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Isotopic evidence for oligotrophication of terrestrial ecosystems

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(Article begins on next page)

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1 **Isotopic evidence for oligotrophication of terrestrial** 2 **ecosystems**

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68 Human societies depend on an Earth System that operates within a constrained range of nutrient
69 availability, yet the recent trajectory of terrestrial nitrogen (N) availability is uncertain.
70 Examining patterns of foliar N concentrations ([N]) and isotope ratios ($\delta^{15}\text{N}$) from more than
71 42,000 samples acquired over 37 years, here we show that foliar [N] declined by 8% and foliar
72 $\delta^{15}\text{N}$ declined by 0.8 – 1.9 ‰. Examining patterns across different climate spaces, foliar $\delta^{15}\text{N}$
73 declined across the entire range of MAT and MAP tested. These results suggest declines in N
74 supply relative to plant demand at the global scale. In all, there are now multiple lines of
75 evidence of declining N availability in many unfertilized terrestrial ecosystems, including
76 declines in $\delta^{15}\text{N}$ of tree rings and leaves from herbarium samples over the past 75-150 years.
77 These patterns are consistent with the proposed consequences of elevated atmospheric CO_2 and
78 longer growing seasons. These declines will limit future terrestrial C uptake and increase
79 nutritional stress for herbivores.
80

81
82 Human societies depend on a resilient, accommodating Earth System with a constrained range of
83 environmental conditions ^{1,2}, yet there is a fundamental uncertainty about the trajectory of
84 nitrogen (N) availability in terrestrial ecosystems. On the one hand, as more and more reactive N
85 has been fixed by humans over time ³, planetary boundaries for N fluxes are thought to have
86 been exceeded, generating wide-scale aquatic and terrestrial eutrophication as well as
87 contributing to terrestrial acidification and aquatic anoxia. Exceeding the planetary N boundary
88 is thought to be destabilizing the Earth system ^{1,2,4-7}. In contrast, atmospheric CO₂ concentrations
89 have increased by >40% over the past 150 years. Elevated atmospheric CO₂ could be reducing
90 N availability in terrestrial ecosystems as plant N demand increases more than N supplies and/or
91 higher ratios of C to N in plants induce greater microbial N limitation ⁸⁻¹¹. Longer growing
92 seasons associated with climate warming could also be increasing plant N demand more than
93 supply in some ecosystems, also reducing N availability ¹². With no global databases to directly
94 assess changes in terrestrial N availability, the lack of resolution of the trajectory of terrestrial N
95 cycling constrains our ability to predict future terrestrial C uptake ¹³, plant biodiversity¹⁴, and
96 herbivore performance ^{15,16}. For example, increasing N availability would generally increase
97 plant productivity in unfertilized ecosystems, reduce plant biodiversity, and increase the growth
98 of herbivores as protein limitation is reduced. Decreasing N availability generally leads to
99 opposite effects. Given the central role of nitrogen in so many ecosystem properties, a basic N
100 trajectory is required to increase the certainty with which regulatory decisions can be made and
101 predict future terrestrial ecosystem function.

102

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

120

121 **Results**

122 Examining patterns for 38,451 unsummarized measurements of foliar $\delta^{15}\text{N}$ from non- N_2 -fixing
123 species, mean foliar $\delta^{15}\text{N}$ was 0.4 ‰ and varied by over 40 ‰ across all samples (-20.6 ‰ to
124 +21.4 ‰). As observed in a previous synthesis¹⁷, using data summarized by species at each site

125 for each year ($n = 10,796$), foliar $\delta^{15}\text{N}$ increased with increasing mean annual temperature
126 (MAT) and decreasing mean annual precipitation (MAP) (Fig 1). With these data, $\delta^{15}\text{N}$ began
127 increasing with increasing MAT above 9.7 ± 1.1 °C which was similar to the 8.5 °C breakpoint
128 observed in the full dataset of the first synthesis¹⁷ and the 9.8 °C breakpoint observed for a
129 global synthesis of soil organic matter $\delta^{15}\text{N}$ ²². As observed previously, in the current synthesis,
130 foliar $\delta^{15}\text{N}$ increases with increasing log-transformed foliar [N] and differed among species with
131 different mycorrhizal associations (Fig 1). Non-mycorrhizal species still had the highest foliar
132 $\delta^{15}\text{N}$, and ericoid species the lowest (Fig 1). Foliar [N] was highest under cold, wet climates and
133 also differed significantly among mycorrhizal types with nonmycorrhizal and arbuscular species
134 having the highest N concentrations (19.2 mg g^{-1}) and ericoid species the lowest (12.4 mg g^{-1}).
135 After accounting for climate, foliar [N], and mycorrhizal type, there were significant differences
136 among continents in foliar $\delta^{15}\text{N}$. For example, samples from Europe were 1.2 ± 0.2 ‰ lower than
137 expected based on climate, mycorrhizal type, and [N] whereas samples from South America
138 were 1.2 ± 0.2 ‰ more than expected (Supplementary Table 1, Supplementary Fig. 4). For foliar
139 [N], leaves from a typical plant with the geometric mean [N] of 17.3 mg g^{-1} would be 11.4 mg g^{-1}
140 if it were from Australia and 20.4 mg g^{-1} from Asia if one held mycorrhizal type and climate
141 constant and only varied the continent of origin (Supplementary Table 1).

142

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

148 geometric mean [N] of 17.3 mg g⁻¹ in 1980 declining 8% to 15.6 mg g⁻¹ in 2017. Given this
149 declining foliar [N] over time and the relationship between foliar [N] and δ¹⁵N, we ran additional
150 regression models that standardized foliar δ¹⁵N for climate, mycorrhizal type, and continent, but
151 did not hold foliar [N] constant over time. Not holding foliar [N] constant over time, residual
152 foliar δ¹⁵N declined by 1.9 ± 0.5 ‰ (*P* < 0.001) over 37 years (Fig 2).

153
154 To test how changes in foliar [N] were affecting the trend in δ¹⁵N given that both were changing
155 over time, a structural equation models (SEM) further examined the role of foliar [N] in
156 determining changes in δ¹⁵N and the changes in δ¹⁵N that were independent of trends in foliar
157 [N]. Doing so allows partitioning of direct effects of time on foliar δ¹⁵N from indirect effects that
158 occur through changes in foliar [N]. Working with site-level residual foliar δ¹⁵N and foliar [N]
159 for non-N₂-fixing species after standardizing for climate, mycorrhizal type, and continent, taking
160 into account [N]-dependent and independent pathways, the SEM resulted in a lower estimate of
161 the decline in foliar δ¹⁵N in non-N₂-fixing species than the regression with the sums of effects
162 via the two pathways generating an estimated decline of 0.8 ± 0.5 ‰ over 37 years
163 (Supplementary Fig. 5, Supplementary Table 2). With this approach, 82% of the decline
164 occurred independent of changes in [N], while the remainder was due to the decline in [N].

165 To explore patterns of changes in foliar δ¹⁵N and [N] over time across climates for non-N₂-fixing
166 species, we ran a series of SEMs using subsets of the data created by serially adjusting the
167 minimum and maximum MAT for inclusion in the SEM. Examining the coefficients for SEMs
168 across ranges of MAT, plants in hot regions have been more likely to increase in foliar [N] over
169 time than plants from cold regions (Supplementary Fig. 6). Yet, the [N]-independent changes in
170 foliar δ¹⁵N were consistently negative across the entire range of MAT tested (Supplementary Fig.

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

177

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

191

192 Discussion

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

209

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

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

220

221 Considered alongside these other lines of evidence, our results suggest that most terrestrial
222 ecosystems are undergoing oligotrophication, even while other ecosystems—particularly
223 intensively fertilized terrestrial ecosystems, urban areas, and their downstream receiving
224 waters—are eutrophying. This global bifurcation of N availability raises questions about whether
225 humanity has exceeded a true planetary boundary for nitrogen availability ³⁵. Broad-scale
226 reductions of anthropogenic N fixation would certainly reduce impacts on aquatic ecosystems,
227 but at the same time could also further constrain terrestrial C uptake as atmospheric CO₂
228 concentrations continue to increase and N deposition rates fall ¹³. Given projected increases in
229 atmospheric CO₂ concentrations and global temperatures over the next century, it is likely that
230 this oligotrophication will continue and the C:N stoichiometry of most terrestrial ecosystems will
231 continue to increase. It remains to be tested whether reduced plant protein accompanying
232 oligotrophication can explain reductions in production in herbivores ³⁶, but declining N
233 availability to plants should cascade up to herbivores ^{15,16}. Even if atmospheric CO₂ is eventually
234 stabilized at low enough levels to mitigate the most serious impacts of climate change ³⁷, many
235 terrestrial ecosystems will increasingly display signs of too little reactive N as opposed to too
236 much. Preventing these declines in N availability further emphasizes the need to reduce
237 anthropogenic CO₂ emissions.

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

241

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920 **Author contributions.** JMC and AE conceived of the research, conducted analyses, generated
921 figures, and prepared the original draft. All authors contributed data and provided comments on
922 manuscripts.

923 **Competing interests**

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

926

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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

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

968

969 **Methods**

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

986 associated with the year the data were collected, location data to generate site latitude and
987 longitude, sufficient identity of the species from which the leaves were collected to identify the
988 mycorrhizal type and N₂-fixing status of the plant, and both foliar N concentration and foliar
989 $\delta^{15}\text{N}$. Out of 146 researchers we attempted to contact, a total of 108 researchers responded that
990 they would send data and 100 sent data by January 10, 2018. Along with data acquired from
991 Dryad and TRY databases, 180 new datasets were added to the 78 datasets of the original paper.

992
993 For each data point in the database, we assigned a mean annual temperature and precipitation
994 based on its geographic location from New et al. 2002. Original climate data were maintained if
995 data from the first database did not have location data associated with them. N₂-fixing status of
996 each species was assigned based on Werner et al.²⁰. Any Fabaceae species not listed in the
997 reference was assumed to be N₂-fixing unless the majority of the species in the genus were non-
998 N₂ fixers. Family identification was assigned from theplantlist.org or ITIS. Mycorrhizal type of
999 the species was derived from Brundrett²¹ using family- and genus-level assignments.

1000

1001 **Data analysis.** Statistical analyses were pre-registered on October 3, 2017 (<https://osf.io/thnyf>)
1002 to reduce post-analysis bias in choosing statistical methods. Analyses were constructed with the
1003 knowledge of patterns from the 2009 analyses, but without access to any subsequent data. All
1004 analyses were conducted in R 3.3.2. All data for a given species at a given site within a year were
1005 averaged. All samples within each 0.1° latitude and longitude were considered to be from the
1006 same site. Statistical analyses were run separately for N₂- and non-N₂-fixing species. Our general
1007 regression approach was to test for trends in foliar $\delta^{15}\text{N}$ after standardizing for as many
1008 covariates as possible that could be skewing the temporal trend due to differential sampling. To

1009 accomplish this, we conducted a set of regressions with species-averaged data followed by a
1010 regression with site-averaged data. In the first set of regressions, foliar $\delta^{15}\text{N}$ (averaged by site,
1011 species, and year) was regressed against log-transformed MAP, log-transformed foliar [N], and
1012 mycorrhizal type. Differences among mycorrhizal types were assessed with pairwise contrasts on
1013 least-squares means. The residuals of this regression were then subjected to a segmented
1014 regression to identify the breakpoint between MAT and foliar $\delta^{15}\text{N}$. A subsequent regression of
1015 foliar $\delta^{15}\text{N}$ (averaged for site, species, and year) then included MAT, the interaction between
1016 MAT and a categorical variable representing whether sites had MAT above or below the
1017 breakpoint, log-transformed MAP, log-transformed foliar [N], and mycorrhizal type. Outliers
1018 were considered as those points having a Cook's $D > 1$, but no points met this threshold for this
1019 data set. To test whether foliar $\delta^{15}\text{N}$ increased or decreased over time, we ran a second regression
1020 on the residual foliar $\delta^{15}\text{N}$ from the previous analysis after averaging the residuals by year and
1021 site. The regression tested the averaged residuals against year of sampling and the identity of the
1022 continent from which the sample was taken. Continent was included to ensure that any trends
1023 over time were not due to differential sampling over time between continents, which had been
1024 previously observed as explaining variation in foliar $\delta^{15}\text{N}$ independent of climate. A similar set
1025 of regressions were run with log-transformed foliar [N] as the response and without foliar [N] as
1026 a predictor. After observing that foliar [N] declined, additional regressions were performed that
1027 paralleled the foliar $\delta^{15}\text{N}$ regressions but did not include log foliar [N] in the regression model in
1028 order to quantify how foliar $\delta^{15}\text{N}$ changed without standardizing for the declines in log foliar
1029 [N]. In this model, the regression was not weighted by sample size for each year, in accordance
1030 with all other models.

1031

1032 **Structural Equation Modelling.** The first set of regressions were designed to test for trends in
1033 foliar $\delta^{15}\text{N}$ after standardizing foliar $\delta^{15}\text{N}$ with respect to foliar [N]. To account for trends in [N]
1034 occurring over time when assessing the potential causes of changes in $\delta^{15}\text{N}$ over time (which
1035 cannot be assessed using regression methods), we also conducted a structural equation model
1036 that used site-level residual $\delta^{15}\text{N}$ after accounting for MAT and its breakpoint, log-transformed
1037 MAP, mycorrhizal type, and identity of the continent from which samples were taken. The SEM
1038 then assessed the influence of time on foliar [N] as well as time and [N] on foliar $\delta^{15}\text{N}$.
1039 Post-registration, the SEM was altered to correct an oversight. The final SEM used residual foliar
1040 [N] after standardizing for MAT, log MAP, mycorrhizal type, and continent as opposed to
1041 unstandardized foliar $\delta^{15}\text{N}$. The SEM also was altered from its original pre-registered
1042 formulation to use site-averaged data rather than unsummarized data, which was another initial
1043 oversight. As an exploratory exercise, we also ran a series of SEMs that explored the response of
1044 foliar $\delta^{15}\text{N}$ as a function of climate. In the first set of SEMs, data were subset by MAT, serially
1045 incrementing the lower bound from -5 to 18 °C and the upper bound from 10 °C more than the
1046 lower bound up to 28°C. All combinations were tested with MAT bounds incremented by 1 °C
1047 between runs. In the second set of SEMs, data were subset by log MAP, serially varying the
1048 lower bound from 2 to 3.1 and the upper bound from 0.4 more than the lower bound to 3.6. log
1049 MAP bounds were incremented by 0.1 and the SEMs explored responses in MAP from 100 mm
1050 to 3981 mm. SEM models were implemented in the R programming language using the Lavaan
1051 package version 0.5-23.1097³⁸. No modification indices were used.
1052 Because all possible pathways between all variables were accounted for in the SEM, i.e. the
1053 models were “just identified” or saturated, we could not test the significance of our models^{22,39-41},
1054 but do report significance values and unstandardized coefficients for each path. Future research

1055 could test more complex SEMs that are not saturated, which would allow for estimation of the
1056 significance of a model as a whole. Given that we could not estimate the significance of the
1057 model, one should not rely on the SEM as support for the causal structure that was tested, but
1058 instead as a technique for generating the individual parameters that were used to assess N-
1059 dependent and N-independent rates of decline in $\delta^{15}\text{N}$.

1060

1061 **Data sources.** Articles from which published data were derived are listed here^{23,42-224}. A table of
1062 the papers examined and their ultimate inclusion or exclusion can be found at Supplementary
1063 Table 4.

1064





