Adesmia volckmanni*, a Patagonian leguminous
517 shrub. *Journal of Arid Environments* **67**, 328-335, doi:10.1016/j.jaridenv.2006.02.005
518 (2006).

519 96 Gos, P. *et al.* Relative contribution of soil, management and traits to co-variations of
520 multiple ecosystem properties in grasslands. *Oecologia* **180**, 1001-1013 (2016).

521 97 Gray, A. *et al.* Does geographic origin dictate ecological strategies in *Acacia senegal* (L.)
522 Willd.? Evidence from carbon and nitrogen stable isotopes. *Plant and Soil* **369**, 479-496,
523 doi:10.1007/s11104-013-1593-4 (2013).

- 524 98 Große-Stoltenberg, A., Hellmann, C., Thiele, J., Oldeland, J. & Werner, C. Invasive
525 acacias differ from native dune species in the hyperspectral/biochemical trait space.
526 *Journal of Vegetation Science* **29**, 325-335 (2018).
- 527 99 Guerrieri, R., Lepine, L., Asbjornsen, H., Xiao, J. & Ollinger, S. V. Evapotranspiration
528 and water use efficiency in relation to climate and canopy nitrogen in US forests. *Journal*
529 *of Geophysical Research-Biogeosciences* **121**, 2610-2629, doi:10.1002/2016jg003415
530 (2016).
- 531 100 Gundale, M. J., Deluca, T. H. & Nordin, A. Bryophytes attenuate anthropogenic nitrogen
532 inputs in boreal forests. *Global Change Biology* **17**, 2743-2753 (2011).
- 533 101 Gundale, M. J., From, F., Bach, L. H. & Nordin, A. Anthropogenic nitrogen deposition in
534 boreal forests has a minor impact on the global carbon cycle. *Global Change Biology* **20**,
535 276-286, doi:10.1111/gcb.12422 (2014).
- 536 102 Gundale, M. J., Hyodo, F., Nilsson, M.-C. & Wardle, D. A. Nitrogen niches revealed
537 through species and functional group removal in a boreal shrub community. *Ecology* **93**,
538 1695-1706 (2012).
- 539 103 Gurmesa, G. A. *et al.* Nitrogen input ¹⁵N signatures are
540 reflected in plant ¹⁵N natural abundances in subtropical forests
541 in China. *Biogeosciences* **14**, 2359-2370, doi:10.5194/bg-14-2359-2017 (2017).
- 542 104 Haberer, K. *et al.* Effects of long-term free-air ozone fumigation on delta N-15 and total
543 N in *Fagus sylvatica* and associated mycorrhizal fungi. *Plant Biology* **9**, 242-252,
544 doi:10.1055/s-2006-924758 (2007).

545 105 Hall, S. J., Hale, R. L., Baker, M. A., Bowling, D. R. & Ehleringer, J. R. Riparian plant
546 isotopes reflect anthropogenic nitrogen perturbations: robust patterns across land use
547 gradients. *Ecosphere* **6**, doi:10.1890/es15-00319.1 (2015).

548 106 Hamerlynck, E. P. & McAuliffe, J. R. Growth and foliar delta N-15 of a Mojave desert
549 shrub in relation to soil hydrological dynamics. *Journal of Arid Environments* **74**, 1569-
550 1571, doi:10.1016/j.jaridenv.2010.06.001 (2010).

551 107 Havik, G., Catenazzi, A. & Holmgren, M. Seabird Nutrient Subsidies Benefit Non-
552 Nitrogen Fixing Trees and Alter Species Composition in South American Coastal Dry
553 Forests. *Plos One* **9**, doi:10.1371/journal.pone.0086381 (2014).

554 108 Hawke, D. *et al.* Foliar and soil N and δ 15N as restoration metrics at Pūtarīngamotu
555 Riccarton Bush, Christchurch city. *Journal of the Royal Society of New Zealand* **47**, 319-
556 335 (2017).

557 109 Hellmann, C., Grosse-Stoltenberg, A., Laustroeer, V., Oldeland, J. & Werner, C.
558 Retrieving nitrogen isotopic signatures from fresh leaf reflectance spectra: disentangling
559 delta N-15 from biochemical and structural leaf properties. *Frontiers in Plant Science* **6**,
560 doi:10.3389/fpls.2015.00307 (2015).

561 110 Hellmann, C., Grosse-Stoltenberg, A., Thiele, J., Oldeland, J. & Werner, C.
562 Heterogeneous environments shape invader impacts: integrating environmental, structural
563 and functional effects by isoscapes and remote sensing. *Scientific Reports* **7**,
564 doi:10.1038/s41598-017-04480-4 (2017).

565 111 Hellmann, C., Rascher, K. G., Oldeland, J. & Werner, C. Isoscapes resolve species-
566 specific spatial patterns in plant-plant interactions in an invaded Mediterranean dune
567 ecosystem. *Tree Physiology* **36**, 1460-1470, doi:10.1093/treephys/tpw075 (2016).

568 112 Hellmann, C. *et al.* Impact of an exotic N-2-fixing Acacia on composition and N status of
 569 a native Mediterranean community. *Acta Oecologica-International Journal of Ecology*
 570 **37**, 43-50, doi:10.1016/j.actao.2010.11.005 (2011).
 571 113 Hellmann, C., Werner, C. & Oldeland, J. A spatially explicit dual-isotope approach to
 572 map regions of plant-plant interaction after exotic plant invasion. *PloS one* **11**, e0159403
 573 (2016).
 574 114 Hobbie, E. A., Rice, S. F., Weber, N. S. & Smith, J. E. Isotopic evidence indicates
 575 saprotrophy in post-fire Morchella in Oregon and Alaska. *Mycologia* **108**, 638-645,
 576 doi:10.3852/15-281 (2016).
 577 115 Hobbie, J. E. *et al.* Mycorrhizal fungi supply nitrogen to host plants in Arctic tundra and
 578 boreal forests: N-15 is the key signal. *Canadian Journal of Microbiology* **55**, 84-94,
 579 doi:10.1139/w08-127 (2009).
 580 116 Hofmeister, J., Hosek, J., Buzek, F. & Rolecek, J. Foliar N concentration and delta N-15
 581 signature reflect the herb layer species diversity and composition in oak-dominated
 582 forests. *Applied Vegetation Science* **15**, 318-328, doi:10.1111/j.1654-109X.2011.01174.x
 583 (2012).
 584 117 Hofmockel, K. S. *et al.* Sources of increased N uptake in forest trees growing under
 585 elevated CO₂: results of a large-scale N-15 study. *Global Change Biology* **17**, 3338-
 586 3350, doi:10.1111/j.1365-2486.2011.02465.x (2011).
 587 118 Hogberg, P. *et al.* Recovery of ectomycorrhiza after 'nitrogen saturation' of a conifer
 588 forest. *New Phytologist* **189**, 515-525, doi:10.1111/j.1469-8137.2010.03485.x (2011).
 589 119 Hogberg, P. & Alexander, I. J. Roles of root symbioses in African woodland and forest:
 590 evidence from ¹⁵N abundance and foliar analysis. *Journal of Ecology*, 217-224 (1995).

591 120 Hoogmoed, M., Cunningham, S. C., Baker, P., Beringer, J. & Cavagnaro, T. R. N-fixing
592 trees in restoration plantings: Effects on nitrogen supply and soil microbial communities.
593 *Soil Biology & Biochemistry* **77**, 203-212, doi:10.1016/j.soilbio.2014.06.008 (2014).

594 121 Houle, D., Moore, J. D., Ouimet, R. & Marty, C. Tree species partition N uptake by soil
595 depth in boreal forests. *Ecology* **95**, 1127-1133, doi:10.1890/14-0191.1 (2014).

596 122 Hudson, J. M. G., Henry, G. H. R. & Cornwell, W. K. Taller and larger: shifts in Arctic
597 tundra leaf traits after 16 years of experimental warming. *Global Change Biology* **17**,
598 1013-1021, doi:10.1111/j.1365-2486.2010.02294.x (2011).

599 123 Hyodo, F., Kusaka, S., Wardle, D. A. & Nilsson, M.-C. Changes in stable nitrogen and
600 carbon isotope ratios of plants and soil across a boreal forest fire chronosequence. *Plant*
601 *and Soil* **364**, 315-323, doi:10.1007/s11104-012-1339-8 (2013).

602 124 Ingram, L. J. & Adams, M. A. Does season and grazing influence the delta C-13 and
603 delta N-15 of C-4 native grasses in semi-arid rangelands of the Pilbara region of NW
604 Australia? *Agriculture Ecosystems & Environment* **236**, 277-284,
605 doi:10.1016/j.agee.2016.12.008 (2017).

606 125 Jiang, C. & Zhang, X. N isotopes and N cycle in the TieShanPing subtropical forest
607 ecosystem, Southwestern China. *Environmental Monitoring and Assessment* **154**, 301-
608 308, doi:10.1007/s10661-008-0398-z (2009).

609 126 Kahmen, A., Wanek, W. & Buchmann, N. Foliar delta(15)N values characterize soil N
610 cycling and reflect nitrate or ammonium preference of plants along a temperate grassland
611 gradient (vol 156, pg 861, 2008). *Oecologia* **158**, 371-371, doi:10.1007/s00442-008-
612 1133-8 (2008).

613 127 Kang, H. *et al.* Variation in foliar delta N-15 among oriental oak (*Quercus variabilis*)
614 stands over eastern China: Patterns and interactions. *Journal of Geochemical Exploration*
615 **110**, 8-14, doi:10.1016/j.gexplo.2011.02.002 (2011).

616 128 Kearsley, E. *et al.* Functional community structure of African monodominant
617 Gilbertiodendron dewevrei forest influenced by local environmental filtering. *Ecology*
618 *and Evolution* **7**, 295-304, doi:10.1002/ece3.2589 (2017).

619 129 Kenzo, T., Tanaka-Oda, A., Mastuura, Y. & Hinzman, L. D. Morphological and
620 physicochemical traits of leaves of different life-forms of various broadleaf woody plants
621 in interior Alaska. *Canadian Journal of Forest Research* **46**, 1475-1482,
622 doi:10.1139/cjfr-2015-0417 (2016).

623 130 Kleinebecker, T. *et al.* Evidence from the real world: N-15 natural abundances reveal
624 enhanced nitrogen use at high plant diversity in Central European grasslands. *Journal of*
625 *Ecology* **102**, 456-465 (2014).

626 131 Klopatek, J. M., Barry, M. J. & Johnson, D. W. Potential canopy interception of nitrogen
627 in the Pacific Northwest, USA. *Forest Ecology and Management* **234**, 344-354,
628 doi:10.1016/j.foreco.2006.07.019 (2006).

629 132 Koba, K. *et al.* delta N-15 of soil N and plants in a N-saturated, subtropical forest of
630 southern China. *Rapid Communications in Mass Spectrometry* **24**, 2499-2506,
631 doi:10.1002/rcm.4648 (2010).

632 133 Koch, P. L. & Fox, L. R. Browsing impacts on the stable isotope composition of
633 chaparral plants. *Ecosphere* **8**, doi:10.1002/ecs2.1686 (2017).

634 134 Korner, C., Leuzinger, S., Riedl, S., Siegwolf, R. T. & Streule, L. Carbon and nitrogen
635 stable isotope signals for an entire alpine flora, based on herbarium samples. *Alpine*
636 *Botany* **126**, 153-166, doi:10.1007/s00035-016-0170-x (2016).

637 135 Kranabetter, J. & Meeds, J. Tree ring $\delta^{15}\text{N}$ as validation of space-for-time substitution in
638 disturbance studies of forest nitrogen status. *Biogeochemistry* **134**, 201-215 (2017).

639 136 Kranabetter, J. M., Dube, S. & Lilles, E. An investigation into the contrasting growth
640 response of lodgepole pine and white spruce to harvest-related soil disturbance. *Canadian*
641 *Journal of Forest Research* **47**, 340-348 (2016).

642 137 Kranabetter, J. M. & MacKenzie, W. H. Contrasts Among Mycorrhizal Plant Guilds in
643 Foliar Nitrogen Concentration and $\delta^{15}\text{N}$ Along Productivity Gradients of a Boreal
644 Forest. *Ecosystems* **13**, 108-117, doi:10.1007/s10021-009-9304-y (2010).

645 138 Kuang, Y. *et al.* Nitrogen deposition influences nitrogen isotope composition in soil and
646 needles of *Pinus massoniana* forests along an urban-rural gradient in the Pearl River
647 Delta of south China. *Journal of Soils and Sediments* **11**, 589-595, doi:10.1007/s11368-
648 011-0342-7 (2011).

649 139 Ladd, B., Pepper, D. A. & Bonser, S. P. Competition intensity at local versus regional
650 spatial scales. *Plant Biology* **12**, 772-779, doi:10.1111/j.1438-8677.2009.00289.x (2010).

651 140 Laiolo, P., Carlos Illera, J., Melendez, L., Segura, A. & Ramon Obeso, J. Abiotic, Biotic,
652 and Evolutionary Control of the Distribution of C and N Isotopes in Food Webs.
653 *American Naturalist* **185**, 169-182, doi:10.1086/679348 (2015).

654 141 Laughlin, D. C., Fule, P. Z., Huffman, D. W., Crouse, J. & Laliberte, E. Climatic
655 constraints on trait-based forest assembly. *Journal of Ecology* **99**, 1489-1499 (2011).

656 142 LeDuc, S. D., Rothstein, D. E., Yermakov, Z. & Spaulding, S. E. Jack pine foliar delta N-
 657 15 indicates shifts in plant nitrogen acquisition after severe wildfire and through forest
 658 stand development. *Plant and Soil* **373**, 955-965, doi:10.1007/s11104-013-1856-0 (2013).
 659 143 Li, Y., Xue, J., Clinton, P. W. & Dungey, H. S. Genetic parameters and clone by
 660 environment interactions for growth and foliar nutrient concentrations in radiata pine on
 661 14 widely diverse New Zealand sites. *Tree Genetics & Genomes* **11**, doi:10.1007/s11295-
 662 014-0830-1 (2015).
 663 144 Liu, X., Wang, G., Li, J. & Wang, Q. Nitrogen isotope composition characteristics of
 664 modern plants and their variations along an altitudinal gradient in Dongling Mountain in
 665 Beijing. *Science China-Earth Sciences* **53**, 128-140, doi:10.1007/s11430-009-0175-z
 666 (2010).
 667 145 Liu, X. *et al.* Foliar delta C-13 and delta N-15 values of C-3 plants in the Ethiopia Rift
 668 Valley and their environmental controls. *Chinese Science Bulletin* **52**, 1265-1273,
 669 doi:10.1007/s11434-007-0165-5 (2007).
 670 146 Ma, L. *et al.* Ecophysiological and foliar nitrogen concentration responses of understorey
 671 Acacia spp. and Eucalyptus sp to prescribed burning. *Environmental Science and*
 672 *Pollution Research* **22**, 10254-10262, doi:10.1007/s11356-015-4223-2 (2015).
 673 147 Makarov, M. I. *et al.* Determinants of N-15 natural abundance in leaves of co-occurring
 674 plant species and types within an alpine lichen heath in the Northern Caucasus. *Arctic*
 675 *Antarctic and Alpine Research* **46**, 581-590, doi:10.1657/1938-4246-46.3.581 (2014).
 676 148 Maranon-Jimenez, S., Castro, J., Ignacio Querejeta, J., Fernandez-Ondono, E. & Allen,
 677 C. D. Post-fire wood management alters water stress, growth, and performance of pine

678 regeneration in a Mediterranean ecosystem. *Forest Ecology and Management* **308**, 231-
679 239, doi:10.1016/j.foreco.2013.07.009 (2013).

680 149 Matsushima, M., Choi, W.-J. & Chang, S. X. White spruce foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
681 indicate changed soil N availability by understory removal and N fertilization in a 13-
682 year-old boreal plantation. *Plant and soil* **361**, 375-384 (2012).

683 150 Mayor, J. R., Schuur, E. A. G., Mack, M. C., Hollingsworth, T. N. & Baath, E. Nitrogen
684 Isotope Patterns in Alaskan Black Spruce Reflect Organic Nitrogen Sources and the
685 Activity of Ectomycorrhizal Fungi. *Ecosystems* **15**, 819-831, doi:10.1007/s10021-012-
686 9548-9 (2012).

687 151 Mayor, J. R., Wright, S. J., Schuur, E. A. G., Brooks, M. E. & Turner, B. L. Stable
688 nitrogen isotope patterns of trees and soils altered by long-term nitrogen and phosphorus
689 addition to a lowland tropical rainforest. *Biogeochemistry* **119**, 293-306,
690 doi:10.1007/s10533-014-9966-1 (2014).

691 152 McGlynn, T. P. *et al.* Spurious and functional correlates of the isotopic composition of a
692 generalist across a tropical rainforest landscape. *BMC ecology* **9**, 23-23,
693 doi:10.1186/1472-6785-9-23 (2009).

694 153 McLauchlan, K. K., Craine, J. M., Nippert, J. B. & Ocheltree, T. W. Lack of
695 eutrophication in a tallgrass prairie ecosystem over 27 years. *Ecology* **95**, 1225-1235,
696 doi:10.1890/13-1068.1 (2014).

697 154 Medina, E., Cuevas, E. & Lugo, A. Substrate Chemistry and Rainfall Regime Regulate
698 Elemental Composition of Tree Leaves in Karst Forests. *Forests* **8**, 182,
699 doi:10.3390/f8060182 (2017).

700 155 Menge, D. N. L., Baisden, W. T., Richardson, S. J., Peltzer, D. A. & Barbour, M. M.
 701 Declining foliar and litter $\delta^{15}\text{N}$ diverge from soil, epiphyte and input $\delta^{15}\text{N}$
 702 along a 120 000 yr temperate rainforest chronosequence. *New Phytologist* **190**, 941-952,
 703 doi:10.1111/j.1469-8137.2010.03640.x (2011).

704 156 Menyailo, O. V., Makarov, M. I. & Cheng, C. H. Isotopic composition of carbon
 705 ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in foliage and soil as a function of tree species.
 706 *Doklady biological sciences : proceedings of the Academy of Sciences of the USSR*,
 707 *Biological sciences sections* **456**, 209-211, doi:10.1134/s0012496614030168 (2014).

708 157 Mercado, A. R., Jr., Van Noordwijk, M. & Cadisch, G. Positive nitrogen balance of
 709 *Acacia mangium* woodlots as fallows in the Philippines based on N-15 natural abundance
 710 data of N-2 fixation. *Agroforestry Systems* **81**, 221-233, doi:10.1007/s10457-010-9309-8
 711 (2011).

712 158 Meyer, W. M., III & Yeung, N. W. Trophic relationships among terrestrial molluscs in a
 713 Hawaiian rain forest: analysis of carbon and nitrogen isotopes. *Journal of Tropical*
 714 *Ecology* **27**, 441-445, doi:10.1017/s0266467411000058 (2011).

715 159 Morford, S. L., Houlton, B. Z. & Dahlgren, R. A. Increased forest ecosystem carbon and
 716 nitrogen storage from nitrogen rich bedrock. *Nature* **477**, 78-U88,
 717 doi:10.1038/nature10415 (2011).

718 160 Msanne, J. *et al.* Ecophysiological responses of native invasive woody *Juniperus*
 719 *virginiana* L. to resource availability and stand characteristics in the semiarid grasslands
 720 of the Nebraska Sandhills. *Photosynthetica* **55**, 219-230, doi:10.1007/s11099-016-0683-y
 721 (2017).

722 161 Murphy, B. P. & Bowman, D. M. J. S. The carbon and nitrogen isotope composition of
723 Australian grasses in relation to climate. *Functional Ecology* **23**, 1040-1049,
724 doi:10.1111/j.1365-2435.2009.01576.x (2009).

725 162 Nielsen, J. A., Frew, R. D., Whigham, P. A., Callaway, R. M. & Dickinson, K. J. M.
726 Thyme travels: N-15 isoscapes of *Thymus vulgaris* L. invasion in lightly grazed pastoral
727 communities. *Austral Ecology* **41**, 28-39, doi:10.1111/aec.12284 (2016).

728 163 Ogaya, R. & Penuelas, J. Changes in leaf $\delta(13)\text{C}$ and $\delta(15)\text{N}$ for three
729 Mediterranean tree species in relation to soil water availability. *Acta Oecologica-*
730 *International Journal of Ecology* **34**, 331-338, doi:10.1016/j.actao.2008.06.005 (2008).

731 164 Pasquini, S. C. & Santiago, L. S. Nutrients limit photosynthesis in seedlings of a lowland
732 tropical forest tree species. *Oecologia* **168**, 311-319, doi:10.1007/s00442-011-2099-5
733 (2012).

734 165 Pellegrini, A. F. A., Hoffmann, W. A. & Franco, A. C. Carbon accumulation and nitrogen
735 pool recovery during transitions from savanna to forest in central Brazil. *Ecology* **95**,
736 342-352, doi:10.1890/13-0290.1 (2014).

737 166 Perakis, S. S. & Kellogg, C. H. Imprint of oaks on nitrogen availability and $\delta\text{N-15}$ in
738 California grassland-savanna: a case of enhanced N inputs? *Plant Ecology* **191**, 209-220,
739 doi:10.1007/s11258-006-9238-9 (2007).

740 167 Perakis, S. S., Tepley, A. J. & Compton, J. E. Disturbance and Topography Shape
741 Nitrogen Availability and $\delta\text{N-15}$ over Long-Term Forest Succession. *Ecosystems* **18**,
742 573-588, doi:10.1007/s10021-015-9847-z (2015).

743 168 Perakis, S. S., Sinkhorn, E. R. & Compton, J. E. $\delta\text{15 N}$ constraints on long-term nitrogen
744 balances in temperate forests. *Oecologia* **167**, 793-807 (2011).

745 169 Peri, P. L. *et al.* Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope composition
 746 in plant and soil in Southern Patagonia's native forests. *Global Change Biology* **18**, 311-
 747 321, doi:10.1111/j.1365-2486.2011.02494.x (2012).

748 170 Pillar, V. D. & Sosinski Jr, E. E. An improved method for searching plant functional
 749 types by numerical analysis. *Journal of Vegetation Science* **14**, 323-332 (2003).

750 171 Pons, T. L., Perreijn, K., van Kessel, C. & Werger, M. J. A. Symbiotic nitrogen fixation
 751 in a tropical rainforest: N-15 natural abundance measurements supported by experimental
 752 isotopic enrichment. *New Phytologist* **173**, 154-167, doi:10.1111/j.1469-
 753 8137.2006.01895.x (2007).

754 172 Powers, J. S. & Tiffin, P. Plant functional type classifications in tropical dry forests in
 755 Costa Rica: leaf habit versus taxonomic approaches. *Functional Ecology* **24**, 927-936,
 756 doi:10.1111/j.1365-2435.2010.01701.x (2010).

757 173 Priyadarshini, K. V. R. *et al.* Overlap in nitrogen sources and redistribution of nitrogen
 758 between trees and grasses in a semi-arid savanna. *Oecologia* **174**, 1107-1116,
 759 doi:10.1007/s00442-013-2848-8 (2014).

760 174 Ren, H. *et al.* Exacerbated nitrogen limitation ends transient stimulation of grassland
 761 productivity by increased precipitation. *Ecological Monographs* **87**, 457-469,
 762 doi:10.1002/ecm.1262 (2017).

763 175 Roa-Fuentes, L. L., Templer, P. H. & Campo, J. Effects of precipitation regime and soil
 764 nitrogen on leaf traits in seasonally dry tropical forests of the Yucatan Peninsula, Mexico.
 765 *Oecologia* **179**, 585-597, doi:10.1007/s00442-015-3354-y (2015).

766 176 Roberts, P., Blumenthal, S. A., Dittus, W., Wedage, O. & Lee-Thorp, J. A. Stable carbon,
 767 oxygen, and nitrogen, isotope analysis of plants from a South Asian tropical forest:

768 Implications for primatology. *American Journal of Primatology* **79**,
769 doi:10.1002/ajp.22656 (2017).

770 177 Roggy, J. C. *et al.* Complementary N Uptake Strategies between Tree Species in Tropical
771 Rainforest. *International scholarly research notices* **2014**, 427194-427194,
772 doi:10.1155/2014/427194 (2014).

773 178 Roggy, J. C., Prevost, M. F., Garbaye, J. & Domenach, A. M. Nitrogen cycling in the
774 tropical rain forest of French Guiana: comparison of two sites with contrasting soil types
775 using delta N-15. *Journal Of Tropical Ecology* **15**, 1-22 (1999).

776 179 Rosado, B. H. P. & de Mattos, E. A. Interspecific variation of functional traits in a CAM-
777 tree dominated sandy coastal plain. *Journal of Vegetation Science* **21**, 43-54,
778 doi:10.1111/j.1654-1103.2009.01119.x (2010).

779 180 Ruiz-Navarro, A., Barbera, G. G., Albaladejo, J. & Querejeta, J. I. Plant delta N-15
780 reflects the high landscape-scale heterogeneity of soil fertility and vegetation productivity
781 in a Mediterranean semiarid ecosystems. *New Phytologist* **212**, 1030-1043,
782 doi:10.1111/nph.14091 (2016).

783 181 Salmon, V. G. *et al.* Nitrogen availability increases in a tundra ecosystem during five
784 years of experimental permafrost thaw. *Global Change Biology* **22**, 1927-1941,
785 doi:10.1111/gcb.13204 (2016).

786 182 Santiago, L., Silvera, K., Andrade, J. & Dawson, T. Functional strategies of tropical dry
787 forest plants in relation to growth form and isotopic composition. *Environmental*
788 *Research Letters* **12**, 115006 (2017).

789 183 Schimann, H. *et al.* Differing nitrogen use strategies of two tropical rainforest late
790 successional tree species in French Guiana: Evidence from N-15 natural abundance and

791 microbial activities. *Soil Biology & Biochemistry* **40**, 487-494,
792 doi:10.1016/j.soilbio.2007.09.011 (2008).

793 184 Scott, E. E., Perakis, S. S. & Hibbs, D. E. delta N-15 patterns of Douglas-fir and red alder
794 riparian forests in the Oregon coast range. *Forest Science* **54**, 140-147 (2008).

795 185 Selmanns, P. C. & Hart, S. C. Substrate age and tree islands influence carbon and nitrogen
796 dynamics across a retrogressive semiarid chronosequence. *Global Biogeochemical Cycles*
797 **22**, doi:10.1029/2007gb003062 (2008).

798 186 Serbin, S. P., Singh, A., McNeil, B. E., Kingdon, C. C. & Townsend, P. A. Spectroscopic
799 determination of leaf morphological and biochemical traits for northern temperate and
800 boreal tree species. *Ecological Applications* **24**, 1651-1669 (2014).

801 187 Shen, J. *et al.* Relationships of leaf nitrogen concentration and delta15N value in
802 *Humulus scandens* with atmospheric NH3 and NO2. *Journal of China Agricultural*
803 *University* **15**, 84-88 (2010).

804 188 Silva, L. C. R., Gomez-Guerrero, A., Doane, T. A. & Horwath, W. R. Isotopic and
805 nutritional evidence for species- and site-specific responses to N deposition and elevated
806 CO2 in temperate forests. *Journal of Geophysical Research-Biogeosciences* **120**, 1110-
807 1123, doi:10.1002/2014jg002865 (2015).

808 189 Smith, K. R., Mathias, J. M., McNeil, B. E., Peterjohn, W. T. & Thomas, R. B. Site-level
809 importance of broadleaf deciduous trees outweighs the legacy of high nitrogen (N)
810 deposition on ecosystem N status of Central Appalachian red spruce forests. *Plant and*
811 *Soil* **408**, 343-356, doi:10.1007/s11104-016-2940-z (2016).

812 190 Song, M., Djabbletey, G., Nkrumah, E. E. & Huang, M. Patterns in leaf traits of
813 leguminous and non-leguminous dominant trees along a rainfall gradient in Ghana.
814 *Journal of Plant Ecology* **9**, 69-76, doi:10.1093/jpe/rtv038 (2016).

815 191 Soper, F. M., Boutton, T. W. & Sparks, J. P. Investigating patterns of symbiotic nitrogen
816 fixation during vegetation change from grassland to woodland using fine scale $\delta^{15}\text{N}$
817 measurements. *Plant, Cell & Environment* **38**, 89-100, doi:10.1111/pce.12373 (2015).

818 192 Soper, F. M. *et al.* Natural abundance ($\delta^{15}\text{N}$) indicates shifts in nitrogen relations of
819 woody taxa along a savanna-woodland continental rainfall gradient. *Oecologia* **178**, 297-
820 308, doi:10.1007/s00442-014-3176-3 (2015).

821 193 Stephan, K., Kavanagh, K. L. & Koyama, A. Comparing the Influence of Wildfire and
822 Prescribed Burns on Watershed Nitrogen Biogeochemistry Using N-^{15} Natural
823 Abundance in Terrestrial and Aquatic Ecosystem Components. *Plos One* **10**,
824 doi:10.1371/journal.pone.0119560 (2015).

825 194 Szpak, P., White, C. D., Longstaffe, F. J., Millaire, J.-F. & Vasquez Sanchez, V. F.
826 Carbon and Nitrogen Isotopic Survey of Northern Peruvian Plants: Baselines for
827 Paleodietary and Paleoecological Studies. *Plos One* **8**, doi:10.1371/journal.pone.0053763
828 (2013).

829 195 Tanaka-Oda, A. *et al.* Variation in leaf and soil $\delta^{15}\text{N}$ in diverse tree species in a lowland
830 dipterocarp rainforest, Malaysia. *Trees* **30**, 509-522 (2016).

831 196 Tanaka-Oda, A., Kenzo, T., Toriyama, J. & Matsuura, Y. Variability in the growth rates
832 and foliage $\delta^{15}\text{N}$ values of black spruce trees across a slope gradient in the Alaskan
833 Interior. *Canadian Journal of Forest Research* **46**, 1483-1490 (2016).

834 197 Tang, B., Yin, C., Yang, H., Sun, Y. & Liu, Q. The coupling effects of water deficit and
835 nitrogen supply on photosynthesis, WUE, and stable isotope composition in *Picea*
836 *asperata*. *Acta Physiologiae Plantarum* **39**, doi:10.1007/s11738-017-2451-4 (2017).

837 198 Templer, P. H. *et al.* Fog as a source of nitrogen for redwood trees: evidence from fluxes
838 and stable isotopes. *Journal of Ecology* **103**, 1397-1407, doi:10.1111/1365-2745.12462
839 (2015).

840 199 Thorpe, A. S., Perakis, S., Catricala, C. & Kaye, T. N. Nutrient limitation of native and
841 invasive N₂-fixing plants in northwest prairies. *PLoS One* **8**, e84593,
842 doi:10.1371/journal.pone.0084593 (2013).

843 200 Van der Colff, D., Dreyer, L. L., Valentine, A. & Roets, F. Comparison of nutrient
844 cycling abilities between the invasive *Acacia mearnsii* and the native *Virgilia divaricata*
845 trees growing sympatrically in forest margins in South Africa. *South African Journal of*
846 *Botany* **111**, 358-364, doi:10.1016/j.sajb.2017.04.001 (2017).

847 201 Viani, R. A. G., Rodrigues, R. R., Dawson, T. E. & Oliveira, R. S. Functional differences
848 between woodland savannas and seasonally dry forests from south-eastern Brazil:
849 Evidence from ¹⁵N natural abundance studies. *Austral Ecology* **36**, 974-982,
850 doi:10.1111/j.1442-9993.2010.02233.x (2011).

851 202 Wang, A. *et al.* Variations in nitrogen-15 natural abundance of plant and soil systems in
852 four remote tropical rainforests, southern China. *Oecologia* **174**, 567-580,
853 doi:10.1007/s00442-013-2778-5 (2014).

854 203 Wang, C. *et al.* Aridity threshold in controlling ecosystem nitrogen cycling in arid and
855 semi-arid grasslands. *Nature Communications* **5**, doi:10.1038/ncomms5799 (2014).

856 204 Wang, L. & Macko, S. A. Constrained preferences in nitrogen uptake across plant species
857 and environments. *Plant Cell and Environment* **34**, 525-534, doi:10.1111/j.1365-
858 3040.2010.02260.x (2011).

859 205 Wang, L., D'Odorico, P., O'Halloran, L. R., Caylor, K. & Macko, S. Combined effects of
860 soil moisture and nitrogen availability variations on grass productivity in African
861 savannas. *Plant and Soil* **328**, 95-108, doi:10.1007/s11104-009-0085-z (2010).

862 206 Wang, L., D'Odorico, P., Ries, L. & Macko, S. A. Patterns and implications of plant-soil
863 delta C-13 and delta N-15 values in African savanna ecosystems. *Quaternary Research*
864 **73**, 77-83, doi:10.1016/j.yqres.2008.11.004 (2010).

865 207 Wang, L., Okin, G. S., D'Odorico, P., Caylor, K. K. & Macko, S. A. Ecosystem-scale
866 spatial heterogeneity of stable isotopes of soil nitrogen in African savannas. *Landscape*
867 *Ecology* **28**, 685-698, doi:10.1007/s10980-012-9776-6 (2013).

868 208 Wang, L., Okin, G. S., Wang, J., Epstein, H. & Macko, S. A. Predicting leaf and canopy
869 15N compositions from reflectance spectra. *Geophysical Research Letters* **34** (2007).

870 209 Wang, L., Shaner, P.-J. L. & Macko, S. Foliar delta N-15 patterns along successional
871 gradients at plant community and species levels. *Geophysical Research Letters* **34**,
872 doi:10.1029/2007gl030722 (2007).

873 210 Watkins, J. E., Jr., Rundel, P. W. & Cardelus, C. L. The influence of life form on carbon
874 and nitrogen relationships in tropical rainforest ferns. *Oecologia* **153**, 225-232,
875 doi:10.1007/s00442-007-0723-1 (2007).

876 211 Werner, C. & Máguas, C. Carbon isotope discrimination as a tracer of functional traits in
877 a Mediterranean macchia plant community. *Functional Plant Biology* **37**, 467-477
878 (2010).

879 212 Williams, M., Shimabokuro, Y. E. & Rastetter, E. B. (ed Oak Ridge National
880 Laboratory Distributed Active Archive Center) (2012).

881 213 Woodcock, P. *et al.* Assessing trophic position from nitrogen isotope ratios: effective
882 calibration against spatially varying baselines. *Naturwissenschaften* **99**, 275-283,
883 doi:10.1007/s00114-012-0896-2 (2012).

884 214 Wu, T. & Huang, J. Effects of grazing on the delta15N values of foliage and soil in a
885 typical steppe ecosystem in Inner Mongolia, China. *Journal of Plant Ecology (Chinese*
886 *Version)* **34**, 160-169 (2010).

887 215 Xiao, L., Yang, H., Sun, B., Li, X. & Guo, J. Stable isotope compositions of recent and
888 fossil sun/shade leaves and implications for palaeoenvironmental reconstruction. *Review*
889 *of Palaeobotany and Palynology* **190**, 75-84, doi:10.1016/j.revpalbo.2012.10.002 (2013).

890 216 Yang, Y. *et al.* Vegetation and Soil N-15 Natural Abundance in Alpine Grasslands on the
891 Tibetan Plateau: Patterns and Implications. *Ecosystems* **16**, 1013-1024,
892 doi:10.1007/s10021-013-9664-1 (2013).

893 217 Yang, Y., Siegwolf, R. T. W. & Koerner, C. Species specific and environment induced
894 variation of delta C-13 and delta N-15 in alpine plants. *Frontiers in Plant Science* **6**,
895 doi:10.3389/fpls.2015.00423 (2015).

896 218 Yao, F. Y., Wang, G. A., Liu, X. J. & Song, L. Assessment of effects of the rising
897 atmospheric nitrogen deposition on nitrogen uptake and long-term water-use efficiency of
898 plants using nitrogen and carbon stable isotopes. *Rapid Communications in Mass*
899 *Spectrometry* **25**, 1827-1836, doi:10.1002/rcm.5048 (2011).

- 219 Ye, L. *et al.* Contrasting impacts of grass species on nitrogen cycling in a grazed
Sudanian savanna. *Acta Oecologica-International Journal of Ecology* **63**, 8-15,
doi:10.1016/j.actao.2015.01.002 (2015).
- 220 Zhang, H.-Y. *et al.* Impacts of leguminous shrub encroachment on neighboring grasses
include transfer of fixed nitrogen. *Oecologia* **180**, 1213-1222, doi:10.1007/s00442-015-
3538-5 (2016).
- 221 Zhao, L. *et al.* The effects of short-term rainfall variability on leaf isotopic traits of desert
plants in sand-binding ecosystems. *Ecological Engineering* **60**, 116-125,
doi:10.1016/j.ecoleng.2013.07.022 (2013).
- 222 Zmudczynska-Skarbek, K., Barcikowski, M., Zwolicki, A., Iliszko, L. & Stempniewicz,
L. Variability of polar scurvygrass *Cochlearia groenlandica* individual traits along a
seabird influenced gradient across Spitsbergen tundra. *Polar Biology* **36**, 1659-1669,
doi:10.1007/s00300-013-1385-6 (2013).
- 223 Sparks, J. A. & Crowley, B. E. Where did people forage in prehistoric Trinidad? Testing
the utility of isotopic tools for tracking terrestrial resource use. *Journal Archaeological of
Science Reports* **19**, 968-978 (2018).
- 224 Mosher, S. *Carbon isotope discrimination and nitrogen isotope values indicate that
increased relative humidity from fog decreases plant water use efficiency in a subtropical
montane cloud forest* M.S. thesis, University of Cincinnati, (2015).

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Competing interests

Although JMC is an owner of Jonah Ventures, a for-profit DNA sequencing company, the authors declare no competing interests in the publication of this research.

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941

942 **Figure 1| Relationships between residual foliar $\delta^{15}\text{N}$ of non- N_2 -fixing species and**
943 **predictors.** Included are (a) MAT, (b) log MAP, (c) log [N], and (d) mycorrhizal type after
944 standardizing for the other three factors. All data were summarized by species for a given
945 location before the regression. Each point represents an average foliar $\delta^{15}\text{N}$ for a given species at
946 a given location in a given year. $n = 10,796$.

947

948 **Figure 2| Results of the regressions of (a) residual foliar $\delta^{15}\text{N}$ and (b) residual log-**
949 **transformed foliar [N].** Results shown after accounting for site climate, mycorrhizal type, and
950 identity of continent from which samples were collected. Included are means for each year
951 (black symbols) and site-averaged data (gray symbols). Thin black line represents regression line
952 on average residual $\delta^{15}\text{N}$ for each year (a: $y = 102.3 - 0.051x$, $r^2 = 0.29$, $P < 0.001$; b: $y = 3.02 -$
953 $0.0015x$, $r^2 = 0.05$, $P = 0.04$) and blue area represent 95% confidence interval for the loess-
954 smoothed curve of average residual values (thick black line).

955

956 **Figure 3| Conceptual diagram summarizing N availability bifurcation hypothesis for global**
957 **terrestrial ecosystems.** The left half of the diagram represents the most anthropogenically
958 influenced areas. These ecosystems are becoming more eutrophic, represented are the increases
959 in N availability, foliar N concentrations, gaseous N loss, and transfers to aquatic ecosystems as
960 well as declining dissolved oxygen (DO) levels in waters. The right half of the diagram
961 represents the least anthropogenically influenced ecosystems, which are becoming more
962 oligotrophic. Here, any increased N deposition is overwhelmed by the consequences of

increasing atmospheric CO₂ concentrations on N availability. These ecosystems are demonstrating oligotrophication with declining N availability, declining foliar N concentrations, declining gaseous N loss, and reduced transfers to aquatic ecosystems. Diagram created by Brianne Walsh, University of Maryland Center for Environmental Science, Integration and Application Network.

Methods

Data acquisition. Data for this synthesis included data from the 2009 synthesis and published and unpublished data acquired from other researchers. To identify data not included in the 2009 synthesis, Web of Science was searched with the terms “(nitrogen isotope or 15-N) and (leaf or leaves or foliar)” for papers published between 2006 and the present. Web of Science was also searched for papers that cited Craine et al. 2009 and these were examined using the same criteria. Google Scholar was searched using similar criteria and the first 300 articles were examined. Articles that potentially were associated with foliar $\delta^{15}\text{N}$ data were downloaded and examined to see if foliar $\delta^{15}\text{N}$ data were collected. Articles were excluded if foliar $\delta^{15}\text{N}$ data were limited to: (1) urban areas (2) agricultural ecosystems (3) non-control samples of manipulative experiments (4) non-vascular plants (5) fertilized plants (6) semi-aquatic or aquatic plants (7) sites with mean annual precipitation < 50 mm. For those papers that did not provide data on-line, we contacted the corresponding author using the provided email and requested the data. First emails were sent on October 3, 2017. Failures to respond within two weeks or bounced email resulted in searching the web for a different email or contacting another author on the paper. If an author was successfully contacted, we asked whether they have additional appropriate foliar $\delta^{15}\text{N}$ data that could be provided to the project. Data were included in the final synthesis if data points were

associated with the year the data were collected, location data to generate site latitude and longitude, sufficient identity of the species from which the leaves were collected to identify the mycorrhizal type and N₂-fixing status of the plant, and both foliar N concentration and foliar $\delta^{15}\text{N}$. Out of 146 researchers we attempted to contact, a total of 108 researchers responded that they would send data and 100 sent data by January 10, 2018. Along with data acquired from Dryad and TRY databases, 180 new datasets were added to the 78 datasets of the original paper.

For each data point in the database, we assigned a mean annual temperature and precipitation based on its geographic location from New et al. 2002. Original climate data were maintained if data from the first database did not have location data associated with them. N₂-fixing status of each species was assigned based on Werner et al.²⁰. Any Fabaceae species not listed in the reference was assumed to be N₂-fixing unless the majority of the species in the genus were non-N₂ fixers. Family identification was assigned from theplantlist.org or ITIS. Mycorrhizal type of the species was derived from Brundrett²¹ using family- and genus-level assignments.

Data analysis. Statistical analyses were pre-registered on October 3, 2017 (<https://osf.io/thnyf>) to reduce post-analysis bias in choosing statistical methods. Analyses were constructed with the knowledge of patterns from the 2009 analyses, but without access to any subsequent data. All analyses were conducted in R 3.3.2. All data for a given species at a given site within a year were averaged. All samples within each 0.1° latitude and longitude were considered to be from the same site. Statistical analyses were run separately for N₂- and non-N₂-fixing species. Our general regression approach was to test for trends in foliar $\delta^{15}\text{N}$ after standardizing for as many covariates as possible that could be skewing the temporal trend due to differential sampling. To

accomplish this, we conducted a set of regressions with species-averaged data followed by a regression with site-averaged data. In the first set of regressions, foliar $\delta^{15}\text{N}$ (averaged by site, species, and year) was regressed against log-transformed MAP, log-transformed foliar [N], and mycorrhizal type. Differences among mycorrhizal types were assessed with pairwise contrasts on least-squares means. The residuals of this regression were then subjected to a segmented regression to identify the breakpoint between MAT and foliar $\delta^{15}\text{N}$. A subsequent regression of foliar $\delta^{15}\text{N}$ (averaged for site, species, and year) then included MAT, the interaction between MAT and a categorical variable representing whether sites had MAT above or below the breakpoint, log-transformed MAP, log-transformed foliar [N], and mycorrhizal type. Outliers were considered as those points having a Cook's $D > 1$, but no points met this threshold for this data set. To test whether foliar $\delta^{15}\text{N}$ increased or decreased over time, we ran a second regression on the residual foliar $\delta^{15}\text{N}$ from the previous analysis after averaging the residuals by year and site. The regression tested the averaged residuals against year of sampling and the identity of the continent from which the sample was taken. Continent was included to ensure that any trends over time were not due to differential sampling over time between continents, which had been previously observed as explaining variation in foliar $\delta^{15}\text{N}$ independent of climate. A similar set of regressions were run with log-transformed foliar [N] as the response and without foliar [N] as a predictor. After observing that foliar [N] declined, additional regressions were performed that paralleled the foliar $\delta^{15}\text{N}$ regressions but did not include log foliar [N] in the regression model in order to quantify how foliar $\delta^{15}\text{N}$ changed without standardizing for the declines in log foliar [N]. In this model, the regression was not weighted by sample size for each year, in accordance with all other models.

Structural Equation Modelling. The first set of regressions were designed to test for trends in foliar $\delta^{15}\text{N}$ after standardizing foliar $\delta^{15}\text{N}$ with respect to foliar [N]. To account for trends in [N] occurring over time when assessing the potential causes of changes in $\delta^{15}\text{N}$ over time (which cannot be assessed using regression methods), we also conducted a structural equation model that used site-level residual $\delta^{15}\text{N}$ after accounting for MAT and its breakpoint, log-transformed MAP, mycorrhizal type, and identity of the continent from which samples were taken. The SEM then assessed the influence of time on foliar [N] as well as time and [N] on foliar $\delta^{15}\text{N}$. Post-registration, the SEM was altered to correct an oversight. The final SEM used residual foliar [N] after standardizing for MAT, log MAP, mycorrhizal type, and continent as opposed to unstandardized foliar $\delta^{15}\text{N}$. The SEM also was altered from its original pre-registered formulation to use site-averaged data rather than unsummarized data, which was another initial oversight. As an exploratory exercise, we also ran a series of SEMs that explored the response of foliar $\delta^{15}\text{N}$ as a function of climate. In the first set of SEMs, data were subset by MAT, serially incrementing the lower bound from -5 to 18 °C and the upper bound from 10 °C more than the lower bound up to 28°C. All combinations were tested with MAT bounds incremented by 1 °C between runs. In the second set of SEMs, data were subset by log MAP, serially varying the lower bound from 2 to 3.1 and the upper bound from 0.4 more than the lower bound to 3.6. log MAP bounds were incremented by 0.1 and the SEMs explored responses in MAP from 100 mm to 3981 mm. SEM models were implemented in the R programming language using the Lavaan package version 0.5-23.1097³⁸. No modification indices were used. Because all possible pathways between all variables were accounted for in the SEM, i.e. the models were “just identified” or saturated, we could not test the significance of our models^{22,39-41}, but do report significance values and unstandardized coefficients for each path. Future research

could test more complex SEMs that are not saturated, which would allow for estimation of the significance of a model as a whole. Given that we could not estimate the significance of the model, one should not rely on the SEM as support for the causal structure that was tested, but instead as a technique for generating the individual parameters that were used to assess N-dependent and N-independent rates of decline in $\delta^{15}\text{N}$.

Data sources. Articles from which published data were derived are listed here^{23,42-224}. A table of the papers examined and their ultimate inclusion or exclusion can be found at Supplementary Table 4.





